EXHIBIT C

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Bishop Field Office
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RE: Casa Diablo IV Project Impacts

Dear Mr. Reinhardt and Ms. Sudoimer:

This letter consists of my expert evaluation, associated comments, and recommendations on the joint Draft Environmental Impact Statement and Draft Environmental Impact Report (Draft EIS/EIR), prepared for the Casa Diablo IV Geothermal Project (Project) pursuant to the requirements of the National Environmental Policy Act (NEPA; 42 SC 4321 *et seq.*) and the California Environmental Quality Act (CEQA; Public Resources Code 2100-21178.1). The Bureau of Land Management (BLM) and the Great Basin Unified Air Pollution Control District (Air District) act as the lead agencies and authors of the Draft EIS/EIR. The agencies assert that the document sufficiently describes and evaluates the environmental impacts that are expected to result from construction, operation, maintenance, and decommissioning of the Project and presents Project Design Measures (PDMs) and mitigation measures.

I am an independent wildlife biologist, with nearly 40 years of professional experience during which I conducted research on, and worked with, large mammals (deer, mountain sheep, elk, and mountain lions) in eastern and southeastern California; more than 20 years were spent working on issues in the eastern Sierra Nevada and, specifically, in Inyo and Mono counties. I previously have served as a consultant to various clients on renewable energy projects — including wind, solar, and geothermal — and their potential impacts to mule deer and mountain sheep, and have testified before the California Energy Commission. I hold Bachelors and Masters Degrees in Zoology and Biology, respectively, from California State University Long Beach, and a Ph.D. in Wildlife Biology from the University of Alaska Fairbanks.

In my comments I offer a specific critique of issues related to the CD-IV Project as described in the Draft EIS/EIR — particularly those involving migratory mule deer, which utilize the project site on a semi-annual basis, as well as resident deer, which occupy the project site on a year-round basis. I am personally familiar with the project site, and my professional background in ungulate ecology, extensive reviews of the contemporary scientific literature, and contacts with other experts on ungulate ecology that are familiar with the location of the Project provided the basis for the findings herein.

A. The Draft EIS/EIR Fails to Adequately Identify and Analyze the Importance of the Project Site to Mule Deer and Resulting Impacts to the Species

Migratory behavior of large mammals is one of the most spectacular, yet threatened, phenomena in the animal kingdom.[1] Mule deer inhabiting the eastern Sierra Nevada are among the large mammals well-known for their migratory behavior, and problems associated with development or intrusions, and effects on habitat fragmentation or alteration of movement corridors have been of substantial concern to managers and conservationists for many years.[2 3] Migration by mule deer clearly has fitness consequences for individuals, as well as ecosystem-level implications.[4 5] Migration by mule deer in the Sierra Nevada is a two-way phenomenon that occurs between areas used during winter and those used during the remainder of the year.[6 7 8] Thus, actions that prevent, or otherwise restrict, the potential for movement of mule deer between seasonal ranges have broad-sweeping implications, not only for the persistence of migratory behavior, but for continued ecosystem function.

Given that migration is a seasonal phenomenon that occurs on a semi-annual basis, the Draft EIS/EIR is woefully inadequate, because it addresses only use by deer during the fall migration, or by "resident" deer prior to the fall migration. Despite the fact that the Draft EIS/EIR acknowledges that the Proposed Action is located in an important mule deer migration path and staging area in the fall and spring, it reports only information on use by mule deer that was obtained during summer (for resident deer) and fall (for migratory deer); noticeably absent is any baseline information or analysis of impacts during the spring (for migratory deer).[9 10 11 12] Moreover, those data were obtained I9-144

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[1] Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320-331.

[2] Kucera, T. E., and C. W. McCarthy. 1988. Habitat fragmentation and mule deer migration corridors: a need for evaluation. Western Section of The Wildlife Society Transactions 24:61–67.

[3] Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

[4] Nicholson, M.C., R.T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

[5] Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1

[6] Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

[7] Loft, E. R., R. C. Bertram, and D. L. Bowman. 1989. Migration patterns of mule deer in the central Sierra Nevada. California Fish and Game 75:11–19.

[8] Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1

[9] Draft EIS/EIR page 1-12.

within a limited time frame (summer and fall 2011), rather than over a series of semi-annual migrations that would be necessary to fully understand, and develop mitigation for, the potential impacts of disruption of that migratory corridor.

The biological reports addressing mule deer issues have indicated the problematic nature of an absence of assessments over multiple years, small sample sizes, and the absence of data collected during spring. For example, routes used by mule deer during migration have been shown to be varied and reticulate over multiple migratory events.[13] The apparent assumption that project impacts would be identical during both spring and fall migrations is speculative at best, and patently wrong at worst. The potential for inter-annual variation in migration routes further confounds the utility of conclusions based on observations obtained during a single migration event. In the absence of information on the spring migration, and in the absence of more than a single year of information on occupancy and use of the project site by mule deer, the Draft EIS/EIR fails to provide an accurate portrayal of use of the Project site by mule deer. This information is critically important for decision makers to fully assess and provide adequate mitigation for the impacts of the Project. Moreover, differences between results obtained during spring and fall may act in synergism to amplify the effects of the project on mule deer and, thus, must be considered further in a cumulative sense. Additionally, the California Department of Fish and Game (now California Department of Fish and Wildlife [CDFW]) clearly identified a requirement to address deer use of the project site during spring migration, as requested in a letter to Mono County regarding the MP-1 replacement project, and its similar importance to the CD-IV Project, as emphasized by CDFW.[14] [15] The consultant has cautioned that, "Given the limited sampling duration, which encompasses a single migration event, the degree to which these results may be generalized to future years or regarded as describing "average use" cannot be known."[16] Indeed, sample size upon which the ability of deer to negotiate the existing Basalt Canyon Pipeline involved an assessment of only 23 attempted crossings.[17] Further, the shortcomings associated with assessing deer use during the unusually late snow conditions also have been recognized.[18]

The Draft EIS/EIR acknowledges that, "Potential interactions between deer and proposed project elements arise from the reasonable notions that migrating deer will not exhibit tolerance to new power plant noise and activity and will not readily adapt to movement

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[10] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.
[11] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[12] Draft EIR/EIS page 3.4-1.
[13] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
[14] Letter from B. Henderson (CDFG) to D. Lyster (Mono County) dated 7 March 2011.
[15] Santos, N. 2011. G-1 Replacement Plant Site Visit Summary dated 22 March 2011.
[16] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[17] Paulus, J. 2011. Memorandum to Ron Leiken, Ormat Corporation, dated 29 December 2011.
[18] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.

across new aboveground pipelines associated with geothermal energy production."[19] The Draft EIS/EIR further states that, "[m]igratory deer ... may not remain long enough to adapt and may be thwarted in their habitat usage for movement along traditional paths by any new installation of linear barriers."[20] Unfortunately, the Draft EIS/EIR fails to analyze these stated potentially significant impacts, relying on a finding that "[t]here [are] not sufficient data to speculate how migrating deer would respond to the new barriers associated with the Proposed Action."[21] This rationale is untrue; scientific literature to the contrary is readily available and that literature addresses the fact that energy development activities yield indirect losses of habitat that are substantially greater than those associated with direct losses, and that acclimation by mule deer to disturbances did not occur over a period of three years.[22] Moreover, numerous recent studies have reiterated the potential for migrating mule deer to be affected by a variety of energy development projects, including geothermal development.[23] [24] [25] [26] [27] By failing to disclose the necessary information, the EIS/EIR analysis of potentially significant impacts is fundamentally flawed. The public and the decision makers are subsequently led to believe that abandonment of habitat is unlikely and impacts are less than significant.[28]

I9-144 cont.

The Draft EIS/EIR relies exclusively on information contained in reports suggesting that the only mule deer that crossed through the proposed Project site during migration were two individuals that had been fitted with GPS telemetry collars.[29] The suggestion made by the report that a "migration route" can be firmly established is in direct conflict with existing scientific evidence.[30] At least 37 female mule deer were fitted with GPS telemetry collars in Round Valley, Inyo and Mono counties, and then tracked during 2002–2004.[31] The Draft EIS/EIR relies on misleading information as an example of deer

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[19] Draft EIS/EIR page 4.4-16.

[20] Draft EIS/EIR page 4.4-16.

[21] Draft EIS/EIR page 4.4-17.

[22] Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

[23] Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

[24] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052--1061.

[25] Lutz, D. W., J. R. Heffelfinger, S. A. Tessmann, R. S. Gamo, and S. Siegel. 2011. Energy development guidelines for mule deer. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

[26] Hebbelwhite, M. 2008. A literature review of the effects of energy development on ungulates: implications for central and eastern Montana. Contract report prepared for the Montana Department of Fish, Wildlife, and Parks, Miles City, USA.

[27] Hebbelwhite, M. 2011. Effects of energy development on ungulates. Pages 71–94 in D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

[28] Draft EIS/EIR page 4.4-16.

[29] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.

[30] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

[31] Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.

movements, rather than a more meaningful population-level assessment of the Project site in terms of its population-level or landscape-level value to mule deer. Indeed, approximately 12 collared animals occurred on or near the project site during 2002–2004, based on my ocular assessment of data presented elsewhere.[32]

The Draft EIS/EIR clearly acknowledges that there will be direct losses of mule deer habitat, but fails to disclose the potentially significant impacts of those losses. For example, bitterbrush is an extremely important component of mule deer diets and is critically important to mule deer occupying the eastern Sierra Nevada.[33][34] The Draft EIS/EIR fails to address the effects of habitat loss, both direct and indirect, on availability of bitterbrush and other shrub components of sagebrush scrub habitats associated with the project site because it does not consider the secondary impacts of the loss of nutritional resources; nutritional resources are extremely important in the life-history strategies of ungulates, and nutrient availability is critically important to the performance of mule deer in the eastern Sierra Nevada.[35][36][37] Loss of nutrient resources associated with direct impacts to foraging habitat or secondary impacts to habitat use resulting from avoidance of the Project and vicinity have implications for individuals that may be affected by the development and, ultimately, for the population of mule deer.

I9-144 cont.

B. The Draft EIS/EIR Fails to Adequately Identify and Analyze the Potential for the Project to Yield Increased Mortality Resulting From Vehicle Collisions

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Highway associated impacts are among the most prevalent and widespread stressors of natural ecosystems, and are especially severe in the western United States as a result, in part, of increased energy development activities.[38][39] Mortality due to vehicle collision is an important source of death among mule deer throughout the range of the species and particularly in Mono County in the eastern Sierra Nevada, where it is the main cause of unintended deer mortality.[40][41] The Draft EIS/EIR acknowledges the potential for vehicle

[32] Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.
[33] Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1
[34] Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.
[35] Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.
[36] Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1
[37] Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.
[38] Farrell, J. E., L. R. Irby, and P. T. McGowan. 2002. Strategies for ungulate-vehicle collision mitigation. Intermountain Journal of Sciences 8:1–18.
[39] Heffelfinger, J. R., and T. A. Messmer. 2002. Introduction. Pages 1–11 *in* J. C. deVos, M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.
[40] V. C. Bleich, California Department of Fish and Game (retired), personal observations 1986–2007.

collisions to increase as a result of the proposed project.[42] No information on the current level of vehicular collisions is in the area is provided; this information, however, is readily available from the California Department of Transportation.[43] [44] Information identifying deer-vehicle collision "hot spots" in the eastern Sierra Nevada exists, two of which have been identified near the project site.[45] In the absence of an assessment of current cause-specific mortality rates, the Draft EIS/EIR fails to provide a meaningful way of assessing what the impacts of an increase in vehicle deaths among mule deer resulting from the Proposed Action would be. It has been established that numerous deer from the Round Valley population are killed in vehicle collisions along U.S. Highway 395 on an annual basis, and collisions with vehicles also accounted for about 15% of known sources of mortality among a sample of female deer from the Casa Diablo population.[46] [47]

I9-145 cont.

"The location of the new power plant and the pipelines running south of it in the Proposed Action would introduce new barriers to mule deer migration moving down slope from north to south to access meadow and riparian communities associated with Mammoth Creek. It is not known whether this would force some migrating deer further west and closer to U.S. Highway 395 where they would be subject to increased mortality due to vehicular collisions."[48] However, implementation of alternative 2 has the potential to reduce the mortality of deer resulting from vehicle collisions, but at the cost of increased impedance to deer movements due to additional pipeline construction.[49] In the absence of data to the contrary, any increase in the current level of mortality resulting from vehicle collisions must be considered to be additive, and additive mortality has the potential to significantly influence the performance of ungulate populations.[50] Thus, the Draft EIS/EIR fails in its discussion of the impacts of potential increases in vehicle collisions in a manner that cannot be evaluated, because the document fails to provide baseline information relative to the current rate of vehicle collisions.

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41 Mono County Planning Department. 2001. Master environmental assessment for Mono County. Mono County Planning Department, Bridgeport, California, USA. Available at: < http://www.monocounty.ca.gov/sites/default/files/fileattachments/planning_division/page/812/2001_mea_and_maps_color.pdf>

42 Joint EIR, page 2-77.

43 Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.

44 T. J. Taylor, California Department of Fish and Wildlife, personal communication. 13 December 2012.

45 Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.

46 Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462–172.

47 Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265–272.

48 Draft EIS/EIR page 4.4-17.

49 Draft EIS/EIR, page 4.4-21.

50 Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342–361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.

C. The Draft EIS/EIR Fails to Acknowledge Prior Planning Documents That Emphasize the Protection of Mule Deer Habitat and Areas Through Which They Move During Migration

The mule deer is an important game species. The impacts of geothermal development on the Round Valley (i.e., the Sherwin Grade and Buttermilk deer herds combined) and Casa Diablo deer herds have been a longstanding management concern of CDFW, and the importance of protecting areas through which deer move during migration has long been emphasized.[51] [52] [53] Much, if not all, of the proposed Project falls outside of the jurisdiction of the city of Mammoth Lakes in Mono County.[54] Mule deer habitat and areas through which mule deer move during migration in Mono County have been of great concern to planners, and the recently revised Mono County General Plan depicts the Project area as being entirely within what the County refers to as the Hot Creek Deer Migration Zone.[55] Further, Mono County has identified deer as an important natural, biological, and recreational resource, and noted that geothermal exploration, development and operations shall be undertaken in a manner that minimizes or prevents adverse effects to the deer population and migration within the deer migration zones.[56] I9-147

Mono County's General Plan states: "[p]rojects outside community areas within identified deer habitat areas, including migration corridors or winter range (see the Biological Resources Section of the Master Environmental Assessment), which may have a significant effect on deer resources shall submit a site-specific deer study performed by a recognized and experienced deer biologist in accordance with Action 1.1."[57] The aforementioned "[s]ite-specific deer study" has failed to provide information adequate to assess the potential impacts of the proposed project on mule deer, as noted in Section A, above, because those studies failed to address spring migration. Moreover, it is my opinion that the deer investigations upon which conclusions were drawn[58] [59] were not performed by a "[r]ecognized and experienced deer biologist" as stipulated in the General

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[51] Blankinship, T. E. 1984. Buttermilk deer herd management plan. California Department of Fish and Game, Bishop, USA.
[52] Thomas, R. D. 1985. Management plan for the Sherwin Grade deer herd. California Department of Fish and Game, Bishop, USA.
[53] Thomas, R. D. 1985. Management plan for the Casa Diablo deer herd. California Department of Fish and Game, Bishop, USA.
[54] Draft EIS/EIR, page 1-5.
[55] County of Mono Community Development Department. 2010. Mono County General Plan. Bridgeport, California, USA. (Drafted July 1997; Revised 2010). Conservation /Open Space Element-2012, Figure 1. Available at: <http://www.monocounty.ca.gov/sites/default/files/fileattachments/planning_division/page/812/2012_conservation.open_space_element.pdf>
[56] Draft EIS/DIR page 3.10-10.
[57] County of Mono Community Development Department. 2010. Mono County General Plan. Bridgeport, California, USA. (Drafted July 1997 and Revised 2010). Page V-14. Available at: <http://www.monocounty.ca.gov/sites/default/files/fileattachments/planning_division/page/812/2012_conservation.open_space_element.pdf>
[58] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[59] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.

Plan. The biologist that prepared the reports has a fine reputation as a botanical consultant, but queries of web-based literature search engines using "deer" and "Paulus" failed to yield any professional publications that would establish him as a "[r]ecognized and experienced deer biologist."[60] [61] Thus, the reports upon which the Draft EIS/EIR is based failed to meet the criteria established by Mono County.[62]

The U.S. Forest Service has identified the conservation of mule deer habitat and areas used by mule deer during migration as important biological resources and has, by reference, incorporated management plans — and, thereby, management objectives — for the Round Valley (i.e., Sherwin Grade Deer Herd and Buttermilk Deer Herd combined) and Casa Diablo deer herds published by CDFW into their planning documents.[63] The Inyo National Forest Land and Resource Management Plan also emphasizes the maintenance and enhancement of the integrity of key mule deer winter ranges, holding areas, migration routes, and fawning areas.[64] [65] Deer and deer habitat clearly are an important resource to the Inyo National Forest. Nevertheless, the Forest Service does not appear to have provided assurances that impacts were appropriately analyzed or mitigated to the extent possible to ensure the viability of deer migration corridors.[66]

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D. <u>The DEIR Does Not Address the Project's Cumulative Impacts to Mule Deer</u>

Cumulative impacts to mule deer include permanent habitat loss, loss of forest cover, loss of special use areas, blockage of areas through which deer move during migration, disturbance, and altered predator-prey relationships. The Draft EIS/EIR provides insufficient analysis of the Project's contribution to these cumulative impacts. Specifically, the Draft EIS/EIR suffers two fundamental flaws:

I9-148

1. The Draft EIR/EIS fails to fully identify infrastructure development and activities that will affect deer use. As a result, the DEIR lacks the information needed to evaluate the cumulative impacts of the Project.

2. The Draft EIR/EIS lacks an analysis of cumulative impacts to deer that will result if the project is developed, particularly with respect to deer movements, which have implications at the levels of the individual, the population(s), and the ecosystem. In the

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[60] Google Scholar. Available at http://scholar.google.com/schhp?hl=en
[61] Proquest. Available at http://search.proquest.com/
[62] County of Mono Community Development Department. 2012. Mono County General Plan. Bridgeport, California, USA. Page V-14. Available at: <http://www.monocounty.ca.gov/sites/default/files/fileattachments/planning_division/page/812/2012_conservation.open_space_element.pdf>
[63] U.S. Forest Service. 1988. Inyo National Forest Plan. Appendix A:398–206. Available at: <http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5352771.pdf>
[64] U.S. Forest Service. 1988. Inyo National Forest Plan. Forest plan standards and guidelines. Chapter IV:98–99. Inyo National Forest, Bishop, California, USA. Available at: <http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_003621.pdf>
[65] Draft EIS/EIR page 3.10-6.
[66] Draft EIS/EIR page 1-10.

absence of baseline information, it is not possible for the Draft EIS/EIR to fully anticipate and analyze the cumulative impacts of the Project.

The abundance of high-quality forage that is generally not available on deer winter range makes the Project site, which is located within the Sherwin Holding Area, a critically important component of habitat used during the annual cycles of the Round Valley and Casa Diablo deer herds.[67] [68] The area identified for project development is crossed during the fall migration by deer moving southward from higher elevations or from west of the Sierra crest.[69] [70] [71] [72] During spring, mule deer from the Round Valley and Casa Diablo deer herds move northward and westward through the Sherwin Holding Area.[73] [74]

The nutritional content of forage has an influence on nearly every life history component of mule deer, including survival and reproduction.[75] The proposed project is located within the Sherwin Holding Area, and the presence of resident and migratory deer in the Project area establishes it as deer habitat with available and high-quality, forage.[76] The Project will eliminate up to 80 acres of habitat within the holding area.[77] More importantly, though, shifts in deer use away from the project area (i.e., avoidance of the project area by mule deer) can, and should, be expected but such shifts are not adequately addressed.[78] [79] Additionally, there is serious concern over the potential to indirectly affect habitat quality by spreading invasive species of vegetation, as pointed out by CDFW during the scoping process.[80] [81] [82] Invasions of exotic species, such as cheatgrass,

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67 Thomas, R. D. 1985. Management plan for the Sherwin Grade deer herd. California Department of Fish and Game, Bishop, USA.
68 Thomas, R. D. 1985. Management plan for the Casa Diablo deer herd. California Department of Fish and Game, Bishop, USA.
69 Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the Eastern Sierra Nevada, California. Ph.D. dissertation, University of California, Berkeley, USA.
70 Taylor, T, 1988. Casa Diablo deer study: Migration and seasonal habitats of the Casa Diablo deer herd. Unpublished report prepared for California Department of Fish and Game, Bishop, USA.
71 Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.
72 Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
73 Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.
74 Monteith, K. L., V. C. Bleich, T. R. Stephenson, and B. M. Pierce. 2009. Population dynamics of mule deer in the eastern Sierra Nevada: implications of nutritional condition. California Department of Fish and Game, Bishop, USA.
75 Monteith, K. L., V.C. Bleich, T.R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):1–34.
76 Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
77 Draft EIS/EIR page 4.4-27.
78 Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.
79 Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
80 Draft EIS/EIR page A-14.

have altered Great Basin ecosystems, and have resulted in deaths of native shrubs from excessive fire intensity, inability of native species to compete with cheatgrass, and subsequent rapid domination by cheatgrass following fires.[83] [84] Bitterbrush, a valuable forage species that occurs on the project site, is extremely important to mule deer, and is one of the native species adversely affected by cheatgrass invasions.[85] [86]

The Round Valley Deer Herd has declined substantially during the last 25 years, from approximately 6,000 individuals in 1985, reaching a low in 1990 of about 950 animals, and then increasing to about 1,900 individuals in 2009.[87] [88] The primary cause of the decline appears to have been a decrease in carrying capacity.[89] Given the importance of nutrient intake to the population performance of mule deer, additional declines in the number of deer inhabiting Round Valley could occur with habitat modifications associated with development of the Project, both in terms of direct habitat loss as well as decreases in habitat use because deer do not occupy the area immediately adjacent to developed sites.[90] [91] Because the Project will affect habitat used by the herd during migration, it will exacerbate the current stressors experienced by the population, and could lead to a further decline in numbers. The Project's potential to contribute further to the decline could be cumulatively considerable as a result of the loss of foraging habitat or forage itself, and must be considered in that context to fully understand its implications for the continued health of the Round Valley Deer Herd, as well as the Casa Diablo Deer Herd.

I9-148 cont.

Other factors make it impossible for the Draft EIS/EIR to have fully assessed cumulative impacts of the Project on mule deer. For example, one of the deer studies focused on the impacts of the proposed Project on "migratory" deer, whereas the other focused on the impacts of the Project on "resident" deer.[92] [93] Further, as pointed out previously, no

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[81] Santos, N. 2011. G-1 Replacement Plant Site Visit Summary dated 22 March 2011.
[82] Letter from B. Henderson (CDFW) to D. Lyster (Mono County) dated 7 March 2011.
[83] Young, J. A., R. A. Evans, and B. L. Kay. 1987. Cheatgrass. Rangelands 9:266-270
[84] Vollmer, J. G., J. L. Vollmer, K. Schoup, and R. Amundson. 2005. Controlling cheatgrass in winter range to restore habitat and endemic fire. Deer and Elk Workshop 6:20-24.
[85] Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the Eastern Sierra Nevada, California. Ph.D. dissertation, University of California, Berkeley, USA.
[86] Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.
[87] Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.
[88] Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. *In press*. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology.
[89] Monteith, K. L., V. C. Bleich, T. R. Stephenson, and B. M. Pierce. 2009. Population dynamics of mule deer in the eastern Sierra Nevada: implications of nutritional condition. California Department of Fish and Game, Bishop, USA.
[90] Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.
[91] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
[92] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.

information on the presence of movements of migratory deer during spring were presented. Although impacts of the Project would contribute cumulatively to both resident and migratory mule deer, there is no coherent, overarching analysis or discussion of the manner in which the Project will affect mule deer or deer migration. This is a fundamental flaw, and can only be addressed with additional information obtained during periods of spring migration, and over an extended timeline; hence, it is not possible to fully assess cumulative impacts associated with the Project.

Track counts along transects provide a measure of relative use and can be used as an index to deer activity or presence, but interpretation of data are subject to numerous assumptions.[94 95] Track surveys in and of themselves cannot be used to estimate the absolute number of deer using a particular area, but density estimates can be derived if additional assumptions are met.[96] Data presented in the Draft EIS/EIR are not adequate to allow the derivation of density estimates. Nevertheless, the most recent estimate of deer wintering in Round Valley was reported to be approximately 2,200 individuals,[97] as referenced by others.[98] Although that figure is cited in the Draft EIS/EIR, information that I have been able to obtain does not include population estimates.[99 100]

I9-148 cont.

Based on my ocular estimate using information available elsewhere, about12 telemetered deer used, or occurred in the vicinity of, the Project site during migration.[101] A total of 37 individuals, however, actually were telemetered. Thus, animals telemetered with GPS collars in the Round Valley population and detected within — or near — the Project site potentially represented 32% of the individuals that could have been expected to be present ([12/37] × 100 = 32), assuming no bias in the distribution of the collars. If animals from both the Casa Diablo herd (population estimate 2,800) and Round Valley herd (population estimate 2,200) used the project site equally, up to 5,000 individuals could have passed through the area.[102 103] That, however, is unlikely because only deer

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[93] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.
[94] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[95] Keegan T. W., B. B. Ackerman, A. N. Aoude, L. C. Bender, T. Boudreau, L. H. Carpenter, B. B. Compton, M. Elmer, J. R. Heffelfinger, D. W. Lutz, B. D. Trindle, B. F. Wakeling, and B. E. Watkins. 2011. Methods for monitoring mule deer populations. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
[96] Overton, W. S. 1969. Estimating the numbers of animals in wildlife populations. Pages 403–456 *in* R. H. Giles, Jr., editor. Wildlife management techniques. Third edition (revised). The Wildlife Society, Washington, D.C., USA. (As cited by Keegan et al. [2011]).
[97] California Department of Fish and Game. 2011. January 2011 and March 2011 deer census data. California Department of Fish and Game, Bishop, USA. (Unable to locate this document).
[98] Final EIS/EIR, p. 3.4-17.
[99] McKeever, J. 2011a. Deer survey summary, post season - 2010. Unpublished memo dated 24 January 2011. California Department of Fish and Game. California Department of Fish and Game, Bishop, USA.
[100] McKeever, J. 2011b. Deer survey summary, spring 2011. Unpublished memo dated 11 April 2011. California Department of Fish and Game, Bishop, USA.
[101] Ferranto, S. P. 2006. Conservation of mule deer in the eastern Sierra Nevada. M.S. thesis, University of Nevada, Reno, USA.
[102] Final EIS/EIR, p. 3.4-17.

from Round Valley were collared. But, if Round Valley deer occurred on, or near, the project site in the same proportion in which they were collared, up to 700 (32% of 2,200) deer could have used the area. This figure is substantially greater than the maximum of 170 deer postulated to have used the project site over an 8-day period in May 2011, a number that was inappropriately derived from unreliable data.[104] [105] Neither of these numbers is likely "correct", but given the discrepancy between them, it is probable that cumulative impacts to individuals, the population, and ecosystem services could be far greater than indicated in the Draft EIS/EIR.

Many of the deer migrating northward and westward through the project site from the Round Valley winter range, or northward and westward from the Casa Diablo winter range continue on to summer ranges west of the Sierra crest, but there has been a substantial decrease in the proportion of animals doing so.[106] Continuing declines in the number of deer moving to the west slope of the Sierra Nevada could result in shifts in the availability of nutrients on the summer range: fewer deer could be present as a result of project implementation, and this potentiality must be discussed cumulatively in an ecosystem-level context. Further, climate change has been linked to a general shift from snowfall to rainfall in the western United States.[107] If such a trend continues, selection could favor migratory ungulates that take advantage of enhanced availability of resources resulting from a warming climate, and partial migration may become a better evolutionary strategy.[108] Given the value of the Sherwin Holding Area both to resident and migratory mule deer, the potential for the Project to yield exacerbated negative impacts must be discussed in (1) the context of direct loss of habitat resulting from development; (2) the indirect losses of habitat because deer avoid an area within some distance threshold around the Project; and (3) changes in habitat quality that will result from the likely proliferation of invasive species. Thus, the cumulative impacts of the project could extend far beyond the present and into the future, and have implications for evolutionary and ecosystem-level processes as well.[109]

I9-148 cont.

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[103] V. Bleich was unable to locate any documents substantiating the population estimates of 2,800 and 2,200 deer comprising the Casa Diablo and Round Valley deer populations, as reported in the Final EIS/EIR.

[104] Santos, N., and T. A. Reed. 2011. Deer track count surveys. MACTEC Project Number 4306080009.

[105] Cashen, S. 2011. 2011. Comments on the draft environmental impact report for the Mammoth Pacific I replacement project. Letter dated 22 August 2011 to Ms. Elizabeth Klebaner, Adams, Broadwell, Joseph, & Cardozo, South San Francisco, California, USA.

[106] Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. doi:10.1890/ES10-00096.1

[107] Knowles, N., M. D. Dettinger, and D. R. Cayan. 2005. Trends in snowfall versus rainfall in the Western
United States. Journal of Climate 19:4545–4559.

[108] Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist 142:59–81.

[109] Monteith, K. L., V.C. Bleich, T.R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):1–34.

E. The Draft EIS/EIR Fails to Adequately Mitigate for Impacts to Mule Deer

The cumulative impacts to mule deer include a decrease in forage availability that will occur as a result of infrastructure development, a decrease in forage availability that will result as a secondary effect as deer avoid use of habitat adjacent to the project, potential blockage of areas that deer move through during migration, and potential increases in mortality resulting from vehicle collisions, all of which impact individual deer but, ultimately, have population-level and even ecosystem-level consequences. The Draft EIS/EIR does not adequately discuss these impacts, in part because the information on which conclusions drawn in the Draft EIS/EIR is incomplete and, thereby, inadequate to formulate suitable mitigation measures. For example, a single seasonal survey of tracks of resident deer during fall, and a single track survey of deer conducted during the fall migration are the only data presented and analyzed.[110] [111] Moreover, there has been no work conducted on the Project site during the spring migration, a phenomenon that is as important as is fall migration, and perhaps even more so from a nutritional perspective. **I9-149**

In the Draft EIS/EIR, Project Design Measure for Environmental Protection BIO-1 proposes that, "A qualified wildlife biologist will walk the pipeline route once each year for the first three years following completion of construction to survey for any signs that the pipeline is impeding wildlife movement. If such evidence is found, the USFS *may require* ORNI 50, LLC to clear one or more areas under the pipeline of at least 16 inches height, or sufficient to allow wildlife to pass under the pipeline, at the points where movement is impeded."[112] BIO-1 is fundamentally flawed due to the vagaries associated with interpreting results of track surveys and the influences of seasonal variation — both within and among years — on deer habitat use and deer movement patterns and resultant influences on survey results.[113] Given these limitations, meaningful information cannot be derived from any such annual "walk" along the pipeline. In the absence of meaningful information, there is no evidence to support the argument that additional elevated pipeline segments would be an effective PDM for environmental protection, as stated in BIO-1.[114] **I9-150**

A minimum of approximately 16 inches above ground height has been the general scientific community's, recommendation for *fences* in areas occupied by mule deer.[115] Nevertheless, the data included in the Draft EIS/EIR are insufficient to conclude that a *pipeline* of that elevation will allow unimpeded passage of those large ungulates and,

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[110] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.

[111] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.

[112] Draft EIS/EIR page 2-48. (emphasis added).

[113] Keegan T. W., B. B. Ackerman, A. N. Aoude, L. C. Bender, T. Boudreau, L. H. Carpenter, B. B. Compton, M. Elmer, J. R. Heffelfinger, D. W. Lutz, B. D. Trindle, B. F. Wakeling, and B. E. Watkins. 2011. Methods for monitoring mule deer populations. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

[114] Draft EIS/EIR page 2-48.

[115] Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, Sr., and A. L. Medina. 2005. Managing rangelands for wildlife. Pages 873–897 *in* C. E. Braun, editor. The wildlife management techniques manual. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

thus, cannot be considered a viable recommendation. There is no guarantee that any aspect of BIO-1 is enforceable *in the absence of wording that will require action.* Moreover, even if a requirement to "[c]lear one or more areas under the pipeline of at least 16 inches height, or to allow wildlife to pass under the pipeline" was stipulated, BIO-1 is so non-specific that it cannot be interpreted to guarantee that any action will be taken to mitigate impacts to blockage of movements by mule deer. Wildlife is a term that can be applied to virtually any species of terrestrial vertebrate; mule deer are the largest native terrestrial vertebrates that occur on the project site, and there must be assurances that any resulting modification(s) will meet passage requirements of mule deer. Additionally, the ability of mule deer to cross under a pipeline constructed 16" above the ground will vary with snow accumulation, a consideration that must be addressed in detail. **I9-150 cont.**

Mitigation measures proposed (for alternatives 1 and 3 only) include the construction of a "[d]eer crossing... [that will resemble]... the existing crossing at the SCE easement." WIL-4 stipulates that said crossing will be designed with input from CDFW, and will enhance movement of mule deer thorough the Project area.[116] [117] I was unable, however, to locate any reference to the efficacy of the existing crossing at the SCE easement. Thus, it is impossible to conclude that there would be any meaningful benefit in terms of the crossing's potential as a mitigation measure. In the absence of any substantiation that the crossing proposed in WIL-4 provides relief to deer moving through the area, it cannot be viewed as appropriate or adequate mitigation. **I9-151**

Placing underground sections of the proposed pipelines in Basalt Canyon parallel to those in the existing pipeline is appropriate, as noted in WIL-5.[118] However, the statement that mule deer habitually use roads for movement is not supported by data included in the Draft EIS/EIR, because transects on which this statement is based were the roads themselves, and *investigators recorded tracks that crossed the roads*, not those running along the road (i.e., in the direction of travel the road provided).[119] [120] Information on deer crossing at buried sections of pipelines suggests that resident deer moved only sparingly across the pipelines at those points, as follows. "If all crossings of transects BB and EE in Basalt Canyon scrub are *assumed* [emphasis added] to represent deer that have crossed the existing (aboveground) Basalt Canyon pipeline, then on average 19 pipeline crossings per night occurred. Of these, an average 0.2 crossings per night utilized existing (underground) dips. The five dips "captured" 1% of crossings, which is roughly proportional to the 1% of pipeline length that dips underground (5 dips x 30 ft/dip)."[121] Mitigation based on the *assumption* that deer leaving tracks detected along transects crossed the pipeline is inappropriate in the absence of data to that effect. Additional **I9-152**

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[116] Draft EIS/EIR page 257.
[117] Draft EIS/EIR page 4.4-30.
[118] Draft EIS/EIR page 257.
[119] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.
[120] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[121] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.

studies that determine whether resident deer crossed under or over the pipeline at areas other than the "dips" are necessary before the proposed mitigation can be viewed as meaningful. Further, the mitigation proposed in WIL-5, that "Segments that are parallel to the existing Basalt Canyon pipeline in areas where there are currently no underground segments shall be installed underground at a prescribed frequency"[122] [123] contains no guarantee that the prescribed frequency will be meaningful in terms of providing for passage of mule deer. In the absence of a definition, the phrase "prescribed frequency" is open to interpretation and, thereby, worthy of question.

WIL-5 further states that, "These underground segments shall be located in alignment with suspected traditional migratory routes (see Figure 4.4-1)."[124] [125] There is no basis for selection of these proposed sites that has a foundation in the deer track survey data west of Highway 395, which indicate deer use is inconsistent in any particular part of the project area as determined from track data of resident deer.[126] Further, similar data are presented for the single year for which use by deer during the fall migration was assessed.[127] Unfortunately, a single year of such data, and absent information for the period of spring migration, fails to incorporate both annual and inter-annual variation that can be expected to occur.[128] The basis for selecting sites for the proposed underground segments thus, cannot be supported in the context of being "in alignment with suspected migratory routes" under conditions that will occur over an extended number of years. In fact, the investigations upon which site selection of the underground segments is based were conducted during unusually snow-free conditions.[129]

I9-152 cont.

WIL-5 clearly states that construction of underground segments in the existing Basalt Canyon pipeline is not proposed as mitigation, because deer readily pass over the single pipeline.[130] Evidence that deer readily pass over the single pipeline, however, is based on the *assumption* that tracks made by deer and detected on transects were made by animals that crossed the pipeline.[131] In the absence of data confirming that those deer actually crossed the existing pipeline, the efficacy of the proposed mitigation is speculative, with no assurance that any benefits would accrue.

In addition to the aforementioned underground segments, WIL-5 stipulates that overhead pipeline segments will be installed at high movement areas, and will be of sufficient

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[122] Draft EIS/EIR page 2-57.
[123] Draft EIS/EIR page 4.4-30.
[124] Draft EIS/EIR page 2-57.
[125] Draft EIS/EIR page 4.4-31.
[126] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.
[127] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[128] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
[129] Paulus, J. 2012. Fall 2011 migratory deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 10 February 2012.
[130] Draft EIS/EIR page 2-57.
[131] Paulus, J. 2011. Fall 2011 resident deer survey for the Casa Diablo, Basalt Canyon, and upper Basalt geothermal areas. 30 October 2011.

height above the substrate to allow "wildlife" to pass under the pipeline.[132] As pointed out earlier in this critique, the term wildlife refers to terrestrial vertebrates in general and, as written, WIL-5 fails to stipulate that these proposed crossings will be of a height adequate to allow mule deer to pass under them. The overhead pipeline segments must be installed at heights sufficient to allow mule deer, not just "wildlife," to pass under the pipeline. I9-152 cont.

Monitoring of the effects of project implementation on mule deer movements is proposed in WIL-6.[133] [134] WIL-6 fails to incorporate performance measures and, therefore, reliance on it makes it impossible to determine just what will constitute an additional migration corridor needing remedial action. For example, if deer repeatedly approach the pipeline at a particular location and then turn away, will that constitute an additional migratory corridor that will initiate remedial action? As currently written such a result could be interpreted as not being evidence of a movement corridor. Further, the problematic nature of the methodology used previously — and that WIL-6 is to be modeled after — has been pointed out earlier in this letter. While the intended "remedial action" of installing earthen ramps over the pipeline proposed in WIL-6 is meritorious, it must be assured that adequate methods of sampling are employed, and that sampling covers a continuum of environmental conditions encountered during spring and fall migrations, as well as periods of presence of resident individuals. It is recommended that revised mitigation proposals include multiple years of sampling because of the variance associated with deer movements, and behavior is influenced by multiple factors, among which are local weather conditions.[135] I9-153

"The Proposed Action would introduce new barriers to mule deer migration moving downslope from north to south to access meadow and riparian communities associated with Mammoth Creek. It is not known whether this would force some migrating deer further west and closer to U.S. Highway 395 where they would be subject to increased mortality due to vehicular collisions."[136] To mitigate the potential for the Proposed Action, there is acknowledgment that erecting any temporary barriers to movement that could redirect deer westward towards Highway 395 is an important consideration. It is then suggested that deer *could* move unimpeded to the east of the project area, and that an additional crossing provided south of the proposed plant site would reduce, but not eliminate the threat to migrating deer.[137] It is unclear, however, that the term "threat" to migrating deer is in reference to collisions between vehicles and deer on Highway 395, or to the pipeline itself. I concur that not erecting barriers that would force deer towards Highway 395 is important; however, there is no assurance that the proposed mitigation (i.e., the deer crossing) will lessen the probability of that happening. Further, if Alternative 2 is implemented the power plant will be shifted further east of Highway 395, but doing so will entail a substantial increase in the length of double pipelines, which I9-154

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[132] Draft EIS/EIR page 2-57.
[133] Draft EIS/EIR page 2-57.
[134] Draft EIS/EIR page 4.4-32.
[135] Sawyer, H., M. J. Kaufmann, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.
[136] Draft EIS/EIR page 4.4-17.
[137] Draft EIS/EIR page 4.4-17.

could further impede deer movement.[138] No performance measures are included for the proposed mitigation; therefore, no opportunity exists to assess its effectiveness.[139] If there is an increase in deer mortality as a result of vehicle collisions, meaningful action should include construction of a highway crossing and fencing appropriate to direct deer through or over that crossing, as has been successfully demonstrated elsewhere.[140] **I9-154 cont.**

In conclusion, the Draft EIS/EIR fails to adequately identify and analyze the importance of the project site to mule deer and the resulting impacts to that species; this shortcoming occurs largely because the Draft EIR/EIS suffers from incomplete baseline information that would allow the reader to draw meaningful conclusions. Further, the Draft EIS/EIR fails to adequately identify and analyze the potential for the project to yield increased mortality among deer that would result from an increase in collisions with vehicles. The Draft EIS/EIR is not consistent with prior planning documents prepared by the Inyo National Forest and Mono County, all of which emphasize the importance of mule deer, protection of mule deer habitat, and protection of areas through which they move during migration. The Draft EIS/EIS further fails to adequately consider the cumulative impacts of the project on mule deer, particularly in the sense of population-level and ecosystem-level changes that will result if the Project causes mule deer to cease using the area that will be developed, are prevented from moving through the infrastructure created by the Project, or if the Project affects nutrient intake by the deer. Finally, the mitigation measures proposed to compensate for impacts to mule deer, mule deer habitat, and areas through which mule deer move during migration, are proposed in the absence of data adequate to ensure their efficacy. This problem exists largely as a result of the absence of data upon which to fully assess the potential impacts, as pointed out in the initial portion of my comments. **I9-155**

Sincerely,

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[138] Draft EIS/EIR page 2.77.
[139] Draft EIS/EIR page 2-57.
[140] Simpson, N. O. 2012. Use of vegetative overpasses by mule deer during migration. M.S. Thesis, University of Nevada, Reno, USA.

Curriculum Vitae

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Personal Interests:

Hockey (I am a former goaltender), family life, autoharp, gardening, hunting, and fishing.

Professional Goals:

To help ensure the persistence of populations of large mammals and their habitats through the study of their ecology and behavior, to apply that knowledge in meaningful conservation efforts, and to impart that knowledge through professional activities including publications, teaching, and other public contacts.

Education:

Ph.D. University of Alaska Fairbanks (Wildlife Biology, 1993). Thesis: "Sexual Segregation in Desert-Dwelling Mountain Sheep."

M.A. California State University, Long Beach (Biology, 1973). Thesis: "Ecology of Rodents at the Seal Beach Naval Weapons Station, Fallbrook Annex, San Diego County, California."

B.S. California State University, Long Beach (Zoology, 1970).

Professional Background:

Senior Conservation Scientist, Eastern Sierra Center for Applied Population Ecology (2008 – present). I provide expertise on natural resource conservation and management issues, particularly as they relate to large mammals in desert, mountain, and plains environments.

Senior Environmental Scientist, California Department of Fish and Game (2001 – 2008; now retired). I served as the project leader for the Sierra Nevada Bighorn Sheep Recovery

Program, a project to conserve mountain sheep in that range and restore them to formerly occupied habitats; I continued to function as the Regional Large Mammal and Desert specialist, with an emphasis on mountain sheep and mule deer in southeastern California. I also served as chair of the Sierra Nevada Bighorn Sheep Scientific Advisory Group, and served on the Peninsular Bighorn Sheep Recovery Team.

Senior Wildlife Biologist, California Department of Fish and Game (1999 – 2001). I served as the Regional Large Mammal and Desert Specialist, with an emphasis on mountain sheep and mule deer in southeastern California.

Senior Wildlife Biologist, California Department of Fish and Game (1993 – 1999). I served as the Regional Large Mammal Specialist and supervised the activities of 5 journeyman wildlife biologists in eastern California. Emphasis species included mountain sheep, mule deer, pronghorn, tule elk, and sage grouse in eastern California.

Associate Wildlife Biologist, California Department of Fish and Game (1986 – 1993). I served as the Regional mountain sheep specialist, and supervised the activities of 5 journeyman wildlife biologists in eastern California. Emphasis species included mountain sheep, mule deer, pronghorn, tule elk, and sage grouse in eastern California.

Project Leader, California Department of Fish and Game, Federal Aid in Wildlife Restoration Project W-26-D (1978 – 1986). I supervised 2 technicians, and planned and implemented habitat management projects designed to benefit waterfowl, sage grouse, mule deer, and mountain sheep in eastern California.

Assistant Wildlife Biologist, California Department of Fish and Game (1975 – 1978). I was an Area Biologist responsible for management of mule deer, mountain sheep, and the Endangered Stephens' kangaroo rat, as well as for environmental review activities in Riverside and San Bernardino counties, California.

Junior Aquatic Biologist, California Department of Fish and Game (1974 – 1975). I was responsible for fisheries management activities, with an emphasis on wild trout and the Endangered unarmored three-spined stickleback in Los Angeles and San Bernardino counties, California.

Park Ranger, Department of Recreation, City of Long Beach, California (1970 – 1973). I was responsible for public education activities, routine patrol, and coordination with other law enforcement agencies in El Dorado Regional Park, Long Beach, California.

Academic Appointments:

Research Professor, Department of Natural Resources and Environmental Science, University of Nevada, Reno (2007 – Present).

Affiliate Faculty, Department of Biological Sciences, Idaho State University, Pocatello, Idaho (2005 – Present).

Senior Research Associate, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska (1998 – Present).

Affiliate Assistant Professor of Wildlife Ecology, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska (1993 – 1998).

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Adjunct Assistant Professor of Natural Resource Science, Department of Natural Resource Science, University of Rhode Island, Kingston (1992 – 1994).

Instructor, Mt. San Jacinto College, San Jacinto, California (1976 – 1986).

Assistant Professor, Department of Biology, Rio Hondo College, Whittier, California (1973 – 1974).

Teaching Assistant, California State University, Long Beach (1972 – 1973).

Graduate Research Assistant, California State University, Long Beach (1970–1972).

Graduate Student Supervision:

Chair of Graduate Committee:

Kevin L. Monteith (Ph.D.), Reproductive ecology of migratory and resident mule deer in the eastern Sierra Nevada, California. Idaho State University, Pocatello. *Graduated July 2011.* Present position: Post-doctoral Researcher, Wyoming Cooperative Fish and Wildlife Research Unit. Co-chair with Dr. R. T. Bowyer.

Michael W. Oehler (M.S.), Ecology of mountain sheep: effects of mining and precipitation. University of Alaska Fairbanks. *Graduated December 1999.* Current position: Wildlife Biologist, National Park Service, Theodore Roosevelt National Park, Medora, North Dakota. Co-chair with Dr. R. T. Bowyer.

Becky M. Pierce (Ph.D.), Predator-prey dynamics between mountain lions and mule deer: effects on distribution, population regulation, habitat selection and prey selection. University of Alaska Fairbanks. *Graduated May 1999.* Current position: Associate Wildlife Biologist, California Department of Fish and Game, Bishop, California. Co-chair with Dr. R. T. Bowyer.

Graduate Committee Membership:

Anthony Bush (M.S.), Responses of mule deer to water development in a Mojave Desert ecosystem. University of Nevada, Reno. Graduation expected June 2014.

Jeffrey T. Villepique (Ph.D.), Interactions between mountain lions and mountain sheep: an assessment of forage benefits and predation risk. Idaho State University, Pocatello (Graduation expected December 2012).

Sabrina Morano (Ph.D.), Reproductive biology of mule deer in the White Mountains, Inyo and Mono counties, California. University of Nevada, Reno (Graduation expected June 2013).

Cody J. McKee (M.S.), Ecology of mule deer in the eastern Mojave Desert, California. University of Nevada, Reno. *Graduated May 2012*. Current position: Wildlife Biologist, Nevada Division of Wildlife, Las Vegas.

Jericho C. Whiting (Ph.D.), Behavior and ecology of reintroduced Rocky Mountain bighorn sheep. Idaho State University, Pocatello. *Graduated December 2008*. Current position: Wildlife Biologist, Idaho National Laboratory, Twin Falls.

Cody A. Schroeder (M.S.), Habitat selection by mountain sheep: forage benefits or risk of predation? Idaho State University, Pocatello. *Graduated September 2007.* Current position: Doctoral Student, University of Nevada, Reno.

Jason P. Marshal (Ph.D.), Foraging ecology and water relationships of mule deer in a Sonoran Desert environment. University of Arizona, Tucson. *Graduated May 2005.* Current position: Senior Lecturer, University of the Witwatersrand, South Africa.

Heather E. Johnson (M.S.), Antler breakage in tule elk in Owens Valley, California: nutritional causes and behavioral consequences. University of Arizona, Tucson. *Graduated January 2004*. Current position: Mammal Research Biologist, Colorado Division of Wildlife, Durango.

Jennifer L. Rechel (Ph.D. [Geography]), Influence of neighborhood effects and friction surfaces on the spatial distribution and movement strategies of desert-dwelling mountain sheep (*Ovis canadensis*). University of California, Riverside. *Graduated August 2003*. Current position: Wildlife Biologist, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Riverside, California.

Holly B. Ernest (Ph.D.), Ecological genetics of mountain lions (*Puma concolor*) in California. University of California, Davis. *Graduated December 2001*. Current position: Research Geneticist, School of Veterinary Medicine, University of California, Davis.

Esther S. Rubin (Ph.D.), The ecology of bighorn sheep (*Ovis canadensis*) in the peninsular ranges of California. University of California, Davis. *Graduated December 2000*. Current position: Research Branch Chief, Arizona Game and Fish Department, Phoenix, Arizona.

Nancy G. Andrew (M.S.), Demography and habitat use of desert-dwelling mountain sheep in the East Chocolate Mountains, Imperial County, California. University of Rhode Island, Kingston. *Graduated May 1994*. Current position: Associate Wildlife Biologist, California Department of Fish and Game.

Awards and Honors:

Service Beyond Self Award, 2011 (Society for the Conservation of Bighorn Sheep)

Honorary Lifetime Membership, 2010 (in recognition of long and continuing service to the Society for the Conservation of Bighorn Sheep)

Wild Sheep Biologist Wall of Fame Award, 2009 (in recognition of significant contributions to the conservation of wild sheep in North America) (Wild Sheep Foundation)

Lifetime Achievement Award, 2008 (In recognition of contributions toward the conservation of mountain sheep in California) (California Chapter of the Foundation for North American Wild Sheep)

Honor Plaque, 2007 (Group Award, in recognition of outstanding contributions toward the recovery of mountain sheep in the Sierra Nevada) (Desert Bighorn Council)

State Statesman Award, 2006 (In recognition of outstanding contributions to the wild sheep of California) (Foundation for North American Wild Sheep)

Trail Blazer Award, 2004 (In recognition of efforts on behalf of mountain sheep conservation in California) (California Chapter of the Foundation for North American Wild Sheep)

Director's Achievement Award, 2004 (In recognition of editorial services for *California Fish and Game* (California Department of Fish and Game)

Annual Achievement Award, 2004 (In recognition of conservation of mule deer and their habitats) (Southern California Chapter, California Deer Association)

Alumni Achievement Award for Professional Excellence, 2002 (University of Alaska Alumni Association)

Outstanding Alumnus Award, 2002 (College of Science, Engineering, and Mathematics, University of Alaska Fairbanks)

Sustained Superior Accomplishment Award, 2002 (California Department of Fish and Game)

The Desert Ram Award, 2001 (Desert Bighorn Council)

Outstanding Publication Award for a Monograph, 1998 (The Wildlife Society)

Award of Appreciation, 1998 (San Fernando Valley Chapter of Safari Club International, CA)

Professional Membership, Boone and Crockett Club, 1998 (Boone and Crockett Club)

Certificate of Appreciation, 1997 (Society for the Conservation of Bighorn Sheep)

"Ol' Irongut" Award, 1996 (California Department of Fish and Game, Division of Air Services)

Resources Agency/University of California Fellowship, 1996 (Sponsored jointly by the California Resources Agency and the University of California, Davis)

Director's Achievement Award, 1992 (California Department of Fish and Game)

Outstanding Biology Department Alumnus, 1988 (California State University, Long Beach)

Professional of the Year, 1985 (Western Section of The Wildlife Society)

California Wildlife Officer of the Year, 1984 (Shikar-Safari Foundation)

Award of Honor, 1984 (Society for the Conservation of Bighorn Sheep)

Honorary Lifetime Membership, 1984 (Banning [California] Sportsman's Club)

Professional and Fraternal Memberships:

American Society of Mammalogists (Life Member)
The Boone and Crockett Club (Professional Member)
The Wildlife Society
Society for Conservation Biology
Southwestern Association of Naturalists
Wild Sheep Foundation
National Rifle Association
California Chapter, Foundation for North American Wild Sheep
Society for the Conservation of Bighorn Sheep
Minnesota-Wisconsin Chapter, Foundation for North American Wild Sheep

Licenses and Certifications:

California Community College Credential (# 45476 [Lifetime])
State of California Blaster's License (# 2087)
Certified in Wildlife Capture Techniques (California Department of Fish and Game)
Certified Wildlife Biologist (1981 – The Wildlife Society)
California Hunter Safety Instructor (# 1984)
Flying in the Wire and Obstruction Environment (2010 - Utilities Aviation Specialists)

Other Professional Activities:

Editorial Activities:

Editor-in-Chief, *California Fish and Game* (2010 – present)

Associate Editor, *California Fish and Game* (1995 – 2009)

Editor, *Transactions of the Western Section of The Wildlife Society* (1988)

Associate Editor, *Transactions of the Western Section of The Wildlife Society* (1986 – 1987)

Reviewer for Journals:

Conservation Biology, Journal of Wildlife Management, Wildlife Society Bulletin, Journal of Mammalogy, The Condor, California Fish and Game, Transactions of the Western Section of the Wildlife Society, Western North American Naturalist, Desert Bighorn Council Transactions, Southwestern Naturalist, Proceedings of the Northern Wild Sheep and Goat Council, Journal of Wildlife Diseases, Great Basin Naturalist, Bulletin of the Southern California Academy of Sciences, Journal of Zoology (London), Vida Silvestre Neotropical, Wildlife Biology, Wildlife Monographs, European Journal of Wildlife Research, Biological Conservation, Journal of Arid Environments (An average of about 12 reviews per year).

Other Activities:

2012 – Present: Member, USDI Bureau of Land Management Resource Advisory Council (Appointed by the Secretary of the Interior)

2012 – Present: Chair, Projects Funding Committee, California Chapter, Wild Sheep Foundation

2011: Member, Jim McDonough Awards Committee, The Wildlife Society

2011 – Present: Co-Chair, Conservation Grants Subcommittee, Boone and Crockett Club

2011 – Present: Member, Conservation Committee, Boone and Crockett Club

2010 – Present: Administrator, Professional Resource Advisory Board, Wild Sheep Foundation

2008 – 2012: Member, Projects Funding Committee, California Chapter, Wild Sheep Foundation

2008 – Present: Member, Big Game Records Committee, Boone and Crockett Club

2007 – Present: Advisory Board Member, Texas Bighorn Society

2007 – Present: Science Advisor, Society for the Conservation of Bighorn Sheep

2006 – Present: Member, *Ad Hoc* Committee on Professional Membership, Boone and Crockett Club.

1998 – 2002: Coach and member of Board of Trustees, Sierra Roller Hockey League.

1995–96: Vice Chairman, The Desert Bighorn Council.

1994–98: Member, Board of Directors, The Wildlife Forensic DNA Foundation.

1993 – Present: Member, Professional Resource Advisory Board, Wild Sheep Foundation

1991: Member, Committee on Support of Symposia and Conferences, The Wildlife Society.

1989–1993: Member, Board of Trustees, Friends of the Eastern California Museum; Vice-chairman, 1991–1992; Chairman, 1993.

1987–1988: Chairman, The Desert Bighorn Council.

1988: Co-chairman, Wildlife Water Development Symposium, Western Section of The Wildlife Society.

Publications in Professional Journals:

Loft, E. R., and **V. C. Bleich**. *In review*. An historical perspective on deer ranges in California: terminology and its relevance to wildlife conservation. California Fish and Game.

Wiedmann, B., and **V. C. Bleich**. *In review*. Responses of bighorn sheep to recreational activities: trial of a trail. Prairie Naturalist.

McKee, C. J., K. M. Stewart, **V. C. Bleich**, J. S. Sedinger, N. W. Darby, and D. L. Hughson. *In review*. Space use patterns of mule deer: responses to provision of water and effects of wildfire. Journal of Arid Environments.

McKee, C. J., K. M. Stewart, J. S. Sedinger, **V. C. Bleich**, N. W. Darby, and D. L. Hughson. *In review*. Mule deer in arid environments: does provision of water improve population performance? European Journal of Wildlife Research.

Monteith, K. M., T. R. Stephenson, **V. C. Bleich**, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. *In review*. Life history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs.

Monteith, K. L., R. A. Long, **V. C. Bleich**, J. R. Heffelfinger, P. R. Krausman, and R. T. Bowyer. *In press*. Size of horn-like structures in trophy ungulates: effects of climate, culture, or harvest? Wildlife Monographs.

Grovenburg, T., R. Klaver, C. Jacques, T. Brinkman, C. Swanson, C. DePerno, K. Monteith, J. Sievers, **V. Bleich**, J. Kie, and J. Jenks. *In press*. Influence of landscape characteristics and ungulate demography on retention of expandable radiocollars. Wildlife Society Bulletin.

Krausman, P. R., and **V. C. Bleich**. *In press*. Conservation and management of ungulates in North America. International Journal of Environmental Science.

Abella, R., **V. C. Bleich**, R. A. Botta, B. J. Gonzales, T. R. Stephenson, S. G. Torres, and J. D. Wehausen. *In press*. Status of bighorn sheep in California — 2011. Desert Bighorn Council Transactions.

Monteith, K., T. Stephenson, **V. Bleich**, M. Conner, B. Pierce, and R. Bowyer. *In press*. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology.

Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and **V. C. Bleich**. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295– 307. [published on line 12 July 2012; DOI: 10.1007/s00442-012-2397-6].

Holl, S. A., **V. C. Bleich**, B. W. Callenberger, and B. Bahro. 2012. Simulated effects of two fire regimes on bighorn sheep: the San Gabriel Mountains, California, USA. Fire Ecology 8(3):88–103. [DOI: 10.4996/fireecology.0803088]

Pierce, B. M., **V. C. Bleich**, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977–988.

Marshal, J. P., **V. C. Bleich**, P. R. Krausman, A. Neibergs, M. L. Reed, and N. G. Andrew. 2012. Habitat use and diets of mule deer and feral ass in the Sonoran Desert. Southwestern Naturalist 57:16–25.

Simpson, N. O., K. M. Stewart, and **V. C. Bleich**. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190–209.

Marshal, J. P., and **V. C. Bleich**. 2011. Evidence of relationships between El Niño Southern Oscillation and mule deer harvest in California. California Fish and Game 97:84–97.

Villepique, J. T., B. M. Pierce, **V. C. Bleich**, and R. T. Bowyer. 2011. Diets of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey. Southwestern Naturalist 56:187–192.

Monteith, K. M., **V. C. Bleich**, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011 Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. DOI:10.1890/ES10-00096.1

Whiting, J. C., R. T. Bowyer, J. T. Flinders, **V. C. Bleich**, and J. G. Kie. 2010. Sexual segregation and use of water by bighorn sheep: implications for conservation. Animal Conservation 13:541–548.

Holl, S. A., and **V. C. Bleich**. 2010. Responses of large mammals to fire and rain in the San Gabriel Mountains, California. Northern Wild Sheep and Goat Council Proceedings 17:139–156.

Schroeder, C. A., R. T. Bowyer, **V. C. Bleich**, and T. R. Stephenson. 2010. Sexual segregation in Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*: ramifications for conservation. Arctic, Antarctic, and Alpine Research 42:476–489.

Bleich, V. C., J. P. Marshal, and N. G. Andrew. 2010. Habitat use by a desert ungulate: predicting effects of water availability on mountain sheep. Journal of Arid Environments 74:638–645.

Bleich, V. C. 2009. Perceived threats to mountain sheep: levels of concordance among states, provinces, and territories. Desert Bighorn Council Transactions 50:32–39.

Krausman, P. R., D. E. Naugle, M. R. Frisina, R. Northrup, **V. C. Bleich**, W. M. Block, M. C. Wallace, and J. D. Wright. 2009. Livestock grazing, wildlife habitat, and rangeland values. Rangelands 31(5):15–19.

Bleich, V. C. 2009. Factors to consider when reprovisioning water developments used by mountain sheep. California Fish and Game 95:153–159.

Holl, S. A., and **V. C. Bleich**. 2009. Reconstructing the San Gabriel Mountains bighorn sheep population. California Fish and Game 95:77–87.

Clifford, D. L., B. A. Schumaker, T. R. Stephenson, **V. C. Bleich**, M. Leonard-Cahn, B. J. Gonzales, W. M. Boyce, and J. A. K. Mazet. 2009. Assessing disease risk at the wildlife-livestock interface: a study of Sierra Nevada bighorn sheep. Biological Conservation 142:2559–2568.

Bleich, V. C., J. H. Davis, J. P. Marshal, S. G. Torres, and B. J. Gonzales. 2009. Mining activity and habitat use by mountain sheep. European Journal of Wildlife Research 55:183–191.

Pease, K. M., A. H. Freedman, J. P. Pollinger, J. E. McCormack, W. Buermann, J. Rodzen, J. Banks, E. Meredith, **V. C. Bleich**, R. J. Schaefer, K. Jones, and R. K. Wayne. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. Molecular Ecology 18:1848–1862.

Duffy, L. K., M. W. Oehler, R. T. Bowyer, and **V. C. Bleich**. 2009. Mountain sheep: an environmental epidemiological survey of variation in metal exposure and physiological biomarkers following mine development. American Journal of Environmental Sciences 5:296–303.

Marshal, J. P., J. W. Cain III, **V. C. Bleich**, and S. S. Rosenstock. 2009. Intrinsic and extrinsic sources of variation in the population dynamics of an arid-environment large herbivore. Canadian Journal of Zoology 87:103–111.

Villepique, J. T., **V. C. Bleich**, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-Science™ Collars and a method for screening location data. California Fish and Game 94:155–168.

Bleich, V. C., H. E. Johnson, S. A. Holl, L. Konde, S. G. Torres, and P. R. Krausman. 2008. Fire history in a chaparral ecosystem: implications for conservation of a native ungulate. Rangeland Ecology and Management 61:571–579.

Marshal, J. P., P. R. Krausman, and **V. C. Bleich**. 2008. Body condition of desert mule deer is related to rainfall. Southwestern Naturalist 53:311–318.

Marshal, J. P., **V. C. Bleich**, and N. G. Andrew. 2008. Evidence for interspecific competition between feral ass and mountain sheep in a desert environment. Wildlife Biology 14:228–236.

Bleich, V. C., and R. A. Weaver. 2007. Status of mountain sheep in California: comparisons between 1957 and 2007. Desert Bighorn Council Transactions 49:55–67.

Wehausen, J. D., and **V. C. Bleich**. 2007. Influence of aerial search time on survey results. Desert Bighorn Council Transactions 49:23–29.

Bowyer, R. T., **V. C. Bleich**, X. Manteca, J. C. Whiting, and K. M. Stewart. 2007. Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. Ethology 113:1048–1060.

Epps, C. W., J. D. Wehausen, **V. C. Bleich**, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714–724.

Bleich, V. C., T. R. Stephenson, B. M. Pierce, and M. J. Warner. 2007. Body condition of mule deer while injured and following recovery. Southwestern Naturalist 52:164–167.

Johnson, H. E., **V. C. Bleich**, and P. R. Krausman. 2007. Mineral deficiencies in tule elk, Owens Valley, California. Journal of Wildlife Diseases 43:61–74.

Johnson, H. E., **V. C. Bleich**, P. R. Krausman, and J. L. Koprowski. 2007. Effects of antler breakage on mating behavior in male tule elk (*Cervus elaphus nannodes*). European Journal of Wildlife Research 53:9–15.

Bleich, V. C. 2006. Mountain sheep in California: perspectives on the past, and prospects for the future. Biennial Symposium of the Northern Wild Sheep and Goat Council 15:1–13.

Marshal, J. P., **V. C. Bleich**, P. R. Krausman, M. L. Reed, and N. G. Andrew. 2006. [Invited paper] Factors affecting habitat use and distribution of mule deer in an arid environment. Wildlife Society Bulletin 34:609–619.

Bleich, V. C., N. G. Andrew, M. J. Martin, G. P. Mulcahy, A. M. Pauli, and S. S. Rosenstock. 2006. [Invited paper] Quality of water available to wildlife: comparisons among artificial and natural sources. Wildlife Society Bulletin 34:627–632.

Bleich, V. C., S. Nelson, P. J. Wood, H. R. Wood, and R. A. Noles. 2006. [Invited paper] Retrofitting gallinaceous guzzlers: enhancing water availability and safety for wildlife. Wildlife Society Bulletin 34:633–636.

Marshal, J. P., P. R. Krausman, **V. C. Bleich**, S. S. Rosenstock, and W. B. Ballard. 2006. [Invited paper] Gradients of forage biomass and ungulate use near wildlife water developments. Wildlife Society Bulletin 34:620–626.

Rominger, E. M., **V. C. Bleich**, and E. J. Goldstein. 2006. [Letter] Bighorn sheep, mountain lions, and the ethics of conservation. Conservation Biology 20:1041.

Marshal, J. P., L. M. Lesicka, **V. C. Bleich**, P. R. Krausman, G. P. Mulcahy, and N. G. Andrew. 2006. Demography of desert mule deer in southeastern California. California Fish and Game 92:55–66.

Bleich, V. C., B. M. Pierce, J. Jones, and R. T. Bowyer. 2006. Variance in survival rates among young mule deer in the Sierra Nevada, California. California Fish and Game 92:24–38.

Johnson, H. E., **V. C. Bleich**, and P. R. Krausman. 2005. Antler breakage in tule elk, Owens Valley, California. Journal of Wildlife Management 69:1747–1752.

Rosenstock, S. S., **V. C. Bleich**, M. J. Rabe, and C. Reggiardo. 2005. Water quality at wildlife water sources in the Sonoran Desert, United States. Rangeland Ecology and Management 58:623–627.

Marshal, J. P., P. R. Krausman, and **V. C. Bleich**. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360–365.

Bleich, V. C., J. T. Villepique, T. R. Stephenson, B. M. Pierce, and G. M. Kutliyev. 2005. Efficacy of aerial telemetry as an aid to capture specific individuals: a comparison of two techniques. Wildlife Society Bulletin 33:332–336.

Bleich, V. C. 2005. [Invited paper] In my opinion: politics, promises, and illogical legislation confound wildlife conservation. Wildlife Society Bulletin 33:66–73.

Wehausen, J. D., **V. C. Bleich**, and R. R. Ramey II. 2005. Correct nomenclature for Sierra Nevada bighorn sheep. California Fish and Game 91:216–218.

Oehler, M. W., **V. C. Bleich**, R. T. Bowyer, and M. C. Nicholson. 2005. Mountain sheep and mining: implications for conservation and management. California Fish and Game 91:149–178.

Marshal, J. P., P. R. Krausman, and **V. C. Bleich**. 2005. Dynamics of mule deer forage in the Sonoran Desert. Journal of Arid Environments 60:593–609.

Bleich, V. C., and S. G. Torres. 2004. [Guest Editorial] International involvement in wildlife conservation. Wildlife Society Bulletin 32:1013–1014.

Krausman, P. R., **V. C. Bleich**, J. W. Cain III, T. R. Stephenson, D. W. DeYoung, P. W. McGrath, P. K. Swift, B. M. Pierce, and B. D. Jansen. 2004. Neck lesions in ungulates from collars incorporating satellite technology. Wildlife Society Bulletin 32:987–991.

Marshal, J. P., **V. C. Bleich**, N. G. Andrew, and P. R. Krausman. 2004. Seasonal forage use by desert mule deer in southeastern California. Southwestern Naturalist 49:501–505.

Holl, S. A., **V. C. Bleich**, and S. G. Torres. 2004. Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967–2002. Wildlife Society Bulletin 32:412–426.

Pierce, B. M., R. T. Bowyer, and **V. C. Bleich**. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533–541.

Bleich, V. C., E. F. Cassirer, L. E. Oldenburg, V. L. Coggins, and D. L. Hunter. 2004. Predation by a golden eagle, *Aquila chrysaetos*, on a juvenile mountain sheep, *Ovis canadensis*. California Fish and Game 90:91–93.

Epps, C. W., D. R. McCullough, J. D. Wehausen, **V. C. Bleich**, and J. L. Rechel. 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18:102–113.

Long, E. S., D. M. Fecske, R. A. Sweitzer, J. A. Jenks, B. M. Pierce, and **V. C. Bleich**. 2003. Efficacy of photographic scent stations to detect mountain lions. Western North American Naturalist 63:529–532.

Bleich, V. C. 2003. The potential for botulism in desert-dwelling mountain sheep. Desert Bighorn Council Transactions 47:2–8.

Epps, C. W., **V. C. Bleich**, J. D. Wehausen, and S. G. Torres. 2003. Status of bighorn sheep in California. Desert Bighorn Council Transactions 47:20–35.

Oehler, M. W., Sr., R. T. Bowyer, and **V. C. Bleich**. 2003. Home ranges of mountain sheep: effects of precipitation in a desert ecosystem. Mammalia 67:385–402.

Weckerly, F. W., **V. C. Bleich**, C.-L. B. Chetkiewicz, and Mark A. Ricca. 2003. Body weight and rumen-reticulum capacity in tule elk and mule deer. Journal of Mammalogy 84:659–664.

Ernest, H. B., W. M. Boyce, **V. C. Bleich**, B. M. May, S. J. Stiver, and S. G. Torres. 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. Conservation Genetics 4:353–366.

Bleich, V. C., T. R. Stephenson, N. J. Holste, I. C. Snyder, J. P. Marshal, P. W. McGrath, and B. M. Pierce. 2003. Effects of tooth extraction on selected biological parameters of female mule deer. Wildlife Society Bulletin 31:233–236.

Marshal, J., P. R. Krausman, **V. C. Bleich**, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, el Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66:1283–1289.

Stephenson, T. R., **V. C. Bleich**, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using *in vivo* and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

Swift, P. K., **V. C. Bleich**, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal. 2002. Tooth extraction from mule deer in the absence of chemical immobilization. Wildlife Society Bulletin 30:253–255.

Bleich, V. C., C. S. Y. Chun, R. W. Anthes, T. E. Evans, and J. K. Fischer. 2001. [Invited Paper] Visibility bias and development of a sightability model for tule elk. Alces 37:315–327.

Drew, M. L., **V. C. Bleich**, S. G. Torres, and R. G. Sasser. 2001. Early pregnancy detection in mountain sheep using a pregnancy-specific protein B assay. Wildlife Society Bulletin 29:1182–1185.

Rosenstock, S. S., J. J. Hervert, **V. C. Bleich**, and P. R. Krausman. 2001. Muddying the water with poor science: a reply to Broyles and Cutler. Wildlife Society Bulletin 29:734–738 [peer edited].

Bleich, V. C. 2001. [Letter] On wildlife management in national monuments. The Wildlifer 306:59.

Andrew, N. G., **V. C. Bleich**, A. D. Morrison, L. M. Lesicka, and P. Cooley. 2001. Wildlife mortalities associated with artificial water sources in the Sonoran Desert. Wildlife Society Bulletin 29:275–280.

Thompson, J. R., **V. C. Bleich**, S. G. Torres, and G. P. Mulcahy. 2001. Translocation techniques for mountain sheep: does the method matter? Southwestern Naturalist 46:87–93.

Bleich, V. C., and B. M. Pierce. 2001. Accidental mass mortality of migrating mule deer. Western North American Naturalist 61:124–125.

Chao-chin, C., B. B. Chomel, R. W. Kasten, R. Heller, K. M. Kocan, H. Ueno, K. Yamamoto, **V. C. Bleich**, B. M. Pierce, B. J. Gonzales, P. K. Swift, W. M. Boyce, S. S. Jang, H.-J. Boulouis, and Y. Piemont. 2000. *Bartonella* spp. isolated from domestic and wild ruminants in North America. Emerging Infectious Diseases 6:306–311.

Singer, F. J., **V. C. Bleich**, and M. A. Gudorf. 2000. [Invited Paper] Restoration of bighorn sheep metapopulations in and near western national parks. Restoration Ecology 8(4S):14–24.

Bleich, V. C., and M. W. Oehler. 2000. [Invited paper] Wildlife education in the United States: thoughts from agency biologists. Wildlife Society Bulletin 28:542–545.

Rubin, E. S., W. M. Boyce, and **V. C. Bleich**. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769–786.

Schaefer, R. J., S. G. Torres, and **V. C. Bleich**. 2000. Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. California Fish and Game 86:127–135.

Pierce, B. M., **V. C. Bleich**, and R. T. Bowyer. 2000. Prey selection by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462–472.

Swift, P. K., J. D. Wehausen, H. B. Ernest, R. S. Singer, A. M. Pauli, H. Kinde, T. E. Rocke, and **V. C. Bleich**. 2000. Desert bighorn sheep mortality due to presumptive type C botulism in California. Journal of Wildlife Diseases 36:184–189.

Pierce, B. M., **V. C. Bleich**, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.

Bleich, V. C. 1999. Wildlife conservation and wilderness management: uncommon objectives and conflicting philosophies. North American Wild Sheep Conference Proceedings 2:195–205.

Bleich, V. C., and A. M. Pauli. 1999. Distribution and intensity of hunting and trapping activity in the East Mojave National Scenic Area, California. California Fish and Game 85:148–160.

Pierce, B. M., **V. C. Bleich**, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986–992.

Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80:283–289.

Bleich, V. C., and B. M. Pierce. 1999. Expandable and economical radio collars for juvenile mule deer. California Fish and Game 85:56–62.

Hill, S. D., and **V. C. Bleich**. 1999. Monitoring wildlife water sources using low Earth orbiting satellites (LEOS). Wildlife Society Bulletin 27:25–27.

Andrew, N. G., **V. C. Bleich**, and P. V. August. 1999. Habitat selection by mountain sheep in the Sonoran Desert: implications for conservation in the United States and Mexico. California Wildlife Conservation Bulletin 12:1–30.

Grigione, M. M., P. Burman, **V. C. Bleich**, and B. M. Pierce. 1999. Identifying individual mountain lions (*Felis concolor*) by their tracks: refinement of an innovative technique. Biological Conservation 88:25–32.

Bleich, V. C. 1998. Importance of observer experience in determining age and sex of mountain sheep. Wildlife Society Bulletin 26:877–880.

de Ropp, J. S., J. H. Theis, J. I. Mead, and **V. C. Bleich**. 1998. Limitations of nuclear magnetic resonance (NMR) analysis of fecal bile for taxonomic identification of contemporary and extinct mammals. California Fish and Game 84:112–118.

Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265–272.

Pierce, B. M., **V. C. Bleich**, C. L.-B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

Andrew, N. G., **V. C. Bleich**, P. V. August, and S. G. Torres. 1997. Demography of mountain sheep in the East Chocolate Mountains, California. California Fish and Game 83:68–77.

Andrew, N. G., L. M. Lesicka, and **V. C. Bleich**. 1997. An improved fence design to protect water sources for native ungulates. Wildlife Society Bulletin 25:823–825.

Bleich, V. C., S. G. Torres, J. D. Wehausen, and T. A. Swank. 1996. [Invited paper] History of transplanting mountain sheep — California. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 10:164–166.

Torres, S. G., **V. C. Bleich**, and J. D. Wehausen. 1996. Status of bighorn sheep in California, 1995. Desert Bighorn Council Transactions 40:27–34.

Oehler, M. W., **V. C. Bleich**, and R. T. Bowyer. 1996. Error associated with LORAN-C: effects of aircraft altitude and geographic location. Desert Bighorn Council Transactions 40:19–21.

Bleich, V. C. 1996. Interactions between coyotes (*Canis latrans*) and mountain sheep (*Ovis canadensis*). Southwestern Naturalist 41:81–82.

Davis, J. L., C. L.-B. Chetkiewicz, **V. C. Bleich**, G. Raygorodetsky, B. M. Pierce, J. W. Ostergard, and J. D. Wehausen. 1996. A device to safely remove immobilized mountain lions from trees and cliffs. Wildlife Society Bulletin 24:537–539.

Bleich, V. C., B. M. Pierce, J. L. Davis, and V. L. Davis. 1996. Thermal characteristics of mountain lion dens. Great Basin Naturalist 56:276–278.

Main, M. B., F. W. Weckerly, and **V. C. Bleich**. 1996. [Invited Paper] Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449–461.

Cronin, M. A., and **V. C. Bleich**. 1995. Mitochondrial DNA variation among populations and subspecies of mule deer in California. California Fish and Game 81:45–54.

Bleich, V. C., and M. V. Price. 1995. Aggressive behavior of *Dipodomys stephensi*, an endangered species, and *Dipodomys agilis*, a sympatric congener. Journal of Mammalogy 76:646–651.

Torres, S. G., **V. C. Bleich**, and J. D. Wehausen. 1994. Status of bighorn sheep in California, 1993. Desert Bighorn Council Transactions 38:17–28.

Bleich, V. C., and S. G. Torres. 1994. [Invited Paper] California's mountain sheep management program. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 9:186–195.

Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes. 1994. [Lead Article] Responses of mountain sheep *Ovis canadensis* to helicopter surveys: ramifications for the conservation of large mammals. Biological Conservation 45:1–7.

Jaeger, J. R., J. D. Wehausen, **V. C. Bleich**, and C. L. Douglas. 1993. Limits in the resolution of LORAN-C for aerial telemetry studies. Desert Bighorn Council Transactions 37:20–23.

Torres, S. G., **V. C. Bleich**, and A. M. Pauli. 1993. Status of bighorn sheep in California, 1992. Desert Bighorn Council Transactions 37:47–52.

Torres, S. G., **V. C. Bleich**, and A. M. Pauli. 1993. An analysis of hunter harvest of mountain sheep in California, 1987–1992. Desert Bighorn Council Transactions 37:37–40.

Jessup, D. A., W. L. Goff, D. Stiller, M. N. Oliver, **V. C. Bleich**, and W. M. Boyce. 1993. A retrospective serologic survey for *Anaplasma* spp. infection in three bighorn sheep (*Ovis canadensis*) populations in California. Journal of Wildlife Diseases 29:547–554.

Thompson, J. R., and **V. C. Bleich**. 1993. A comparison of mule deer survey techniques in the Sonoran Desert of California. California Fish and Game 79:70–75.

Bleich, V. C. 1993. Comments on research, publications, and California's longest continuously published journal. California Fish and Game 79:42–43.

Bleich, V. C., M. C. Nicholson, A. T. Lombard, and P. V. August. 1992. Preliminary tests of mountain sheep habitat models using a geographic information system. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 8:256–263.

Bleich, V. C., R. T. Bowyer, D. J. Clark, and T. O. Clark. 1992. Quality of forages eaten by mountain sheep in the eastern Mojave Desert, California. Desert Bighorn Council Transactions 36:41–47.

Bleich, V. C., S. G. Torres, D. A. Jessup, and G. P. Mulcahy. 1992. Status of mountain sheep in California, 1991. Desert Bighorn Council Transactions 36:76–77.

Krausman, P. R., **V. C. Bleich**, J. A. Bailey, D. Armentrout, and R. R. Ramey II. 1992. What is a minimum viable population? Desert Bighorn Council Transactions 36:68–75.

Jaeger, J. R., J. D. Wehausen, and **V. C. Bleich**. 1991. Evaluation of time-lapse photography to estimate population parameters. Desert Bighorn Council Transactions 35:5–8.

Bleich, V. C., and D. A. Jessup. 1991. Status of bighorn sheep in California, 1990. Desert Bighorn Council Transactions 35:11–12.

Bleich, V. C., and D. Racine. 1991. Mountain beaver (*Aplodontia rufa*) from Inyo County, California. California Fish and Game 77:153–155.

Bleich, V. C., J. G. Stahmann, R. T. Bowyer, and J. E. Blake. 1990. Osteoporosis, osteomalacia, and cranial asymmetry in a mountain sheep (*Ovis canadensis*). Journal of Wildlife Diseases 26:372–376.

Bleich, V. C. 1990. On Calcium deficiency and brittle antlers. Journal of Wildlife Diseases 26:588.

Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4:383–390.

Bleich, V. C., R. T. Bowyer, A. M. Pauli, R. L. Vernoy, and R. W. Anthes. 1990. Responses of mountain sheep to aerial sampling using helicopters. California Fish and Game 76:197–204.

Bleich, V. C., J. D. Wehausen, J. A. Keay, J. G. Stahmann, and M. W. Berbach. 1990. Radiotelemetry collars and mountain sheep: a cautionary note. Desert Bighorn Council Transactions 34:6–8.

Bleich, V. C., J. D. Wehausen, K. R. Jones, and R. A. Weaver. 1990. Status of bighorn sheep in California, 1989 and translocations from 1971 through 1989. Desert Bighorn Council Transactions 34:24–26.

Pauli, A. M., and **V. C. Bleich**. 1988. Additional records of the spotted bat (*Euderma maculatum*) from California. Great Basin Naturalist 48:563.

Wehausen, J. D., **V. C. Bleich**, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. Journal of Wildlife Management 51:86–98.

Holl, S. A., and **V. C. Bleich**. 1987. Mineral lick use by mountain sheep in the San Gabriel Mountains, California. Journal of Wildlife Management 51:381–383.

Wehausen, J. D., **V. C. Bleich**, and R. A. Weaver. 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. Western Section of The Wildlife Society Transactions 23:65–74.

Schwartz, O. A., **V. C. Bleich**, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. Biological Conservation 37:179–190.

Bleich, V. C. 1986. Early breeding in free-ranging mountain sheep. Southwestern Naturalist 31:530–531.

Schwartz, O. A., and **V. C. Bleich**. 1985. Optimal foraging in Barn Owls? Rodent frequencies in diet and fauna. Bulletin of the Southern California Academy of Science 84:41–45.

Bowyer, R. T., and **V. C. Bleich**. 1984. Distribution and taxonomic affinities of mule deer, *Odocoileus hemionus*, from Anza-Borrego Desert State Park, California. California Fish and Game 70:53–57.

Bowyer, R. T., and **V. C. Bleich**. 1984. Effects of cattle grazing on selected habitats of southern mule deer. California Fish and Game 70:240–247.

Bleich, V. C., and R. A. Weaver. 1983. "Improved" sand dams for wildlife habitat management. Journal of Range Management 36:130.

Bleich, V. C. 1983. Comments on helicopter use by wildlife agencies. Wildlife Society Bulletin 11:304–306.

Bleich, V. C. 1982. Additional notes on species richness of mammals at Bodie, California. Southwestern Naturalist 27:121–122.

Bleich, V. C., L. J. Coombes, and J. H. Davis. 1982. Horizontal wells as a wildlife habitat improvement technique. Wildlife Society Bulletin 10:324–329.

Bleich, V. C. 1982. An illustrated guide to aging the lambs of mountain sheep. Desert Bighorn Council Transactions 26:59–62.

Bleich, V. C., L. J. Coombes, and G. W. Sudmeier. 1982. Volunteers and wildlife habitat management: twelve years together. CAL-NEVA Wildlife Transactions 1982:64–68.

Bleich, V. C. 1982. Horizontal wells for mountain sheep: desert bighorn "Get the shaft". Desert Bighorn Council Transactions 26:63–64.

Bleich, V. C., L. J. Coombes, and G. W. Sudmeier. 1982. Volunteer participation in California wildlife habitat management projects. Desert Bighorn Council Transactions 26:56–58.

Paysen, T. E., J. A. Derby, H. Black, **V. C. Bleich**, and J. W. Mincks. 1980. A vegetation classification system applied to southern California. USDA Forest Service General Technical Report PSW-45:1–33.

Bleich, V. C. 1979. *Microtus californicus scirpensis* not extinct. Journal of Mammalogy 60:851–852.

Bleich, V. C., and B. Blong. 1978. A magnificent frigatebird in San Bernardino County, California. Western Birds 9:129.

Bleich, V. C. 1978. Breeding bird census: annual grassland. American Birds 32:121.

Bleich, V. C. 1977. Dipodomys stephensi. Mammalian Species 73:1–3.

Schwartz, O. A., and **V. C. Bleich**. 1976. The development of thermoregulation in two species of woodrats, *Neotoma lepida* and *Neotoma albigula*. Comparative Biochemistry and Physiology 54A:211–213.

Bleich, V. C. 1975. Roadrunner predation on ground squirrels in California. Auk 92:147–149.

Bleich, V. C., and O. A. Schwartz. 1975. Water balance and fluid consumption in the southern grasshopper mouse, *Onychomys torridus*. Great Basin Naturalist 35:62–64.

Bleich, V. C., and O. A. Schwartz. 1975. Observations on the home range of the desert woodrat, *Neotoma lepida intermedia*. Journal of Mammalogy 56:518–519.

Bleich, V. C. 1975. Diving times and distances in the Pied-billed Grebe. Wilson Bulletin 87:278–280.

Bleich, V. C., and O. A. Schwartz. 1975. Parturition in the white-throated woodrat. Southwestern Naturalist 20:271–272.

Schwartz, O. A., and **V. C. Bleich**. 1975. Comparative growth in two species of woodrats, *Neotoma lepida intermedia* and *Neotoma albigula venusta*. Journal of Mammalogy 56:653–656.

Bleich, V. C. 1974. Muskrats (*Ondatra zibethicus*) in Amargosa Canyon, Inyo and San Bernardino counties, California. Murrelet 55:7–8.

Bleich, V. C. 1974. Abnormal dentition in a grizzly bear. Murrelet 55:11.

Bleich, V. C., and O. A Schwartz. 1974. Interspecific and intergeneric maternal care in woodrats *(Neotoma)*. Mammalia 38:381–387.

Bleich, V. C., and O. A. Schwartz. 1974. Western range extension of Stephens' kangaroo rat (*Dipodomys stephensi*), a threatened species. California Fish and Game 60:208–210.

Book Chapters and Proceedings of Symposia:

Whiting, J. C., **V. C. Bleich**, R. T. Larsen, and R. T. Bowyer. *In press*. [Invited contribution] Water availability and bighorn sheep: life-history characteristics and persistence of populations. Pages 131–163 *in* J. A. Daniels, editor. Advances in environmental research, Volume 21. Nova Science Publishers, New York, New York, USA.

Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, Sr., and A. L. Medina. 2012. [Invited contribution] Managing rangelands for wildlife. Pages 75–94 *in* N. J. Silvy, editor. The wildlife management techniques manual. Volume 2: Management. Seventh edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Krausman, P. R., **V. C. Bleich**, W. M. Block, D. E. Naugle, and M. C. Wallace. 2011. [Invited contribution] An assessment of rangeland activities on wildlife populations and habitats. Pages 253–290 *in* D. D. Briske, editor. Conservation benefits of rangeland practices. USDA Natural Resource Conservation Service, Washington, DC, USA.

Gibson, R. M., **V. C. Bleich**, C. W. McCarthy, and T. L. Russi. 2011. [Invited contribution] Hunting lowers population size in Greater Sage-grouse. Pages 307–315 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. Studies in Avian Biology 39. University of California Press, Berkeley, USA.

Bleich, V. C., and B. M. Pierce. 2005. [Invited contribution] Management of mountain lions in California. Pages 63–69 *in* E. L. Buckner and J. Reneau, editors. Records of North American big game. 12th edition. Boone and Crockett Club, Missoula, Montana, USA.

Rubin, E. S., and **V. C. Bleich**. 2005. [Invited contribution] Sexual segregation: a necessary consideration in wildlife conservation. Pages 379–391 *in* K. E. Ruckstuhl and P. Neuhaus, editors. Sexual segregation in vertebrates: ecology of the two sexes. Cambridge University Press, Cambridge, United Kingdom.

Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, Sr., and A. L. Medina. 2005. [Invited contribution] Managing rangelands for wildlife. Pages 873–897 *in* C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Pierce, B. M., and **V. C. Bleich**. 2003. [Invited Contribution] Mountain lion. Pages 744–757 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland.

Torres, S. G., and **V. C. Bleich**. 1999. [Invited Contribution] Desert bighorn sheep: California. Pages 170–173 *in* D. E. Toweill and V. Geist, editors. Return of royalty: a celebration of success. Boone and Crockett Club, Missoula, Montana.

Bleich, V. C., and S. G. Torres. 1999. [Invited Contribution] California bighorn sheep: California. Pages 130–133 *in* D. E. Toweill and V. Geist, editors. Return of royalty: a celebration of success. Boone and Crockett Club, Missoula, Montana.

Bleich, V. C. 1998. [Invited Contribution] *Microtus californicus* (Peale 1848). Pages 90–92 *in* D. J. Haffner, E. Yensen, and G. L. Kirkland, Jr., editors. North American rodents: status survey and conservation action plan. International Union for the Conservation of Nature, Gland, Switzerland.

Kie, J. G., **V. C. Bleich**, A. L. Medina, J. D. Yoakum, and J. W. Thomas. 1996. [Invited Contribution] Managing rangelands for wildlife. Pages 663–688 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland.

Bleich, V. C., J. D. Wehausen, R. R. Ramey II, and J. L. Rechel. 1996. [Invited Contribution] Metapopulation theory and mountain sheep: implications for conservation. Pages 353–373 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Covelo, California.

Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1995. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Pages 102–109 *in* D. Ehrenfeld, editor. Readings from Conservation Biology: wildlife and forests. The Sheridan Press, Hanover, Pennsylvania. [Reprinted from Conservation Biology 4:383–390].

Bleich, V. C., J. D. Wehausen, and S. A. Holl. 1995. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Pages 71–78 *in* D. Ehrenfeld, editor. Readings from Conservation Biology: the landscape perspective. The Sheridan Press, Hanover, Pennsylvania. [Reprinted from Conservation Biology 4:383–390].

Bleich, V. C. 1992. History of wildlife water developments, Inyo County, California. Pages 100–106 *in* C. A. Hall, V. Doyle-Jones, and B. Widawski, editors. The history of water: eastern Sierra Nevada, Owens Valley, White-Inyo Mountains. University of California White Mountain Research Station, Bishop.

Bleich, V. C., and D. B. Koch. 1992. [Abstract] Tule elk on private lands: species preservation, habitat protection, or wildlife commercialization? Page 78 *in* R. D. Brown, editor. The biology of deer. Springer-Verlag, New York, New York.

Bleich, V. C., C. D. Hargis, J. A. Keay, and J. D. Wehausen. 1991. Interagency coordination and the restoration of wildlife populations. Pages 277–284 *in* J. Edelbrock and S. Carpenter, editors. Natural areas and Yosemite: prospects for the future. U.S. National Park Service, Denver Service Center, Denver, Colorado.

Bleich, V. C. 1990. [Invited contribution] Horizontal wells for wildlife water development. Pages 51–58 *in* G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.

Bleich, V. C., and A. M. Pauli. 1990. Mechanical evaluation of artificial watering devices built for mountain sheep in California. Pages 65–72 *in* G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.

Bleich, V. C. 1990. Affiliations of volunteers participating in California wildlife water development projects. Pages 187–192 *in* G. K. Tsukamoto and S. J. Stiver, editors. Wildlife water development. Nevada Department of Wildlife, Reno.

Bleich, V. C. 1990. Costs of translocating mountain sheep. Pages 67–75 *in* P. R. Krausman and N. S. Smith, editors. Managing wildlife in the southwest. Arizona Chapter of The Wildlife Society, Phoenix.

Bleich, V. C., and S. A. Holl. 1982. [Invited Contribution] Management of chaparral habitat for mule deer and mountain sheep in southern California. Pages 247–254 *in* C. E. Conrad and W. C. Oechel, Technical Coordinators. Proceedings of the symposium on the dynamics and management of Mediterranean-type ecosystems. USDA Forest Service, General Technical Report PSW-58.

Bleich, V. C. 1982. [Invited Contribution] Review comments. Pages 567–568 *in* C. E. Conrad and W. C. Oechel, Technical Coordinators. Proceedings of the symposium on the dynamics and management of Mediterranean-type ecosystems. USDA Forest Service, General Technical Report PSW-58.

Bowyer, R. T., and **V. C. Bleich**. 1980. Ecological relationships between southern mule deer and California black oak. Pages 292–296 *in* T. R. Plumb, Technical Coordinator. Proceedings of the Symposium on the ecology, management, and utilization of California oaks. USDA Forest Service, General Technical Report PSW-44.

Agency Reports:

Brewer, C., et al. 2012. Recommendations for domestic sheep and goat management in wild sheep habitat. Western Association of Fish and Wildlife Agencies Wild Sheep Working Group, Cheyenne, Wyoming.

Bleich, V. C., N. J. Kogut, and D. Hamilton. 2011. Information for contributors to *California Fish and Game*. California Fish and Game 97:47-57.

Hurley, K., et al. 2010. Recommendations for domestic sheep and goat management in wild sheep habitat. Western Association of Fish and Wildlife Agencies Wild Sheep Working Group, Cheyenne, Wyoming. Available at http://www.wafwa.org/documents/wswg/WSWGManagementofDomesticSheepandGoatsinWildSheepHabitatReport.pdf

Hurley, K., et al. 2007. Recommendations for domestic sheep and goat management in wild sheep habitat. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming. Available at http://www.mwvcrc.org/bighorn/wafwawildsheepreport.pdf

Monteith, K. L., **V. C. Bleich**, T. R. Stephenson, and B. M. Pierce. 2009. Population dynamics of mule deer in the eastern Sierra Nevada: implications of nutritional condition. California Department of Fish and Game, Bishop.

Sierra Nevada Bighorn Sheep Recovery Program [**V. C. Bleich**, H. E. Johnson, B. M. Pierce, C. R. Schroeder, T. R. Stephenson, and J. T. Villepique]. 2006. Sierra Nevada bighorn sheep in 2006. Outdoor California 67(2):10–17.

Bleich, V. C. 2005. Sierra Nevada bighorn sheep. Pages 226–227 *in* California Department of Fish and Game (compiler). The status of rare, threatened, and endangered plants and animals of California 2002–2004. California Department of Fish and Game, Sacramento, California, USA.

Bleich, V. C. 2005. Peninsular bighorn sheep. Pages 228–230 in California Department of Fish and Game (compiler). The status of rare, threatened, and endangered plants and animals of California 2002–2004. California Department of Fish and Game, Sacramento, California, USA.

Sierra Nevada Bighorn Sheep Recovery Program [**V. C. Bleich**, B. M. Pierce, T. R. Stephenson, J. T. Villepique, and J. D. Wehausen]. 2004. Sierra Nevada Bighorn Sheep Progress Report 2003. Outdoor California 65(1):4–17.

U.S. Fish and Wildlife Service [C. Benz, **V. Bleich**, W. Boyce, D. Craig, D. Graber, H. Quigley, P. Stine, S. Torres, and J. Wehausen]. 2003. Recovery plan for the Sierra Nevada bighorn sheep. U.S. Fish and Wildlife Service, Portland, Oregon.

U.S. Fish and Wildlife Service [D. Armentrout, **V. Bleich**, W. Boyce, T. Davis, J. DeForge, D. Freeman, M. Jorgensen, S. Ostermann, E. Rubin, O. Ryder, P. Sorensen, S. Torres, and J. Wehausen]. 2000. Recovery plan for bighorn sheep in the peninsular ranges, California. U.S. Fish and Wildlife Service, Portland, Oregon.

Singer, F., W. Adrian, F. Allendorf, J. Bailey, J. Berger, **V. Bleich**, M. Bogan, P. Brussard, S. Buskirk, N. T. Hobbs, T. Smith, D. Stevens, C. Van Riper III, E. Vyse, and G. White. 1996. Bighorn sheep in the Rocky Mountain region. National Biological Service, Ft. Collins, Colorado. 55 pp.

Gudorf, M., P. Y. Sweanor, F. J. Singer, A. Blankenship, **V. Bleich**, T. Easterly, J. Emmerich, C. Eustace, L. Irby, D. Jaynes, B. Jellison, R. Kissell, J. Lindsay, J. Parks, T. Peters, K. Reid, S. Stewart, and T. Voss. 1996. Bighorn sheep habitat assessment of the greater Bighorn Canyon National Recreation Area. National Park Service and National Biological Service Cooperative Report, Bighorn Canyon National Recreation Area, Lovell, Wyoming. 43 pp.

Gudorf, M., P. Sweanor, F. Singer, **V. Bleich**, J. Cordova, C. Hake, L. Lee, T. Lytle, P. Perrotti, S. Petersburg, and B. Sloan. 1995. Bighorn sheep habitat assessment of the greater Colorado National Monument area. National Park Service and National Biological Service Cooperative Report, Colorado National Monument, Fruita, Colorado. 52 pp.

Holl, S. A., and **V. C. Bleich**. 1983. San Gabriel mountain sheep: biological and management considerations. USDA Forest Service, San Bernardino National Forest, San Bernardino, California. 136 pp.

Bleich, V. C. 1980. Amargosa vole study. California Department of Fish and Game, Nongame Wildlife Investigations Job Final Report W-54-R-10. 8 pp.

Gould, G. I., Jr., and **V. C. Bleich**. 1977. Amargosa vole study: progress report. Nongame Wildlife Investigations Job Progress Report W-54-R-10 California Department of Fish and Game, Sacramento. 4pp.

Bleich, V. C. 1975. Wildlife section including habitat and vegetation types in the Lake Mathews study area. Pages 84–130 *in* A study of the fish and wildlife resources of the Metropolitan Water District property at Lake Mathews with habitat improvement recommendations. California Department of Fish and Game, Long Beach.

Bleich, V. C. 1972. An annotated checklist of the mammals occurring in the Tecopa-Dumont Sand Dunes Study Area. Pages 75–77, appendix *in* M. A. Romero, editor. Amargosa Canyon-Dumont Dunes Proposed Natural Area. House of Impressions, Sun Valley, California.

Bleich, V. C. 1972. Checklist of the terrestrial vertebrates of the Seal Beach Naval Weapons Station, Fallbrook Annex, San Diego County, California. U.S. Navy, WPNSTAFBAINST 11015.2:7–13.

Book Reviews and Obituaries:

Bleich, V. C. 2012. Stephen A. Holl (1949–2012). California Wild Sheep, Winter 2012:12–13.

Bleich, V. C. 2012. Earl M. Lauppe (1929–2011). California Fish and Game 97:211–212 [unsigned].

Bleich, V. C. 2012. In memory of Stephen Holl. Bleats and Blats (Official Newsletter of the Desert Bighorn Council) March, 2012:7–9.

Weaver, R. A., and **V. C. Bleich**. 2011. Bonnar Blong, 1923–2009. Desert Bighorn Council Transactions 50:iii.

Bleich, V. C. 1994. Marvin Wood, 1909–1994. Wild Sheep 17(4):8.

Bleich, V. C. 1992. [Review of] Midnight wilderness: journeys in Alaska's Arctic National Wildlife Refuge, by D. S. Miller. California Fish and Game 78:85–86.

Bleich, V. C. 1992. [Review of] Natural history of the White-Inyo Range, eastern California, edited by C. A. Hall, Jr. California Fish and Game 78:84–85.

Bleich, V. C. 1987. James C. Bicket, 1947–1986. Wildlife Society Bulletin 15:477–478.

Bleich, V. C. 1987. J. D. "Don" Landells, 1926–1986. Western Section of The Wildlife Society Transactions 22:iv.

Bleich, V. C. 1987. James C. Bicket, 1947–1986. Western Section of The Wildlife Society Transactions 22:v.

Bleich, V. C. 1979. [Review of] Wild geese, by M. A. Ogilvie. California Fish and Game 66:282–283.

Bleich, V. C. 1977. [Review of] Mammals of the world, by E. P. Walker. California Fish and Game 63:73.

Bleich, V. C. 1975. [Review of] The carnivores, by R. F. Ewer. California Fish and Game 61:255–256.

Popular Articles:

Bleich, V. C. 2012. Solar energy and bighorn sheep: habitat fragmentation, mitigation, and sportsmen. Part II. California Wild Sheep, Fall 2012:10–11.

Bleich, V. C. 2012. Solar energy and bighorn sheep: habitat fragmentation, mitigation, and sportsmen. Part I. California Wild Sheep, Summer 2012:12–14.

Bleich, V. C. 2012. The basis for bighorn sheep harvest recommendations in California. California Wild Sheep, Spring 2012:28–29.

Bleich, V. C. 2012. Correction needed. California Wild Sheep, Spring 2012:29.

Bleich, V. C. 2012. "This is like déjà vu all over again!" Sheep Sheet 2012(1):9–11.

Bleich, V. C. 2011. "This is like déjà vu all over again!"—Again! California Wild Sheep, Winter 2011:17.

Bleich, V. C. 2011. "This is like déjà vu all over again!" California Wild Sheep, Summer 2011:13–14.

Bleich, V. C. 2011. California's twenty-fifth bighorn sheep season will occur in 2011! Sheep Sheet 2011(2):11–13.

Bleich, V. C. 2011. How agencies rate challenges to the management of wild sheep. California Wild Sheep, Spring 2011:30–31.

Bleich, V. C. 2011. California's 25th bighorn sheep season will occur in 2011! California Wild Sheep, Spring 2011:22–23.

Bleich, V. C. 2010. The potential for death at the waterhole. Sheep Sheet 2010(6):2–3.

Bleich, V. C. 2010. Some more "Pahs". Sheep Sheet 2010(5):9.

Bleich, V. C., and N. G. Andrew. 2010. Mountain sheep, mule deer, and donkeys in the desert. California Wild Sheep, Fall 2010:26–27.

Bleich, V. 2010. Some more "pahs". Sheep Sheet 2010(3):9.

Bleich, V. 2010. Some thoughts on "Water dispensaries keep mountain bighorn sheep alive. Sheep Sheet 3:9–12 [reprinted from California Wild Sheep, Fall 2009:28–30].

Bleich, V. C. 2010. Deer capture activities in Mojave National Preserve, 25–30 April 2010. California Wild Sheep, Summer 2010:8–9.

Bleich, V. C. 2010. A brief history of the CDFG bighorn sheep habitat enhancement program. Sheep Sheet 2010(2):8–11. [Reprinted from California Wild Sheep, Winter 2009:8–10].

Bleich, V. C. 2010. Wildlife biology is a meaningful, but dangerous, profession. California Wild Sheep, Spring 2010:8–9.

Bleich, V. C. (Editor). 2009. Domestic and bighorn sheep don't mix. Bighorn, Fall 2009:20–25.

Bleich, V. C. 2009. A brief history of the CDFG bighorn sheep habitat enhancement program. California Wild Sheep, Winter 2009:8–10.

Bleich, V. C. 2009. Some thoughts on "Water dispensaries" keep mountain bighorn sheep alive. California Wild Sheep, Fall 2009:28–30.

Bleich, V. C. 2009. Parting shots [letter]. Bighorn (The Official Magazine of the Texas Bighorn Society), Spring 2009:30.

Bleich, V. C. 2009. Implications of fire history for conserving bighorn sheep. Boone and Crockett Club Trophy Points 3 (July 2009). Available at: http://www.boone-crockett.org/news/featured_story.asp?area=news&ID=52

Darby, N., J. Dungan, K. Stewart, **V. Bleich**, and D. Hughson. 2009. Responses of mule deer to experimental manipulation of water sources: preliminary results from the first year. Mojave National Preserve Science Newsletter 1:1–3.

Bleich, V. C., H. E. Johnson, S. A. Holl, L. Konde, S. G. Torres, and P. R. Krausman. 2009. Implications of fire history for conserving bighorn sheep. California Wild Sheep, Summer 2009:29.

Bleich, V. C. 2009. Some thoughts on water development in wilderness. California Wild Sheep, Spring 2009:8–9.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part IV). California Wild Sheep, Fall 2008:14–15.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part III). California Wild Sheep, Summer 2008:10–11.

Bleich, V. C. 2008. Mountain sheep in California: some perspectives on the past, and prospects for the future (Part II). California Wild Sheep, Spring 2008:12–13.

Bleich, V. C. 2007. Mountain sheep in California: some perspectives on the past and some prospects for the future (Part I). California Wild Sheep, Winter 2007:12–13.

Bleich, V. C. 2007. The Sierra Nevada bighorn sheep recovery program. Conservation Connection 16:11.

Bleich, V. C. 2007. The Sierra Nevada bighorn sheep recovery program. California Wild Sheep, Fall 2007:16–17.

Bleich, V. C., and B. M. Pierce. 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part II] Conservation Connection 15:12. Reprinted with permission from Records of North American Big Game, 12th Edition).

Monteith, K. L., and **V. C. Bleich**. 2007. Mule deer fawn survival in central Sierra Nevada. Outdoor California 6(3):26–29.

Bleich, V. C., and B. M. Pierce. 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part II]. California Wild Sheep, Summer 2007:8–9. Reprinted with permission from Records of North American Big Game, 12th Edition)

Bleich, V. C., and B. M. Pierce. 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part I]. Conservation Connection 14:18–19. Reprinted with permission from Records of North American Big Game, 12th Edition

Bleich, V. C., and B. M. Pierce. 2007. Management of mountain lions in California: history, basic biology, and citizen initiatives [part I]. California Wild Sheep, Spring 2007:18–19. Reprinted with permission from Records of North American Big Game, 12th Edition)

Monteith, K. L., and **V. C. Bleich**. Mule deer fawn survival in the central Sierra Nevada. California Deer, Winter 2007:6–8.

Bleich, V. C. 2006. The potential for death at the waterhole. Conservation Connection 12:13. [Reprinted from California Wild Sheep, Fall 2006:8–9].

Monteith, K. L., and **V. C. Bleich**. 2006. Fawn survival: central Sierra Nevada. Mule Deer Foundation Magazine 9:16–18.

Bleich, V. C., and N. G. Andrew. 2006. Bighorn sheep in California: how many are there, and how are they doing? Foundation for North American Wild Sheep Conservation Connection 11:5–6. [Reprinted from California Wild Sheep, Summer 2006:4–5].

Bleich, V. C. 2006. The potential for death at the waterhole. California Wild Sheep, Fall 2006:8–9.

Bleich, V. C., and N. G. Andrew. 2006. Bighorn sheep in California: how many are there, and how are they doing? California Wild Sheep, Summer 2006:4–5.

Bleich, V. C. 2002. Restoring bighorn sheep to the Sierra Nevada: a project of interest to the Boone and Crockett Club. Fair Chase 17(1):22–26.

Bleich, V. C. 2001. Restoring bighorn sheep to the Sierra Nevada: a new challenge for wildlife biologists. Wild Sheep 24(4):47–50,52.

Bleich, V. C. 2001. Summer ranges, winter ranges, and migratory mule deer: putting the parts of a puzzle in place. Outdoor California 62(4):20–23.

Anderson, L. A., and **V. C. Bleich**. 2000. Desert bighorns in California: a success story for wildlife biologists and sheep hunters. Fair Chase 15(4):13–15.

Bleich, V. C., B. M. Pierce, S. G. Torres, and T. Lupo. 2000. Using space age technology to study mountain lion ecology. Outdoor California 61(3):24–25.

Torres, S. G., and **V. C. Bleich**. 2000. Mountain lions — California's elusive predator. Outdoor California 61(3):4–6.

Bleich, V. C., and N. G. Andrew. 2000. Mountain sheep, mule deer, and burros in the brush: flourishing wild burros impact habitats and native big game. Tracks 17:10–12.

Pauli, A. M., and **V. C. Bleich**. 1999. Gambel's quail hunting opportunities abundant within Mojave National Preserve. Pages 8–9,14 *in* A. J. Kenward, editor. Upland Game California. California Department of Fish and Game, Sacramento.

Bleich, V. C. 1999. Desert deer investigation launched. Outdoor California 60(5):13–15.

Bleich, V. C. 1999. [Letter] America's wilderness. National Geographic Magazine 195(3):xv.

Bleich, V. C. 1997. Securing large carnivores. Wildlife Control Technology 4(2):39.

Bleich, V. C. 1996. Assisting researchers can augment your income. Wildlife Control Technology 3(6):4.

Pierce, B. M., and **V. C. Bleich**. 1996. Round Valley deer study. Mule Deer 2(4):10–13.

Bleich, V. C. 1995. California's newest sheep hunting opportunity: the East Chocolate Mountains. Wild Sheep 18(4):19–22.

Pierce, B. M., and **V. C. Bleich**. 1995. California deer management: the Round Valley investigation. California Hunter Magazine 4(4):32–33.

Bleich, V. C., and S. G. Torres. 1995. The "book" rams are still out there. Tracks 12:9.

Bleich, V. C., and S. G. Torres. 1993. History and current status of mountain sheep in California. Wild Sheep 16(4):15–19.

Bleich, V. C. 1993. Sexual segregation in desert-dwelling mountain sheep. Wild Sheep 16(4):13–14.

Bleich, V. C. 1993. Mountain sheep habitat: using a geographic information system. Boone and Crockett Club News Journal 8(4):39–40.

Bleich, V. C. 1992. Round Valley deer facing long comeback trail. Tracks 9:9,15.

Bleich, V. C. 1990. Status of bighorn sheep in California: a brief synopsis. Wild Sheep 13(2):55.

Bleich, V. C. 1988. Distribution and early history of mountain sheep in California. Pages 1–3 *in* B. W. Wilson, editor. California desert bighorn sheep: a guidebook for the hunter. Society for the Conservation of Bighorn sheep, Los Angeles, California.

Bleich, V. C. 1988. Modern management of mountain sheep in California. Pages 4–6 *in* B. W. Wilson, editor. California desert bighorn sheep: a guidebook for the hunter. Society for the Conservation of Bighorn sheep, Los Angeles, California.

Bleich, V. C. 1983. Big game guzzlers and mountain sheep. Outdoor California 44(6):10.

Davis, J. H., and **V. C. Bleich**. 1980. Time-lapse photography: a new focus on wildlife. Outdoor California 41(4):7–9.

Coombes, L. J., and **V. C. Bleich**. 1979. Horizontal wells: the DFG's new slant on water for wildlife. Outdoor California 40(3):10–12.

Presentations at Professional Meetings

From 1972 to the present, I have been an author or coauthor of more than 100 presentations at professional meetings. I was selected to present a keynote address, "Ecology of mountain sheep: Ramifications for disease transmission and population persistence" at the April 2007 Workshop on Respiratory Disease in Mountain Sheep: Knowledge Gaps and Future Research which was held at the University of California, Davis. Details pertaining to these presentations are available upon request.

Grants and Fellowships

During 1973 through 2007, I competed successfully for and received project-specific funding in the amount of $1,636,247 from internal and external sources. Details of grants and other funding received are available upon request.

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Comment Letter I9

Management and Conservation Article

Influence of Well Pad Activity on Winter Habitat Selection Patterns of Mule Deer

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ABSTRACT Conversion of native winter range into producing gas fields can affect the habitat selection and distribution patterns of mule deer (*Odocoileus hemionus*). Understanding how levels of human activity influence mule deer is necessary to evaluate mitigation measures and reduce indirect habitat loss to mule deer on winter ranges with natural gas development. We examined how 3 types of well pads with varying levels of vehicle traffic influenced mule deer habitat selection in western Wyoming during the winters of 2005–2006 and 2006–2007. Well pad types included producing wells without a liquids gathering system (LGS), producing wells with a LGS, and well pads with active directional drilling. We used 36,699 Global Positioning System locations collected from a sample ($n = 31$) of adult (>1.5-yr-old) female mule deer to model probability of use as a function of traffic level and other habitat covariates. We treated each deer as the experimental unit and developed a population-level resource selection function for each winter by averaging coefficients among models for individual deer. Model coefficients and predictive maps for both winters suggested that mule deer avoided all types of well pads and selected areas further from well pads with high levels of traffic. Accordingly, impacts to mule deer could probably be reduced through technology and planning that minimizes the number of well pads and amount of human activity associated with them. Our results suggested that indirect habitat loss may be reduced by approximately 38–63% when condensate and produced water are collected in LGS pipelines rather than stored at well pads and removed via tanker trucks. The LGS seemed to reduce long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1052–1061; 2009)

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KEY WORDS gas development, habitat selection, liquids gathering system (LGS), mule deer, *Odocoileus hemionus*, predation risk, resource selection function, Wyoming.

Increased energy development on public lands has generated concern because of potential impacts to wildlife populations and their habitats (Lyon and Anderson 2003, Sawyer et al. 2006, Bergquist et al. 2007, Walker et al. 2007). Because many of the largest natural gas reserves in the Intermountain West, North America, occur in shrub-dominated basins (e.g., Powder River Basin, Piceance Basin, Green River Basin), management concerns have focused on native shrub communities and associated species, including mule deer (*Odocoileus hemionus*; Sawyer et al. 2006). Changes to mule deer habitat are often obvious and direct, such as replacement of native vegetation with well pads, access roads, and pipelines. More difficult to quantify, however, are indirect habitat losses that occur when animals avoid areas around infrastructure due to increased human activity.

Understanding effects of human activity on wildlife is key to successful management and conservation (Knight and Gutzwiller 1995, Gill et al. 1996, Taylor and Knight 2003). The influence of human-related disturbances on wildlife energetics, demography, and habitat selection is particularly important among temperate ungulates whose survival depends on minimizing energy expenditures during winter (Parker et al. 1984, Hobbs 1989). Across western North America, restricting human activity in crucial ungulate winter ranges has been a common management practice for decades (Lyon and Christensen 2002). However, limiting human activity on many native winter ranges has become complicated, as the dominant land use has shifted from agriculture to energy extraction (Bureau of Land Management [BLM] 2005) and recreation (Knight and Gutzwiller 1995). Although many wintering ungulate herds are exposed to human activities, our understanding of how ungulates react to such disturbances is limited.

It has been demonstrated that wintering mule deer respond to natural gas well pads by selecting habitats ≥ 3 km away (Sawyer et al. 2006), but we do not know how mule deer behavior changes with levels of human activity. For example, do well pads receiving 2 vehicle trips per day elicit a different behavioral response than those with 10 vehicle trips per day? Ungulates tend to avoid human disturbances such as roads (Rowland et al. 2000, Nellemann et al. 2001, Dyer et al. 2002), energy development (Nellemann and Cameron 1996, Bradshaw et al. 1997, Dyer et al. 2001, Nellemann et al. 2003), bicyclists (Taylor and Knight 2003), hikers (Miller et al. 2001, Papouchis et al. 2001), and snowmobiles (Freddy et al. 1986, Seip et al. 2007). However, it remains unclear how behavioral responses scale with the level of human activity.

As gas development expands across the Intermountain West (BLM 2005), identifying mitigation measures that reduce human disturbance and associated indirect habitat loss will become increasingly important, as will our ability to

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understand and predict animal responses to disturbance. Levels of human activity vary across most developing gas fields, with higher levels of activity at well pads with active drilling operations and lower levels of activity at well pads with producing wells. This development scenario provides an excellent opportunity to quantify how behavioral responses of ungulates vary as a function of disturbance level. Our objective was to determine whether mule deer habitat selection in winter was influenced by well pads with varying levels of traffic in a developing gas field in western Wyoming. Our intent was to provide a quantitative assessment of how wintering mule deer respond to active drilling operations versus producing well pads with different traffic regimes, such that future development and mitigation strategies may be improved.

STUDY AREA

The Pinedale Anticline Project Area (PAPA) is located in the upper Green River Basin, approximately 5 km southwest of Pinedale, Wyoming, USA. The PAPA consisted primarily of federal lands (80%) administered by the BLM, with elevations of 2,070–2,400 m (BLM 2000). The PAPA supported livestock grazing and provided crucial winter range for 4,000 to 5,000 migratory mule deer that summer in portions of 4 mountain ranges 80–160 km away (Sawyer et al. 2005). Although the PAPA covered 799 km^2, most mule deer spend winter in the northern third, an area locally known as the Mesa. The 260-km^2 Mesa is bounded by the Green River on the west and the New Fork River on the north, south, and east, and it is vegetated primarily by Wyoming big sagebrush (*Artemisia tridentata*) and sagebrush–grassland communities. Our study was restricted to the Mesa portion of the PAPA, where we previously modeled predevelopment distribution patterns of mule deer during winters 1998–1999 and 1999–2000 (Fig. 1; Sawyer et al. 2006).

The PAPA also contains some of the largest natural gas reserves in the region, which the BLM approved for development in 2000 (BLM 2000). Due to a series of regulatory decisions (BLM 2000, 2004*a*, *b*), the PAPA contained 3 basic types of well pads during 2005 and 2006, including 1) active drilling pads, 2) producing well pads with liquids gathering systems (LGS), and 3) producing well pads without LGS. All active drilling pads implemented directional drilling, where multiple wells were drilled and completed from one pad. Most human activity in gas fields is vehicle traffic on unpaved roads and is highest at active drilling pads. However, once drilling is completed and wells are in production phase, traffic levels decline at well pads. Among producing well pads, those with LGS have the lowest levels of traffic because water and condensate by-products are collected in pipelines rather than by tanker trucks. During the 2005–2006 winter, our study area contained 6 active drilling pads and approximately 60 and 66 LGS and non-LGS well pads, respectively. During the 2006–2007 winter, our study area contained 5 active drilling pads and approximately 71 and 72 LGS and non-LGS well pads, respectively.

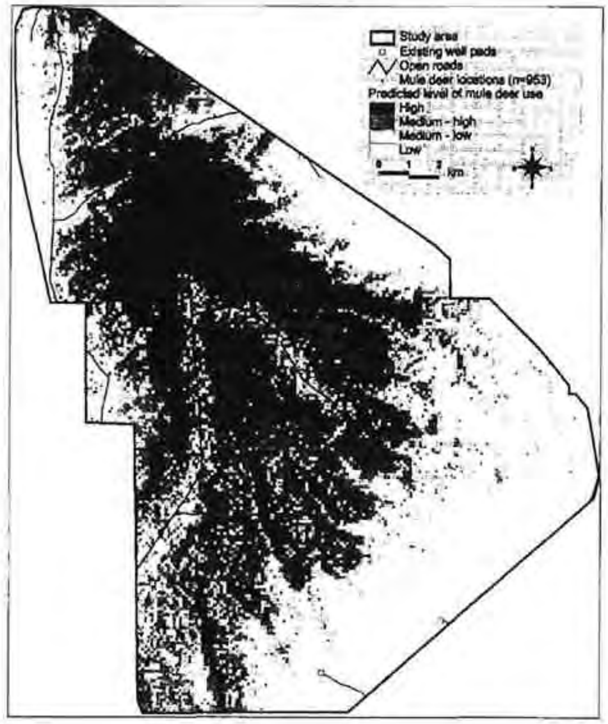

Figure 1. Population-level model predictions and associated categories of mule deer habitat use before gas development, during winters 1998–1999 and 1999–2000 in western Wyoming, USA (from Sawyer et al. 2006).

METHODS

We captured adult ($\geq$1.5-yr-old) female mule deer using helicopter net-gunning in the northern portion of the PAPA, where deer congregate in early winter before moving to their individual winter ranges throughout the Mesa (Sawyer and Lindzey 2001). Previous work showed that capturing deer in this area during early winter provides the best opportunity to obtain a representative sample of the wintering population (Sawyer et al. 2006). We fitted deer with store-on-board Global Positioning System (GPS) radiocollars (Telonics, Inc., Mesa, AZ) equipped with remote-release mechanisms and programmed to attempt a location fix every 2 hours. Potential fix-rate bias (Frair et al. 2004, Nielson et al. 2009) was not a concern because of the high (99%) fix-rate success of the GPS collars in the open terrain of our study area.

We used active infrared sensors (Trailmaster® TM 1550 sensor; Goodson and Associates, Inc., Lenexa, KS) to monitor vehicle traffic at a sample of 18 well pads during 13 January–27 March 2006 and 10 January–17 March 2007. We placed monitors approximately 1.2 m off the ground and set them at a sensitivity level that required the infrared beam to be broken for 0.30 seconds. We designed this configuration to minimize the sensor recording multiple hits for trucks pulling trailers. We estimated mean daily traffic volume for the 3 well pad types: those with LGS, those without LGS, and active drilling pads. We also observed 235 traffic (175 pickup trucks, 38 utility trucks, 18 tractor-trailers, 8 cars) crossings across the 18 sites to assess accuracy of the monitoring system. Of the 235 vehicle observations, 229 (97%) were accurately recorded. We used analysis of variance to test for differences in mean daily traffic volume among well pad types.

Resource Selection

Whereas traditional resource selection function methods (Manly et al. 2002) commonly use logistic regression to compare a discrete set of used units with a set of unused or available units (Thomas and Taylor 2006), our approach used multiple regression to model probability of use as a continuous variable (Marzluff et al. 2004; Sawyer et al. 2006, 2007). Our approach consisted of 5 basic steps in which we 1) measured predictor variables at 4,500 randomly selected circular sampling units, 2) estimated relative frequency of use in the sampling units for each radiocollared deer, 3) used relative frequency as the response variable in a generalized linear model (GLM) to estimate probability of use for each deer as a function of predictor variables, 4) averaged coefficients from models of each individual deer to develop a population-level model, and then 5) mapped predictions of the population-level model.

This method treats the marked animal as the experimental unit, thereby eliminating 2 of the most common problems with resource selection analyses: pooling data across individuals and ignoring spatial or temporal correlation in animal locations (Thomas and Taylor 2006). An additional benefit of treating each animal as the experimental unit is that interanimal variation can be examined (Thomas and Taylor 2006), while still providing population-level inference via averaging coefficients (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). Finally, by modeling use as a continuous variable, we considered resource use in a probabilistic manner that relies on actual time spent by an animal in a sampling unit, rather than presence or absence of the animal (Marzluff et al. 2004, Millspaugh et al. 2006).

We used the study area of Sawyer et al. (2006), which was based on the distribution (i.e., min. convex polygon) of 39,641 locations from 77 mule deer over 6 years (1998–2003). Based on 7 years of previous modeling efforts, we identified 3 variables as potentially important predictors of winter mule deer distribution, including elevation, slope, and distance to well pad type (Sawyer et al. 2006). We did not include vegetation as a variable because the sagebrush–grassland was homogeneous across the study area, and vegetation maps that divide this habitat into finer classes did not exist. We used ArcView to calculate slope from a 26-m × 26-m digital elevation model (United States Geological Survey 1999). We digitized roads and well pads from high-resolution (10-m) satellite images provided by Spot Image Corporation (Chantilly, VA). Images were collected in September 2005 and 2006, after most annual construction activities (e.g., well pad and road building) were complete, but before snow accumulation. Images were geo-processed by SkyTruth (Sheperdstown, WV). We categorized well pads as active drilling, LGS, or non-LGS.

Our sampling units for measuring habitat variables consisted of 4,500 circular units with 100-m radii randomly distributed across the study area. Ideally, the sampling unit should be small enough to detect changes in animal movement or habitat selection (Millspaugh et al. 2006, Sawyer et al. 2006) but large enough to ensure the number of locations within the sampling units approximates a known error distribution (e.g., Poisson or negative binomial). Size of the sampling units may vary depending on mobility of the animal, frequency of GPS locations, and heterogeneity of the landscape. Previously, we evaluated units with 75-m, 100-m, and 150-m radii and found units with 100-m radii worked well for mule deer data collected at 2-hour intervals in the PAPA study area (Sawyer et al. 2006). Alternatively, we could have used square sampling units, but regardless of the shape or number, the sampling units cannot cover the entire study area because our modeling approach requires the total number of locations for each animal occurring in the sampling units be treated as a random variable. We took a simple random sample with replacement to ensure independence of sampling units. We counted the number of deer locations within each sampling unit and measured elevation, slope, and distance to well pad type at the center of each sampling unit.

Before modeling resource selection, we conducted a Pearson's pairwise correlation analysis to identify possible multicollinearity issues and to determine whether we should exclude any variables from our modeling ($|r| > 0.60$). Among the well pad variables, distance to active drilling and non-LGS pads were correlated ($r = 0.72$) during the 2005–2006 winter. However, we retained both covariates because this made the models more interpretable, and the correlation did not seem to influence model stability (i.e., regression coefficient did not switch signs and SEs did not increase substantially as we added variables). During the 2006–2007 winter, distance to active drilling and non-LGS pads were highly correlated ($r = 0.90$); thus, we excluded distance to active drilling well pad as a covariate from the 2006–2007 model.

The relative frequency of locations from each radiocollared deer found in each sampling unit was an empirical estimate of probability of use by that deer, and we used it as a continuous response variable in a GLM. We used an offset term (McCullagh and Nelder 1989) in the GLM to estimate probability of use for each radiocollared deer as a function of a linear combination of predictor variables, plus or minus an error term assumed to have a negative binomial distribution. We preferred the negative binomial distribution over the Poisson because the negative binomial allows for overdispersion (White and Bennetts 1996), which in this application is due to many sampling units with zero locations. We began our modeling by first estimating coefficients for each radiocollared deer with the following equation:

$$\ln(E[l_i]) = \ln(total) + \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \qquad (1)$$

which is equivalent to

$$\ln(E[l_i/total]) = \ln(E[\text{Relative Frequency}_i]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \quad (2)$$

where l_i is number of locations for a radiocollared deer within sampling unit i (i = 1, 2, ..., 4,500), *total* is total number of locations for the deer within the study area, β_0 is an intercept term, $\beta_1, \ldots, \beta_p$ are unknown coefficients for habitat variables $X_1, \ldots, X_p$, and $E[.]$ denotes the expected value. The offset term, ln(*total*), converts the response variable from an integer count (e.g., 0, 1, 2) to a frequency (e.g., 0, 0.003, 0.005) by dividing the number of deer locations in each sampling unit (l_i) by the total number of locations for the individual deer (*total*; Fig. 2). At the level of an individual animal, this approach estimates true probability of use for each sampling unit as a function of predictor variables and is referred to as a resource selection probability function (RSPF; Manly et al. 2002). However, it is important to note that if we average coefficients from individual deer RSPFs to obtain a population-level model, the predictions reflect geometric means of individual probabilities rather than true probabilities. Also, because our sampling units may overlap, they are not mutually exclusive and thus predictions from equation 1 are not subject to a unit-sum constraint.

We followed the Marzluff et al. (2004) approach by fitting one model with all variables to each animal. Next, we treated the estimated coefficients as random variables, because they represent independent, replicated measures of resource use (Marzluff et al. 2004, Millspaugh et al. 2006). This approach quantifies the resource selection of individuals and provides a valid method of assessing population-level use by averaging coefficients among marked individuals (Marzluff et al. 2004, Millspaugh et al. 2006). We considered quadratic terms for distance to well pad and slope variables (Sawyer et al. 2006), and following convention, we also included the linear form of each variable. We did not use an information theoretic approach such as Akaike's Information Criterion (AIC; Burnham and Anderson 2002) for model selection because there is no standard method by which AIC can be properly applied to retain the animal as the experimental unit and build a population-level model with a common set of predictor variables. To evaluate population-level resource selection we assumed GLM coefficients for predictor variable t for each deer were a random sample from an approximate normal distribution (Seber 1984), with the mean of the distribution representing the population-level effect of predictor variable t on probability of use (Marzluff et al. 2004; Millspaugh et al. 2006; Sawyer et al. 2006, 2007). This approach implicitly assumes that population-level effects are accurately reflected by averaging coefficients among animals, which yields predictions that are equivalent to the geometric mean of predictions made from individual RSPFs. Importantly, the geometric mean of a set of numbers is always less than or equal to the arithmetic mean, with the difference between the two increasing with increasing variance in the numbers being averaged (Morris and Doak 2002). We recognize that

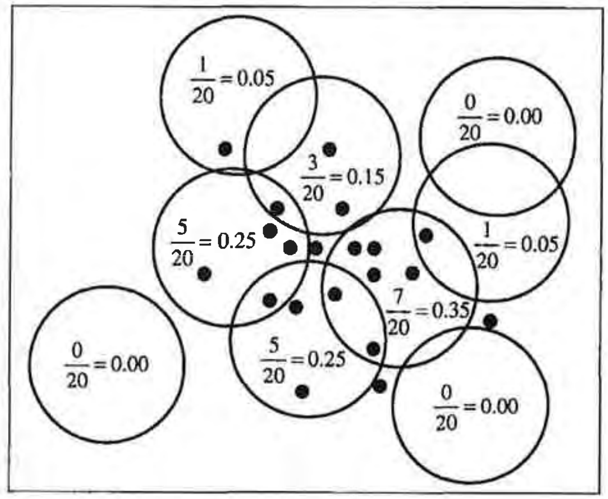

Figure 2. Dividing the number of deer locations in each circular sampling unit by total number of locations converts the response variable to relative frequency of use (e.g., 0.05, 0.15, 0.20), rather than integer counts (e.g., 1, 3, 5). This hypothetical example uses a random sample of circular sampling units and a total of 20 deer locations. Note that 3 locations occurred outside of the sampling units.

an alternative approach for estimating population-level effects is to calculate the arithmetic mean, cell by cell, from the mapped predictions of individual RSPFs; however, this approach only produces a population-level predictive map, not a population-level model. Given that predictions from both approaches were highly correlated (r_s = 0.65 in 2005–2006 and r_s = 0.80 in 2006–2007) and our goal was to produce a population-level model, we averaged coefficients of the s individual deer RSPFs, using

$$\hat{\hat{\beta}}_t = \frac{1}{n}\sum_{s=1}^{n} \hat{\beta}_{ts}, \quad (3)$$

where $\hat{\hat{\beta}}_{ts}$ was the estimate of coefficient t (t = 1, 2, ..., p) for individual s (s = 1, 2, ..., n). We estimated the variance of each coefficient in the population-level model using the variation among individual deer and the equation

$$\text{var}\left(\hat{\hat{\beta}}_t\right) = \frac{1}{n-1}\sum_{s=1}^{n}\left(\hat{\beta}_{ts} - \hat{\beta}_t\right)^2 \quad (4)$$

Population-level inferences using equations 3 and 4 are unaffected by biases in estimated coefficients caused by potential spatial autocorrelation because we selected sampling units at random with replacement (Thompson 1992). Similarly, temporal autocorrelation is not an issue in this analysis because the response variable is the count of relocations within each sampling unit and does not have an associated time stamp other than the study period. To evaluate significance of explanatory variables, we used univariate analyses (i.e., t-tests) with each coefficient as the response variable (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). This approach to evaluating ecological significance is considered conservative because the interanimal variation is included in the calculation of

Table 1. Coefficients for population-level models of radiocollared mule deer during winters 2005–2006 and 2006–2007 in western Wyoming, USA.

Predictor variable	Winter 2005–2006			Winter 2006–2007		
	$\hat{\beta}$	SE	*P*	$\hat{\beta}$	SE	*P*
Intercept	−60.089	12.640	<0.001	−73.969	15.364	<0.001
Elevation (m)	0.012	0.004	0.010	0.020	0.007	0.012
Slope (°)	0.168	0.052	0.004	0.359	0.052	<0.001
Slope² (°)	−0.013	0.003	0.001	−0.024	0.003	<0.001
Non-LGS[a] well pad (m)	3.060	0.003	0.001	5.748	1.545	0.004
Non-LGS well pad² (m)	−0.182	0.109	0.110	−0.653	0.156	0.001
LGS well pad (m)	1.316	0.880	0.151	3.397	1.013	0.007
LGS well pad² (m)	−0.437	0.109	<0.001	−0.421	0.126	0.007
Active drilling pad (m)	3.121	1.204	0.178	na[b]		
Active drilling pad² (m)	−0.197	0.073	0.014	na		

[a] LGS = liquids gathering system.
[b] na = not applicable.

variance, thereby making rejection of the null hypothesis ($\hat{\beta}_i$ = 0) less likely (Marzluff et al. 2004). Nevertheless, ecological significance of explanatory variables is based on the consistency of selection coefficients among collared deer; our sample size was the number of marked mule deer, not sampling units or GPS locations.

We mapped predictions of population-level models for each winter on a 104-m × 104-m grid that covered the study area. We checked predictions to ensure all values were in the interval [0,1], to verify that we would not extrapolate outside the range of model data (Neter et al. 1996). We then assigned the model prediction for each grid cell a value of 1 to 4 based on the quartiles of the distribution of predictions for each map, and we classified areas as high use, medium-high use, medium-low use, or low use. We calculated the mean value of model variables for each of the 4 categories and used high-use values as a reference for assessing how mule deer responded to different well pad types. As a predevelopment reference, we developed a map depicting predicted levels of mule deer use before gas development, as presented by Sawyer et al. (2006).

To evaluate predictive ability of the population-level models we developed for 2005–2006 and 2006–2007 we applied each of them to the 2007–2008 winter landscape. We then used 7,578 GPS locations collected from an independent sample (n = 9) of mule deer during the 2007–2008 winter to calculate a Spearman rank correlation (r_s) characterizing the number of GPS locations that occurred in 10 equal-sized prediction bins based on each of the population-level models (Boyce et al. 2002). We performed all statistical analyses in R language and environment for statistical computing (R Development Core Team 2006).

RESULTS

In winter 2005–2006, traffic levels varied from 2 to 5 vehicle passes per day at LGS well pads, from 4 to 9 at non-LGS well pads, and from 86 to 145 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.3 (SE = 0.30, n = 9), 7.3 (SE = 0.62, n = 6), and 112.4 (SE = 17.3, n = 3) vehicle passes per day, respectively. Mean daily traffic volumes differed across well pad types (F_2 = 119.38, $P \leq 0.001$) and 95% confidence intervals did not overlap.

In winter 2006–2007, traffic levels varied from 2 to 6 vehicle passes per day at LGS well pads, from 6 to 12 at non-LGS well pads, and from 86 to 90 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.6 (SE = 0.50, n = 8), 8.4 (SE = 1.16, n = 7), and 85.3 (SE = 2.91, n = 3) detections per day, respectively. Mean daily traffic volumes differed across well pad types (F_2 = 981.31, $P \leq 0.001$) and 95% confidence intervals did not overlap.

Resource Selection

We used 24,955 locations from 20 GPS-collared mule deer to estimate individual models during the 2005–2006 winter (1 Dec–15 Apr). Most deer (17 of 20) had positive coefficients for elevation, indicating a preference for higher elevations. Based on the relationship between linear and quadratic terms for slope, distance to LGS pad, distance to non-LGS pad, and distance to active drill pad, most deer selected for areas with moderate slopes (14 of 20), away from non-LGS well pads (16 of 20), away from LGS well pads (13 of 20), and away from active drill pads (13 of 20).

Coefficients from the population-level model and associated P-values suggested that most deer selected for areas with higher elevations, moderate slopes, and away from all well pad types (Table 1). Areas with the highest predicted level of use had an average elevation of 2,239 m; a slope of 4.98°; and were 2.61 km from LGS well pads, 4.30 km from non-LGS well pads, and 7.49 km from active drill pads (Table 2). In contrast, areas with the lowest predicted level of use had an average elevation of 2,183 m; a slope of 3.07°; and were 4.03 km, 1.44 km , and 2.78 km from LGS, non-LGS, and active drill well pads, respectively (Table 2). The predictive map indicated that deer use was lowest in areas at low elevation and near clusters of non-LGS and active drill pads (Fig. 3). Predicted levels of mule deer use were noticeably different than those observed prior to development (Fig. 1).

Using the predicted high-use areas as a reference, mule deer distanced themselves from all types of well pads and tended to select areas progressively further from well pads with higher levels of traffic. Specifically, areas with the highest predicted deer use were 2.61 km, 4.30 km, and 7.49 km away from LGS, non-LGS, and active drill pads, respectively. We used these avoidance distances as a metric

Table 2. Average values of population-level model variables in low-, medium-low-, medium-high-, and high-use mule deer categories during winters 2005–2006 and 2006–2007 in western Wyoming, USA.

	Predicted mule deer use							
	High		Medium-high		Medium-low		Low	
Model variables	2005–2006	2006–2007	2005–2006	2006–2007	2005–2006	2006–2007	2005–2006	2006–2007
Elevation (m)	2,239	2,243	2,224	2,203	2,238	2,233	2,183	2,206
Slope (°)	4.98	4.55	3.64	3.61	3.26	3.52	3.07	3.27
Distance to LGS[a] pad (km)	2.61	3.46	3.33	3.43	2.87	2.53	4.03	2.12
Distance to non-LGS pad (km)	4.30	4.35	3.53	3.97	2.50	2.83	1.44	0.69
Distance to active drill pad (km)	7.49	na[b]	5.47	na	3.93	na	2.78	na

[a] LGS = liquids gathering system.
[b] na = not applicable.

to assess indirect habitat loss associated with well pad types. Using a straight line distance, mule deer avoidance of LGS pads was approximately 40% less than that of non-LGS pads (i.e., 1 – [2.6/4.3] = 0.40; Fig. 4). However, assuming a circular area of behavioral response from the point of disturbance (well pad), the indirect habitat loss was reduced by 63% (i.e., 1 – [21/58] = 0.63; Fig. 4) relative to non-LGS pads. Conversely, the straight line distance mule deer selected away from active drill pads was approximately 2.8 times greater than LGS pads and 1.7 times greater than non-LGS pads. Assuming a circular area of behavioral response, indirect habitat loss associated with active drill pads was approximately 3.0 times more than non-LGS pads and 8.4 times more than LGS pads.

Figure 3. Population-level model predictions and associated categories of mule deer habitat use during winter 2005–2006 in western Wyoming, USA. LGS = liquids gathering system, GPS = Global Positioning System.

We used 11,744 locations collected from 11 GPS-collared mule deer to estimate individual models during the 2006–2007 winter. Most deer (9 of 11) had positive coefficients for elevation, indicating a preference for higher elevations. All deer selected for areas with moderate slopes and most selected for areas away from non-LGS well pads (9 of 11) and LGS well pads (9 of 11). We did not include distance to active drill pad as a variable during this winter because it was strongly correlated with distance to non-LGS well pads.

Coefficients from the population-level model and associated *P*-values suggested that deer selected for areas with higher elevations, moderate slopes, and away from LGS and non-LGS well pads (Table 1). Areas with the highest predicted level of use had an average elevation of 2,243 m; slope of 4.55°; and were 3.46 km and 4.35 km from LGS and non-LGS well pads, respectively (Table 2). In contrast, areas with the lowest predicted level of use had an average elevation of 2,206 m; slope of 3.27°; and were 2.12 km and 0.69 km from LGS and non-LGS well pads, respectively (Table 2). Within high use habitats, deer used areas closer to LGS pads compared with non-LGS. The predictive map indicated that deer use was lowest in areas with low elevations and clusters of non-LGS well pads (Fig. 5). Predicted levels of mule deer use were noticeably different than those observed before development (Fig. 1).

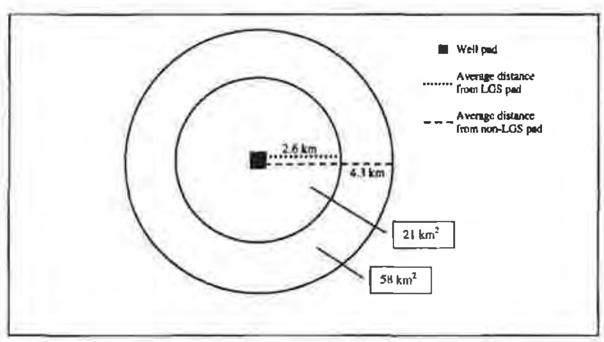

Figure 4. Relationship between straight-line avoidance distances and circular area of impact as a measure of indirect mule deer habitat loss associated with liquids gathering system (LGS) and non-LGS well pads during the 2005–2006 winter in western Wyoming, USA.

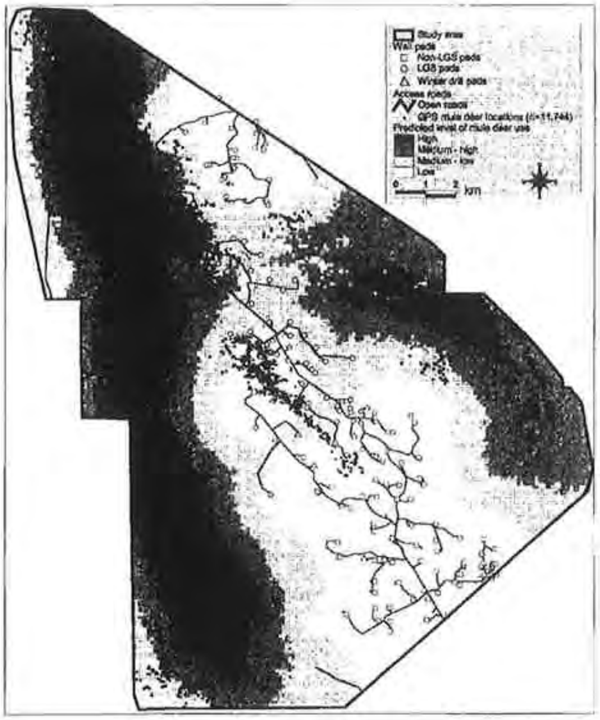

Figure 5. Population-level model predictions and associated categories of mule deer habitat use during winter 2006–2007 in western Wyoming, USA. LGS = liquids gathering system, GPS = Global Positioning System.

Mule deer distanced themselves from LGS and non-LGS well pads and tended to select areas progressively further from well pads that received higher levels of traffic. Areas with the highest predicted deer use were 3.46 km and 4.35 km away from LGS and non-LGS well pads, respectively. Mule deer avoidance of LGS pads was approximately 21% less than that of non-LGS pads. However, assuming a circular area of avoidance from the point of disturbance (well pad), the indirect habitat loss was reduced by 38% relative to non-LGS pads.

When the 2005–2006 and 2006–2007 population-level models were applied to the 2007–2008 landscape, which included new well pad development, their predictions produced Spearman rank correlations (r_s) of 0.903 and 0.939, respectively. The high r_s values indicated that both models effectively predicted the distribution of an independent set of locations (l = 7,578) collected from 9 mule deer.

DISCUSSION

Consistent with our previous work on this mule deer population, we found that deer habitat selection was influenced by well pads (Sawyer et al. 2006). Mule deer avoided all types of well pads but tended to select areas farther from well pads with higher levels of traffic. The reduced response of mule deer to low traffic levels suggests that impacts of gas development on mule deer may be reduced by minimizing traffic. Avoidance distances calculated from predicted high-use areas provided a useful metric to estimate indirect habitat loss associated with different types of well pads. Indirect habitat loss associated with LGS well pads was 38–63% less than with non-LGS well pads, which is noteworthy given that the expected production life of gas wells in the PAPA is 40 years (BLM 2006). Indirect habitat loss associated with active drilling pads was much higher than that at producing well pads; however, all active drill pads in our study were used for directional drilling, which is generally a short-term (6 months–2 yr) disturbance, whereas producing well pads represent a long-term (i.e., decades) disturbance. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios (e.g., clustered development; Theobald et al. 1997).

Evaluating wildlife responses to disturbance is conceptually similar to how ecologists have evaluated prey response to predation risk (Lima and Dill 1990, Lima 1998). Like predation risk, human-related disturbances can divert time and energy away from foraging, resting, and other activities that improve fitness (Gill et al. 1996, Frid and Dill 2002), which could be important to wintering ungulates whose nutritional condition is closely linked to survival. Similar to Gavin and Komers (2006) and Haskell and Ballard (2008), we found it useful to evaluate our findings in relation to predation risk theory. Predation risk (Lima and Dill 1990) predicts that antipredator behavior has a cost to other activities (e.g., foraging, resting) and that the trade-off is optimized when the antipredator behavior (e.g., fleeing, vigilance, habitat selection) tracks short-term changes in predation risk (Frid and Dill 2002). Given that risk of predation can vary across seasons, days, or even hours, antipredator behaviors of prey species should be sensitive to the current risk of predation (Lima and Dill 1990) or level of disturbance. Our results suggested that reducing traffic from 7 to 8 (non-LGS well pads) vehicle passes per day to 3 (LGS well pads) was sufficient for mule deer to perceive less risk and alter their habitat selection behavior such that LGS well pads were avoided less than non-LGS well pads, effectively reducing indirect habitat loss associated with producing well pads.

The trade-offs associated with maximizing foraging opportunities and minimizing predation have been well studied (e.g., Lima and Dill 1990, Bleich et al. 1997, Brown and Kotler 2004). Importantly, however, trade-offs can only occur if foraging benefits and predation risks are positively correlated (Bowyer et al. 1998, Pierce et al. 2004). If the most energetically profitable foraging areas are not perceived as the most dangerous, then there is no trade-off between maximizing foraging and minimizing predation (Lima 1998). Because many of the well pads were constructed in habitats identified as highly preferred by mule deer before development (Fig. 1; Sawyer et al. 2006), we believe that tangible trade-offs existed and that mule deer reduced foraging opportunities by avoiding well pads. High levels of predation risk may indirectly affect survival and reproduction by reducing the amount of time, energy, and resources needed to maintain healthy body condition (Frid and Dill 2002). Furthermore, animals displaced from disturbed sites may experience greater intraspecific competition or density-dependent effects when congregating into smaller areas of undisturbed or suboptimal habitat (Gill and Sutherland 2000). However, the link between antipredator behavior and reduced population performance is difficult to demonstrate (Lima 1998) and has not yet been documented for mule deer and energy development.

Drilling during winter (15 Nov–30 Apr) in areas designated as crucial winter range is a recent phenomenon. Traditionally, seasonal timing restrictions have limited development activities (e.g., construction, drilling, well completion) to nonwinter months and represent the most common, and sometimes the only, mitigation measure required by the BLM for reducing disturbance to wintering ungulates on federal lands. Because of seasonal timing restrictions, the energy industry typically was not allowed to drill during the winter in crucial winter ranges. However, winter drilling will likely become a more common practice across the Intermountain West, as evidenced by recent National Environmental Policy Act decisions in western Wyoming, where stakeholders identified year-round directional drilling as the preferred method to develop the necessary number of wells to recover natural gas reserves, regardless of winter range designation (BLM 2004*a*, *b*, 2006). Wildlife managers have expressed concerns about year-round drilling in crucial winter range because seasonal timing restrictions would be waived and levels of human disturbance would increase substantially during winter (BLM 2004*a*), when mule deer are most vulnerable (Parker et al. 1984, Hobbs 1989). Although significant indirect habitat loss may occur with seasonal timing restrictions in place (Sawyer et al. 2006), our results suggest that wintering mule deer are sensitive to varying levels of disturbance and that indirect habitat loss may increase by a factor of >2 when seasonal restrictions are waived.

Both directional drilling and construction of the LGS were large-scale, multimillion dollar decisions that involved an assortment of local, state, and national stakeholders (BLM 2004*a*). Although Wyoming currently produces the most natural gas in the contiguous United States, the scale and intensity of gas development is predicted to increase elsewhere in the Intermountain West, especially in Colorado, Utah, New Mexico, and Montana (BLM 2005). As gas development becomes more widespread, wildlife and development conflicts will be inevitable. Although the wildlife species of concern (e.g., mule deer, greater sage-grouse [*Centrocercus urophasianus*], pronghorn [*Antilocapra americana*]) may differ across states or regions, the available development strategies (e.g., directional drilling, LGS) will probably be similar. If human disturbances such as vehicle traffic are analogous to predation risk (Gill et al. 1996, Frid and Dill 2002, Gavin and Komers 2006), then mule deer responses to directional drilling and LGS development strategies should be qualitatively similar in other areas across the Intermountain West.

The conceptual framework of predation risk provides a useful context for interpreting responses of ungulates to human disturbances (e.g., Rowland et al. 2000, Nellemann et al. 2003, Taylor and Knight 2003, Gavin and Komers 2006). However, given the rapid and widespread energy exploration and development across the Intermountain West (BLM 2005), manipulative studies will be necessary to advance our understanding of wildlife responses to human disturbance and habitat perturbations. Unfortunately, many of the systems we study are too large or too expensive to manipulate (Macnab 1983). In addition, when experiments are conducted at large spatial scales, such as the 799-km^2 PAPA, replication and randomization are rarely options (Nichols 1991, Sinclair 1991). When the treatment or manipulation is commodity driven, such as mineral extraction or gas development, randomization becomes especially difficult to achieve. Recognizing the constraints that limit our ability to conduct large-scale manipulative studies, researchers have been encouraged to treat management prescriptions, such as fire or harvest regimes, as a form of experimentation (Macnab 1983, Nichols 1991, Sinclair 1991) and as an opportunity for adaptive management (Walters and Holling 1990). Gas development will probably continue to be a dominant activity on federal lands across the Intermountain West. As such, we encourage researchers to consider energy development strategies and mitigation measures as large-scale experimentation that, if properly monitored, can improve our knowledge of energy development impacts to wildlife.

MANAGEMENT IMPLICATIONS

Because mule deer selected for habitats progressively further from well pads with higher levels of traffic, our results suggest that potential impacts of gas development on mule deer may be reduced by technology and planning that minimizes the number of well pads (e.g., directional drilling) and the level of human activity associated with them (e.g., LGS). Our results suggest indirect habitat loss to mule deer could potentially be reduced by 38–63% when condensate products are collected in LGS pipelines rather than being stored at well pads and removed via tanker trucks. In addition, because a LGS can be installed underground and usually in existing roadway or pipeline corridors, associated direct habitat losses are minimal. The LGS seemed to be an effective means for reducing long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss.

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LITERATURE CITED

Bergquist, E., P. Evangelista, T. J. Stohlgren, and N. Alley. 2007. Invasive species and coal bed methane development in the Powder River Basin, Wyoming. Environmental Monitoring and Assessment 128:381–394.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415–524.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in Northeastern Alberta. Journal of Wildlife Management 61:1127–1133.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Bureau of Land Management [BLM]. 2000. Record of decision: environmental impact statement for the Pinedale Anticline natural gas field exploration and development project. Pinedale Field Office, Pinedale, Wyoming, USA.

Bureau of Land Management [BLM]. 2004*a*. Environmental assessment for Questar year-round drilling proposal, Sublette County, Wyoming. Pinedale Field Office, Pinedale, Wyoming, USA.

Bureau of Land Management [BLM]. 2004*b*. Finding of no significant impact, decision record and environmental assessment for Questar year-round drilling proposal, Sublette County, Wyoming. Pinedale Field Office, Pinedale, Wyoming, USA.

Bureau of Land Management [BLM]. 2005. Oil and gas activity on public lands in the United States and Wyoming. Wyoming State Office, Cheyenne, USA.

Bureau of Land Management [BLM]. 2006. Supplemental environmental impact statement for the Pinedale Anticline Oil and Gas Exploration and Development Project. Wyoming State Office, Cheyenne, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer–Verlag, New York, New York, USA.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65:531–542.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80:839–845.

Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPs collar bias in habitat selection studies. Journal of Applied Ecology 41:201–212.

Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63–68.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as predation risk? Canadian Journal of Zoology 84:1775–1780.

Gill, J. A., and W. J. Sutherland. 2000. Predicting the consequences of human disturbance from behavioral decisions. Pages 51–64 *in* L. M. Gosling and W. J. Sutherland, editors. Behavior and conservation. Cambridge University Press, Cambridge, United Kingdom.

Gill, J. A., W. J. Sutherland, and A. R. Watkins. 1996. A method to quantify the effects of human disturbance for animal populations. Journal of Applied Ecology 33:786–792.

Haskell, S. P., and W. B. Ballard. 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. Canadian Journal of Zoology 86:1–11.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101.

Knight, R. L., and K. J. Gutzwiller, editors. 1995. Wildlife and recreationists: coexistence through management and research. Island Press, Washington D.C., USA.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25–34.

Lima, S. L., and L. M. Dill. 1990. Behavioral decision making under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Lyon, L. J., and A. G. Christensen. 2002. Elk and land management. Pages 557–581 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, London, United Kingdom.

Macnab, J. 1983. Wildlife management as scientific experimentation. Wildlife Society Bulletin 11:397–401.

Manly, B. F., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and steller's jays. Ecology 85:1411–1427.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, Boca Raton, Florida, USA.

Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29:124–132.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Nelleman, C., and R. D. Cameron. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49:23–28.

Nellemann, C., I. Vistnes, P. Jordhøy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. Biological Conservation 101:351–360.

Nellemann, C., I. Vistnes, P. Jordhøy, O. Strand, and A. Newton. 2003. Progressive impact on piecemeal infrastructure development on wild reindeer. Biological Conservation 113:307–317.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. McGraw-Hill, Boston, Massachusetts, USA.

Nichols, J. D. 1991. Science, population ecology, and the management of the American black duck. Journal of Wildlife Management 55:790–799.

Nielson, R. M., B. F. J. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. Ecology 90:in press.

Papouchis, C., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65:573–582.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533–541.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.

Sawyer, H., and F. Lindzey. 2001. The Sublette mule deer study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.

Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266–1273.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a non-forested environment. Journal of Wildlife Management 71:868–874.

Sawyer, H., R. M. Nielson, F. G. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.

Seber, G. A. F. 1984. Multivariate observations. John Wiley and Sons, New York, New York, USA.

Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71:1539–1544.

Sinclair, A. R. E. 1991. Science and the practice of wildlife management. Journal of Wildlife Management 55:767–773.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13:951–963.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

Thompson, S. K. 1992. Sampling. John Wiley and Sons, New York, New York, USA.

United States Geological Survey. 1999. 30-meter National Elevation Dataset (tiled for Wyoming). United States Geological Survey EROS data center, Sioux Falls, South Dakota, USA.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060–2068.

White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77:2549–2557.

Associate Editor: McCorquodale.

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Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics

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Abstract. Phenological events of plants and animals are sensitive to climatic processes. Migration is a life-history event exhibited by most large herbivores living in seasonal environments, and is thought to occur in response to dynamics of forage and weather. Decisions regarding when to migrate, however, may be affected by differences in life-history characteristics of individuals. Long-term and intensive study of a population of mule deer (*Odocoileus hemionus*) in the Sierra Nevada, California, USA, allowed us to document patterns of migration during 11 years that encompassed a wide array of environmental conditions. We used two new techniques to properly account for interval-censored data and disentangle effects of broad-scale climate, local weather patterns, and plant phenology on seasonal patterns of migration, while incorporating effects of individual life-history characteristics. Timing of autumn migration varied substantially among individual deer, but was associated with the severity of winter weather, and in particular, snow depth and cold temperatures. Migratory responses to winter weather, however, were affected by age, nutritional condition, and summer residency of individual females. Old females and those in good nutritional condition risked encountering severe weather by delaying autumn migration, and were thus risk-prone with respect to the potential loss of foraging opportunities in deep snow compared with young females and those in poor nutritional condition. Females that summered on the west side of the crest of the Sierra Nevada delayed autumn migration relative to east-side females, which supports the influence of the local environment on timing of migration. In contrast, timing of spring migration was unrelated to individual life-history characteristics, was nearly twice as synchronous as autumn migration, differed among years, was related to the southern oscillation index, and was influenced by absolute snow depth and advancing phenology of plants. Plasticity in timing of migration in response to climatic conditions and plant phenology may be an adaptive behavioral strategy, which should reduce the detrimental effects of trophic mismatches between resources and other life-history events of large herbivores. Failure to consider effects of nutrition and other life-history traits may cloud interpretation of phenological patterns of mammals and conceal relationships associated with climate change.

Key words: climate change; life-history characteristics; mule deer; NDVI; nutritional condition; *Odocoileus hemionus*; plant phenology; risk averse; risk prone; Sierra Nevada; snow depth; trophic mismatch.

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Introduction

Climate change is expected to alter ecosystem structure and function, including community composition and distributions of species (Walther et al. 2002). Overwhelming evidence from long-term research supports the influence of climate change on phenology (i.e., timing of seasonal activities) of plants and animals (Stenseth et al. 2002, Badeck et al. 2004, Gordo and Sanz 2005). Spring activities of numerous taxa have occurred progressively earlier and in the direction expected from climate change since the 1960s, including breeding by birds, arrival of migrant birds, appearance of butterflies, chorusing and spawning of amphibians, and flowering in plants (Walther et al. 2002, Parmesan and Yohe 2003 for reviews). Corresponding delays in the initiation of autumn events also have been reported, but those phenological shifts are less apparent (Walther et al. 2002, Carey 2009). For example, during a 42-year study of migration in eight species of birds, three species advanced, three delayed, and two did not change the timing of autumn migration (Adamik and Pietruszkova 2008). Indeed, the timing of seasonal activities may be one of the simplest processes to track changes in the ecology of a species responding to climatic change (Walther et al. 2002). Addressing questions related to climate change, however, requires long-term studies to disentangle influences of large-scale climate and individual life-history patterns on phenological events.

Migration is a well-recognized life-history strategy involving numerous taxa over the globe (Baker 1978, Swingland and Greenwood 1983, Fryxell et al. 1988, Alerstam et al. 2003); effective conservation actions are necessary to maintain intact patterns of migration (Berger 2004, Bolger et al. 2008). Nevertheless, our understanding of the biology of migration by large herbivores is fragmentary, and consequences of climate change on those phenological patterns remain largely unknown (Bolger et al. 2008, Wilcove 2008). In strongly seasonal environments, large herbivores typically migrate between discrete ranges, which is thought to have evolved in response to the dynamic patterns of forage quality and availability (Morgantini and Hudson 1989, Albon and Langvatn 1992, Hebblewhite et al. 2008), predation risk (Fryxell et al. 1988), and weather patterns (Nelson and Mech 1981, Loft et al. 1989, Kucera 1992, Grovenburg et al. 2009). Indeed, migrants often acquire a selective advantage through enhanced fitness (Dingle 1985, Fryxell et al. 1988), avoid resource bottlenecks by obtaining access to greater food supplies in larger and less densely inhabited ranges, and obtain forage in the most nutritious phenological stages (McCullough 1985, Fryxell and Sinclair 1988, Fryxell et al. 1988, Albon and Langvatn 1992, Holdo et al. 2009, Zeng et al. 2010).

At most mid- to high-latitude regions, frost-free periods have increased with a concomitant 10% decrease in snow cover since the late 1960s (Walther et al. 2002). Temporal and spatial advance in seasonal resource availability by a warming climate may reduce the reproductive success of animals that fail to adjust life-history events to correspond with temporal changes in peak forage availability, resulting in a trophic mismatch (Post and Forschhammer 2008, Post et al. 2008). Nevertheless, large herbivores may be capable of adjusting their timing of migration to enhance nutrient gain in an attempt to compensate for the trophic mismatch at a large spatial scale (Post and Forschhammer 2008), unless their migratory patterns are fixed by day length rather than other environmental cues (Garrott et al. 1987, Post and Forschhammer 2008). If large herbivores respond to milder winter conditions with flexibility in timing of migration, animals should depart winter range earlier in spring and remain on summer ranges for a longer duration in autumn to gain access to forage under circumstances of reduced intraspecific competition (Albon and Langvatn 1992), increased plant diversity (Mysterud et al. 2001), and at a more nutritious phenological stage (Klein 1965, Pettorelli et al. 2007, Hamel et al. 2009). Consequently, natural selection should favor those individuals that respond to climatic change by timing seasonal migration to correspond with phenological advances in plant growth, resulting in improved nutritional gains (White 1983, Mysterud et al. 2001, Voeten et al. 2009).

Although effects of climatic patterns and plant phenology on the timing of migratory events for large herbivores have been documented (Albon and Langvatn 1992, Kucera 1992, Nelson 1995, Sabine et al. 2002, Fieberg et al. 2008), the influence of intrinsic factors, such as age, location of summer residency (which may differ for populations using the same winter range), and reproductive and nutritional state, rarely have been considered (White et al. 2010). Failure to recognize other important factors related to individual life-history characteristics may lead to spurious correlations between indices of climate and the timing of migration.

The behavioral responses of an individual may be affected by their current nutritional state. For instance, studies of avian ecology have suggested that the timing of long-distance migration in bird species may be under strong endogenous control (Mitrus 2007, Pulido 2007). Despite the well-recognized carry over of nutritional condition from the energetic costs and benefits from previous seasons (Parker et al. 2009), few studies have considered whether differences in nutritional condition among individuals affect the timing of migration by large herbivores (Bolger et al. 2008). Maternal females, or those in poor nutritional condition, may be less able to afford the presumed risk associated with altering timing of migration (Ruckstuhl and Festa-Bianchet 1998, Ciuti et al. 2006). Large herbivores are long-lived and those in adequate nutritional condition have the opportunity to reproduce annually; consequently, females should adopt a strategy to promote their survival and opportunity for future reproduction, while simultaneously protecting their current reproductive investment (Stearns 1992).

Most knowledge on timing and synchrony of migration in large herbivores has been derived from short-term studies, which limits the probability of observing variable weather conditions (Fieberg et al. 2008), and precludes the evaluation of effects of large-scale climate on migratory events (Forchhammer and Post 2004). Our objective was to assess a long-term dataset to evaluate effects of climatic conditions, plant phenology, and individual life-history characteristics of mule deer (*Odocoileus hemionus*) in the western Great Basin on timing and synchrony of seasonal migration. Our first objective was to evaluate the influence of extrinsic variables including, broad-scale climate, local weather, and plant phenology on timing of migration. Global climate change is expected to alter the phenological patterns of life-history events for numerous taxa, including seasonal migration by vertebrates (Walther et al. 2002, Forchhammer and Post 2004). Effects of winter weather and snow depth, as well as progression in plant phenology, on timing of seasonal movements by large herbivores have been well documented (Garrott et al. 1987, Kucera 1992, Albon and Langvatn 1992, Sabine et al. 2002, Fieberg et al. 2008, Zeng et al. 2010). Therefore, we expected current weather conditions, driven by broad-scale climate, to influence the timing of seasonal migrations among mule deer. Furthermore, progression in plant phenology, particularly in spring, should correspond to the timing of migratory events between seasonal ranges across years. Following the identification of extrinsic factors that affected seasonal migration of mule deer, we evaluated the influence of intrinsic factors among individual mule deer on timing of migration. We hypothesized that timing of migration would be influenced by individual life-history characteristics including nutritional condition, reproductive status, age, and location of summer residency. Migration by large herbivores is a spectacular phenomenon occurring across a wide array of landscapes, however, many of these migrations are imperiled by anthropogenic disturbances, which is likely indicative of major ecological changes (Berger 2004, Bolger et al. 2008, Wilcove 2008). Our approach will provide a better understanding of the mechanisms underpinning this biological process and should aid in the conservation of these large, vagile mammals and their unique behaviors.

Study Area

We monitored the timing of migration for a population of mule deer that wintered on the east side of the Sierra Nevada in Round Valley (37°24′ N, 118°34′ W), Inyo and Mono counties, California, USA (Fig. 1). Mule deer inhabited approximately 90 km^2 of Round Valley during November-April, but the size of this area was dependent on snow depth (Kucera 1988). Annual snow depth in a drainage adjacent to Round Valley (Station ID: RC2, California Department of Water Resources) was highly variable during our study; the coefficient of variation of snow depth in April was 57% and ranged from 25.4 to 139.7 cm. Precipitation in the study area is strongly seasonal, with 75% occurring between November

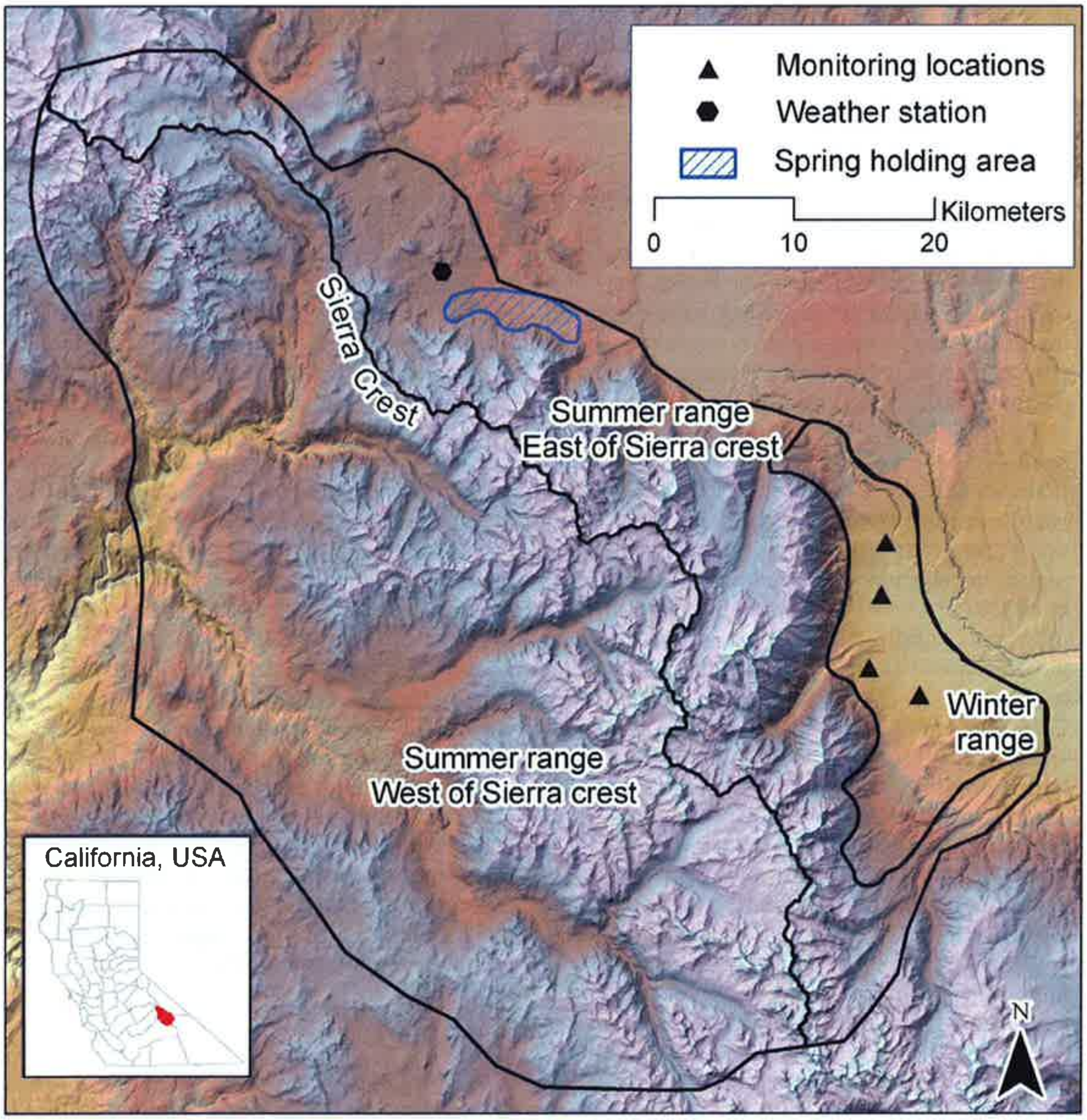

Fig. 1. Seasonal ranges occupied by female mule deer during winter, and the distinct ranges on both sides of the crest of the Sierra Nevada (Sierra crest), California, USA during summer. The four monitoring locations on winter range are indicated as well as the spring holding area for deer and location of the weather station near Mammoth Lakes, California.

and March (Kucera 1988). Daily temperatures near Mammoth Lakes, California, USA during 1999–2009 ranged from −27 to 33°C (Western Regional Climate Center). The region is typified by dry, hot summers (June–September), short, mild autumns with cooling temperature and increasing precipitation (October), and long, cold winters, with most annual precipitation accumulating as snow (November–April). Spring is short and characterized by decreasing precipitation and increasing temperatures (May; Fig. 2).

Round Valley is bounded to the west by the

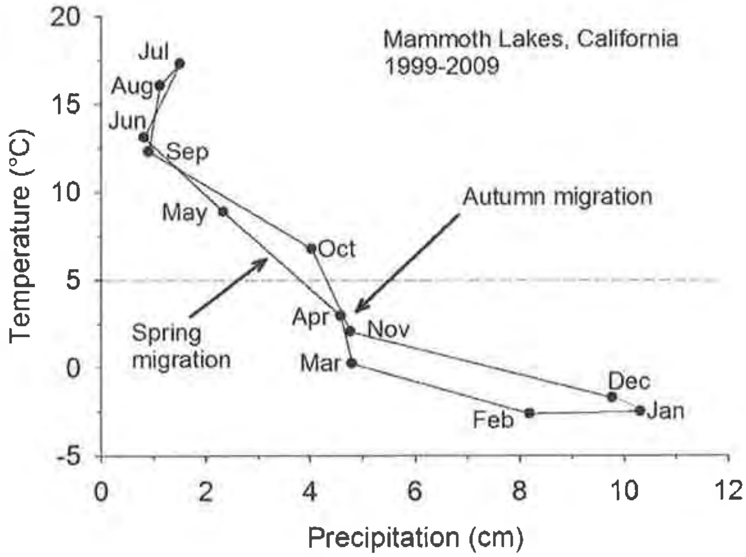

Fig. 2. Climograph of the mean monthly temperature and precipitation at Mammoth Lakes, California, USA, 1999–2009, which is located adjacent to summer range and the traditional migratory route for mule deer occupying winter range in Round Valley. Autumn and spring migration correspond to average timing of seasonal migration, 1999–2009, and dashed line represents an index to a temperature threshold (5°C) for growth of plants (Chapin 1983).

Sierra Nevada, to the south by large boulders and granite ridges of the Tungsten Hills and Buttermilk Country, and to the east by US Highway 395. The northern end of Round Valley gradually rises from the valley floor at 1,375 m to the top of the Sherwin Grade at 2,135 m. Open pastures comprised about 18.3 km^2 of the eastern portion of the valley; 3.2 km^2 was low-density residential housing (Pierce et al. 2004). Vegetation in Round Valley was characteristic of the western Great Basin and sagebrush-steppe ecosystem (Storer et al. 2004).

Summer range for mule deer that winter in Round Valley occurred on both sides of the crest of the Sierra Nevada (hereafter Sierra crest; Fig. 1) at elevations ranging from 2,200 to >3,600m (Kucera 1988). Winter storms from the Pacific Ocean deposit moisture as they move up the western slope with a substantial rain shadow, resulting in a more arid landscape on the eastern slope, where the Great Basin Desert begins (Storer et al. 2004, Bleich et al. 2006). The dense pine-fir (*Pinus-Abies*) stands and rivers on the west side of the Sierra crest contrast with the sparse forests transitioning to sagebrush scrub with only a few small streams on the east side. Indeed, the formidable Sierra crest sharply delineates the western slope from the eastern slope of the Sierra Nevada, and is traversable only by a series of passes that increase in elevation from north to south (Kucera 1988). Mule deer typically migrate northward and westward to high-elevation ranges in spring (Kucera 1992, Pierce et al. 1999); most migrate over the aforementioned passes to the west side of the Sierra Crest (Fig. 1), while some remain on the east side (Kucera 1992, Pierce et al. 2000). Prior to completion of migration to summer range, mule deer from Round Valley make extensive use of a spring holding area at higher elevation (>1,200 m) located on the east side of the Sierra Nevada, just southeast of Mammoth Lakes, California, USA (Kucera 1992; Fig. 1). Mule deer often remain on the spring holding area until snow on summer range has receded (Kucera 1992).

Methods

Animal capture

During March 1997–2009 and November 2002–2008, we captured adult female (>1 yr old) mule deer on winter range in Round Valley using a hand-held net gun fired from a helicopter (Krausman et al. 1985). We hobbled and blindfolded each animal prior to moving it by helicopter to a central processing station with shelter for animals and handling crews. To allow age determination by cementum annuli (Matson's Laboratory, Milltown, Montana, USA), we removed one incisiform canine using techniques described by Swift et al. (2002); this procedure has no effect on body mass, percent body fat, pregnancy rate, or fetal rate of mule deer (Bleich et al. 2003). We fitted each animal with standard, VHF radiocollars (Telonics, Inc., Mesa, Arizona, USA; Advanced Telemetry Systems, Isanti, Minnesota, USA) equipped with a mortality sensor. We attempted to maintain radiocollars on >75 adult females by capturing new, unmarked animals to replace animals lost to mortality.

We conducted ultrasonography using an Aloka 210 portable ultrasound device (Aloka, Wallinford, CT), with a 5-MHz transducer, to measure maximum thickness of subcutaneous fat deposition at the thickest point cranial to the cranial process of the tuber ischium to the nearest 0.1 cm (Stephenson et al. 2002). We complemented ultrasonography with palpation to determine a body-condition score, validated for mule deer (Cook et al. 2007), to estimate nutritional condition of deer that have mobilized subcutaneous fat reserves (<5.6% ingesta-free body fat). We calculated rLIVINDEX as subcutaneous rump-fat thickness plus rump body-condition score (Cook et al. 2007). We then used rLIVINDEX to calculate ingesta-free body fat (IFBFat), where IFBFat = 2.920 × rLIVINDEX − 0.496 (Cook et al. 2007). During deer captures in March, we used an ultrasound with a 3-MHz linear transducer to determine pregnancy and fetal rates (number of fetuses per female) of females during the second one-third of gestation (Stephenson et al. 1995).

During each autumn, we attempted to determine reproductive status of all marked females as they arrived on winter range in late-October through November. We located radiocollared females using ground-based telemetry and stalked to within visible range of deer (<200 m). We observed each female using binoculars or spotting scopes until we could confidently determine the number of young-at-heel. We identified the number of young-at-heel by observing nursing and other maternal behavior (Miller 1971), and determined recruitment status based on the presence or absence of young-at-heel identified each autumn. Animal capture and research methods were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (protocol #: 650-0410), were in accordance with guidelines of research on large mammals by the American Society of Mammalogists (Ganon et al. 2007), and followed California Department of Fish and Game protocols for wildlife restraint.

Timing of migration

We determined the presence or absence of radiomarked mule deer on winter range with radio telemetry from four monitoring locations, which were strategically distributed across Round Valley during 1999–2009 (Fig. 1). Although we did not attempt to determine exact locations of animals by triangulation, the topography of the Sierra Nevada that bounded Round Valley on three sides conveniently blocked the signal of animals that were not present in the valley. We conducted telemetry from fixed-wing aircraft to locate animals that were not present in Round Valley. Aerial telemetry also was used to locate all females on their summer range during mid-summer and to categorize animals based on the side of the Sierra crest (east or west) that they occupied (Fig. 1).

We attempted to monitor animals from the ground a minimum of 3 days per week beginning on 1 October and continuing through 30 April each winter. Logistical constraints during some years, however, affected the frequency and duration of monitoring. We censored animals that died prior to migration in either autumn or spring because, in some instances, we were unable to determine exact date of death. We assumed that censoring of individuals was independent of the migratory strategy exhibited by deer.

Local weather and climate

We obtained data on daily weather from a station located near the town of Mammoth Lakes, California, USA (Western Regional Climate Center 1998–2009), which was near the summer range of deer, and was immediately adjacent to the traditional migratory route and spring holding area for mule deer from Round Valley (Kucera 1992; Fig. 1). Daily data on weather were not available for winter range; therefore, we used weather data from the nearby station at Mammoth Lakes, California, for all analyses (Appendix). Because deer also likely respond to changing weather patterns rather than simply absolute daily measurements of weather (Sabine et al. 2002, Grovenburg et al. 2009), we calculated a metric of change in weather to represent a change in weather on a particular day relative to previously experienced weather patterns. This metric reflected the difference in the daily weather relative to the mean of that particular weather variable during the previous 2 weeks, which we arbitrarily chose to represent the relative magnitude of change in weather on a day.

Annual weather patterns in the western US have been correlated with the annual mean of the southern oscillation index (SOI; Trenberth and Hurrell 1994, Marshal et al. 2002, Stenseth et al. 2003). Accordingly, we used the standardized SOI (National Oceanic and Atmospheric Administration, Climate Prediction Center) as a measure of variation in large-scale climate (Stone et al. 1996). For autumn migration, we used the annual mean of the SOI during the previous October through September, and for spring we used the mean SOI during the previous April through March in migration models.

Plant phenology

Temperature is one of the most critical factors influencing phenology in plants (Rachlow and Bowyer 1991). Therefore, we calculated an index to growth and senescence of plants based on mean daily temperatures (Chapin 1983). For each spring, we calculated the number of growing-degree days per day (the number of degrees that the mean daily temperature was >5°C, summed across all previous days beginning on 1 January) as an index to growth of plants (Chapin 1983). For each autumn, we calculated a metric of senescence of plants by the opposite of growing-degree days, which we termed senescent-degree days (the number of degrees that the mean daily temperature was <5°C, summed across all previous days beginning on 15 September).

The normalized difference vegetation index (NDVI) is derived from satellite imagery that measures the greenness of vegetation. NDVI is sensitive to environmental change (Pettorelli et al. 2005), is associated with fluctuations in dietary quality (Christianson and Creel 2009, Hamel et al. 2009), and thus, is related to numerous aspects of the ecology of large herbivores (Loe et al. 2005, Pettorelli et al. 2007). From the Earth Resources and Observation Science Center of the U.S. Geological Survey, we obtained a time series of 14-day composite NDVI with 1-km^2 spatial resolution recorded by the Advanced Very High Resolution Radiometer aboard the polar-orbiting weather satellites of the National Oceanic and Atmospheric Administration. Data were further processed to remove effects of atmospheric contamination with the method of Swets et al. (1999). We extracted mean NDVI values for each 2-week interval from 1999–2009 for pixels that occurred within the winter range and spring holding area for mule deer (Kucera 1988; Fig. 1). We extracted data for the spring holding area rather than the extensive summer range occupied by deer from Round Valley (Fig. 1), because habitat on the spring holding area was comparable with that occurring on winter range and deer made extensive use of holding areas in spring (Kucera 1992). We calculated a daily NDVI for both areas by interpolating between 14-day composites of NDVI, assuming a linear progression between change in NDVI composites and time increment for each period. We also expected deer to respond to progressive changes in NDVI; therefore, analogous to metrics of change for weather variables, we also calculated a metric of daily change in NDVI by the difference in daily NDVI relative to the mean NDVI during the previous 2 weeks. To describe annual deviations in patterns of green-up and senescence, we used program TIMESAT (Jönsson and Eklundh 2004) to calculate variables derived from NDVI data including: Julian date of onset of spring and onset of autumn, rate of increase in NDVI at the beginning of the season, rate of decrease in NDVI at the end of the season, and maximum and minimum NDVI for seasonal ranges (Reed et al. 1994, Pettorelli et al. 2005).

Statistical analyses

We evaluated relationships between the annual mean (October–September) of the SOI and the corresponding annual sum in snowfall and precipitation, and the annual average of mean daily temperature using linear regression (Neter et al. 1996), with one-tailed tests, because the direction of the expected relationships have been established previously (Trenberth and Hurrell 1994, Marshal et al. 2002). We used two-tailed *t*-tests to evaluate differences in annual phenological metrics between winter range and the spring holding area (Zar 1999), to determine if patterns of plant phenology differed between seasonal ranges.

Daily weather.—We used principal component analysis (PCA) of local weather data, based on the variance–covariance matrix (McGarigal et al. 2000), to reduce the dimensionality of those variables and derive independent composite variables that described daily weather. In the PCA, we included 12 variables representing absolute daily weather and a metric of change in daily weather for: minimum, maximum, and average temperature (°C), snowfall (cm), snow depth (cm), and precipitation (cm). We selected 5 principal components because they each explained >1% of the variation in daily weather and were biologically relevant (Appendix). Principal component 1 explained 74.2% of the variation in daily weather and represented an absolute measure of daily depth of snow from lower (negative loadings) to higher snow depths (positive loadings). Principal component 2 explained 12.1% of the variation in daily weather and reflected daily changes in snow depth from decreasing snow depth (negative loadings) to increasing snow depth (positive loadings). Absolute daily temperatures from cold temperatures (negative loading) to warm temperatures (positive loading) were represented by principal component 3, which explained 8.1% of the variation in daily weather. Daily snowfall and precipitation from lower (negative loadings) to higher (positive loadings) was reflected by principal component 4, which explained 3.0% of the variation in daily weather. Finally, a metric of change in daily temperatures from cooling temperatures (negative loadings) to warming temperatures (positive loadings) was represented by principal component 5, which explained 1.7% of the variation in daily weather.

Migration timing.—We censored 1 deer that was resident all year on winter range in Round Valley, and 2 deer that failed to return to winter range in 2006 and 2007. We censored those individuals because we were not interested in testing hypotheses regarding mixed-migration strategies (Nicholson et al. 1997); ≥99% of deer in Round Valley were obligate migrators. We also chose to restrict analyses of timing of migration in autumn to the period between 15 September and 31 December, because events beyond that date in any particular year were sparse. Restriction of analyses for autumn migration resulted in the censoring of 14 migratory events that occurred after 31 December, during 1999–2009. We also censored 1 migratory event during spring migration when an individual deer migrated on 15 January, whereas all other migratory events occurred after 6 March.

Logistical constraints precluded continuous sampling to identify the exact day of departure and arrival on winter range in our study. Average monitoring interval per season ranged from 11.5 days for autumn 1999 to 1.3 days for spring 1999. Average censor interval for migratory events per season ranged from 20 days for autumn 2000 to 1 day for spring 2002. The timing of a migratory event could only be attributed to an interval of time. Data collected under this coarse sampling regime are known as interval-censored and require proper accounting for the uncertainty of the timing of events (Johnson et al. 2004, Fieberg and DelGiudice 2008).

To properly account for interval-censored data, we applied the method of Johnson et al. (2004) to calculate a robust measure of mean date of migration and a corrected measure of the SD of the distribution of migratory events to determine synchrony (Gochfeld 1980). This method is an extension of Sheppard's correction, which allows unequal sampling intervals (bin size; Johnson et al. 2004). We used the method of Johnson et al. (2004) and the associated 95% CI to evaluate differences in timing of migration among years, recruitment status of females in autumn (presence of young-at-heel), and summer residency (east versus west side of the Sierra crest). We used multiple-regression analysis (Neter et al. 1996) to evaluate the relationship between annual mean and synchrony (SD) of seasonal migration with annual metrics of large-scale climate and plant phenology including: annual

SOI; Julian date of onset of spring and onset of autumn; and rate of increase or decrease in NDVI between seasons, respectively. Before interpreting results of our multiple-regression analyses, we evaluated residual plots for compliance with assumption of normality and homogeneity of variance (Neter et al. 1996). We did not include annual averages of local weather variables in the multiple-regression analysis, because of collinearity with SOI and Julian date of onset of spring ($r > 0.50$). We examined fit of multiple regression models with R^2_{adj} and the contribution of each variable by reporting partial correlations ($r^2_{partial}$; Neter et al. 1996, Zar 1999). We determined whether mean date of seasonal migration of mule deer was advancing or receding during 1999–2009 using simple linear regression (Neter et al. 1996). We also used linear regression to determine if there were directional changes in annual precipitation, snowfall, mean temperature, SOI, Julian date of start of season, and Julian date of end of season relative to time (Neter et al. 1996).

Migration modeling.—We adopted methods of survival analysis that have been developed for interval-censored data, which are used to analyze data addressing the time of a specific event (Dinsmore et al. 2002); events in our study were the dates of arrival to and departure from winter range. We used interval-censored models to evaluate effects of extrinsic and intrinsic factors on the distribution of migratory events for seasonal migration in mule deer. We estimated daily probability of not migrating as a function of Julian date using the nest-survival option in Program MARK (White and Burnham 1999, Dinsmore et al. 2002) and subsequently, we calculated daily probability of migrating as one minus the daily probability of not migrating. These models were developed to analyze nest-survival data (Dinsmore et al. 2002), but provide a powerful tool to investigate other biological phenomena, including timing of migration in relation to time-specific and individual-based covariates (Fieberg and DelGiudice 2008). Nevertheless, nest-survival models do not account for repeated measurements between years (although it does account for them within years). We partitioned our dataset into individuals monitored during ≤3 years versus individuals monitored >3 years and calculated mean date of seasonal migration (±95% CI) using Johnson et al. (2004) to evaluate whether repeated monitoring of some individuals had an effect on our analyses. There was no difference in timing of migration between individuals monitored for ≤3 years compared with >3 years, which indicated that repeated sampling of individuals likely did not have a strong influence on our analyses.

Input files for Program MARK included three variables required for each deer: the day since the beginning of the interval that the deer was available to migrate (i), the day the deer was monitored immediately prior to a migratory event (j), and the day the deer was monitored immediately after a migratory event (k; notation follows Dinsmore et al. 2002). We scaled the beginning of the monitoring interval for each season (i) so that the first day of the monitoring interval was the same Julian date across all years. For autumn, j_i represented the last observation when absent from winter range, and k_i represented the first observation on winter range. For spring, j_i represented the last day present on winter range, and k_i represented the subsequent observation when absent from winter range. Each autumn, a few individuals arrived on winter range prior to the initiation of monitoring of radio signals in Round Valley. In those instances, we assigned j_i as 15 September of the current autumn, which we assumed was prior to the earliest date expected for individuals to arrive on winter range. Each spring, a few individuals also remained on winter range when we ceased monitoring in Round Valley. For those individuals, we assigned k_i to 15 May of the current spring, which we assumed was the latest date any individual would be expected to depart winter range.

We employed an information-theoretic approach to identify extrinsic and intrinsic factors that influenced timing of migration in mule deer. In the first stage of the modeling, we examined all possible combinations of extrinsic predictor variables that might influence timing of migration in mule deer: annual SOI, daily weather variables and weather change metrics from the PCA, growing- or senescent-degree days, daily range-specific NDVI and change in NDVI, and a quadratic time-trend. We included year as a nuisance parameter to account for variation among years that was not specifically addressed by our other annual environmental variables. We also fit a quadratic time-trend that allowed daily probability of migration to follow a curvilinear pattern, which we expected to occur because seasonal patterns of migration commonly occur in a pulse with tails on either side (Garrott et al. 1987, Kucera 1992, Brinkman et al. 2005, Grovenburg et al. 2009). We expected potential interactions between principal components for weather and NDVI, but did not include those interactions because of multicollinearity between the interaction terms and principal components representative of those weather variables ($r > 0.70$). For each model, we calculated Akaike's information criterion adjusted for small sample size (Akaike 1973; AIC_c), ΔAIC_c, and Akaike weight (w_i; Burnham and Anderson 2002). We then calculated model-averaged parameter estimates and unconditional standard errors (SE) for each predictor variable (Burnham and Anderson 2002). We determined if model-averaged parameter estimates differed from zero by examining whether their 95% CI, based on unconditional SEs, overlapped zero. We evaluated the relative importance of variables based on their importance weights, which we calculated as the sum of w_i across all models that contained a particular variable (Burnham and Anderson 2002).

After we identified the extrinsic variables that affected the timing of seasonal migration among mule deer, we added intrinsic covariates characterizing the life-history of groups (e.g., summer residency) and individuals (e.g., nutritional condition), to evaluate whether life-history traits among individuals affected their timing of migration. We partitioned the dataset to include only those individuals where data on life-history characteristics were available. We believe the sample of individual animals with data on life-history characteristics was representative of the population, because we attempted to determine reproductive status of all marked females on winter range during autumn, captured 50% of collared females in November, and attempted to capture every marked female each March.

We modeled all possible combinations of the extrinsic variables that were significant (based on 95% *CI*) in the first stage of the modeling approach, and individual life-history characteristics that we hypothesized would affect the timing of seasonal migration including: age (years); summer residency (east versus west side of the Sierra crest); nutritional condition (ingesta-free body fat; IFBFat); fetal rate (for spring migration only); and recruitment (presence or absence of young-at-heel for autumn migration only). We also evaluated interactions based on ΔAIC_c and confidence intervals of interaction terms for life-history characteristics (e.g., recruitment × IFBFat), and between life-history characteristics and daily weather (e.g., IFBFat × PC1). None of the interactions we investigated were significant, or resulted in a significant improvement of model fit. Interaction terms were removed from subsequent analyses. For both spring and autumn models, we also included age as a quadratic term (age^2) to allow timing of migration to be a curvilinear function of age. Finally, we again used model averaging, 95% CI, and importance weights to evaluate the effects of life-history characteristics on the timing of migration (Burnham and Anderson 2002). Following the identification of important life-history variables on the timing of migration by mule deer, we calculated the daily probability of migration for east- and west-side females (i.e., summer residency), for females in relatively poor nutritional condition (4% IFBFat), and good nutritional condition (18% IFBFat), and for old (12.4 years old) and young females (2.4 years old) to illustrate the effects of age, summer residency, and nutritional condition on the daily probability of seasonal migration of mule deer. All assigned values for each life-history characteristic were within the range we observed for deer in Round Valley and were in accordance with that reported for mule deer elsewhere (Gaillard et al. 2000, Cook et al. 2007).

Results

We monitored spring and autumn migration of radiocollared mule deer each year during 1999–2009. We documented 850 and 882 migratory events by mule deer in the autumn and spring, respectively, by monitoring 297 individual deer for 1 to 22 seasonal migrations. During 1999–2009, female mule deer resided on summer range ($\bar{X} = 191$, $SD = 12.6$ days) 10% longer than on winter range ($\bar{X} = 174$, $SD = 8.9$ days). The southern oscillation index (SOI) was negatively related to total snowfall ($\beta = -129.6$, $r^2 = 0.26$, $P = 0.053$), and approached a significant positive relationship with mean annual temperature ($\beta = 0.54$, $r^2 = 0.17$, $P = 0.13$), but exhibited little correlation with total precipitation ($\beta = -7.32$, $r^2 = 0.06$, $P = 0.36$; Appendix). In addition, there was no directional change during 1999–2009 in annual precipitation ($\beta = -2.06$, $r^2 = 0.02$, $P = 0.67$), snowfall ($\beta = -10.61$, $r^2 = 0.02$, $P = 0.65$), average temperature ($\beta = 0.06$, $r^2 = 0.10$, $P = 0.34$), SOI ($\beta = 0.04$, $r^2 = 0.01$, $P = 0.80$), Julian date of start of season ($\beta = -0.40$, $r^2 = 0.01$, $P = 0.85$), or Julian date of end of season ($\beta = -2.54$, $r^2 = 0.15$, $P = 0.24$).

Julian date of onset of spring (as derived from NDVI) was similar between seasonal ranges, but rate of green-up differed and occurred at more than twice the rate on the spring holding area compared with winter range (Table 1). Likewise, date of the onset of senescence was similar between ranges, whereas the rate of senescence was significantly faster on the spring holding area (Table 1). Maximum greenness of vegetation, as indicated by peak values in NDVI, was significantly greater on the spring holding area compared with winter range (Table 1). Moreover, during 1999–2009, daily mean NDVI remained significantly greater (based on 95% CI) on the spring range compared with winter range in Round Valley from 2 April until the end December (Fig. 3). Annual minimum values of NDVI during winter did not differ between seasonal ranges (Table 1), which would be expected when snow covered those ranges. Nevertheless, snow cover was sparse during some winters in Round Valley.

Autumn migration

Snowfall during October ranged from 0 to 110 cm (CV = 196%), whereas mean daily temperature ranged from 4.2 to 10.2°C (CV = 28%), during 1999–2009. Despite such variation in winter weather during October, mean date of autumn migration (28 October) for mule deer only ranged from 18 October to 8 November, and generally was not different among years (Fig. 4). In addition, mean date of autumn migration coincided with the onset of winter as temperatures declined below 5°C, and winter precipitation began to increase (Fig. 2). Mean date of annual migration did not exhibit directional change during 11 years ($\beta = -0.21$, $r^2 = 0.01$, $P = 0.74$). Multiple-regression analysis revealed little relation between annual metrics of large-scale climate and plant phenology, and the annual mean and synchrony of autumn migration ($R^2_{adj} = 0.35$, $P = 0.12$, $R^2_{adj} = 0.23$, $P = 0.20$, respectively). Synchrony (SD) within years was highly variable ranging from 17.1 to 62.1 days (mean SD = 39.0 days).

Migration models that included year received nearly 100% of the Akaike weight. Indeed, model-averaged daily probability of migration varied considerably in shape and magnitude among years, and the annual cumulative proportion of mule deer migrating increased at different rates among years (Fig. 5). Although mean date of autumn migration did not differ statistically during 1999–2009, based on predictive models, the date at which 90% of adult female mule deer had completed autumn migration ranged from 29 October in 2004 when early snowfall and cold temperatures occurred, to 2 December in 1999, which was characterized by a mild autumn (Fig. 5).

Extrinsic factors affecting the daily probability of autumn migration among years included daily snow depth (PC1), daily temperature (PC3), daily snowfall (PC4), and daily change in temperature (PC5; Table 2). Daily probability of migration increased as daily snowfall and snow depth increased, and as daily temperature and rate of change in temperature decreased. Based on Akaike importance weights, those four weather variables all had comparable roles in determining the daily probability of autumn migration in female mule deer (Table 2). For example, early snowfall in the absence of cold temperatures caused only modest increases in the daily probability of migration (Fig. 6a, b), whereas snowfall events coincident with cold and declining temperatures resulted in dramatic increases in the expected proportion of individual deer migrating that day (Fig. 6b, c).

Metrics of plant senescence, including daily senescent degree-days, daily NDVI, daily change in NDVI, end of season date, and rate of decrease in NDVI at end of season, received minimal support (importance weights <0.51) and their model-averaged parameter estimates did not differ from zero (Table 2). Indeed, mean date of autumn migration occurred prior to senescence of plants on summer range (Fig. 3), which supports the association between patterns of

Table 1. Mean, SE, and statistical results from *t*-tests to evaluate differences in annual phenology metrics between winter range and the spring holding area (Fig. 1) for mule deer in the Sierra Nevada, California, USA, 1999–2009. Phenology metrics were calculated following Reed et al. (1994).

Phenology metric	Seasonal range: Winter Mean	Winter SE	Spring Mean	Spring SE	*t*-test: *t*	*df*	*P*
Date of onset of spring†	92.50	4.30	94.60	4.70	0.33	20	0.750
Rate of increase in NDVI	0.03	2×10^{-3}	0.07	4×10^{-3}	7.10	20	<0.001
Date of end of season†	364.60	5.00	366.20	6.50	0.19	20	0.850
Rate of decrease in NDVI	0.03	3×10^{-3}	0.07	7×10^{-3}	5.30	20	<0.001
Maximum NDVI	0.34	0.01	0.60	7×10^{-3}	19.30	20	<0.001
Minimum NDVI	0.11	0.01	0.15	0.02	1.80	20	0.083

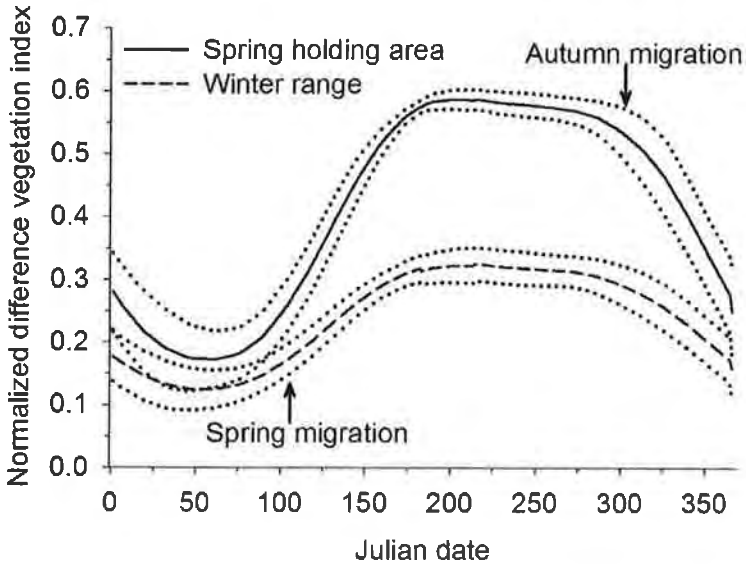

Fig. 3. Normalize difference vegetation index (NDVI) for winter range in Round Valley and the spring holding area (Fig. 1) for mule deer in the Sierra Nevada, California, USA, 1999–2009. Data are mean ±95% CI (dotted lines), and were scaled between 0 and 200. Arrows for autumn and spring migration correspond to average timing of seasonal migration.

winter weather and autumn migration.

Spring migration

During 1999–2009, mean snow depth adjacent to the spring holding area (Fig. 1) during April varied considerably from 0.13 to 87.7 cm (CV = 179%), while mean daily temperatures for April ranged from 0.54 to 5.4°C (CV = 60%). Mean date of departure from winter range for mule deer in Round Valley during 1999–2009 was 18 April, which was coincident with the onset of spring as precipitation declined and temperatures increased above 5°C (Fig. 2). Mean date of spring migration differed among years (Fig. 4), with early departure dates in 2002 and 2007, and delayed departure in 2005 and 2006. Mean date of spring migration did not exhibit a directional change during 1999–2009 ($\beta = -0.02$, $r^2 < 0.001$, $P = 0.98$). Spring migration (SD = 17.3 days) within years was significantly more synchronous than autumn migration (SD = 39.0 days; $t = 4.15$, $df = 20$, $P = 0.001$). Although there was no relation between annual metrics of climate and plant phenology, and synchrony of spring migration

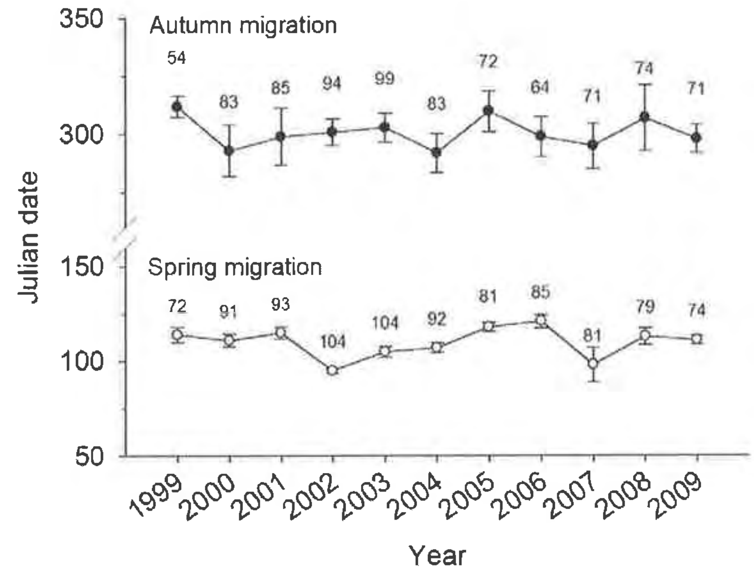

Fig. 4. Mean Julian date (±95% CI) of spring and autumn migration for female mule deer occupying winter range in Round Valley in the eastern Sierra Nevada, California, USA, 1999–2009. Values above means are number of deer monitored during each season.

($R^2_{adj} < 0.001$, $P = 0.77$), a strong relationship existed between those metrics and annual mean date of migration ($R^2_{adj} = 0.71$, $P = 0.014$). Both SOI and Julian date of onset of spring were positively related to the mean date of spring migration, but SOI ($\beta = 5.90$, $r^2_{partial} = 0.20$) accounted for slightly more variation in date of spring migration than the Julian date of onset of spring ($\beta = 0.33$, $r^2_{partial} = 0.15$).

Interval-censored models for spring migration supported an effect of year, with models that contained year having nearly 100% of the Akaike weight (Table 2). The shape and magnitude of the daily probability of spring migration varied markedly among years, as did the date of initiation and trajectory of the cumulative proportion of deer departing winter range (Fig. 7). Of the variables we hypothesized to influence the timing of spring migration, only daily snow depth (PC1), daily NDVI, and daily ΔNDVI had high importance weights and model-averaged parameter estimates that differed from zero (Table 2). As absolute daily snow depth decreased with a concomitant increase in daily NDVI and a positive ΔNDVI, daily probability of departure from winter range increased. Indeed, years of low snow depth with early increases in NDVI resulted in earlier initiation and mean dates of spring migration (Fig. 8b), whereas late snowfall events delayed spring migration (Fig. 8a). Moreover, years with substantial snowfall and later green-up resulted in substantial delays in departure from winter range by mule deer (Fig. 8c). Based on model-averaged estimates of the cumulative proportion migrated in spring, the date at which 90% of adult females had completed spring migration ranged from 13 April in 2002, which was characterized by low snow depth with early advances in plant phenology (Fig. 7, 8b), to 3 May in 2006, when heavy snow pack delayed advances in plant phenology (Fig. 7, 8c).

Effects of life-history characteristics

Following the identification of the extrinsic variables that influenced patterns of seasonal migration of mule deer, we subset our data to include only those individuals for which we had complete data on life-history characteristics in each season. For autumn migration, we obtained data on location of summer residency (side of the Sierra crest), age (years), recruitment (presence of young-at-heel), and nutritional condition (ingesta-free body fat; IFBFat) in November for 312

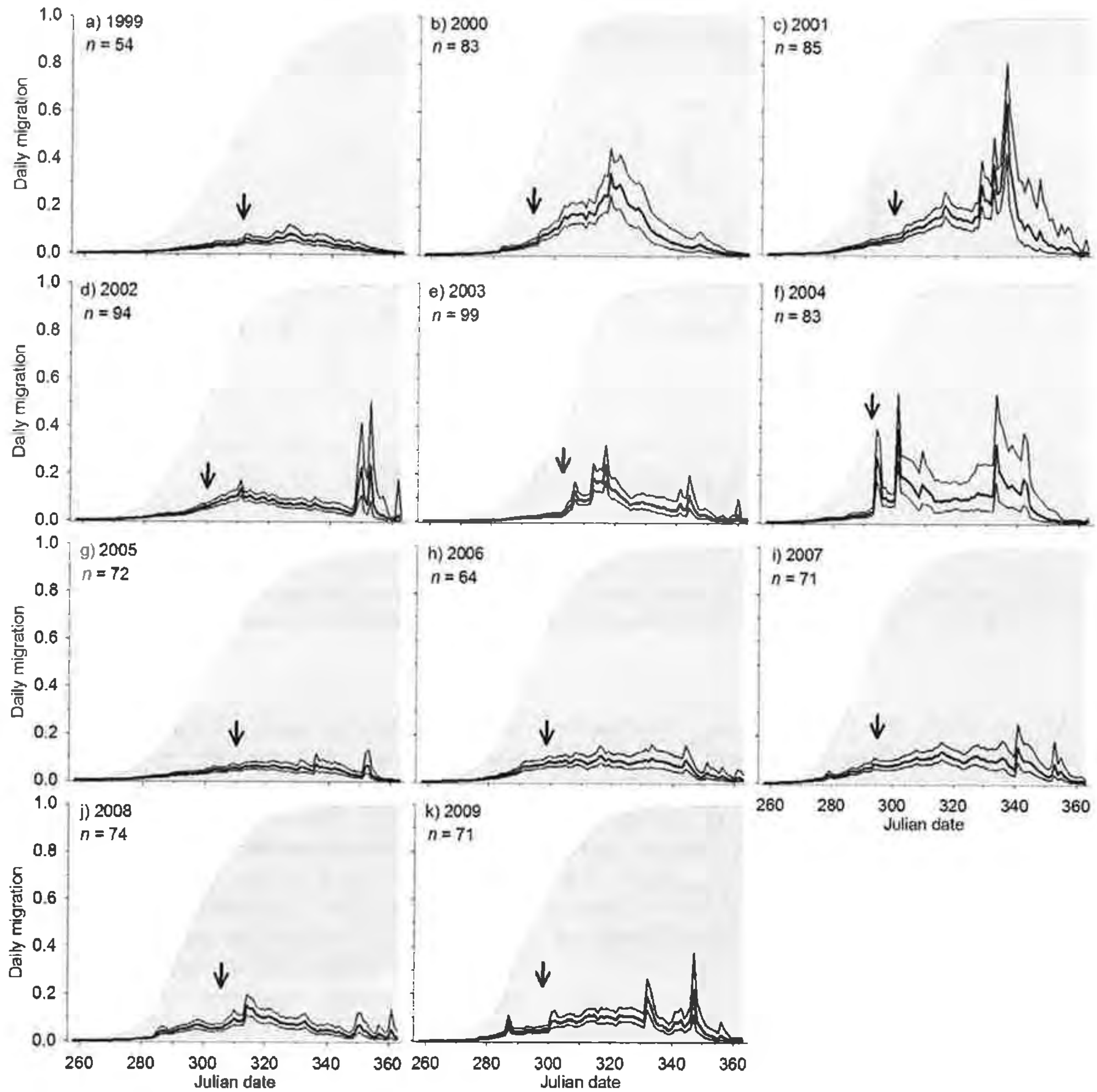

Fig. 5. Model-averaged estimates of the daily probability of migration (heavy line ±95% CI) and cumulative proportion migrated (shaded region) during autumn for adult (>1 year old) female mule deer relative to Julian date, Sierra Nevada, California, USA, 1999–2009. Black arrows indicate mean date of migration.

adult females during 7 years, 2002–2008. Of those females, 153 summered on the east side of the Sierra crest, and 159 on the west side. Age of females monitored in autumn ranged from 1.4 years to 15.4 years ($\bar{X} = 7.4$ years, SD = 2.8), and IFBFat ranged from 0.5% to 23.4% ($\bar{X} = 8.7\%$, SD = 5.3).

For spring migration, we obtained data on summer residency, age, fetal rate and IFBFat in March for 720 females during 11 years, 1999–2009. Of those females, 316 summered on the east-side of the Sierra crest and 404 summered on the west-side. Age of females monitored during spring ranged from 1.8 to 15.8 years ($\bar{X}$ = 6.8 years, SD = 2.7), and fetal rate (number of fetuses per female) ranged from 0 to 3 ($\bar{X} = 1.6$, SD = 0.6). Ingesta-free body fat in March ranged from 0.5% to 15.5% ($\bar{X}$ = 5.1%, SD = 2.5), and was

Table 2. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship between the daily probability of autumn and spring migration of mule deer and 13 extrinsic variables, Sierra Nevada, California, USA, 1999–2009. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Autumn				Spring			
		95% CI				95% CI		
Parameter	Estimate	Lower	Upper	Importance weight	Estimate	Lower	Upper	Importance weight
PC1	0.75*	0.12	1.37	0.85	−0.99*	−1.36	−0.62	1.00
PC2	0.22	−0.11	0.55	0.58	0.09	−0.03	0.20	0.59
PC3	−0.69*	−0.96	−0.41	1.00	0.13	−0.02	0.28	0.68
PC4	0.13*	0.01	0.24	0.84	1×10^{-3}	−0.04	0.04	0.26
PC5	−0.58*	−0.82	−0.35	1.00	0.06	−0.04	0.16	0.50
Degree-days	-2×10^{-3}	-6×10^{-3}	1×10^{-3}	0.51	-5×10^{-4}	-2×10^{-3}	9×10^{-4}	0.10
NDVI	0.72	−1.52	2.94	0.37	53.42*	46.02	60.78	1.00
ΔNDVI	3.20	−3.26	9.60	0.33	93.98*	28.42	159.32	0.99
Seasondate	-2×10^{-5}	-8×10^{-5}	2×10^{-5}	1×10^{-3}	-1×10^{-3}	-9×10^{-3}	6×10^{-3}	4×10^{-3}
ΔSeason	1×10^{-5}	-4×10^{-5}	7×10^{-5}	6×10^{-4}	n/a	n/a	n/a	n/a
SOI	8×10^{-4}	-8×10^{-4}	2×10^{-3}	1×10^{-3}	n/a	n/a	n/a	n/a
T	0.16*	0.13	0.18	1.00	0.11*	0.07	0.15	1.00
TT	-1×10^{-3}*	-1×10^{-3}	-1×10^{-3}	1.00	-1×10^{-3}*	-2×10^{-3}	-1×10^{-3}	1.00
Year	n/a	n/a	n/a	1.00	n/a	n/a	n/a	1.00

Notes: Factors in interval-censored models for seasonal migration included: daily snow depth (PC1), daily metric of change in snow depth (PC2), daily temperature (PC3), daily snowfall and precipitation (PC4), daily metric of change in temperature (PC5), cumulative degree days above or below 5°C for spring and autumn, respectively (degree-days), daily normalized difference vegetation index (NDVI), daily change in NDVI relative to previous 14 days (ΔNDVI), Julian date of start and end of season for spring and autumn respectively (Seasondate), rate of increase and decrease in NDVI at changing seasons for spring and autumn respectively (ΔSeason), mean of the southern oscillation index during 1 year previous to season (SOI), quadratic time trend (T and TT), and year (Year). Year was included as a nuisance parameter in models, however, the parameter estimates for each year are not biologically meaningful and were thus, not included.

significantly lower than IFBFat in November ($t = 14.4$, $df = 1{,}030$, $P < 0.001$).

Autumn migration.—Daily snow depth (PC1), absolute daily temperature (PC3), change in daily temperature (PC5), and the quadratic time trend all maintained their importance and significance for explaining the phenology of autumn migration in mule deer when life-history characteristics were included (Table 3). Daily snowfall (PC4) maintained a high importance weight, but the model-averaged parameter estimate was no longer significant. In addition, the effect of year as a nuisance parameter declined substantially in importance, compared with the first stage of the analysis that included only extrinsic variables (Table 3). Partitioning our dataset from 11 to 7 years may have affected that result; nevertheless, 2002–2008 included years with both extremes in weather patterns and expected probability of migration (Fig. 5).

Mean date of autumn migration was nearly identical between females with young-at-heel and those without young (Fig. 9a). Indeed, the model-averaged parameter estimate for recruitment status was not significant (Table 3). Three other life-history characteristics of individual mule deer, however, were highly important and significant for explaining timing of autumn migration: summer residency, age, and nutritional condition. Mean date of autumn migration between females that summered on either side of the Sierra crest approached a significant difference during most years, with east-side females generally exhibiting earlier dates of migration (Fig. 9b). Accordingly, interval-censored models of migration indicated that summer residency affected the daily probability of migration with east-side females arriving to Round Valley earlier than west-side females (Table 3). Older females had a lower daily probability of migration and, thus, tended to migrate to winter range later than younger females (Table 3). Lastly, ingesta-free body fat of individual females was negatively related to the daily probability of migration. Therefore, females in poor nutritional condition arrived to winter range earlier than females in good nutritional condition.

For example, on Julian date 300 during 2005, predictive models indicated that only 11% of young females in poor nutritional condition

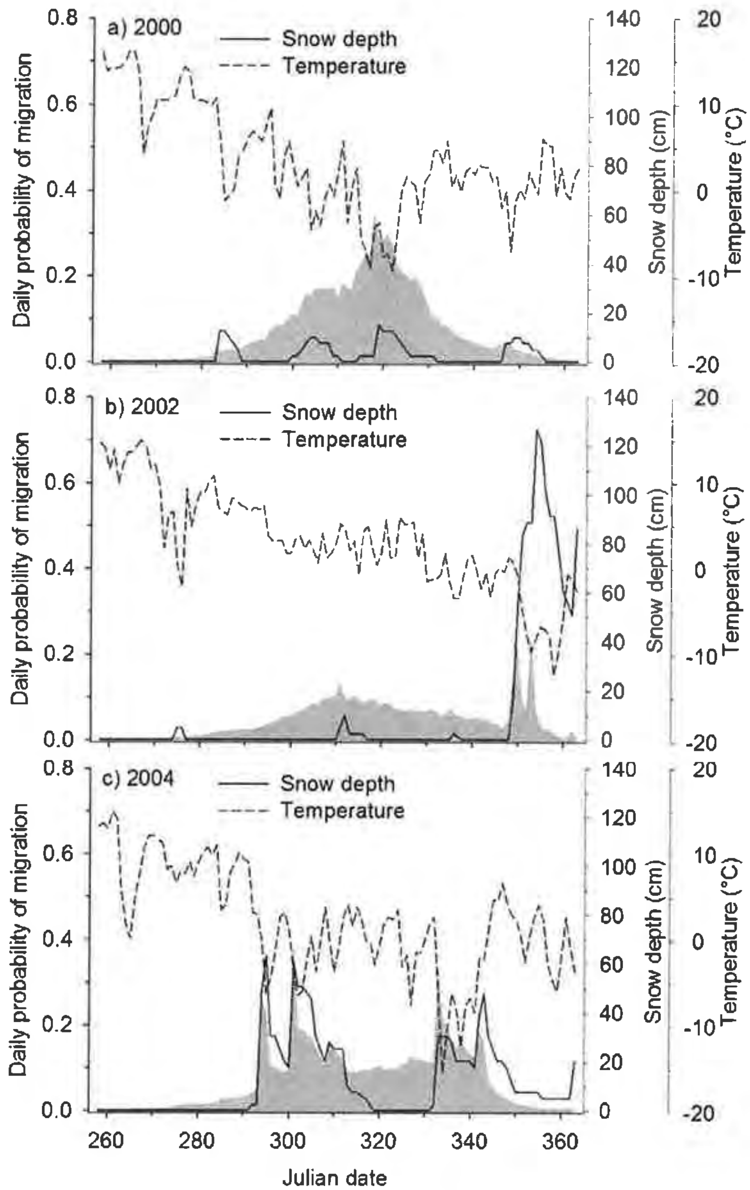

Fig. 6. Model-averaged estimates of the daily probability (shaded region) of autumn migration for adult (>1 year old) female mule deer, daily snow depth (cm), and average daily temperature relative to Julian date, Sierra Nevada, California, USA, during 3 years exhibiting differences in severity of autumn weather: 2000 (a), 2002 (b), and 2004 (c).

remained on summer range compared with 51% of old females in good nutritional condition (Fig. 10a). Furthermore, daily probability of migration for east-side females was higher than west-side females, with further effects of nutritional condition (Fig. 10d). On Julian date 300 during 2007, 92% of east-side females in poor nutritional condition had migrated to winter range, whereas 74% of west-side females in similar nutritional condition had migrated (Fig. 10c).

Spring migration.—In the second stage of the analysis that included life-history characteristics,

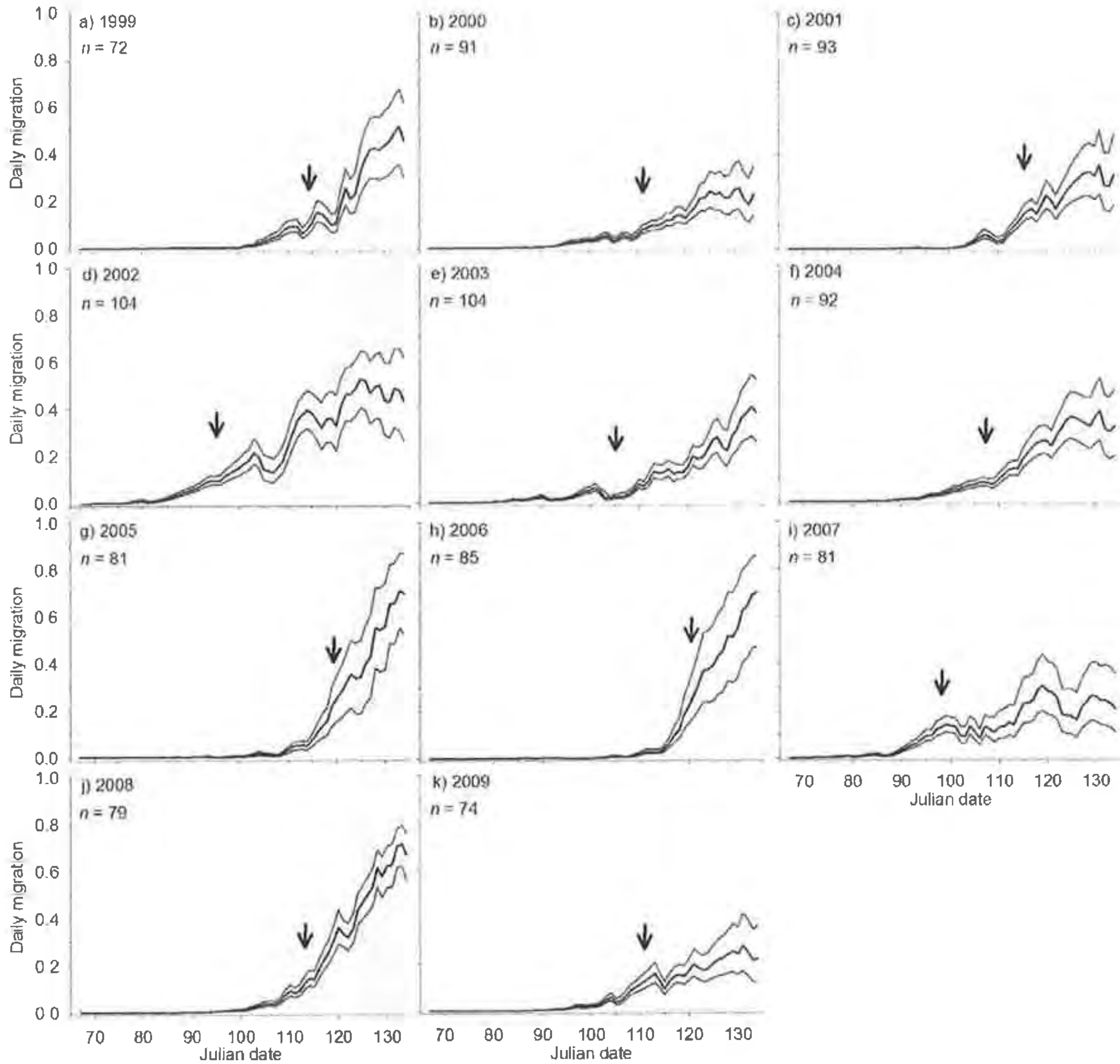

Fig. 7. Model-averaged estimates of the daily probability of migration (heavy line ±95% CI) and cumulative proportion migrated (shaded region) during spring for adult (>1 year old) female mule deer relative to Julian date, Sierra Nevada, California, USA, 1999–2009. Black arrows indicate mean date of migration.

departure from winter range by mule deer in spring was coincident with decreased snow depth (PC1) and increasing plant growth (NDVI and ΔNDVI), which was identical to the first stage of modeling that included only extrinsic factors. We did not detect significant effects of individual life-history characteristics on the daily probability of migration in spring (Table 4). Based on importance weights, summer residency, nutritional condition, and fetal rate were of negligible value in explaining patterns of spring migration. Likewise, mean date of departure from winter range was nearly identical for east-side and west-side females (Fig. 9a). Although the importance weight for age was >0.7, the model-average parameter estimate overlapped zero (Table 4).

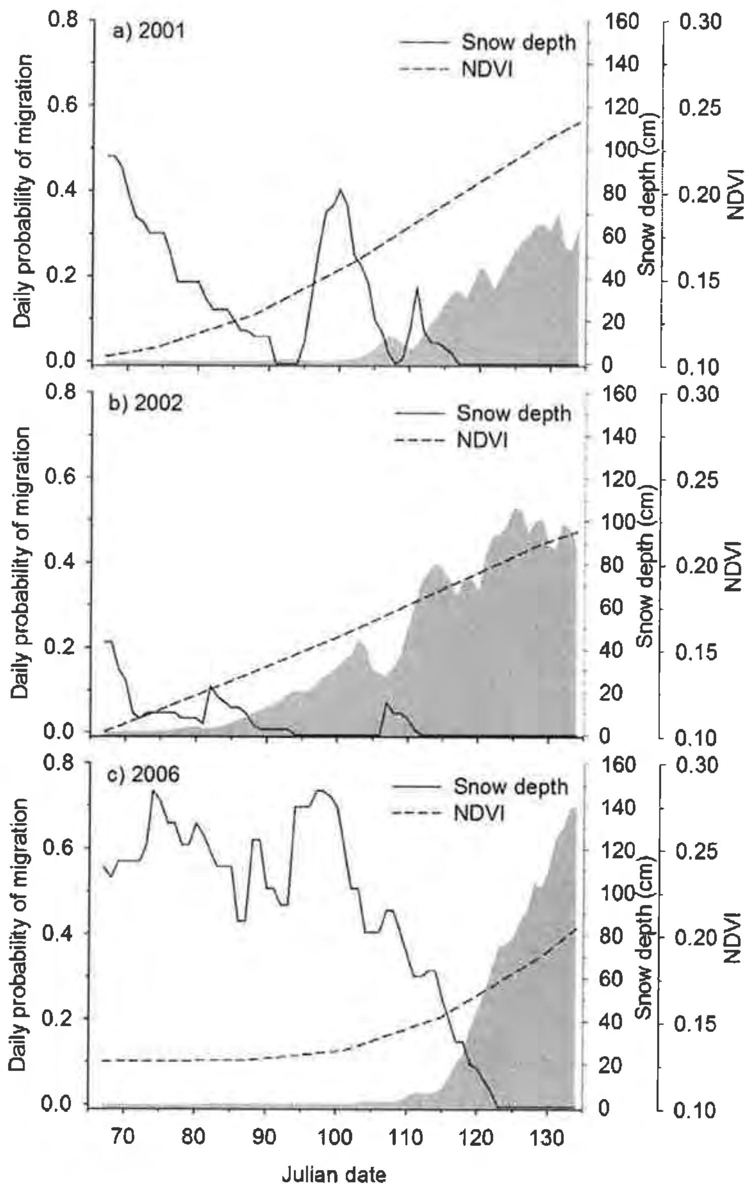

Fig. 8. Model-averaged estimates of the daily probability (shaded region) of spring migration for adult (>1 year old) female mule deer, daily snow depth (cm), and daily normalized difference vegetation index (NDVI) relative to Julian date, Sierra Nevada, California, USA, during 3 years exhibiting different patterns of snow melt and plant phenology: 2000 (a), 2002 (b), and 2006 (c).

Discussion

Long-term studies across a range of environmental conditions may be the key to understanding large-scale effects of climate on the phenological events of animals (Fieberg et al. 2008), a daunting task, especially for large, vagile mammals (McCullough 1979, Pierce et al. 2000, Stewart et al. 2005). Long-term and intensive study of a population of mule deer in the Sierra Nevada, California, USA, allowed us to monitor patterns of migration during years that encom-

Table 3. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship of the daily probability of autumn migration of mule deer with six extrinsic variables (variables that differed from zero in first stage of modeling), and four individual-based covariates with a quadratic term for age, Sierra Nevada, California, USA, 2002–2008. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Autumn			
		95% CI		
Parameter	Estimate	Lower	Upper	Importance weight
PC1	0.87*	0.40	1.35	0.97
PC3	−0.99*	−1.39	−0.59	1.00
PC4	0.10	−0.24	0.04	0.64
PC5	−0.75*	−1.03	−0.47	1.00
T	0.20*	0.13	0.26	1.00
TT	-1×10^{-3}*	2×10^{-3}	-8×10^{-4}	1.00
Year	n/a	n/a	n/a	0.35
Age	−0.07*	−0.13	−0.01	0.98
Age^2	1×10^{-4}	-2×10^{-3}	2×10^{-3}	0.22
Summer Residency	0.66*	0.36	0.95	1.00
IFBFat	−0.04*	−0.06	−0.01	0.94
Recruitment	3×10^{-3}	-5×10^{-3}	0.01	0.03

Notes: Extrinsic factors in interval-censored models for autumn migration with individual covariates included: daily snow depth (PC1), daily temperature (PC3), daily snowfall and precipitation (PC4), daily metric of change in temperature (PC5), quadratic time trend (T and TT), and year (Year). Year was included as a nuisance parameter in models, however the parameter estimates for each year are not biologically meaningful and were thus, not included. Individual covariates included: age in years (Age), side of Sierra crest occupied during summer (summer residency), nutritional condition in November measured as ingesta-free body fat (IFBFat), and the presence or absence of young-at-heel in autumn (Recruitment).

passed a wide array of severity in patterns of weather, and consequently, plant phenology. This dataset allowed us to disentangle the influence of a suite of climatic and life-history variables thought to be responsible for migratory behavior (Table 5). These hypotheses included effects of broad-scale climate, weather patterns, plant phenology, and the effects of life-history characteristics on migration of individual deer (Table 5).

In support of our hypotheses, patterns of local weather and plant phenology were related to the timing of seasonal migration in mule deer, with some detectable effects of large-scale climate (Table 5). Although annual mean date of autumn migration was not statistically different among years, the phenological patterns of autumn migration among individuals varied markedly and were driven by the severity of arriving winter weather. In contrast, mean date of spring migration differed among years and was related to the southern oscillation index (SOI), and onset of spring green-up. Within years, phenological patterns of spring migration were more synchronous than autumn migration, and were clearly associated with snow melt and plant phenology. We also hypothesized, however, that life-history characteristics of individual females would influence their patterns of seasonal migration (Table 5). In accordance with that hypothesis, patterns of autumn migration were affected by location of summer residency, age, and nutritional condition of individual females. Females that summered on the east side of the Sierra crest tended to arrive at Round Valley earlier than females that summered on the west side (Table 5). In addition, older females and those in good nutritional condition remained on summer ranges longer in autumn compared with young females and those in poor nutritional condition (Table 5). During spring migration, however, life-history characteristics of individual females had little influence on timing of migration, which was closely linked to snow depth and plant phenology (Table 5).

The acquisition of continuous data on timing of migration or other life-history events under field conditions is challenging and sometimes impossible to achieve (Garrott et al. 1987, Johnson et al. 2004, Pulido 2007, Fieberg et al. 2008, Meunier et al. 2008), unless animal location data are obtained from collars with global positioning system technology (White et al. 2010). Because of logistical constraints, we were unable to monitor presence or absence of mule

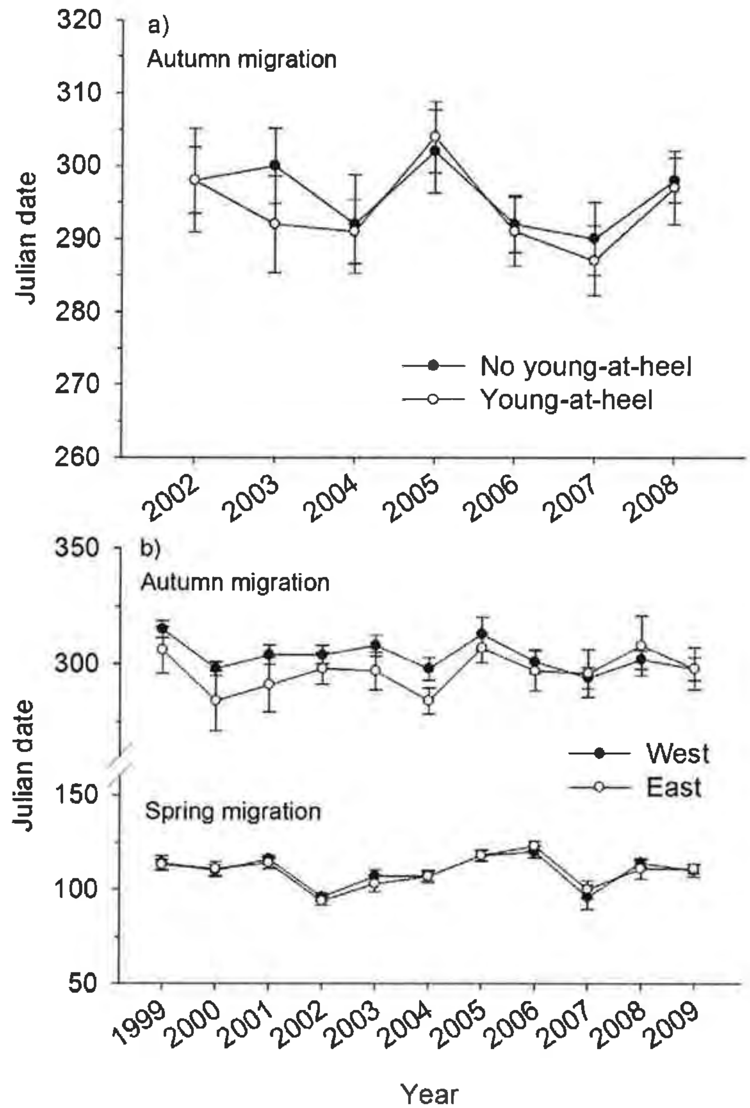

Fig. 9. Mean Julian date (±95% CI) of autumn migration of mule deer (a) relative to reproductive status, 2002–2008; and (b) mean Julian date (±95% CI) of spring and autumn migration relative to the location of summer residency (east or west of the crest of the Sierra Nevada), 1999–2009 for mule deer occupying winter range in Round Valley in the eastern Sierra Nevada, California, USA.

deer on winter range on a daily basis or at regularly spaced intervals (bins). The usual technique for coping with the absence of known dates of life-history events has been to assign the event date to the median date within the interval the event was known to occur (Nelson 1995, Sabine et al. 2002, Meunier et al. 2008). That procedure, however, often underestimates variance, may affect the estimates of regression parameters, and thus, bias their interpretation (Johnson et al. 2004, Fieberg and DelGiudice 2008). We used a procedure for estimating the timing of life-history events developed by Johnson et al. (2004), which is unbiased and allows for unequal time intervals (bins) in sampling, thereby providing a valid comparison of the mean dates and synchrony among years or groups of animals.

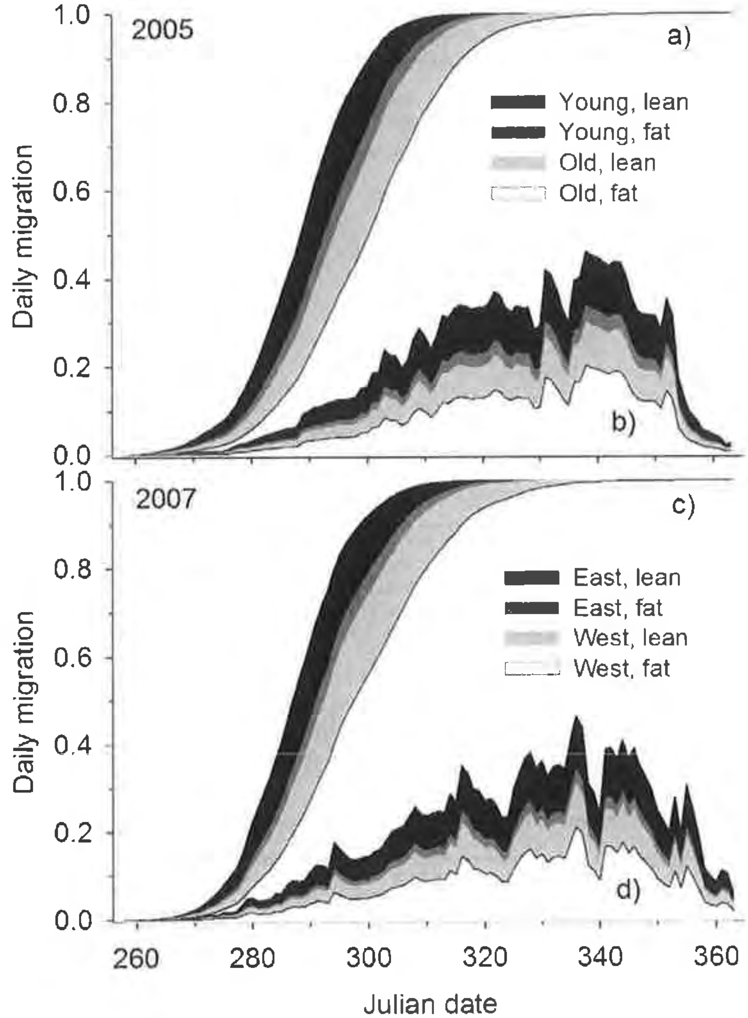

Fig. 10. Model-averaged estimates of the cumulative proportion migrated (a,c) and daily probability of migration (b,d) during autumn for adult (>1 year old) female mule deer illustrating the effects of age (young = 2.4 years old, old = 12.4 years old) and nutritional condition (lean = 4% IFBFat, fat = 18% IFBFat) during 2005 (a, b), as well as the effects of summer residency (east or west of the crest of the Sierra Nevada) and nutritional condition during 2007 (c, d), Sierra Nevada, California, USA.

Despite the marked variability in the timing of migration among individuals within a single population (Brinkman et al. 2005, Fieberg et al. 2008, Grovenburg et al. 2009), seasonal migration often is interpreted at the population level by using point estimates or thresholds in relation to summarized weather patterns. Consequently, the distribution of migratory events among individuals within a season has received little attention until recently (e.g., Meunier et al. 2008, Fieberg et al. 2008). Failure to incorporate the broad range of heterogeneity in timing of migration among individuals likely has hampered our understanding of the factors that affect the phenological patterns of migration of large herbivores. Indeed, analyses at the level of the population fail to ascertain the various migratory strategies among individuals or to identify the selective pressures operating on individuals (Williams 1966, Dingle 2006). To overcome the limitations of analyses at

Table 4. Model-averaged parameter estimates, 95% confidence intervals (95% CI), and Akaike importance weights for interval-censored models describing the relationship of the daily probability of spring migration of mule deer with five extrinsic variables (variables that differed from zero in first stage of modeling), and four individual-based covariates with a quadratic term for age, Sierra Nevada, California, USA, 1999–2009. Asterisks adjacent to parameter estimates indicate 95% CI do not overlap zero.

	Spring			
		95% CI		
Parameter	Estimate	Lower	Upper	Importance weight
PC1	−0.97*	−1.29	−0.64	1.00
NDVI	61.37*	61.23	61.50	1.00
ΔNDVI	99.57*	28.18	170.97	0.95
T	0.11*	0.06	0.16	1.00
TT	-1×10^{-3}*	-2×10^{-3}	-1×10^{-3}	1.00
Year	n/a	n/a	n/a	1.00
Age	−0.02	−0.07	0.03	0.76
Age^2	-4×10^{-4}	-2×10^{-3}	1×10^{-3}	0.15
Summer residency	0.01	−0.02	0.03	0.08
IFBFat	2×10^{-3}	−0.01	0.02	0.34
Fetalrate	-2×10^{-3}	−0.04	0.04	0.23

Notes: Extrinsic factors in interval-censored models for spring migration with individual covariates included: daily snow depth (PC1), daily normalized difference vegetation index (NDVI), daily change in NDVI relative to previous 14 days (ΔNDVI), quadratic time trend (T and TT), and year (Year). Year was included as a grouping variable in models, however the parameter estimates for each year are not biologically meaningful and were thus, not included. Individual covariates included: age in years (Age), side of Sierra crest occupied during summer (summer residency), nutritional condition in March measured as ingesta-free body fat (IFBFat), and fetal rate in March (Fetalrate).

Table 5. Hypotheses and general predictions tested regarding timing of migration for mule deer in the Sierra Nevada, California, USA, during autumn and spring, and the relative support (Yes or No) and direction of the relationship (+ or −) where relevant, 1999–2009.

Hypotheses	Predictions	Autumn	Spring
Broad-scale climate	SOI	No	Yes (+)
Weather patterns	Snow depth	Yes (+)	Yes (−)
	Snowfall	Yes (+)	No
	Temperature	Yes (−)	No
Plant phenology	Degree days	No	No
	NDVI	No	Yes (+)
	Onset of season	No	No
Life-history characteristics	Age	Yes (−)	No
	Nutritional condition	Yes (−)	No
	Summer residency	Yes	No
	Recruitment - Fetalrate	No	No

Notes: Abbreviations are: southern oscillation index (SOI), and normalized difference vegetation index (NDVI). Degree days represent the cumulative degree days above or below 5°C for spring (growing-degree days) and autumn (senescent-degree days), respectively.

the population level, we employed interval-censored, time-to-event models in program MARK, which incorporated the distribution of migratory events to assess their relationship to annual metrics of climate and plant phenology, time-specific covariates of local weather patterns and plant phenology, and allowed the integration of covariates specific to each individual monitored (sensu Dinsmore et al. 2002). Although there are potential weaknesses in using interval-censored models in program MARK, which include the absence of goodness-of-fit testing and the inability to account for repeated sampling of individuals between years, the congruence between migration models and direct hypothesis testing (Johnson et al. 2004) support the legitimacy of this approach.

Autumn migration

The initiation and daily probability of migration for mule deer during autumn was affected by changes in the severity of winter weather, namely increasing snow depth with coincident cooling temperatures (Fig. 6). Increased snow depth with concurrent reduction in ambient temperature results in a concomitant increase in the energetic costs associated with thermoregulation and locomotion in cervids (Telfer and Kelsall 1979, Parker et al. 1984). Furthermore, depth of snow experienced by large herbivores has direct effects on availability of forage (Fancy and White 1985), thereby affecting nutritional condition and probability of winter survival (Garroway and Broders 2005). During most years, however, a large proportion (≥43%) of our marked animals already had migrated to winter range prior to the onset of severe winter weather (i.e., occurrence of snow with average temperatures below freezing) when daily probability of migration was highest (Fig. 5). Likewise, white-tailed deer commonly migrate in response to, and prior to, the accumulation of substantial snow (Nelson 1995, Sabine et al. 2002, Brinkman et al. 2005, Grovenburg et al. 2009).

By delaying autumn migration, deer risk being "trapped" on summer range by sudden winter storms that would increase nutritional, thermoregulatory, and locomotive costs (Parker et al. 1984), and may increase susceptibility to predation or other sources of mortality (Berger 1986, Patterson and Messier 2000, Bleich and Pierce 2001). Nevertheless, individuals that delay autumn migration, but successfully arrive on winter range, may benefit from a greater abundance, diversity, and higher-quality forage on summer range (Albon and Langvatn 1992, Mysterud et al. 2001). Forage quality in our study, as indicated by NDVI, remained significantly higher on summer range throughout autumn (Fig. 3), which supports the energetic advantage of mule deer remaining on summer ranges as long as possible. Even slight changes in diet quality through time can have multiplicative effects on the net energy available for somatic investment, growth, and reproduction (White 1983, Parker et al. 2009).

Spring migration

Mean date of departure from winter range by mule deer in the eastern Sierra Nevada differed over 11 years in response to the duration of snow cover and the timing of plant green-up. We documented strong association between daily snow depth and the probability of spring migration by mule deer. The parameter estimate for the relationship between change in snow depth (PC2) and daily migration for mule deer, however, was not significant, which indicated that the absolute depth of snow was more important in affecting long-distance movement by mule deer than was the rate of snow accumulation or disappearance (Table 2). Likewise, delayed spring migration following winters with heavy snow pack, and early migration in years with low snow pack and early vegetation green-up is common among large herbivores (Garrott et al. 1987, Nelson 1995, Brinkman et al. 2005, Grovenburg et al. 2009, White et al. 2010). The effect of snow pack on large herbivores can severely restrict mobility and exhaust energy reserves (Parker et al. 1984). During all years except 2003, when a late snowstorm occurred in mid-April, mean date of spring migration occurred when snow depth on the spring holding area was ≤12 cm. That snow depth is well below the point at which energy costs of locomotion for mule deer increase significantly (25 cm), regardless of the density of snow (Parker et al. 1984).

Migration to higher elevation during spring may allow the selection of the same plant at an earlier phenological stage (Klein 1965, Morgantini and Hudson 1989), when protein and digestibility are highest (Van Soest 1994, Barboza et al. 2009, Parker et al. 2009). Timing of altitudinal migration of red deer and North American elk (*Cervus elaphus*) coincided with the phenological delay in emergent vegetation at higher elevation (Morgantini and Hudson 1989, Boyce 1991, Albon and Langvatn 1992). Multiple altitudinal movements by golden takin (*Budorcas taxicolor*) in China were determined by the corresponding fluctuations in plant phenology and solar radiation (Zeng et al. 2010). Likewise, female mule deer departed winter range as NDVI began to increase and, thereafter, the daily probability of migration increased in response to both the absolute and daily change in NDVI (Table 2; Fig. 8).

Spring migration for female mule deer was nearly twice as synchronous as autumn migration (Fig. 4). Nutritional demands of pregnant females increase throughout gestation, with most fetal growth (>90%) occurring during the last one-third of gestation (Moen 1978, Robbins and Robbins 1979, Pekins et al. 1998). Inadequate nutrition during gestation may result in fetal loss (Verme 1965), low birth weight and reduced probability of survival of young (Keech et al. 2000, Lomas and Bender 2007), and life-long consequences on the physical characteristics and quality of the individual (Hamel et al. 2009, Monteith et al. 2009). Extended duration of confinement on a traditional winter range can lead to depletion of available browse resulting in increased competition for limited forage (Nicholson et al. 2006). Mule deer wintering in Round Valley exhibited progressive shifts in diet from their main winter forage (*Purshia tridentata*) to forage of low nutritional value (*Artemesia tridentata*) as winter progressed and as population density increased (Kucera 1997, Pierce et al. 2004). Therefore, departure from winter range as soon as snow cover and foraging conditions allow was probably advantageous for mule deer in Round Valley.

Effects of life-history characteristics

The general stimulus for autumn migration is thought to be severe winter weather (Kucera 1992, Sabine et al. 2002, Brinkman et al. 2005, Grovenburg et al. 2009). The great variation among individuals within a single population, however, cannot be explained by this factor alone, especially because weather patterns generally are consistent across local areas. We tested the hypothesis that life-history characteristics of individuals would affect the timing of seasonal migration by incorporating individual-based covariates into interval-censored models. Although individual life-history characteristics were not related to timing of spring migration, location of summer residency, age, and nutritional condition were strongly related to the timing of autumn migration by female mule deer (Table 3).

Females that summered on the east-side of the Sierra crest generally arrived on winter range earlier than west-side females (Fig. 10b). Females inhabiting the west side occupied vast expanses of the Sierra Nevada, and migrated farther than females that occupied the more arid landscape on the east side of the Sierra crest (Kucera 1992). We do not believe greater distances migrated by females from the west side of the Sierra crest were responsible for their delayed arrival on winter range. Although autumn migration is typically rapid with little delay following severe weather (Kucera 1992), females summering on the west side of the Sierra crest may take advantage of comparatively milder conditions after crossing the crest for foraging and resting before proceeding to winter range (Sawyer et al. 2009). Likewise, Mysterud (1999) and White et al. (2010) reported little correlation between the timing of autumn migration and distance migrated in roe deer (*Capreolus capreolus*) and North American elk, respectively. The absence of a relationship between location of summer residency and the phenology of spring migration (Table 4) implies that individuals respond to their local environment. The population of mule deer occupied similar habitat within 90 km^2 in Round Valley during winter, whereas habitats and environmental conditions on summer range, which encompassed >2,800 km^2, differed markedly on either side of the Sierra crest (Bleich et al. 2006). We postulate that behavioral responses of individuals are implemented at fine-scales in the local environment they occupy; this pattern, in conjunction with individual life-history characteristics, holds the greatest potential to influence the timing of seasonal migration.

Understanding age-specific patterns in life-history traits remains a central issue in the ecology of iteroparous organisms (Stearns 1992, Nussey et al. 2008). The terminal-investment hypothesis predicts that mothers should exhibit increased investment in reproduction as they age in relation to their residual reproductive value (Clutton-Brock 1984, Bercovitch et al. 2009). Old female (sensu Gaillard et al. 2000) mule deer in the Sierra Nevada risked encountering severe weather by delaying autumn migration (Fig. 10), and were thus risk-prone (Stephens and Krebs 1986) with respect to the potential loss of foraging opportunities as a result of deep snow. Consequently, old females occupied summer range longer, which provided increased diversity and higher quality forage (Fig. 3), along with less intraspecific competition, when compared with the limited forage and high-density of animals on winter range (Morgantini and Hudson 1989, Albon and Langvatn 1992, Kucera 1992, Pierce et al. 2004). Conversely, young females were risk-averse (sensu Stephens and Krebs 1986) and tended to arrive on winter range earlier in autumn (Fig. 10), ostensibly trading off risk of early winter storms on summer range against obtaining lower-quality, but predictable forage on winter range. Indeed, those age-specific patterns of migration support the terminal-investment hypothesis (Clutton-Brock 1984, Stearns 1992), where old females attempt to maximize nutritional gain in support of reproduction, in spite of increased risk of mortality.

The linear relationship between age and timing of autumn migration (Table 3), however, also supports an experiential explanation. Increased experience with age often is associated with enhanced reproductive performance in large herbivores (Cameron et al. 2000, Gaillard et al. 2000, Weladji et al. 2006; 2010), as well as the potential for improved knowledge of spatial and temporal patterns in the distribution and availability of forage (Mirza and Provenza 1992, Ortegareyes and Provenza 1993). Additional experience with weather patterns in autumn and distribution of forage may have allowed older females to enhance nutritional gain by delaying autumn migration (White 1983) without a detriment to survival, because older females may have better knowledge of the true risk associated with delayed migration. Although we failed to document mortality that was related to delaying autumn migration over 11 years (based on monitoring of collared individuals), late autumn migration can have fatal consequences (Berger 1986, Bleich and Pierce 2001). Despite the impending risk of mortality, older females delayed autumn migration, which could be explained by a combination of a more comprehensive knowledge of true risk, and differential strategies relative to residual reproductive value.

Body fat is the primary energy reserve of the body and is related to multiple demographic factors of large herbivores including timing of breeding (Cook et al. 2004), pregnancy and twinning rate (Keech et al. 2000, Stewart et al. 2005), gestation length (Garcia et al. 2006), birth mass (Keech et al. 2000, Lomas and Bender 2007), and survival (Cook et al. 2004, Bender et al. 2007). Although demographic factors may be directly affected by animal nutrition, we documented that behavioral decisions regarding when to migrate during autumn also had nutritional underpinnings for mule deer. Female mule deer that were nutritionally stressed (sensu Cook et al. 2007) exhibited risk-averse behavior by migrating to winter range early (Fig. 10), where forage resources were likely less palatable and diverse, but more predictable. In contrast, migratory patterns for birds reveal delayed migration for individuals in poor physical condition (Mitrus 2007, Pulido 2007). Energy expenditure and catabolism of somatic reserves associated with thermoregulation and locomotion in large herbivores, however, increases with reduced temperature, rising snow depth, and with the decline in availability and quality of forage (Mautz 1978). In response to those conditions, individuals use various physiological, morphological, and behavioral adaptations to conserve energy and promote survival (Moen 1976, Mautz 1978).

Parker et al. (2009) proposed that behavioral strategies for large herbivores are based on lessening the primary detriment to fitness and that the basis of the strategies is nutritional. Mule deer in the Sierra Nevada may be capable of sequestering better forage resources on summer range in autumn by delaying migration to winter range; however, the primary detriment to adult females in poor nutritional condition may be mortality if they encounter deep snow that increases energetic costs and nutritional loss. We hypothesize that the lower energetic buffer against the potential loss of forage and energetic costs of locomotion in deep snow were responsible for the negative relationship between the daily probability of autumn migration and nutritional condition in mule deer (Table 3; Fig. 10). Similarly, bison (*Bison bison*) arrived earlier to low-elevation winter range as population density increased in Yellowstone National Park, USA, likely in response to negative effects of density dependence on nutritional condition (Plumb et al. 2009).

For spring migration, Garrott et al. (1987) hypothesized that deer must improve their physiological condition prior to incurring the energetic costs associated with migration, which aligns with predictions based on the somatic control of avian migration (Mitrus 2007, Pulido 2007). Contrary to that hypothesis, we observed no relation between date of departure from winter range and nutritional condition, and documented the opposite pattern in autumn. Indeed, no life-history characteristic that we measured was strongly associated with the timing of spring migration (Table 4). Likewise, White et al. (2010) reported little support for effects of age or pregnancy status on timing of spring migration in North American elk. Winter foraging conditions for most large herbivores act as an equalizer by lowering the level and variability of nutritional condition of all deer by spring (Mautz 1978, Barboza et al. 2009, Parker et al. 2009), which likely reduces individual variability in timing of migration and lessens the flexibility in advantageous strategies between individuals during spring migration. Our results indicate that spring migration likely is caused by a direct response to seasonal stimuli of receding snow and new plant growth, and is equally advantageous for female mule deer regardless of age, destination (summer residency), fetal rate, or nutritional condition.

Climate

Phenological traits of both plants and animals are sensitive to climatic processes, with several characteristics advancing in chronology in response to climate change. For example, avian migration is related to plant and invertebrate phenology, with earlier spring migrations corresponding to earlier arrival of spring (Forchhammer et al. 2002, Sparks et al. 2005, Jonzén et al. 2006, Carey 2009). Indeed, the ability of species to advance or recess their timing of migration may have a direct effect on their ability to persist in the face of a changing climate (Walther et al. 2002, Møller et al. 2008, Carey 2009). Mule deer in our study adjusted their timing of seasonal migration to correspond with climatic conditions and plant phenology (Fig. 6, Fig. 8), which may enhance fitness when climate change alters seasonal dynamics of forage quality and availability, so long as that change is not too severe.

In some instances, timing of parturition by large herbivores may respond rapidly to effects of climatic warming on plant phenology (Rachlow and Bowyer 1991, Loe et al. 2005). Timing of migration and parturition by caribou in West Greenland, however, has failed to keep pace with the advancement of the plant-growing season; consequently, recruitment of young has declined fourfold during a single decade (Post and Forchhammer 2008). Plasticity in timing of migration may allow large herbivores to partially compensate for trophic mismatches between seasonal peaks in resource availability and peak energetic demands for reproduction, when phenological patterns of reproduction are less plastic (Post and Forchammer 2008). Plasticity in migration may be an adaptive trait (Gotthard and Nylin 1995), because it likely holds fitness consequences in a changing climate. For example, Møller et al. (2008) reported that populations of migratory birds that failed to exhibit a phenological response to climate change were declining. Species that coordinate life-history phenomena with patterns that remain unaffected by climate change, such as photoperiod, are more likely to encounter trophic mismatches because they fail to synchronize with food supplies that are affected by climate (Carey 2009). Our data indicate, however, that large herbivores may be capable of buffering negative effects of shifts in climate, because patterns of migration are flexible and individuals are responsive to environmental conditions.

Despite clear relationships between the phenological patterns of migration and local weather, timing of autumn migration by mule deer in the Sierra Nevada was influenced by life-history characteristics. Failure to consider effects of nutrition and other life-history traits on phenological patterns of mammals may confound relationships associated with outcomes expected from climate change. For example, progressive changes in nutritional condition or age within a particular population, as a result of density-dependent feedbacks (McCullough 1979, Kie et al. 2003), may yield directional shifts in the timing of migration, even in the absence of a shift in climate (e.g., Plumb et al. 2009). Even in a stochastic environment, fluctuations in population size with bottom-up underpinnings yield dramatic fluctuations in nutritional condition and age structure (Kie et al. 2003, Bowyer et al. 2005), both of which influenced phenological patterns of autumn migration for mule deer (Table 5, Fig. 10). Consequently, climatic change may affect phenological patterns of migration directly, through seasonal weather patterns (Table 1), and indirectly when climatic effects on migration are mediated through life-history characteristics (Fig. 10).

Recently, Barnett et al. (2008) provided evidence of anthropogenic effects on the changes in snow pack and the hydrological regime in the western United States. Between 1950 and 1999, precipitation in montane regions in the western US exhibited a general shift from snow to rain (Knowles et al. 2005), declining snow pack (Hamlet et al. 2005), and snowmelt occurred progressively earlier (Hamlet et al. 2005, Mote et al. 2005). If the occurrence of heavy snowfall wanes with the changing climatic regime, risk of delaying departure from summer range lessens and the nutritional benefits of remaining on summer range increase. Hence, individuals that exhibit risk-prone behavior by delaying departure from summer range will sequester more and higher-quality resources, likely yielding greater fitness than individuals arriving on winter range early. As a result, differences in nutritional condition among individuals within a population may inherently determine the direction of selection with respect to migratory strategies. Likewise, the relation between nutritional condition and the timing of migration, as well as the fitness consequences of that timing, are well documented in birds (Newton 2006, Pulido 2007). Although delayed arrival to and early departure from winter range could bear the cost of encountering inclement weather conditions, individuals employing such tactics may benefit from greater abundance and diversity of food (Albon and Langvatn 1992), yielding higher fitness in the face of a warming climate. Partial migration is common in some populations of large herbivores and, if a warming climate does not compel migration to winter range, we hypothesize that differential selection among individuals employing such strategies will favor the evolution and maintenance of partial migration with permanent residents on summer range (Kaitala et al. 1993).

Phenological relationships for autumn migration also are less conclusive in other taxa compared with spring migration (Walther et al. 2002, Adamik and Pietruszkova 2008, Carey 2009), perhaps because patterns of autumn migration are confounded by life-history characteristics. Thus, we recommend obtaining long-term data on the timing of spring migration to assess the effects of climate change on those phenological patterns because patterns of spring migration may be less confounded by individual life-history characteristics and provide more definitive patterns with respect to climate change. Furthermore, effects of nutritional condition on the timing of migration and how that timing, in turn, influences nutrition and selective pressures among various strategies, requires further investigation across other species of large herbivores.

Conclusions

The persistent movement of thousands of animals across large spatial scales on a seasonal basis is among the most spectacular and well-recognized phenomena of the natural world. Nevertheless, long-distance migrations are being altered by burgeoning human populations and ensuing disturbance and barriers to movement, including habitat loss (Berger 2004, Bolger et al. 2008). In addition, phenological patterns of seasonal migration are likely to be affected by climate change (Walther et al. 2002, Stenseth et al. 2003, Bolger et al. 2008). The need for effective conservation of animal migration warrants a more complete understanding of the biology of this complex behavior (Bolger et al. 2008, Wilcove 2008). We employed an extension of an analytical approach used for survival analyses (Dinsmore et al. 2002, Fieberg and DelGiudice 2008) to consider the distribution of migratory events among individuals and assess the effects of life-history characteristics on timing of migration, which has heretofore received little attention. This methodology should be useful for assessing questions related to timing in most migratory species. We documented that autumn migration of mule deer in the Sierra Nevada was highly variable and associated with patterns of winter weather (cold and snow), whereas spring migration was coincident with decreasing snow depth and advances in plant phenology (Table 5). Although we did not observe directional changes in chronology of spring or autumn migration during our 11-year study, the association between seasonal migration and environmental conditions provides convincing evidence that those migratory patterns may be altered by global climate change. Nevertheless, the close association of the phenology of seasonal migration with environmental conditions may reduce the potential for migratory patterns to be mismatched (sensu Post and Forschhammer 2008) with food availability as climate change alters seasonal patterns of plant growth.

The response of individual mule deer to environmental conditions during autumn was influenced by their life-history characteristics, which may conceal expected relationships with climate change. The risk-prone strategy of delaying autumn migration, which was exhibited by older females, lends support to both the terminal-investment hypothesis, and an experiential explanation (Fig. 10a), and the effects of summer residency on autumn migration indicate that individuals respond to fine-scale patterns of weather within their local environment (Fig. 10b). We demonstrated that unlike birds, mule deer did not accumulate a threshold of fat reserves prior to initiating migration during either season, but in contrast, delayed autumn migration when fat reserves were abundant (Table 3), and yet were unaffected by fat reserves in spring (Table 4). Clearly, our results illustrate the potential problems with extending models developed for avian taxa to large herbivorous mammals (sensu Ralls 1977). Nutritional underpinnings of the timing of autumn migration for mule deer support the hypothesis that behavioral decisions by large herbivores are based on lessening the primary detriment to fitness (Parker et al. 2009), and that those decisions may be underpinned by current nutritional state. We emphasize the importance of considering the influence of individual life-history characteristics on behavior of large herbivores and the underlying effects of nutrition on their life-history strategies. For large herbivores, failure to consider the effects of life-history characteristics when attempting to elucidate relationships between phenological patterns of life-history events and climate may, at best, lead to equivocal relationships or, at worst, be entirely misleading.

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Literature Cited

Adamik, P., and J. Pietruszkova. 2008. Advances in spring but variable autumnal trends in timing of inland wader migration. Acta Ornithologica 43:119–128.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petran and F. Csaki, editors. International symposium on information theory. Second edition.

Akademiai Kiado, Budapest, Hungary.
Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.
Alerstam, T., A. Hendenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–260.
Badeck, F.-W., A. Bondeau, K. Böttcher, D. Doktor, W. Lucht, J. Schaber, and S. Sitch. 2004. Responses of spring phenology to climate change. New Phytologist 162:295–309.
Baker, R. B. 1978. The evolutionary ecology of animal migration. Holmes and Meier Publishers, Inc. New York, New York, USA.
Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer-Verlag, Berlin, Heidelberg, Germany.
Barnett, T. P. et al. 2008. Human-induced changes in the hydrology of the western United States. Science 319:1080–1083.
Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.
Bercovitch, F. B., C. P. Loomis, and R. G. Rieches. 2009. Age-specific changes in reproductive effort and terminal investment in female Nile lechwe. Journal of Mammalogy 90:40–46.
Berger, J. 1986. Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago, USA.
Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–331.
Bleich, V. C., and B. M. Pierce. 2001. Accidental mass mortality of migrating mule deer. Western North American Naturalist 61:124–125.
Bleich, V. C., B. M. Pierce, J. L. Jones, and R. T. Bowyer. 2006. Variance in survival of young mule deer in the Sierra Nevada, California. California Fish and Game 92:24–38.
Bleich, V. C., T. R. Stephenson, N. J. Holste, I. C. Snyder, J. P. Marshal, P. W. McGrath, and B. M. Pierce. 2003. Effects of tooth extraction on body condition and reproduction of mule deer. Wildlife Society Bulletin 31:233–236.
Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.
Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for biodiversity. Pages 342–361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.
Boyce, M. S. 1991. Migratory behaviour and management of elk (*Cervus elaphus*). Animal Behaviour Science 29:249–250.
Brinkman, T. J., C. S. DePerno, J. A. Jenks, B. S. Haroldson, and R. G. Osborn. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. Journal of Wildlife Management 69:1099–1111.
Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, USA.
Cameron, E. Z., W. L. Linklater, K. J. Stafford, and E. O. Minot. 2000. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? Behavioral Ecology and Sociobiology 47:243–249.
Carey, C. 2009. The impacts of climate change on the annual cycles of birds. Philosophical Transactions of the Royal Society of London B 364:3321–3330.
Chapin, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology 2:47–52.
Christianson, D., and S. Creel. 2009. Fecal chlorophyll describes the link between primary production and consumption in a terrestrial herbivore. Ecological Applications 19:1323–1335.
Ciuti, S., P. Bongi, S. Vassale, and M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology 268:97–107.
Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist 123:212–229.
Cook, J. C., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs No 155.
Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934–1943.
Dingle, H. 1985. Migration and life histories. Pages 27–42 *in* M. A. Rankin, editor. Migration: Mechanisms and Adaptive Significance. Contributions in Marine Science, Volume 27. University of Texas Marine Science Institute, Port Arkansas, Texas, USA.
Dingle, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147:212–220.
Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.
Fancy, S. G., and R. G. White. 1985. Energy expendi-

Comment Letter I9

tures by caribou while cratering in snow. Journal of Wildlife Management 49:987–993.

Fieberg, J., and G. DelGiudice. 2008. Exploring migration data using interval-censored time-to-event models. Journal of Wildlife Management 72:1211–1219.

Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. Journal of Mammalogy 89:1529–1539.

Forchhammer, M. C., and E. Post. 2004. Using large-scale climate indices in climate change ecology studies. Population Ecology 46:1–12.

Forchhammer, M. C., E. Post, and N. C. Stenseth. 2002. North Atlantic Oscillation timing of long- and short-distance migration. Journal of Animal Ecology 71:1002–1014.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237–241.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gannon, W. L., R. S. Skies, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Garcia, A. J., T. Landete-Castillejos, D. Carrion, E. Gaspar-Lopez, and L. Gallego. 2006. Compensatory extension of gestation length with advance of conception in red deer (*Cervus elaphus*). Journal of Experimental Biology 305A:55–61.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in Northwest Colorado. Journal of Wildlife Management 51:634–643.

Garroway, C. J., and H. G. Broders. 2005. The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. Canadian Journal of Zoology 83:1246–1256.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pages 207–265 *in* J. Burger, B. L. Olla, and H. E. Winn, editors. Behavior of marine animals, Volume 4, Marine birds. Plenum Press, New York, New York, USA.

Gordo, O., and J. J. Sanz. 2005. Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia 146:484–495.

Gotthard, K., and S. Nylin. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. Oikos 74:3–17.

Grovenburg, T. W., J. A. Jenks, R. W. Klaver, C. C. Swanson, C. N. Jacques, and D. Todey. 2009. Seasonal movements and home ranges of white-tailed deer in north-central South Dakota. Canadian Journal of Zoology 87:876–885.

Hamel, S., M. Garel, M. Festa-Bianchet, J.-M. Gaillard, and S. D. Côté. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Hamlet, A. F., P. W. Mote, M. P. Clark, and D. P. Lettenmaier. 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate 18:4545–4561.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. American Naturalist 173:431–445.

Johnson, D. S., R. P. Barry, and R. T. Bowyer. 2004. Estimating timing of life-history events with coarse data. Journal of Mammalogy 85:932–939.

Jönsson, P., and L. Eklundh. 2004. TIMESAT—a program for analyzing time-series of satellite sensor data. Computers and Geosciences 30:833–845.

Jonzén, N. et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312:1959–1961.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist 142:59–81.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

Kie, J. G., R. T. Bowyer, and K. M. Stewart. 2003. Ungulates in western forests: habitat relationships, population dynamics, and ecosystem processes. Pages 296–340 *in* C. Zabel and R. Anthony, editors. Mammal community dynamics in western coniferous forests: management and conservation. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Klein, D. R. 1965. Ecology of deer range in Alaska. Ecological Monographs 35:259–284.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2005. Trends in snowfall versus rainfall in the Western

Comment Letter I9

United States. Journal of Climate 19:4545–4559.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the Eastern Sierra Nevada, California. Ph.D. Dissertation. University of California, Berkeley, California, USA.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

Kucera, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. Journal of Wildlife Management 61:550–560.

Loe, L. E., C. Bonenfant, A. Mysterud, J. M. Gaillard, R. Langvatn, F. Klein, C. Calenge, T. Ergon, N. Pettorelli, and N. C. Stenseth. 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. Journal of Animal Ecology 74:579–588.

Loft, E. R., R. C. Bertram, and D. L. Brown. 1989. Migration patterns of mule deer in the central Sierra Nevada. California Fish and Game 75:11–19.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884–894.

Marshal, J. P., P. R. Krausman, V. C. Bleich, W. B. Ballard, and J. S. McKeever. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66:1283–1289.

Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. The University of Michigan Press, Ann Arbor, Michigan, USA.

McCullough, D. R. 1985. Long range movements of large terrestrial mammals. Pages 444–465 *in* M. A. Rankin, editor. Migration: mechanisms and adaptive significance. Contributions in Marine Science, Volume 27. University of Texas Marine Science Institute, Port Arkansas, Texas, USA.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York, USA.

Meunier, J., R. Song, R. S. Lutz, D. E. Anderson, K. E. Doherty, J. G. Bruggink, and E. Oppelt. 2008. Proximate cues for a short-distance migratory species: an application of survival analysis. Journal of Wildlife Management 72:440–448.

Miller, F. L. 1971. Behaviour of maternal black-tailed deer (*Odocoileus hemionus columbianus*). Zeitschrift für Tierpsychologie 28:527–533.

Mirza, S. N., and F. D. Provenza. 1992. Effects of age and conditions of exposure on maternally mediated food selection by lambs. Applied Animal Behavior Science 33:35–42.

Mitrus, C. 2007. Is the later arrival of young male red-breasted flycatchers (*Ficedula parva*) related to their physical condition? Journal of Ornithology 148:53–58.

Moen, A. N. 1976. Energy conservation in white-tailed deer in winter. Ecology 57:192–198.

Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. Journal of Wildlife Management 42:715–738.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences, USA 105:16195–16200.

Monteith, K. L., L. E. Schmitz, J. A. Jenks, J. A. Delger, and R. T. Bowyer. 2009. Growth of male white-tailed deer: consequences of maternal effects. Journal of Mammalogy 90:651–660.

Morgantini, L. E., and R. J. Hudson. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Research 21:288–295.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Mysterud, A. 1999. Seasonal migration patterns and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology, London 247:479–486.

Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 2001:915–923.

Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology 73:1069–1076.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs No 77.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. WCB McGraw-Hill, Boston, Massachusetts, USA.

Newton, I. 2006. Can conditions experienced during migration limit the population levels the population levels of birds? Journal of Ornithology 147:146–166.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 2006. Forage selection by mule deer: does niche breadth increase with population density? Journal of Zoology 269:39–49.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J.-M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Functional Ecology 22:393–406.

Ortegareyes, L., and F. D. Provenza. 1993. The amount of experience and age effect the development of foraging skills of goats browsing blackbrush (*Coleogyne ramosissima*). Journal of Animal Science 71:380–383.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 420:168–171.

Patterson, B. R., and F. Messier. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. Journal of Wildlife Management 64:721–732.

Pekins, P. J., K. S. Smith, and W. W. Mautz. 1998. The energy cost of gestation in white-tailed deer. Canadian Journal of Zoology 76:1091–1097.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth vs. rapid green-up: impact on juvenile mountain goats. Ecology 88:381–390.

Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20:503–510.

Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986–992.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462–472.

Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533–541.

Plumb, G. E., P. J. White, M. B. Coughenour, and R. L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. Biological Conservation 142:2377–2387.

Post, E., and M. D. Forchhammer. 2008. Climate change reduces reproductive success of an arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B 363:2369–2375.

Post, E., C. Pederson, C. C. Wilmers, and M. C. Forchhammer. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proceedings of the Royal Society of London B 275:2005–213.

Pulido, F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. Climate Research 35:5–23.

Rachlow, J. L., and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammalogy 72:487–492.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 111:917–938.

Reed, B. C., J. F. Brown, D. VanderZee, T. R. Loveland, J. W. Merchant, and D. O. Ohlen. 1994. Measuring phenological variability from satellite imagery. Journal of Vegetation Science 5:703–714.

Robbins, C. T., and B. L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. American Naturalist 114:101–116.

Ruckstuhl, K. E., and M. Festa-Bianchet. 1998. Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? Ethology 104:941–954.

Sabine, D. L., S. F. Morrison, H. A. Whitlaw, W. B. Ballard, G. J. Forbes, and J. Bowman. 2002. Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. Journal of Wildlife Management 66:718–728.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Sparks, T. H., F. Bairlein, J. G. Bojarinova, O. Hüppop, E. A. Lehikoinen, K. Rainio, L. V. Sokolov, and D. Walker. 2005. Examining the total arrival distribution of migratory birds. Global Change Biology 11:22–30.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, New York, USA.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N. G. Yoccoz, and J. Adlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society of London B 270:2087–2096.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory.

Princeton University Press, Princeton, New Jersey, USA.

Stephenson, T. R., J. W. Testa, G. P. Adams, R. G. Sasser, C. C. Schwartz, and K. J. Hundertmark. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167–172.

Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

Stone, R. C., G. L. Hammer, and T. Marcussen. 1996. Prediction of global rainfall probabilities using phases of the Southern Oscillation Index. Nature 384:252–255.

Storer, T. I., R. L. Usinger, and D. Lukas. 2004. Sierra Nevada Natural History. University of California Press, Berkeley, California, USA.

Swets, D. L., B. C. Reed, J. D. Rowland, and S. E. Marko. 1999. A weighted least-squares approach to temporal NDVI smoothing. 1999 ASPRS Annual Conference: From Image to Information, Portland, Oregon, May 17–21. Proceedings. Bethesda, Maryland, American Society for Photogrammetry and Remote Sensing.

Swift, P. K., V. C. Bleich, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal. 2002. Tooth extraction from live-captured mule deer in the absence of chemical immobilization. Wildlife Society Bulletin 30:253–255.

Swingland, I. R., and P. J. Greenwood. 1983. The ecology of animal movement. Oxford University Press, London, UK.

Telfer, E. S., and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Canadian Journal of Zoology 57:2153–2159.

Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303–319.

Van Soest, P. J. 1994. Nutritional ecology of the ruminant, Second edition. Cornell University Press, Ithaca, New York, USA.

Verme, L. J. 1965. Reproduction studies of penned white-tailed deer. Journal of Wildlife Management 29:74–79.

Voeten, M. M., C. A. D. M. van de Vijver, H. Olff, and F. van Langevelde. 2009. Possible causes of decreasing migratory ungulate populations in an East African savannah after restrictions in their seasonal movements. African Journal of Ecology 48:169–179.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Barilein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Weladji, R. B., J.-M. Gaillard, N. G. Yoccoz, Ø. Holand, A. Mysterud, A. Loison, M. Nieminen, and N. C. Stenseth. 2006. Good reindeer mothers live longer and become better in raising offspring. Proceedings of the Royal Society of London B 273:1239–1244.

Weladji, R. B., Ø. Holand, J.-M. Gaillard, N. G. Yoccoz, A. Mysterud, M. Nieminen, and N. C. Stenseth. 2010. Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? Oecologia 162:261–271.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

White, P. J., K. M. Proffitt, L. D. Mech, S. B. Evans, J. A. Cunningham, and K. L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy 91:827–837.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

Wilcove, D. S. 2008. No way home. Island Press, Washington, D.C., USA.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey, USA.

Zar, J. H. 1999. Biostatistical Analysis. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zeng, Z.-G., P. S. A. Beck, T.-J. Wang, A. K. Skidmore, Y.-L. Song, H.-S. Gong, and H. H. T. Prins. 2010. Effects of plant phenology and solar radiation on seasonal movement of golden takin in the Qinling Mountains, China. Journal of Mammalogy 91:92–100.

Appendix

Table A1. Summary statistics for daily temperature, daily snow depth during winter (November–March), total annual snowfall and precipitation for Mammoth Lakes, California, USA, and annual mean of the southern oscillation index (SOI), 1999–2009.

Weather variable	Mean	SD	Range
Maximum temperature (°C)	13.6	9.2	−13.3–32.8
Average temperature (°C)	5.9	8.0	−20.0–23.3
Minimum temperature (°C)	−1.7	7.3	−26.7–16.7
Snow depth (cm)	39.4	39.1	0–167.6
Annual snowfall (cm)	469.4	163.1	152.4–714.2
Annual precipitation (cm)	49.5	14.9	13.6–66.5
SOI	0.08	0.6	−0.7–1.0

Table A2. Loadings for principle components (1–5) for daily weather variables included in principle components analysis. Weather variables are daily measurements and daily change (Δ) in weather relative to the mean for the previous 2 weeks, Mammoth Lakes, California, USA, 1999–2009.

Weather variable	Principle component 1	2	3	4	5
Maximum temperature (°C)	−0.180	−0.021	0.568	−0.083	0.183
Average temperature (°C)	−0.155	0.001	0.518	−0.004	0.198
Minimum temperature (°C)	−0.129	0.024	0.468	0.076	0.212
Snowfall (cm)	0.071	0.191	0.008	0.623	−0.007
Snow depth (cm)	0.945	−0.188	0.242	−0.012	0.110
Precipitation (cm)	0.005	0.015	0.000	0.051	0.000
ΔMaximum temperature (°C)	−0.013	−0.144	0.222	−0.012	−0.612
ΔAverage temperature (°C)	−0.011	−0.110	0.196	0.072	−0.520
ΔMinimum temperature (°C)	−0.010	−0.076	0.170	0.157	−0.429
ΔSnowfall (cm)	0.012	0.193	0.007	0.702	0.076
ΔSnow depth (cm)	0.171	0.922	0.119	−0.265	−0.187
ΔPrecipitation (cm)	0.005	0.015	0.001	0.058	0.007

Essays

The Last Mile: How to Sustain Long-Distance Migration in Mammals

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Abstract: *Among Earth's most stunning, yet imperiled, biological phenomena is long-distance migration (LDM). Although the understanding of how and why animals migrate may be of general interest, few site-specific strategies have targeted ways in which to best retain such increasingly rare events. Contrasts among 29 terrestrial mammals from five continents representing 103 populations indicate that remnant long-distant migrants have poor long-term prospects. Nonetheless, in areas of low human density in the Western Hemisphere, five social and nongregarious species, all from the same region of the Rocky Mountains (U.S.A.), still experience the most accentuated of remaining New World LDMs south of central Canada. These movements occur in or adjacent to the Greater Yellowstone region, where about 75% of the migration routes for elk (*Cervus elaphus*), bison (*Bison bison*), and North America's sole surviving endemic ungulate, pronghorn (*Antilocapra americana*), have already been lost. However, pronghorn still migrate up to 550 km (round-trip) annually. These extreme movements (1) necessitate use of historic, exceptionally narrow corridors (0.1–0.8 km wide) that have existed for at least 5800 years, (2) exceed travel distances of elephants (*Loxodonta africana*) and zebras (*Equus burchelli*), and (3) are on par with those of Asian chiru (*Pantholops hodgsoni*) and African wildebeest (*Connochaetes taurinus*). Although conservation planners face uncertainty in situating reserves in the most biologically valued locations, the concordance between archaeological and current biological data on migration through specific corridors in these unprotected areas adjacent to the Yellowstone system highlights their retention value. It is highly likely that accelerated leasing of public lands for energy development in such regions will truncate such migrations. One landscape-level solution to conserving LDMs is the creation of a network of national migration corridors, an action in the Yellowstone region that would result in de facto protection for a multispecies complex. Tactics applied in this part of the world may not work in others, however, therefore reinforcing the value of site-specific field information on the past and current biological needs of migratory species.*

La Última Milla: Como Sostener la Migración de Larga Distancia en Mamíferos

Resumen: *Entre los fenómenos biológicos más asombrosos, pero en peligro, de la Tierra está la migración de larga distancia (MLD). Aunque el entendimiento de cómo y porque migran los animales puede ser de interés general, pocas estrategias sitio-específicas han encontrado formas para retener tales eventos cada vez más raros. Los contrastes entre 29 mamíferos terrestres de cinco continentes que representar a 103 poblaciones indican que las MLD remanentes tienen perspectivas pobres a largo plazo. No obstante, en áreas con bajas densidades humanas en el Hemisferio Occidental, cinco especies sociales y no gregarias, todas de las misma región de las Montañas Rocallosas (E.U.A.) aun experimentan las MLD más acentuadas al sur de Canadá. Estos movimientos ocurren en la región de Yellowstone o adyacentes a la misma, donde se han perdido cerca del 75% de las rutas de migración de alces (*Cervus elaphus*), bisontes (*Bison bison*) y el único ungulado endémico sobreviviente de Norteamérica,* Antilocapra americana*. Sin embargo,* Antilocapra americana *aun migra hasta 550 km (viaje redondo) anualmente. Estos movimientos extremos (1) necesitan el uso de corredores históricos, excepcionalmente angostos (0.1-0.8 km de ancho) que han existido por lo menos por 5800 años, (2) exceden las distancias de viaje de elefantes (*Loxodonta africana*) y cebras (*Equus burchelli*) y (3) son similares a*

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los de Pantholops hodgsoni *y* Connochaetes taurinus. *Aunque los planificadores de conservación enfrentan la incertidumbre de situar reservas en las localidades biológicamente más valiosas, la concordancia entre datos arqueológicos y actuales sobre migración por corredores específicos en estas áreas no protegidas adyacentes al sistema Yellowstone resalta su valor de retención. Es altamente probable que las migraciones se trunquen por el arrendamiento acelerado de tierras públicas para el desarrollo energético en tales áreas. Una solución a nivel de paisaje para conservar a las MLD es la creación de una red de corredores nacionales de migración, una acción que resultaría en la protección de hecho de un complejo multi-específico en la región de Yellowstone. Sin embargo, las tácticas empleadas en esta parte del mundo pueden no funcionar en otras, por lo cual se refuerza el valor de la información de campo sitio-específica sobre las necesidades pasadas y actuales de especies migratorias.*

Introduction

Despite increasing attention to biological conservation, most terrestrial surfaces on Earth remain unprotected. Consequently, extraordinary events that once occurred across vast landscapes, playing significant ecological roles, have been truncated. Long-distance migration (LDM) is one such event. Globally, spectacular LDMs still exist and involve volant taxa including diverse species of birds and butterflies (Brower 1995) and well-known cetacean journeys that traverse seas from Arctic to Mexican waters (Baker 1978). Many of the massive and historically described overland treks by herd-dwelling mammals, however, have been lost from Asian steppes, African savannas, and North American grasslands (Table 1). The development of effective strategies to maintain these events has been problematic.

Conservation planners, in trying to capture the essence of both ecological processes and diversity, continue to face uncertainty in reserve placement because landscapes vary in biological value (Groves et al. 2002), events beyond protected borders alter the efficacy of reserves (Newmark 1987, 1995), and changing environments impede knowledge about the relative importance of fixed areas on species persistence (Wilcove 1999). Although LDMs are far from the mainstream of conservation biology, and the movements of gregarious herds in Africa are well-chronicled (Fryxell & Sinclair 1988*a*; Williamson 1997), asocial species also migrate. These species are not typically associated with such movements and include Mountain tapirs (Downer 1996, 1997), black-tailed jackrabbits (Smith et al. 2002), and boreal moose, the latter covering round-trip distances of up to 390 km (Mauer 1998). (Scientific names for species used in analyses are provided in Appendix 1.) Other taxa of terrestrial vertebrates also undertake impressive migrations, including spotted frogs (*Rana luteiventris*) and newts (Pilliod et al. 2002), but how migration is linked with corridor use and especially population persistence has not been well studied (Simberloff et al. 1992; Beier & Noss 1998).

The broader issue, of course, is not whether migratory species are social or large or small, but whether and how to sustain migration so that it does not become a transitional or endangered phenomenon. A fundamental challenge to conservation-minded governments is how best to devise strategies that retain LDMs as part of a rich biological heritage. As a first step in bringing this fleeting ecological process to the conservation table, I offer (1) an analysis of where and which mammalian long-distance migrants have been lost and remain, (2) a potential correlate—body mass—of long-distance migrants, and (3) a relatively straightforward but site-specific conservation plan to retain the longest LDMs in the Western Hemisphere that involve species other than caribou.

Methods

Definitions and Rationale

Migration has been defined in various ways (Sinclair 1983; Rankin 1985). For my purposes a simple operational definition seems best: seasonal round-trip movement between discrete areas not used at other times of the year. For example, a mouse that moves from my house in winter to the outside woodpile during summer and back again would be migratory, and the one-way distance traversed is between house and woodpile. By contrast, a mouse that moves 15 km but not back again is not migratory (Maier 2002). Similarly, a wolverine (*Gulo gulo*) covering a 1000-km^2 region between mountain ranges throughout the year would not be migratory because it fails to show seasonal use of discrete ranges. Many researchers, although not specifically addressing questions about migration distance, have used measures to discern distinct areas of seasonal use (Pierce et al. 1999; Appendix 1), from which migration distances between them could be estimated. Other researchers evaluated distances between formal geometric centers of seasonally discrete home ranges (e.g., Kufeld et al. 1989; Nicholson et al. 1997).

A definition of *long-distance migration* is more troublesome because the distance traversed by species that differ in life-history traits may only be relative. Although

Table 1. Summary of selected major migrations confirmed or suspected lost in historic times, and remnants for three species within the Greater Yellowstone region (*n* is sample for total migration routes).

Continental			*Greater Yellowstone Ecosystem*	
species	*location*	*Reference*[a]	*species*	*percent lost* (n)[b]
Springbok[b]	karoo, Kalahari, South Africa, Namibia	1,2	pronghorn	78 (11)
Wildebeest[b]	Namibia, South Africa	2,3	bison	100 (14)
White-eared kob[c]	The Sudd, Sudan	4	elk	58 (36)
Bison[b]	Canda, U.S.A.	5		
African elephant[b]	Kenya	6		
Asian elephant[b]	India	7		
Saiga[b]	Kazakhastan, Russia, Mongolia	8		

[a] *1, Child & LeRiche 1967; 2, Gasaway et al. 1996; 3, Williamson et al. 1988 and Williamson 1997; 4, Fryxell & Sinclair 1988; 5, Roe 1970; 6, Waithaka 1994; 7, Sukumar 1989; 8, Milner-Gulland et al. 2001.*
[b] *Confirmed lost.*
[c] *Suspected lost.*

either ecological or life-history definitions of LDM may be estimated with allometric criteria to account for body size, my interest lies more in absolute rather than relative distance because conservation strategies have rarely, if ever, been based on relative measures of species size (Groves et al. 2002). With this as a caveat, both European and North American authors have offered provisional definitions that infer "long distance" when one-way movements exceed 10–12 km (Fuller & Keith 1981; Sandgren & Sweanor 1988). Here, I suggest that a long-distance migrant may be species or population dependent and let readers decide for themselves what is "long" and what is not pertinent to conservation objectives.

Choice of Species, Limitations of Data, and Analyses

I collated information on migration from both published and gray literature. I elected to include the latter given the immense number of state-agency reports and bulletins in the United States with information on radio collared animals and attendant analyses of movement patterns in relation to seasonal use. For example, 140 radio collared mule deer were studied at a Wyoming site for multiple years (Sawyer & Lindzey 1999), yet the mere exclusion of such data on migration simply because they were unpublished would represent the loss of significant information. I have not, however, attempted to summarize data from every agency report on movement patterns.

For some taxa (e.g., cervids, camelids), migration may be a polymorphic trait, with members of a population showing great fidelity to areas they either migrate to or remain within (Ortega & Franklin 1995; Bowyer et al. 1996; Nicholson et al. 1997). My measures on distance traversed reflect those of migratory segments of studied populations only, and these were estimated from data presented within the cited study or from the original calculations of the author. The reported measure is the mean for round-trip migrations. Where data stem from multiple populations, I calculated a species mean and, when relevant, standard errors (SEm) and 95% confidences intervals (CI).

Most studies of migration in terrestrial mammals are of hooved mammals (artiodactyls, perrisodactyls, and proboscideans; Appendix 1), but I also included those for carnivores and one lagomorph. For some species (mostly but not exclusively those from North America), multiple data sets exist that tend to reflect populations from geographically different regions. In other areas of the world, data are more restricted, especially when radio collars were not used. For comparative purposes, I included data on these latter migration distances when justified by the author and published in the peer-reviewed literature (e.g., Schaller 1998).

For the approximately 10.8 million ha of the Greater Yellowstone Ecosystem (GYE; Noss et al. 2002), the number of migration routes that have changed or been lost during the last 100 years were estimated by relying on recent historical records (i.e., trapper's journals; Schullery & Whittlesey 1995) and published and agency data. In the GYE this calculation has been possible because, at a coarse level, interest in migration has been great, yielding analyses of track counts, sightings, and estimates of travel routes since the 1950s. Efforts to mark visually (i.e., with neck bands or ear tags) and subsequently to radio-tag elk (Anderson 1958; Craighead et al. 1972) have now spanned portions of >5 decades (Smith & Robbins 1994; B. L. Smith personal communication). Although pronghorn and bison remain less studied, I based estimates of routes lost or retained on point counts of discrete winter and summer ranges. These derive from observations of these ungulates at past known locations, coupled with landscape-level analyses that involved the distribution and change of local human densities, agricultural practices, and winter snow depth. For instance, where towns replaced open habitat in what were once historic pathways (Fig. 1), a route was designated as

Figure 1. Example of the hard edge between a town and open habitat for wildlife (in this case, the National Elk Refuge and town of Jackson, Wyoming) and the blockage of migration (arrow) for bighorn sheep, elk, and pronghorn.

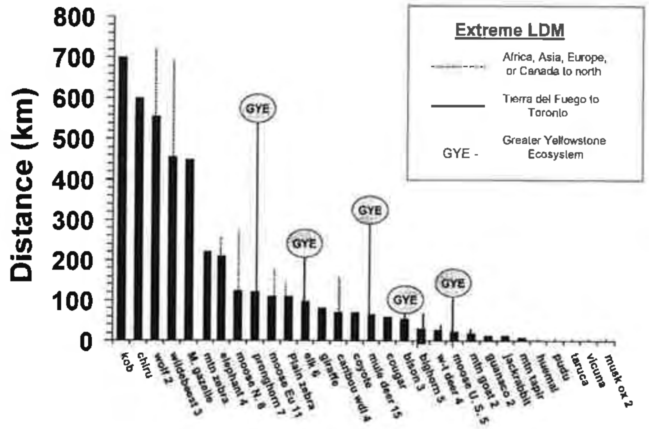

Figure 2. Mean and extreme (extended lines) long-distance migration round-trip distances for terrestrial mammals (excluding barren-ground caribou). Numbers after name are studies/species. If unnumbered, data are based on one study (see Appendix 1 for scientific names and references). Moose from geographically disparate regions are: N, Alaska and Yukon; Eu, Scandinavia; U.S., south of Canada.

"lost." Measures of chest height in pronghorn, bison, and elk relative to snow depth also enable crude prediction of winter occurrence (Telfer & Kelsall 1984).

Although analyses of the potential conduciveness of habitats to movement between two discrete points may be in error because the scale of inquiry affects interpretations (Bowyer et al. 1996) and it is impossible to be certain whether a movement corridor has been lost, I adopted a more conservative measure. Rather than assuming a route was lost, I included data only when discrete summering or wintering sites were known and one remained unused. For instance, the Gallatin Valley of Montana currently harbors a human population of over 40,000. Elk once crossed the valley but no longer can. Whether multiple migration pathways or a single one occurred historically is unknown. To be conservative, which undoubtedly underestimates real losses, I recorded only one lost route, although given the approximate size of Gallatin Valley—over 200,000 ha—and given that elk use summer ranges in at least four adjacent mountain ranges, it is likely that more than a single route has been truncated.

To evaluate whether life-history traits are associated with migration distance, I attempted to fit linear and nonlinear (quadratic, power, exponential) models to non-transformed and log-transformed data on migration distance (mean, median, and longest). Outliers for species or populations were excluded first, and then carnivores were removed to determine whether a global pattern emerged. Subsequently, I restricted analyses to potential migrations that still persist between the southern tip of South America and central Canada, a procedure that excluded more northern latitudes where human effects have been smaller (Sanderson et al. 2002*a*) and caribou mostly unhindered (Appendix 1, but see Mahoney & Schaefer 2002). Although comparative analyses with unequally weighted samples tend to use median values (Gittleman 1986) and measures of migration distance do not occur without error, mean and median distances were highly correlated for all studies ($r^2 = 0.918; p < 0.0001$); therefore, I used average values.

Results

The striking variation in body size that characterizes terrestrial mammals (Eisenberg 1981) is paralleled by migration distances that show great dissimilarities. Although wildebeest and Mongolian gazelles migrate more than 450 km (round-trip) (Fig. 2), for species that may differ in size by more than 40-fold, distances can be both small and similar. For example, mountain tapirs and black-tailed jackrabbits both move <12 km. By contrast, within-species variability can be great. Mule deer average 66 km (±12.7 [SEm]; 95% CI = 38-93; $n = 15$ studies), but in the Upper Green River Basin of Wyoming, distances exceed 285 km (Fig. 2). On a geographically broader scale are barren-ground caribou, with extreme LDMs ($\bar{x} = 1673 \pm 491$ km; $n = 3$; longest = 2500 km). Woodland caribou, however, move far less $\bar{x} = 71 \pm 28$; $n = 4$; Fig. 2).

Although the spatial area used by a species is often associated with its body size (Gompper & Gittleman 1991), this relation appears not to hold, even with the exclusion of such obvious outliers as barren-ground caribou (less than the 99.5% upper CI). Only an exponential model that was restricted geographically to the log mass of species occurring between Canada and the southern tip of South

America explained more than 15% of the variance in migration ($r^2 = 0.178$; $n = 15$; $p = 0.117$), and the explanatory value of this single variable is generally low. It did not improve when analyses were restricted further to only herbivores ($r^2 = 0.015$; $p = 0.986$). These findings, based on a more expansive sample, are consistent with the lack of relationship anticipated by others (Baker 1978; Sinclair & Arcese 1995), presumably because either local ecological conditions, population densities, or other factors are more important, or there is no simple association between body mass and migration distance.

It may be of more immediate relevance to conservation to gain an understanding of how migration has fared in areas with profound anthropogenic impacts. Omitting caribou and other species from the Arctic and other areas with relatively low human impacts (Sanderson et al. 2002*a*) enables a focus on remnant LDMs of the Western Hemisphere. Of 57 populations representing 17 species, the 5 with the extreme LDMs rely on lands within or adjacent to the Greater Yellowstone Ecosystem (GYE) (Fig. 2). Although the Yellowstone area has long been recognized for geothermal distinctiveness and, recently, a restored large-carnivore community (Clark et al. 1999; Noss et al. 2002), what previously has been unrecognized is its ability to support some ecological phenomena—especially the accentuated treks of pronghorn, elk, mule deer, moose, and bison (Fig. 2).

To improve insights into the type of planning necessary to conserve these LDMs, I examined the fates of historic and current routes (Craighead et al. 1972; Smith & Robbins 1994) traversed by three species: pronghorn, bison, and elk (Table 1). A conservative estimate of the frequency of routes truncated indicates that many have already been lost: pronghorn, 78% ($n = 11$); bison, 100% ($n = 14$); and elk, 58% ($n = 36$).

Discussion

Bottlenecks: a Link between the Holocene and Modern Threats

Effective conservation involves obvious complexities and approaches that vary from science and planning to policy and site-specific measures. It is this last category, however, that may be most relevant for achieving conservation of LDMs. Despite the loss of many spectacular treks (Table 1), the longest (caribou excluded) and perhaps most jeopardized in the Western Hemisphere occur in the GYE. Although causes vary for the loss of routes by migratory bison, elk, and pronghorn, four stand out: (1) little tolerance for bison outside protected areas, (2) concentrations of elk on 23 winter feeding grounds in Wyoming, (3) a 20% increase in the human population in the last decade to (currently) more than 370,000, and (4) associated loss of habitat, especially areas crucial to approximately 100,000 wintering ungulates in the southern part of this ecosystem. This last point is central if extreme and highly fragile LDMs are to be retained, especially as the effectiveness of conservation planning shifts from general paradigms to site-specific implementation (Groves et al. 2002; Sanderson et al. 2002*a*).

At the southern terminus of migration routes for pronghorn and mule deer from the GYE in southwestern Wyoming (Fig. 3), about 8500 energy-extraction sites exist on public lands, with up to 10,000–15,000 more forecast during the next decade. The potential to seriously alter winter habitats and subsequently sever migration is genuine. For pronghorns, the extreme LDM that connects the Upper Green River Basin to Grand Teton National Park faces additional challenges (Sawyer & Lindzey 2000) because it winds through at least four narrow corridors (A-D in Fig. 3), beginning with a 0.8-km constriction at an elevation of 2226 m.

This first bottleneck, officially known as Trapper's Point (A in Fig. 3), has existed for 5800–6800 years and is known from three mid-Holocene early Archaic procurement sites. Like today, it was used in the past by pregnant females during spring migration, an inference based on the presence of fetal bones of a size similar to those of pregnant pronghorn during late gestation (Miller & Saunders 2000). Toward the north, a second bottleneck (B) occurs along a 5-km-long sagebrush gap between floodplain and forest that narrows to a strip only 100–400 m wide. The additional two bottlenecks (Fig. 3) are C, a high-elevation hydrographic divide at 2774 m that is often filled with deep snow and distinguishes the Upper Green River Basin from the Gros Ventre Mountains, and D, 30–40 km farther west of C, a 100- to 200-m constriction between sandstone cliffs, road, and the Gros Ventre River.

That any LDM endures in this system is remarkable given increasing impediments to pronghorn treks at lower elevation that include at least 105 fences (Sawyer & Lindzey 2000; J.B., unpublished data), highways, housing subdivisions, and the proliferation of petroleum development in winter habitats. Critically, however, confidence in the existence of future migrations by both pronghorn and mule deer at the scale of past migrations is tenuous. Although much of the wintering areas and migration bottlenecks involve federal land in the Upper Green River Basin (Fig. 3), habitat protection is no longer assured because of possible incompatibilities with U.S. energy policies. Federal permits to drill are being fast-tracked under Presidential Order 13212, which expedites the review and approval of proposals to facilitate the rapid permitting of energy-related projects in the western United States (Berger 2003). Unlike the plethora of Alaskan studies designed to understand possible petroleum-related disruption to migratory caribou (Berger et al. 2001), no peer-reviewed scientific literature exists to assess possible energy-related effects on migration in the GYE.

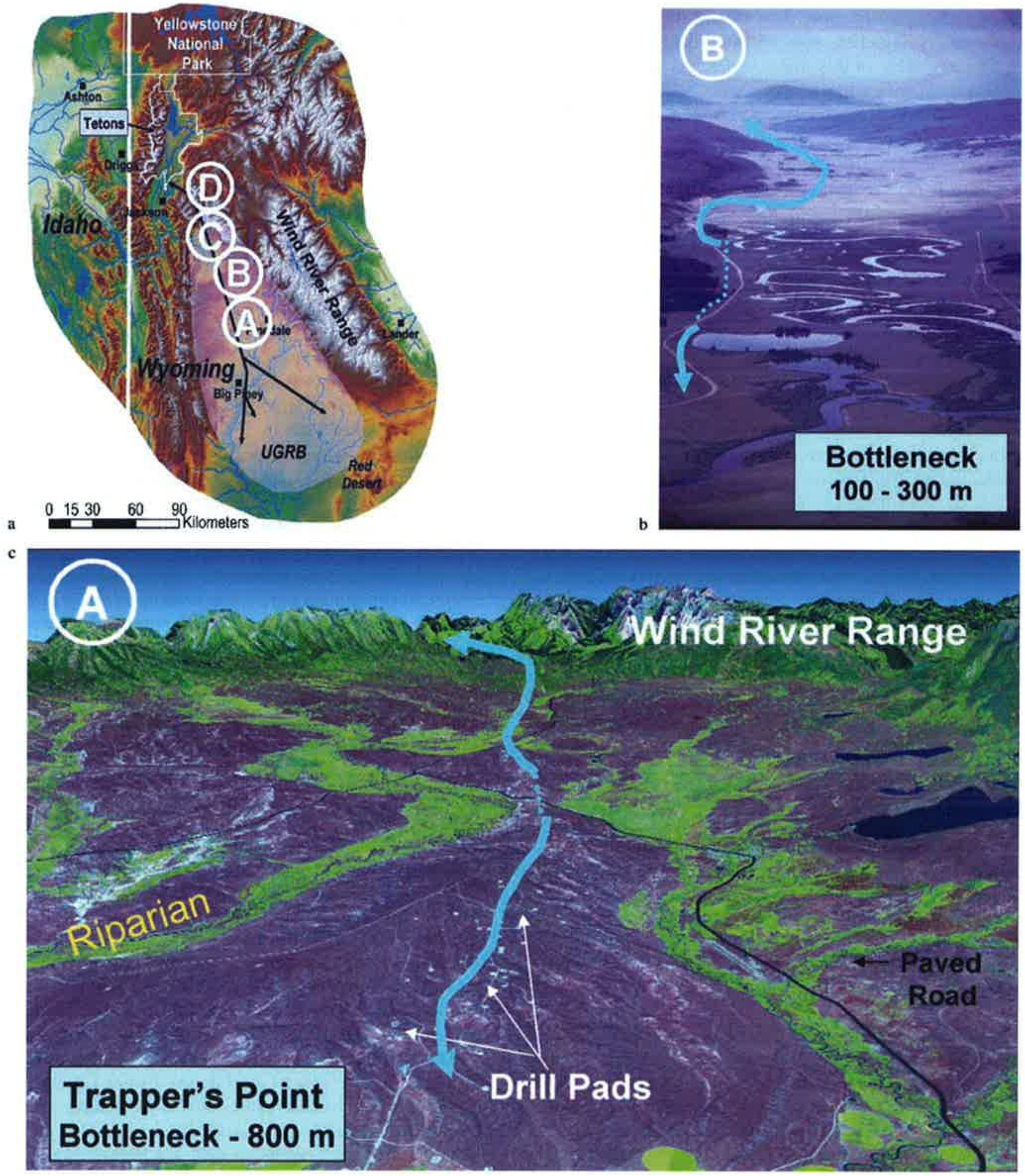

Figure 3. Location of pronghorn migration route in western Wyoming with placement of bottlenecks A to D (described in the text) as indicated in map and enhanced images of A and B (courtesy of Sky Truth and J. Catton, respectively). Solid lines reflect migration routes, and dotted lines are narrow pathways with maximal restriction (e.g., bottleneck) (UGRB, Upper Green River Basin).

Conclusions and a Simple Action Plan

Although American scientists, conservation advocates, private industry, and elected officials seemingly share in the goal of increasing domestic security, efforts to do so must involve serious attempts to develop alternate sources of energy while not sacrificing national or international biological treasures. Despite an association between energy consumption and loss of biodiversity (Ehrlich 1994), the protection of increasingly rare ecological events that include LDMs is possible (Brussard 1991).

Conservation efforts at the southern terminus of the GYE extend back to 1898, and, although largely ignored, have variously called for establishment of nationally designated parks, monuments, and landscapes (Dunham 1898; Wyoming Outdoor Council 2002). A more modest plan to conserve what few truly stunning LDMs remain between central Canada and Tierra del Fuego is to enhance protection for highly sensitive areas and bottlenecks. For the southern GYE these migration routes traverse existing U.S. public lands under the jurisdiction of the Bureau of Land Management (BLM) and U.S. Forest Service (USFS), and can receive real protection if a broader and more formally designated national wildlife migration corridor is instituted for all citizens. Precedents are numerous in the United States, including national scenic highways, historic trails, and rivers.

In this particular instance, details for a statutory migration corridor would need to be resolved. The BLM has the capacity to formally protect habitats by declaring them "areas of critical environmental concern" (ACEC), an idea once proposed between two reserves in the northern Great Basin Desert (Uselman 1998), and not unlike that proposed for connecting elephant refuges through communal lands in Zimbabwe (Osborn & Parker 2003). For the Upper Green River Basin, however, the designating of a formally protected corridor, rather than an ACEC, would represent a landmark victory nationally and internationally because not only would it offer greater protection but it would bring an ecological process, long-distance migration, to the attention of the public. As such, this proposal could sustain a macroscale phenomenon not repeated in grandeur between Tierra del Fuego and central Canada.

The use of process-driven approaches to conserve small and large areas has been effective (Brussard 1991; Sanderson et al. 2002*a*): for example, not only are Monarch butterflies (*Danaus plexippus*) now protected in central Mexico (Brower 1995), but the Serengeti ecosystem is defined by its migratory wildebeest (McNaughton & Banyikawa 1995). Although past boundaries of the GYE were generally denoted by wide-ranging species such as brown bears (*Ursus arctos*) (Craighead 1979; Noss et al. 2002), this species-centric approach may include an error of omission because the extreme LDMs of this region were not previously known. But whether the protection of critical corridors can be achieved by use of species or fleeting ecological processes (Sanderson et al. 2002*b*) is less important than achieving actions on the ground that will effectively result in protecting the remnant and narrow corridors currently used by migrating Upper Green River Basin ungulates. Although theory will help us understand more about the dynamics of connectivity in other systems, enough is known about the concordance between the pronghorn's use of corridors during the mid-Holocene and today to suggest that protective action should not be delayed. Otherwise, we will squander a biological legacy that may be enjoyed by our future descendants.

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Literature Cited

Akenson, J. J., and H. A. Akenson. 1994. Bighorn sheep movements and summer lamb mortality in central Idaho. Symposium of Northern Wild Sheep and Goat Council **8**:14–27.

Anderson, C. C. 1958. The elk of Jackson Hole: a review of Jackson elk studies. Bulletin 10. Wyoming Game and Fish Commission, Cheyenne.

Baker, R. J. 1978. The evolutionary ecology of animal migration. Hoddes and Sloughton, Seven Oaks, United Kingdom.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs **114**.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs **135**.

Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology **12**:1241–1252.

Berger, J. 2003. Is it acceptable to let a species go extinct in a national park? Conservation Biology **17**:1451–1454.

Berger, J., A. Hoylman, and W. A. Weber. 2001. Perturbation in vast ecosystems in the absence of adequate science: Alaska's Arctic Refuge. Conservation Biology **15**:539–542.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1996. Sexual segregation in black-tailed deer: effects of scale. Journal of Wildlife Management. **60**:10–17.

Bright, J. L., and C. Van Riper III. 2000. Pronghorn home ranges, habitat selection, and distribution around water sources in Northern Arizona. Technical report series USGSFRESC/COPL/2000 18. U. S. Geological Service, Denver.

Brower, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly in North America: 1857–1995. Journal of Lepidopteran Society **49**:304–385.

Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management **56**:246-253.
Brussard, P. F. 1991. The role of ecology in biological conservation. Ecological Applications **1**:6-12.
Cain, S. L., T. J. Roffe, J. Berger, and C. Cunningham. 2001. Reproduction and demography of brucellosis-infected bison in the southern Greater Yellowstone Ecosystem. Annual progress report. National Park Service, Moose, Wyoming.
Carrel, W. K., R. A. Ocknefels, and R. E. Schweinsburg. 1999. An evaluation of annual migration patterns of the Paunsaugunt mule deer herd between Utah and Arizona. Technical report 29. Arizona Game Fish, Phoenix.
Child, G., and J. D. Le Riche. 1967. Recent springbok treks (mass movements) in southwestern Botswana. Mammalia **33**:499-504.
Clark, T. W., A. P. Curlee, S. C. Minta, and P. M. Kareiva. 1999. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut.
Craighead, F. J. 1979. Track of the grizzly, Sierra Club Books, San Francisco.
Craighead, J. J., G. Atwell, and B. O'Gara. 1972. Elk migrations in and near Yellowstone National Park. Wildlife Monographs **29**.
Cumming, H. G., and D. B. Beange. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. Journal of Wildlife Management **51**:69-79.
Dalke, P. D., R. D. Beeman, F. J. Kindel, R. J. Robel, and T. R. Williams. 1965. Seasonal movements of elk in the Selway River Drainage. Journal of Wildlife Management **29**:333-338.
Darby, W. R., and W. O. Pruitt Jr. 1984. Habitat use, movements, and grouping behaviour of Woodland caribou (*Rangifer tarandus caribou*) in southeastern Manitoba. Canadian Field Naturalist **98**:184-190.
Deblinger, R. D. 1980. Ecology and behavior of pronghorn in the Red Desert, Wyoming with reference to energy development. Ph. D. dissertation. Colorado State University, Ft. Collins.
Diaz, N. I., and J. Smith-Fluek. 2000. The Patagonian huemal: a mysterious deer on the brink of extinction. Literature of Latin America, Buenos Aires.
Downer, C. C. 1996. The mountain tapir, endangered 'flagship' of the high Andes. Oryx **30**:45-58.
Downer, C. C. 1997. Status and action plan for the mountain tapir (*Tapirus pinchaque*). Pages 100-122 in D. M. Brooks, R. E. Bodmer, and S. M. Matola, editors. Tapirs: status survey and conservation action plan. World Conservation Union, Morges, Switzerland.
Dunham, F. 1898. A winter game reserve. Recreation **9**:271-272.
Edmonds, E. J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. Canadian Journal of Zoology **66**:817-826.
Ehrlich, P. R. 1994. Energy use and biodiversity loss. Philosophical Transactions of the Royal Society of London Series B **344**:99-104.
Eisenberg, J. F. 1981. The mammalian radiations. University of Chicago Press, Chicago.
Eldridge, W. D., M. MacNamara, and N. Pacheco. 1987. Activity patterns and habitat utilization of pudus (*Pudu pudu*) in south central Chile. Pages 352-370 in C. M. Wemmer, editor. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C.
Fancy, S. G., L. F. Pank, K. R. Whitten, and W. L. Regelin. 1988. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology **67**:644-650.
Ferguson, M. A. D., and F. Messier. 2000. Mass emigration of Arctic tundra caribou from a traditional wintering range: population dynamics and physical condition. Journal of Wildlife Management **64**:168-178.
Forbes, G. J., and J. B. Theberge. 1995. Influences of a migratory deer herd on wolf movements and mortality in and near Algonquin Park, Ontario. Pages 303-314 in L. H. Carbyn, S. H. Fritts, and D. R. Seip. Ecology and conservation of wolves in a changing world. Circumpolar Polar Press, Edmonton, Alberta, Canada.
Franklin, W. L. 1982. Biology, ecology, and relationship to man of the South American camelids. Pages 457-490 in M. A. Mares and H. H. Genoways, editors. Mammalian biology in South America. Special publication. Pymatuning Lab, University of Pittsburgh, Pennsylvania.
Fryxell, J. M., and A. R. E. Sinclair. 1988*a*. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution **3**:237-241.
Fryxell, J. M., and A. R. E. Sinclair. 1988*b*. Seasonal migration by white-eared kob in relation to resources. African Journal of Ecology **26**:17-31.
Fuller, T. K., and L. B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management **45**:197-213.
Garrot, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Allredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management. **51**:634-643.
Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs **84**.
Gasaway W. C., et al. 1996. Persistent low densities of plain's ungulates in Etosha National Park, Namibia: testing the food regulation hypothesis. Canadian Journal of Zoology **84**:1556-1572.
Gittleman, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. The American Naturalist **127**:744-771.
Gompper, M. E., and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia **87**:343-348.
Gray, D. R. 1979. Movements and behavior of tagged muskoxen (*Ovibos moschatus*) on Bathurst Island, Northwest Territories, Canada. Musk-Ox **25**:29-46.
Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: putting conservation science into practice. BioScience **52**:499-512.
Gruel, G. E., and N. J. Papez. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Management **27**:414-422.
Hamlin, K. L., and Mackie, R. J. 1989. Mule deer: population ecology in a fluctuating environment. Job completion report. Federal aid W-120-R. Montana Fish, Wildlife, and Parks, Helena.
Hansen, C. G. 1965. Management units and bighorn sheep herds on the Desert Game Range, Nevada. Desert Bighorn Council Transactions. **9**:11-14.
Haugen T. M., and L. B. Keith. 1981. Dynamics of moose populations in northeastern Alberta. Journal of Wildlife Management **45**:573-597.
Hofer, H., and M. East. 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. Pages 332-363 in A. R. E. Sinclair and P. Arcese, editors. Seregenti II. University of Chicago Press, Chicago.
Hoskinson, R. L., and J. R. Tester. 1980. Migration behavior of pronghorn in southeastern Idaho. Journal of Wildlife Management **44**:132-144.
Houston, D. B., E. G. Schreiner, B. B. Moorhead, and K. A. Krueger. 1990. Elk in Olympic National Park: will they persist over time? Natural Areas Journal **10**:6-11.
Johnson, R. L. 1980. Mountain goats and mountain sheep of Washington. Biological Bulletin (Washington) **18**:1-196.
Joubert, E. 1972. The social organization and associated behaviour in the Hartmann zebra, *Equus zebra hartmannae*. Madoqua **6**:17-56.
Kahurrananga, J., and F. Silkiluwasha. 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania in 1972 and recent trends. African Journal of Ecology **35**:179-185.
Knight, R. R. 1970. The Sun River elk herd. Wildlife Monographs **23**.
Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1989. Distribution and movements of female mule deer in the Rocky Mountain foothills. Journal of Wildlife Management **53**:871-877.
LeResche, R. E. 1974. Moose migration in North America. Naturaliste Canada **101**:393-415.

Leslie, D. M., and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildlife Monographs **66**.

Loft, E. R., J. W. Menke, and T. S. Burton. 1984. Seasonal movements and summer habitats of female black-tailed deer. Journal of Wildlife Management **48**:1317–1325.

Mahoney, S. P., and J. A. Schaefer, 2002. Hydroelectric development and the disruption of migration in caribou. Biological Conservation **107**:147–153.

Maier, T. J. 2002. Long-distance movements by female white-footed mice, *Peromyscus leucopus*, in extensive mixed wood forest. Canadian Field Naturalist **116**:108–111.

Mauer, F. J. 1998. Moose migration: northeast Alaska to western Yukon Territory, Canada. Alces **34**:75–81.

McCorquodale, S. M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management **63**:861–871.

McCullough, D. R. 1985. Long range movements of large terrestrial mammals. Contributions to Marine Science **27**:444–465.

McNaughton, S., and F. F. Banyikawa. 1995. Plant communities and herbivory. Pages 49–70 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago.

McQuivey, R. P. 1976. The status and trend of desert bighorn sheep in Nevada: McCullough Mountains. Federal aid, job report. Nevada Fish and Game, Reno.

Meagher, M. 1973. The bison of Yellowstone National Park. National Park Fauna Series **1**:1–161.

Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. Journal of Mammalogy **70**:670–675.

Merkt, J. R. 1987. Reproductive seasonaility and grouping patterns of the North Andean deer or Taruca (*Hippocamelus antisensis*) in southern Peru. Pages 388–401 in C. M. Wemmer, editor. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C.

Miller, M. E., and P. H. Saunders. 2000. The Trapper's Point site (48SU1006): early Archaic adaptations and pronghorn procurement in the Upper Green River Basin, Wyoming. Plain's Anthropologist **45**:39–52.

Milner-Gulland, E. J., M. V. Kholodova, A. Bekenov, O. M. Bukreeva, I. A. Grachev, L. Amgalan, and A. A. Lushchekina. 2001. Dramatic decline in saiga antelope populations. Oryx **35**:340–345.

Mitchell, G. J. 1980. The pronghorn antelope in Alberta. Alberta Department of Energy and Natural Resources, Edmonton.

Morgantini, L. E., and R. J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus*, in Banff National Park, Alberta. Canadian Field Naturalist **102**:12–19.

Murray, M. G. 1995. Specific nutrient requirements and migration of wildebeest. Pages 31–56 in A. R. E. Sinclair, and P. Arcese, editors. Seregenti II. University of Chicago Press, Chicago.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs **77**.

Newmark, W. D. 1987. Mammalian extinctions in western North American parks: a land-bridge island perspective. Nature **325**:430–432.

Newmark, W. D. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology **9**:512–526.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: trade-offs associated with migration. Journal of Mammalogy **78**:483–504.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology **16**:895–908.

Ockenfels, R. A., C. L. Alexander, C. Ticer, and W. K. Carrel. 1994. Home ranges, movement patterns, and habitat selection of pronghorn in central Arizona. Technical report 13. Arizona Game Fish, Phoenix.

Ortega I. M., and W. L. Franklin. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural **68**:489–500.

Osborn, F. V., and G. E. Parker. 2003. Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. African Journal of Ecology **41**: 68–74.

Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns for mountain lions: implications for social regulation and conservation. Journal of Mammalogy **80**: 986–992.

Pilliod, D. S., C. R. Peterson, and P. I. Ritson. 2002. Season migration of Columbian spotted frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. Canadian Journal of Zoology **80**:1849–1860.

Rankin, M. A., editor. 1985. Migration: mechanisms and adaptive significance. Contributions to Marine Science **27**:1–868.

Reynolds, P. E. 1998. Dynamics and range expansion of a re-established muskoxen population. Journal of Wildlife Management **62**:734–744.

Roe, F. G. 1970. The North American buffalo, University of Toronto Press, Toronto.

Rudd, W. J., A. L. Ward, and L. L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? Wildlife Society Bulletin **11**:328–331.

Sandgren, F., and P. Y. Sweanor, 1998. Migration distance of moose populations in relation to river drainage length. Alces **24**:112–117.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002*a*. The human footprint and the last of the wild. BioScience **52**:891–904.

Sanderson, E. W., K. H. Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002*b*. A conceptual model for conservation planning based on landscape species requirements. Landscape and Urban Planning **58**:41–56.

Sawyer, H., and F. Lindzey. 1999. Sublette Mule deer study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie.

Sawyer, H., and F. Lindzey. 2000. Jackson Hole pronghorn study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie.

Sawyer, H., F. Lindzey, D. McWhirter, and K. Andrews. 2002. Potential effects of oil and gas development on mule deer and pronghorn populations in western Wyoming. Transactions of the North American Wildlife and Natural Resource Conference **67**:350–365.

Schaller, G. B. 1998. Wildlife of the Tibetan steppe. University of Chicago Press, Chicago.

Schoen, J. W., and M. D. Kirchhoff. 1985. Seasonal distribution and home range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. Journal of Wildlife Management. **49**:96–103.

Schullery, P., and L. Whittlesey. 1995. Summary of the documentary record of wolves and other wildlife species in the Yellowstone National Park area prior to 1882. Pages 63–76 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.

Semmens, W. J. 1996. Seasonal movements and habitat use of the Highland/Pioneer Mountains bighorn sheep herd of southwest Montana. Symposium of Northern Wild Sheep and Goat Council **10**:35–44.

Simberloff, D. J., A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology **6**:493–504.

Sinclair, A. R. E., 1983. The function of distance movements in vertebrates. Pages 240–258 in I. R. Swingland and P. J. Greenwood, editors. The ecology of animal movements. Oxford University Press, Oxford, United Kingdom.

Sinclair, A. R. E., and P. Arcese. 1995. Serengeti in the context of worldwide conservation efforts. Pages 31–46 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago Press, Chicago.

Smith, B. L., and R. L. Robbins. 1994. Migrations and management of the Jackson Elk herd. Technical report series. Research Bulletin **199**. United States Department of Interior, Washington, D.C.

Smith, G. W., L. C. Stoddardt, and F. F. Knowlton. 2002. Long-distance movements of black-tailed jackrabbits. Journal of Wildlife Management **66**:463–469.

Sukumar, R. 1989. The Asian elephant: ecology and management. Cambridge University Press, Cambridge, United Kingdom.

Tchamba, M. N. 1993. Number and migration patterns of savanna elephants (*Loxodonta africana africana*) in Northern Cameroon. Pachyderm **16**:66-71.

Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology **65**:1828-1834.

Thompson, M. E., J. R. Gilbert, G. J. Matula, and K. I. Morris. 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. Alces **31**:233-245.

Thoules, C., and A. Dyer. 1992. Radio-tracking of elephants in Laikipia District, Kenya. Pachyderm **15**:34-39.

Uselman, S. 1998. ONDA proposes Pronghorn ACEC. Oregon Natural Desert Association **11**:1, 3.

Van Ballenberghe, V. 1977. Migratory behavior of moose in southcentral Alaska. International Congress of Game Biologists **13**:103-109.

Van Deelen, T. R., H. Campa III, M. Hamady, and J. B. Hausfler. 1998. Migration and seasonal range dynamics of deer using adjacent deer yards in northern Michigan. Journal of Wildlife Management **62**:205-213.

Van Vuren, D., and M. P. Bray 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 506-511.

Verlinden, A., and I. K. N. Gavor. 1998. Satellite tracking of elephants in northern Botswana. African Journal of Ecology **36**:105-116.

Waithaka, J. M. 1994. The ecological role of elephants in restructuring habitats. Ph.D. dissertation. Kenyatta University, Nairobi.

Walton, L. R., H. D. Cluff, P. C. Paquet, and M. A. Ramsey. 2001. Movement patterns of barren-ground wolves in the central Canadian Arctic. Journal of Mammalogy **82**:867-876.

Wilcove, D. S. 1999. The condor's shadow. W. H. Freeman, New York.

Williamson, D. 1997. The future of antelope migrations in a changing physical and socio-economic environment. Pages 59-68 in Proceedings of a convention on migratory species. United Nations Environmental Programme, Bonn.

Williamson, D., J. Williamson, and K. T. Ngwamotsoko. 1988. Wildebeest migration in the Kalahari. African Journal of Ecology **26**:269-280.

Wood, K. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Monograph. Montana Department of Fish, Wildlife, and Parks, Helena.

Wyoming Outdoor Council. 2000. Frontline report: saving the Red Desert: 50,000 antelope can't be wrong. Wyoming Outdoor Council, Lander, Wyoming. Available from www.wyomigoutdoorcouncil.org (accessed September 2002).

Zallunardo, R. A. 1965. The seasonal distribution of a migratory mule deer herd. Journal of Wildlife Management **29**:345-351.

Comment Letter I9

Appendix 1. Summary of estimated round-trip migration by species, population, and site.

Species	*Scientific name*	*Location*	*Mean (km)*[a]	*Longest (km)*	*Reference*
Cougar	*Felis concolor*	Sierra Nevada, CA, USA	60		Pierec et al. 1999; V. Bleich, personal communication
Coyote	*Canis latrans*	Jackson Hole, WY, USA	70	80	K. Berger, unpublished data
Wolf	*Canis lupus*	Brooks Range, AK USA	370		Ballard et al. 1997
		Bathhurst region, NWT, Canada	743		Walton et al. 2001
Spotted hyena	*Crocuta crocuta*	Serengeti, Tanzania	120	160	Hofer & East 1995
Elk	*Cervus elaphus*	Banff, AB, Canada	73	138	Mogantini & Hudson 1988
		Yellowstone, WY, USA	70	220	Craighead et al. 1972
		Olympic, WA, USA	60		Houston et al. 1990
		Selway Drainage, ID, USA	<64		Dalke et al. 1965
		Sun River, MT, USA	96		Knight 1970
		Absaroka Divide, WY, USA	90		Rudd et al. 1983
		Jackson Hole, WY, USA	200	220	Smith & Robbins 1994
White-tailed deer	*Odocoileus virginianus*	Algonquin, ON, Canada	60		Forbes & Theberge 1995
		Cheery Creek, MT, USA	14	26	Wood et al. 1989
		Hiawatha Forest, MN, USA	10		Van Deelen et al. 1998
		Superior Forest, MN, USA	34		Nelson & Mech 1981
Mule deer	*Odocoileus hemionus*	Green River Basin, WY, USA	168	288	Sawyer & Lindzey 1999; Sawyer et al. 2002
		Salmon-Trinity Alps, CA, USA	42	70	Loft et al. 1984
		Cheery Creek, MT, USA	11		Wood et al. 1989
		Missouri River Breaks, MT, USA	12		Hamlin & Mackie 1989
		Klickkitat Basin, WA, USA	56		McCorquodale 1999
		Great Basin, NV, USA	141	280	Gruel & Papez 1963
		Silver Lake, OR, USA	60	256	Zallunardo 1965
		Piceance Basin, CO, USA	65	220	Garrot et al. 1987
		Lory State Park, CO, USA	58		Kufeld et al. 1989
		Transverse Ranges, ID, USA	52		Brown 1992
		Paunsaugunt Plateau, UT, USA	102	144	Carrel et al. 1999
		Kaibab Plateau, AZ, USA	45	116	Carrel et al. 1999
		Round Valley, CA, USA	134	192	Pierec et al.1999; V. Bleich, personal communication
		Admiralty Isle, AK, USA	15	90	Schoen & Kirchhoff 1985
		San Bernadino Mountains, CA, USA	23		Nicholson et al. 1997
Moose	*Alces alces*	Old Crow, YT, Canada	246	392	Mauer 1998
		Lower Koyukuk, AK, USA	84	136	Mauer 1998
		Upper Susitna, AK, USA	96	186	Ballard et al. 1991
		White Mountains, AK, USA	130	204	Mauer 1998
		Nelchina Basin, AK, USA	70	220	Van Ballenberghe 1977
		North Slope, YT, Canada	194	276	Mauer 1998
		Tanana Flats, AK, USA	120	280	Gasaway et al. 1983
		northeast Alberta, Canada	40		Haugen & Keith 1981
		Sorsele, Sweden	220	310	Sandgren & Sweanor 1998
		Slussfors, south Sweden	46		Sandgren & Sweanor 1998[b]
		Hornefors, Sweden	41		Sandgren & Sweanor 1998
		Klitten, Sweden	42		Sandgren & Sweanor 1998
		Tennanget, Sweden	68		Sandgren & Sweanor 1998
		Furudal, Sweden	156		Sandgren & Sweanor 1998
		Stottingfjallet, Sweden	118		Sandgren & Sweanor 1998
		Trehorningsjo, Sweden	149		Sandgren & Sweanor 1998
		Slussfors, north Sweden	144		Sandgren & Sweanor 1998
		Nordheden, Sweden	196		Sandgren & Sweanor 1998
		Rosvik, Sweden	66		Sandgren & Sweanor 1998
		Mooseleuk and St. Croix, ME, USA	14		Thompson et al. 1995
		northwest Minnesota, MN, USA	20		LeResche 1974
		northeast Minnesota, MN, USA	12		LeResche 1974
		Gravelly Mountains, MT, USA	14		LeResche 1974
		Teton, WY, USA	61	114	J. Berger, unpublished data
Musk ox	*Ovibos moschatus*	Bathurst Isle, NT, Canada	0		Gray 1979
		Arctic Refuge, AK, USA	0		Reynolds 1998
Caribou[c] (barren-ground)	*Rangifer tarandus*	Arctic Refuge, AK, USA	4355	5055	Fancy et al. 1988
		Central Arctic, AK, USA	3031		Fancy et al. 1988
		Baffin Isle, Canada	800		Ferguson & Messier 2000
Caribou (woodland)	*Rangifer tarandus*	Grand Cache, AB, Canada	136	300	Edmonds 1988
		Birch Mtn, Alberta, Canada	56	142	Fuller & Keith 1981
		Lake Nipigon, ON, Canada	92	160	Cumming & Beange 1987
		Aikens Lake, Manitoba, Canada	0		Darby & Pruitt 1984
Bison	*Bison bison*	Yellowstone, WY, USA	44		Meagher 1973, 1989
		Grand Teton, WY, USA	70	75	Cain et al. 2001
		Henry Mountains, UT, USA	50		Van Vuren & Bray 1986

continued

Appendix 1. (continued)

Species	Scientific name	Location	Mean (km)[a]	Longest (km)	Reference
Bighorn	*Ovis canadensis*	McCullough Mountains, NV, USA	60	64	McQuivey 1976
		River Mountains, NV, USA	7		Leslie & Douglas 1979
		Highland Mountains, MT, USA	19		Semmens 1996
		Salmon River Mountains, ID, USA	74	75	Akenson & Aksenson 1994
		Sheep Range, NV, USA	32		Hansen 1965
Mountain goat	*Oreamos americanus*	Mount Baker, Washington	12		Johnson 1980
		Barometer Mountain, WA, USA	29	29	Johnson 1980
Pronghorn	*Antilocapra americana*	Upper Snake River Plain, ID, USA	89		Hoskinson & Tester 1980
		Wupatki, AZ, USA	30		Bright & Van Riper 2000
		Cordes Junction, AZ, USA	30	80	Ockenfels et al. 1994
		Mingus Mountain, AZ, USA	26	40	Ockenfels et al 1994
		Saskatchewan, Canada	220		Mitchell 1980
		Red Desert, WY, USA	128	164	Deblinger 1980
		Tetons, WY, USA	434	548	Sawyer & Lindzey 2000; Sawyer et al 2002
Huemal	*Hippocamelus bisulcus*	Patagonia, Argentina	6		Diaz & Smith-Fluek 2000
Pudu	*Pudu puda*	Islote Rupanco, Chile	0		Eldridge et al 1987
Taruca	*Hippocamelus antisenis*	La Roya, Peru	0		Merkt 1987
Guanaco	*Lama guanicoe*	Torres del Paine, Argentina	0		Franklin 1982
		Patagonia, Chile	24		Ortega & Franklin 1995
Vicuna	*Vicugna vicugna*	Pampa Galeras, Peru	0		Franklin 1982
Mountain tapir	*Tapirus pinchaque*	Sangay, Ecuador	9	10	Downer 1996, 1997
Mongolian gazelle	*Procapra gutturrosa*	Dornab, Mongolia	500		J Ginsberg, personal communication
White-eared kob	*Kobus kob*	Sudd Region, Sudan	700		Fryxell & Sinclair 1988*b*
Wildebeest	*Connochaetes taurinus*	Serengeti, Tanzania	600–800		Murray 1995 & Web sites[d]
		Kalahari, Botswana	550		Williamson et al 1988
		Tarangire, Tanzania	120		Kahurananga & Silkiluwasha 1997
Springbok	*Antidorcas marsupialis*	Karoo, South Africa	360, one way		Child & LeRiche 1967
Chiru	*Pantholops hodgsoni*	Chang Tang, China	600		Schaller 1998
Mountain zebra	*Equus zebra*	Namib Desert, Namibia	240		Joubert 1972
Plain's zebra	*Equus burchelli*	Tarangire, Tanzania	110		Kahurananga & Silkiluwasha 1997
Elephant	*Loxodonta africana*	northern Botswana	200		Verlinden & Gavor 1998
		Laikipia District, Kenya	200		Thoules & Dyer 1992
		Kalamalove Park, Cameroon	240		Tchamba 1993
		Waza Park, Cameroon	200		Tchamba 1993
Giraffe	*Giraffa camelopadia*	northern Serengeti	80		P. Arcese, personal communication
Black-tailed jackrabbit	*Lepus californicus*	Curlew Valley, UT, USA	12		Smith et al 2002

[a]*Mean is the estimated round-trip distance (km) for migratory segment; otherwise, all data for that population are averaged.*
[b]*Based on means of four longest migration distances.*
[c]*Estimates are total annual movements (based on satellite data), but those in text reflect means between average annual home ranges (seasonal) in brochures of the U.S. Fish and Wildlife Service (Arctic National Wildlife Refuge)*
[d]*Web site: www.africaencounters.com/tanzania/serengel.htm; www.awf.org/wildlives/4547*

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EDMUND G. BROWN JR, Governor
JOHN McCAMMAN, Director

March 7, 2011

Mr. Dan Lyster
Mono County Economic Development and Special Projects
P.O. Box 2415
Mammoth Lakes, Ca 93546

Subject: Mammoth Pacific (MP-1) Replacement Project (State Clearinghouse Number: 2011022020)

Dear Mr. Lyster:

The Department of Fish and Game, hereinafter referred to as Department has reviewed the Notice of Preparation (NOP) of the Draft Environmental Impact Report (DEIR) for the above mentioned project relative to impacts to biological resources. The Department appreciates this opportunity to comment on the above-referenced project, relative to impacts to biological resources.

The Department is a Trustee Agency pursuant to the California Environmental Quality Act (CEQA). A Trustee Agency has jurisdiction over certain resources held in trust for the people of California. Trustee agencies are generally required to be notified of CEQA documents relevant to their jurisdiction, whether or not these agencies have actual permitting authority or approval power over aspects of the underlying project (CEQA Guidelines, Section 15386). As the trustee agency for fish and wildlife resources, the Department provides requisite biological expertise to review and comment upon CEQA documents, and makes recommendations regarding those resources held in trust for the people of California.

The Department may also assume the role of Responsible Agency. A Responsible Agency is an agency other than the lead agency that has a legal responsibility for carrying out or approving a project. A Responsible Agency actively participates in the Lead Agency's CEQA process, reviews the Lead Agency's CEQA document and uses that document when making a decision on the project. The Responsible Agency must rely on the Lead Agency's environmental document to prepare and issue its own findings regarding the project (CEQA Guidelines, Sections 15096 and 15381). The Department most often becomes a responsible agency when a 1600 Streambed Alteration Agreement or a 2081(b) California Endangered Species Act Incidental Take Permit is needed for a project. The Department relies on the environmental document prepared by the Lead Agency to make a finding and decide whether or not to issue permit or agreement. It is important that the Lead

Agency's EIR considers the Department's responsible agency requirements. For example, CEQA requires the Department to include additional feasible alternatives or feasible mitigation measures within its powers that would substantially lessen or avoid any significant effect the project would have on the environment (CEQA Guidelines, section 15096 (g) (2). In rare cases, the Department may need to prepare additional CEQA analysis.

Pursuant to California Fish and Game Code section 711.4, the Department collects a filing fee for all projects subject to CEQA. These filing fees are collected to defray the costs of managing and protecting fish and wildlife resources including, but not limited to, consulting with public agencies, reviewing environmental documents, recommending mitigation measures, and developing monitoring programs. Project applicants need not pay a filing fee in cases where a project will have no effect on fish and wildlife, as determined by the Department, or where their project is statutorily or categorically exempt from CEQA.

Mammoth Pacific, LP, hereinafter referred to as MPLP, operates the existing geothermal development complex northeast of the junction of US Highway 395 and State Route 203, and located about 2.5 miles east of the town of Mammoth Lakes in Mono County, California. MPLP proposes to replace Mammoth Pacific I (MP-1) geothermal power plant with a more modern and efficient plant using advanced technology. The replacement plant will be called M-1. The existing MP-1 plant and the replacement M-1 plant would each be located on a 90-acre parcel of private land owned by MPLP. The replacement M-1 plant would be built approximately 500 feet northeast of the existing MP-1 plant. The new M-1 plant and associated structures and equipment would occupy a little more than 3 acres. The existing entrances to the MPLP geothermal complex would provide access to the new M-1 plant site. The existing MP-1 plant has a design capacity of 14 megawatts (MW). The M-1 replacement plant would have a design capacity of approximately 18MW. During the M-1 plant startup operations, the existing MP-1 plant would continue to operate for a period of time, after which MPLP would close and dismantle the old MP-1 plant, The transition period during which both MP-1 and M-1 operations would overlap may be up to a maximum of two years after the M-1 plant is commissioned. Thereafter, the MP-1 power plant facilities would be removed from the site; plant foundations and above ground pipeline would be removed; and a retention pond on the MP-1 site would be removed. The former MP-1 site would then be graded and the pad covered with gravel to provide an all weather surface for continuing MPLP operations on the site.

To enable Department staff to adequately review and comment on the proposed project, we recommend the following information be included in the DEIR, as applicable:

1. The project description should provide additional information about the proposed project. Will additional wells be drilled, and where would they would be located? Will the capacity of the new plant differ from

the existing facility? Will changes be made that could affect aquifer temperatures , pressures, and spring flows?

2. Explain how the proposed project comports with existing court orders and settlement agreements stemming form the development of the MP1 and PLES plants.

3. A complete assessment (direct, indirect, and cumulative impacts) of the flora and fauna within and adjacent to the project area, with particular emphasis upon identifying special status species including, but not limited to rare, threatened, and endangered species. This assessment should also address locally unique species and rare natural communities.

   a. A thorough assessment of potential impacts to the sage grouse (*Centrocercus urophasianus*) which is a Federal Candidate species and the Federal and State endangered Owens tui chub (*Siphateles bicolor snyderi*).

   b. A thorough site-specific study for mule deer (*Odocoileus hemionus* ssp. *hemionus*) conducted during the appropriate time of year (April 15-June15) by a qualified biologist. The purpose is to quantify the timing and amount of deer use.

   c. The DEIR should include survey methods, dates, and results; and should list all plant and animal species detected within the project study area. Special emphasis should be directed toward describing the status of rare, threatened, and endangered species in all areas potentially affected by the project. All necessary biological surveys should be conducted in advance of DEIR circulation, and should not be deferred.

   d. Rare, threatened, and endangered species to be addressed should include all those which meet the California Environmental Quality Act (CEQA) definition (see CEQA Guidelines, § 15380).

   e. Species of Special Concern status applies to animals generally not listed under the federal Endangered Species Act or the California Endangered Species Act, but which nonetheless are declining at a rate that could result in listing, or historically occurred in low numbers and known threats to their persistence currently exist. At a minimum, Species of Special Concern are considered to be "rare" under CEQA.

   f. A thorough assessment of rare plants and rare natural communities, following the Department's November 2009

Protocols for Surveying and Evaluating Impacts to Special Status Native Plant Populations and Natural Communities (Attachment 1).

g. A detailed vegetation map should be prepared, preferably overlaid on an aerial photograph. The map should be of sufficient resolution to depict the locations of the project site's major vegetation communities, and view project impacts relative to vegetation communities. The vegetation classification system used to name the polygons should be described.

h. A complete assessment of rare, threatened, and endangered invertebrate, fish, wildlife, reptile, and amphibian species should be presented in the DEIR. Seasonal variations in use of the project area should also be addressed. Focused species-specific surveys, conducted at the appropriate time of year and time of day when the species are active or otherwise identifiable, are required. Acceptable species-specific survey procedures should be developed in consultation with the Department and the U.S. Fish and Wildlife Service.

i. The Department's California Natural Diversity Data Base (CNDDB) in Sacramento should be searched to obtain current information on previously reported sensitive species and habitat, including Significant Natural Areas identified under Chapter 12 of the Fish and Game Code. In order to provide an adequate assessment of special-status species potentially occurring within the project vicinity, the search area for CNDDB occurrences should include all U.S.G.S 7.5-minute topographic quadrangles with project activities, and all adjoining 7.5-minute topographic quadrangles. The EIR should discuss how and when the CNDDB search was conducted, including the names of each quadrangle queried.

4. A thorough discussion of direct, indirect, and cumulative impacts expected to adversely affect biological resources, with specific measures to offset such impacts, should be included.

   a. The EIR should present clear thresholds of significance to be used by the Lead Agency in its determination of the significance of environmental effects. A threshold of significance is an identifiable quantitative, qualitative or performance level of a particular environmental effect.

b. CEQA Guidelines, § 15125(a), direct that knowledge of the regional setting is critical to an assessment of environmental impacts and that special emphasis should be placed on resources that are rare or unique to the region.

c. Impacts associated with initial project implementation as well as long-term operation and maintenance of a project should be addressed in the EIR.

d. In evaluating the significance of the environmental effect of a project, the Lead Agency should consider direct physical changes in the environment which may be caused by the project and reasonably foreseeable indirect physical changes in the environment which may be caused by the project. Expected impacts should be quantified (e.g., acres, linear feet, number of individuals taken, volume or rate of water extracted, etc. to the extent feasible).

e. Project impacts should be analyzed relative to their effects on off-site habitats. Specifically, this may include public lands, open space, downstream aquatic habitats, or any other natural habitat that could be affected by the project.

f. Impacts to and maintenance of wildlife corridor/movement areas and other key seasonal use areas should be fully evaluated and provided.

g. A discussion of impacts associated with increased lighting, noise, human activity, changes in drainage patterns, changes in water volume, velocity, quantity, and quality, soil erosion, and/or sedimentation in streams and water courses on or near the project site, with mitigation measures proposed to alleviate such impacts should be included. Special considerations applicable to linear projects include ground disturbance that may facilitate infestations by exotic and other invasive species over a great distance.

h. A cumulative effects analysis should be developed as described under CEQA Guidelines, § 15130. General and specific plans, as well as past, present, and anticipated future projects, should be analyzed relative to their impacts to similar plant communities and wildlife habitats.

5. A range of project alternatives should be analyzed to ensure that the full spectrum of alternatives to the proposed project are fully considered and

evaluated. Alternatives which avoid or otherwise minimize impacts to sensitive biological resources should be identified.

a. If the project will result in any impacts described under the Mandatory Findings of Significance (CEQA Guidelines, § 15065) the impacts must be analyzed in depth in the EIR, and the Lead Agency is required to make detailed findings on the feasibility of alternatives or mitigation measures to substantially lessen or avoid the significant effects on the environment. When mitigation measures or project changes are found to be feasible, the project should be changed to substantially lessen or avoid the significant effects.

6. Mitigation measures for adverse project-related impacts to special status species including, but not limited to rare, threatened and endangered species, sensitive plants, animals, and habitats should be thoroughly discussed. Mitigation measures should first emphasize avoidance and reduction of project impacts. For unavoidable impacts, the feasibility of on-site habitat restoration or enhancement should be discussed. If on-site mitigation is not feasible, off-site mitigation through habitat creation, enhancement, land acquisition and preservation in perpetuity should be addressed.

a. The Department generally does not support the use of relocation, salvage, and/or transplantation as mitigation for impacts to rare, threatened, or endangered species. Studies have shown that these efforts are experimental in nature and largely unsuccessful.

b. Areas reserved as mitigation for project impacts should be legally protected from future direct and indirect impacts. Potential issues to be considered include limitation of access, conservation easements, monitoring and management programs, water pollution, and fire.

c. Plans for restoration and revegetation should be prepared by persons with expertise in the eastern Sierra environment, and native plant revegetation techniques. Each plan should include, at a minimum: (a) the location of the mitigation site; (b) the plant species to be used, container sizes, and seeding rates; (c) a schematic depicting the mitigation area; (d) planting schedule; (e) a description of the irrigation methodology; (f) measures to control exotic vegetation on site; (g) specific success criteria; (h) a detailed monitoring program; (i) contingency measures should the success criteria not be met; and (j) identification of the party responsible for meeting the success criteria and providing for long-term conservation of the mitigation site.

7. Take of species of plants or animals listed as endangered or threatened under the California Endangered Species Act (CESA) is unlawful unless authorized by the Department. However, a CESA 2081(b) Incidental Take Permit may authorize incidental take during project construction or over the life of the project. The DEIR must state whether the project would result in incidental take of any CESA listed organisms. CESA Permits are issued to conserve, protect, enhance, and restore State-listed threatened or endangered species and their habitats. Early consultation is encouraged, as significant modification to a project and mitigation measures may be required in order to obtain a CESA Permit.

   The Department's issuance of a CESA Permit for a project that is subject to CEQA will require CEQA compliance actions by the Department as a responsible agency. The Department as a responsible agency under CEQA may consider the local jurisdiction's (lead agency) Negative Declaration or Environmental Impact Report for the project. The Department may issue a separate CEQA document for the issuance of a CESA Permit unless the project CEQA document addresses all project impacts to listed species and specifies a mitigation monitoring and reporting program that will meet the requirements of a CESA Permit.

   To expedite the CESA permitting process, the Department recommends that the DEIR addresses the following CESA Permit requirements:

   a. The impacts of the authorized take are minimized and fully mitigated;
   b. The measures required to minimize and fully mitigate the impacts of the authorized take and: (1) are roughly proportional in extent to the impact of the taking on the species; (2) maintain the applicant's objectives to the greatest extent possible, and (3) are capable of successful implementation;
   c. Adequate funding is provided to implement the required minimization and mitigation measures and to monitor compliance with and the effectiveness of the measures; and
   d. Issuance of the permit will not jeopardize the continued existence of a State-listed species.

8. The Department has responsibility for wetland and riparian habitats. It is the policy of the Department to strongly discourage development in wetlands or conversion of wetlands to uplands. We oppose any development or conversion which would result in a reduction of wetland

acreage or wetland habitat values, unless, at a minimum, project mitigation assures there will be "no net loss" of either wetland habitat values or acreage. The EIR should demonstrate that the project will not result in a net loss of wetland habitat values or acreage.

a. If the project site has the potential to support aquatic, riparian, or wetland habitat, a jurisdictional delineation of lakes, streams, and associated riparian habitats potentially affected by the project should be provided for agency and public review. This report should include a jurisdictional delineation that includes wetlands identification pursuant to the U. S. Fish and Wildlife Service wetland definition[1] as adopted by the Department[2]. Please note that some wetland and riparian habitats subject to the Department's authority may extend beyond the jurisdictional limits of the U.S. Army Corps of Engineers. The jurisdictional delineation should also include mapping of ephemeral, intermittent, and perennial stream courses potentially impacted by the project. In addition to federally protected wetlands, the Department considers impacts to wetlands (as defined by the Department) potentially significant.

b. The project may require a Lake or Streambed Alteration Agreement, pursuant to Section 1600 et seq. of the Fish and Game Code, with the applicant prior to the applicant's commencement of any activity that will substantially divert or obstruct the natural flow or substantially change the bed, channel, or bank (which may include associated riparian resources) of a river, stream or lake, or use material from a streambed. The Department's issuance of a Lake or Streambed Alteration Agreement for a project that is subject to CEQA will require CEQA compliance actions by the Department as a responsible agency. The Department as a responsible agency under CEQA may consider the local jurisdiction's (lead agency) Negative Declaration or Environmental Impact Report for the project. To minimize additional requirements by the Department pursuant to Section 1600 et seq. and/or under CEQA, the document should fully identify the potential impacts to the lake, stream or riparian resources and provide adequate avoidance,

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[1] Cowardin, Lewis M., et al. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service.

[2] California Fish and Game Commission Policies: Wetlands Resources Policy; Wetland Definition, Mitigation Strategies, and Habitat Value Assessment Strategy; Amended 1994

mitigation, monitoring and reporting commitments for issuance of the agreement.

Thank you for the opportunity to comment. Questions regarding this letter and further coordination on these issues should be directed to Mr. Steve Parmenter, Senior Biologist, at (760) 872-1123 or by email at spar@dfg.ca.gov.

Sincerely,

Original signed by Steve Parmenter for:

Brad Henderson
Habitat Conservation Supervisor

Attachment 1: Department's November 2009 *Protocols for Surveying and Evaluating Impacts to Special Status Native Plant Populations and Natural Communities.*

cc: Department of Fish and Game
Chron, Bishop
William Condon, Renewable Energy Program, CDFG
State Clearinghouse, Sacramento

Invited Article

Winter Habitat Selection of Mule Deer Before and During Development of a Natural Gas Field

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Abstract

*Increased levels of natural gas exploration, development, and production across the Intermountain West have created a variety of concerns for mule deer (*Odocoileus hemionus*) populations, including direct habitat loss to road and well-pad construction and indirect habitat losses that may occur if deer use declines near roads or well pads. We examined winter habitat selection patterns of adult female mule deer before and during the first 3 years of development in a natural gas field in western Wyoming. We used global positioning system (GPS) locations collected from a sample of adult female mule deer to model relative frequency or probability of use as a function of habitat variables. Model coefficients and predictive maps suggested mule deer were less likely to occupy areas in close proximity to well pads than those farther away. Changes in habitat selection appeared to be immediate (i.e., year 1 of development), and no evidence of well-pad acclimation occurred through the course of the study; rather, mule deer selected areas farther from well pads as development progressed. Lower predicted probabilities of use within 2.7 to 3.7 km of well pads suggested indirect habitat losses may be substantially larger than direct habitat losses. Additionally, some areas classified as high probability of use by mule deer before gas field development changed to areas of low use following development, and others originally classified as low probability of use were used more frequently as the field developed. If areas with high probability of use before development were those preferred by the deer, observed shifts in their distribution as development progressed were toward less-preferred and presumably less-suitable habitats.* (JOURNAL OF WILDLIFE MANAGEMENT 70(2):396–403; 2006)

Key words

generalized linear model (GLM), Global Positioning System (GPS), habitat selection, mule deer, natural gas development, negative binomial, Odocoileus hemionus, *resource selection probability function (RSPF), Wyoming.*

Natural gas development on public lands in Wyoming has steadily increased since 1984 (Bureau of Land Management 2002) and created much concern over potential impacts to wildlife. Public lands with high gas potential often coincide with regions of Wyoming that support large mule deer (*Odocoileus hemionus*) populations, such as the Green River Basin (Bureau of Land Management 2000*a*), Great Divide Basin (Bureau of Land Management 2000*b*), and Powder River Basin (Bureau of Land Management 2003). Impacts of natural gas development on mule deer may include the direct loss (i.e., surface disturbance) of habitat to well pad, access road, and pipeline construction. Additional indirect habitat losses may occur if increased human activity (e.g., traffic, noise) associated with infrastructure cause mule deer to be displaced or alter their habitat use patterns. Although it is relatively easy to quantify the direct habitat losses that result from conversion of native vegetation to infrastructure, it is much more difficult to document indirect habitat losses. Nonetheless, because indirect impacts can affect a substantially larger area than direct impacts, understanding them may be a key component to maintaining mule deer seasonal ranges and populations in regions with high levels of natural gas development. Accordingly, there is a need among land management and wildlife agencies to better understand how natural gas development can lead to indirect habitat loss to ensure informed land-use decisions are made, reasonable and effective mitigation measures identified, and appropriate monitoring programs implemented. Our objective was to determine whether natural gas development affected the habitat selection patterns and, thus, distribution of wintering mule deer in western Wyoming.

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Study Area

Beginning in 2000, the Bureau of Land Management (BLM) approved the construction of 700 producing well pads, 645 km of pipeline, and 444 km of roads to develop a natural gas field in the Pinedale Anticline Project Area (PAPA; Bureau of Land Management 2000*a*). The PAPA contains one of the largest and highest density (19 to 30 deer/km^2) mule deer winter ranges in Wyoming (S. Smith, Wyoming Game and Fish Department, Cheyenne, Wyo., USA, unpublished data). The PAPA is located in the upper Green River Basin of western Wyoming, approximately 5 km southwest of Pinedale. The PAPA consists primarily of federal lands (80%) and minerals administered by the BLM (83%). The state of Wyoming owns 5% (39 km^2) of the surface and another 15% (121 km^2) is private (Bureau of Land Management 2000*a*). The study area contains abundant deep gas reserves, supports a variety of agricultural uses, and provides winter range for 4,000 to 5,000 migratory mule deer that summer in portions of 4 different mountain ranges 80 to 200 km away (Sawyer and Lindzey 2001). Although the PAPA covers 799 km^2, most mule deer wintered in the northern one-third, an area locally known as the Mesa. The Mesa is 260 km^2 in size, bounded by the Green River on the west and the New Fork River on the north, south, and east, and vegetated primarily by Wyoming big sagebrush (*Artemisia tridentata*) and sagebrush–grassland communities. Elevation ranges from 2,070 to 2,400 m. Our study was restricted to the Mesa portion of the PAPA.

Methods

Capture

We captured adult ($\geq$1 year) female mule deer using helicopter net-gunning in the northern portion of the PAPA where deer congregated in early winter before moving to their individual winter ranges throughout the Mesa (Sawyer and Lindzey 2001). We believed attempting to randomly capture deer in this area during early winter provided the best opportunity to achieve a representative sample from the wintering population. In years before development (winters 1998–1999 and 1999–2000), we fitted deer with standard, very high frequency (VHF) radio collars (Advanced Telemetry Systems, Isanti, Minnesota). We located radio-collared deer from the ground or air every 7 to 10 days during the 1998–1999 and 1999–2000 winters (1 Dec to 31 Mar). During years of gas field development (winters 2000–2001, 2001–2002, and 2002–2003), we fitted deer with store-on-board global positioning system (GPS) radio collars (Telonics, Inc., Mesa, Arizona) equipped with VHF transmitters and remote-release mechanisms programmed to release at specified dates and times. We fitted GPS radio collars to a sample of different deer each winter; however, 3 deer had collars that collected GPS locations for both the 2001–2002 and 2002–2003 winters. We programmed GPS radio collars to attempt location fixes every 1 or 2 hrs, depending on model type. We did not differentially correct GPS locations because 3-dimensional fixes typically have <20 m error (Di Orio et al. 2003), and previous work in the study area indicated 99% fix-rate success with 80% of successful fixes 3-dimensional locations (Sawyer et al. 2002). Potential fix-rate bias was not a concern because of the high fix-rate success of the GPS collars.

Modeling Procedures

Defining availability.—We defined the study area by mapping 39,641 locations from 77 mule deer over a 6-year period (1998 to 2003), creating a minimum convex polygon (MCP), and then clipping the MCP to the boundary of the PAPA. This was consistent with the McClean et al. (1998) recommendation that the study-area level of habitat availability should be based on the distribution of radio-collared animals.

Habitat variables.—We identified 5 variables as potentially important predictors of winter mule deer distribution, including elevation, slope, aspect, road density, and distance to well pad. We did not include vegetation as a variable because the sagebrush–grassland was relatively homogeneous across the study area and difficult to divide into finer vegetation classes. Further, we believed differences in sagebrush characteristics could be largely explained by elevation, slope, and aspect. We used the SPATIAL ANALYST extension for ArcView (Environmental Systems Research Institute, Redlands, California) to calculate slope and aspect from a 26 × 26-m digital elevation model (U.S. Geologic Survey 1999). Grid cells with slopes >2 degrees were assigned to 1 of 4 aspect categories: northeast, northwest, southeast, or southwest. Grid cells with slopes of $\leq$2 degrees were considered flat and assigned to a fifth category that was used as the reference (Neter et al. 1996) during habitat modeling. We obtained elevation, slope, and aspect values for each of the sampled units using the GET GRID extension for ArcView. The sample units consisted of approximately 4,500 circular units with 100-m radii distributed across the study area. We annually digitized roads and well pads from LANDSAT thematic satellite images acquired from the U.S. Geologic Survey and processed by SkyTruth (Sheperdstown, West Virginia). The LANDSAT images were obtained every fall, before snow accumulation, but after most annual development activities were complete. We calculated road density by placing a circular buffer with a 0.5-km radius on the center of the sample unit and measuring the length of road within the buffer. We used the NEAREST NEIGHBOR extension for ArcView to measure the distance from the center of each sampled unit to the edge of the nearest well pad. We did not distinguish between developing and producing well pads. We assumed habitat loss was similar among all well pads because development of the field was in its early stages (i.e., <5 years), and there was no evidence of successful shrub reclamation. Additionally, there was no evidence that suggested the type of well pad was an accurate indicator of the amount of human activity (e.g., traffic) that occurred at each site. Without an accurate measure of human activity, we believed it was inappropriate to distinguish between producing and developing well pads.

Statistical analyses.—Our approach to modeling winter habitat use consisted of 4 basic steps: 1) estimate the relative frequency of use (i.e., an empirical estimate of probability of use) for a large sample of habitat units for each radiocollared deer, during each winter; 2) use the relative frequency as the response variable in a multiple regression analysis to model the probability of use for each deer as a function of predictor variables; 3) develop a population-level model from the individual deer models, for each winter; and 4) map predictions of population-level models from each winter. Our analysis treated each winter period separately to allow mule deer habitat use and environmental characteristics (e.g., road density or number of well pads) to change through time. We treated radiocollared deer as the experimental unit to avoid pseudo-replication (i.e., spatial and temporal autocorrelation) and to accommodate population-level inference (Otis and White 1999, Johnson et al. 2000, Erickson et al. 2001).

We estimated relative frequency of use for each radio-collared deer using a simple technique that involved counting the number of deer locations in each of approximately 4,500 randomly sampled, circular habitat units across the study area. We took a simple random sample with replacement for each winter to ensure independence of the habitat units (Thompson 1992:51). We chose circular habitat units that had a 100-m radii; an area small enough to detect changes in animal movements but large enough to ensure multiple locations could occur in each unit. Previous analyses suggested model coefficients were similar across a variety of unit sizes, including 50, 75, and 150-m radii (R. Nielson, Western Ecosystems Technology, Inc., Cheyenne, Wyo., USA, unpublished data). We measured predictor variables on each of the sampled habitat units and conducted a Pearson's pairwise correlation analysis (PROC CORR; SAS 2000) before modeling to identify multicolinearities and to determine whether any variables should be excluded from the modeling ($|r| > 0.60$).

The relative frequency of locations from a radio-collared deer found in each habitat unit was an empirical estimate of the probability of use by that deer and was used as a continuous response variable in a generalized linear model (GLM). We used an offset term (McCullagh and Nelder 1989) in the GLM to estimate probability of use for each radiocollared deer as a function of a linear combination of predictor variables, plus or minus an error term assumed to have a negative binomial distribution (McCullagh and Nelder 1989, White and Bennetts 1996). We preferred the negative binomial distribution over the more commonly used Poisson because it allows for overdispersion (White and Bennetts 1996).

We obtained a population-level model for each winter by first estimating coefficients for each radiocollared deer. We used PROC GENMOD (SAS 2000) and the negative binomial distribution to fit the following GLM for each radiocollared deer during each winter period:

$$\ln[E(r_i)] = \ln(total) + \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \qquad (1)$$

which is equivalent to

$$\ln[E(r_i/total)] = \ln[E(\text{Relative frequency}_i)]$$
$$= \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p \qquad (2)$$

where r_i is the number of locations for a radio-collared deer within habitat unit i ($i = 1, 2, \ldots, 4{,}500$), *total* is the total number of locations for the deer within the study area, β_0 was an intercept term, $\beta_1, \ldots, \beta_p$ are unknown coefficients for habitat variables $X_1, \ldots, X_p$, and $E(.)$ denotes the expected value. We used the same offset term for all sampled habitat units of a given deer, thus the term ln(*total*) was absorbed into the estimate of β_0 and ensured we were modeling relative frequency of use (e.g., 0, 0.003, 0.0034, . . .) instead of integer counts (e.g., 0, 1, 2, . . .). Because some locations for each deer were not within a sampled habitat unit, inclusion of the offset term in Eq. (1) was not equivalent to conditioning on the total number of observed locations (i.e., multinomial distribution). In fact, one could drop the offset term and simply scale the resulting estimates of frequency of use by the total number of observed locations to obtain predictions of relative frequency identical to those obtained by Eq. (1). This approach to modeling resource selection estimates the relative frequency or absolute probability of use as a function of predictor variables, so we refer to it as a resource selection probability function (RSPF; Manly et al. 2002).

We assumed GLM coefficients for predictor variable k, for each deer, were a random sample from a normal distribution (Seber 1984, Littell et al. 1996), with the mean of the distribution representing the average or population-level effect of predictor variable k on probability of use. We estimated coefficients for the population-level RSPF for each winter using

$$\hat{\bar{\beta}}_k = \frac{1}{n}\sum_{j=1}^{n} \hat{\beta}_{kj}, \qquad (3)$$

Where $\hat{\beta}_{kj}$ was the estimate of coefficient k for individual j ($j = 1, \ldots, n$). We estimated the variance of each population-level model coefficient using the variation between radiocollared deer and the equation

$$\text{var}(\hat{\bar{\beta}}_k) = \frac{1}{n-1}\sum_{j=1}^{n} (\hat{\beta}_{kj} - \bar{\beta}_k)^2. \qquad (4)$$

This method of estimating population-level coefficients using Eqs. (3) and (4) was used by Marzluff et al. (2004) and Glenn et al. (2004) for evaluating habitat selection of Steller's jays (*Cyanocitta stelleri*) and northern spotted owls (*Strix occidentalis caurina*), respectively. Population-level inferences using Eqs. (3) and (4) are unaffected by potential autocorrelation because temporal autocorrelation between deer locations or spatial autocorrelation between habitat units do not bias model coefficients for the individual radiocollared deer models (McCullagh and Nelder 1989, Neter et al. 1996).

Standard criteria for model selection such as Akaike's Information Criterion (Burnham and Anderson 2002) might be appropriate for individual deer but do not apply for building a model for population-level effects because the same model (i.e., predictor variables) is required for each deer within a winter. Therefore, we used a forward-stepwise model-building procedure (Neter et al. 1996) to estimate population-level RSPFs for winters 2000–2001, 2001–2002, and 2002–2003. The forward-stepwise model-building process required fitting the same models to each deer within a winter and using Eqs. (3) and (4) to estimate population-level model coefficients. We used a t-statistic to determine variable entry ($\alpha \leq 0.15$) and exit ($\alpha > 0.20$; Hosmer and Lemeshow 2000). We considered quadratic terms for road density, distance to nearest well pad, and slope during the model-building process and following convention, the linear form of each variable was included if the model contained a quadratic form.

We conducted stepwise model building for all winters except for the predevelopment period that included winters 1998–1999 and 1999–2000. The limited number of locations recorded for radiocollared deer during that period precluded fitting individual models. Rather, we estimated a population-level model for the predevelopment period by pooling location data across 45 deer that had a minimum of 10 locations. We took simple random samples of 30 locations from deer with >30 locations to ensure that approximately equal weight was given to each deer in the analysis. We fit a model containing slope, elevation, distance to roads, and aspect for the predevelopment period. Distance to well pad was not included as a variable in the predevelopment model because there were only 11 existing well pads on the Mesa before development, and most were >10 years old, with little or no human activity associated with them. We used bootstrapping to estimate the standard errors and P values of the predevelopment population-level model coefficients.

We mapped predictions of population-level RSPFs for each winter on 104 × 104-m grids that covered the study area. We checked predictions to ensure all values were in the [0,1] interval, such that we were not extrapolating outside the range of the model data (Neter et al. 1996). The estimated probability of use for each grid cell was assigned a value of 1 to 4 based on the quartiles of the distribution of predictions for each map. We assigned grid cells with the highest 25% of predicted probabilities of use a value of 1 and classified them as high-use areas, assigned grid cells in the 51 to 75 percentiles a value of 2 and classified them as medium- to high-use areas, assigned grid cells in the 26 to 50 percentiles a value of 3 and classified them as medium- to low-use areas, and assigned grid cells in the 0 to 25 percentiles a values of 4 and classified them as low-use areas. We used contingency tables to identify changes in the 4 habitat-use categories across the 4 winter periods.

Results

Predevelopment: Winters 1998–1999 and 1999–2000

The population-level RSPF was estimated from 953 VHF deer locations collected from 45 adult female mule deer during the winters (1 Dec to 15 Apr) of 1998–1999 and 1999–2000 (Table 1). Units with the highest probability of use (Fig. 1) had an average elevation of 2,275 m, an average slope of 5 degrees, and an average road density of 0.14 km/km^2. Aspects with the highest probability of use were northwest and southwest.

Year 1 of Development: Winter 2000–2001

Individual models were estimated for 10 radiocollared deer during the winter (1 Jan to 15 Apr) of 2000–2001. Eight of the 10 deer had positive coefficients for elevation and negative coefficients for road density, indicating selection for higher elevations and low road densities. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, all 10 deer selected for moderate slopes, and 7 of 10 deer selected areas away from well pads.

The population-level RSPF was estimated from 18,706 GPS locations collected from 10 radiocollared deer during the winter of 2000–2001 (Table 1). The RSPF included elevation, slope, road density, and distance to well pad (Table 1). Deer selected for areas with higher elevations, moderate slopes, low road densities, and away from well pads. Habitat units with the highest probability of use (Fig. 2) had an average elevation of 2,266 m, slope of 5 degrees, road density of 0.16 km/km^2, and were 2.7 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well pads and access roads (Fig. 2). Shifts in deer distribution between predevelopment and year 1 of development were evident through the changes in the 4 deer use categories (Table 2). Of the habitat units classified as high deer use before development, only 60% were classified as high deer use during year 1 of development (Table 2). Of the areas classified as low deer use before development, 58% remained classified as low deer use during year 1 of development (Table 2).

Year 2 of Development: Winter 2001–2002

Individual models were developed for 15 radiocollared deer during the winter (4 Jan to 15 Apr) of 2001–2002. Fourteen of the 15 deer had positive coefficients for elevation, indicating selection of higher elevations. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, all 15 deer selected for moderate slopes, and 12 of 15 deer selected areas away from well pads.

The population-level RSPF was estimated from 14,851 GPS locations collected from 15 radiocollared deer during the winter of 2001–2002 (Table 1). The RSPF included elevation, slope, and distance to well pad (Table 1). Deer selected for areas with higher elevations, moderate slopes, and away from well pads. Habitat units with the highest probability of use (Fig. 3) had an average elevation of 2,255 m, slope of 5 degrees, and were 3.1 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well pads (Fig. 3). Shifts in deer distribution between predevelopment, year 1, and year 2 of development were evident through the changes in the 4 deer-use categories (Table 2). Of the habitat units classified as high deer use before development, only 49% were classified as high deer use during year 2 of development (Table 2). Of the areas classified as low deer use before development, 48% remained classified as low deer use during year 2 of development (Table 2).

Year 3 of Development: Winter 2002–2003

Individual models were developed for 7 radiocollared deer during the winter (20 Dec to 15 Apr) of 2002–2003. All 7 deer had positive coefficients for elevation, indicating selection of higher elevations. Based on the relationship between the linear and quadratic terms for slope and distance-to-well-pad variables, 6 of 7 deer selected for moderate slopes, and 6 of 7 deer selected areas away from well pads.

The population-level RSPF was estimated from 4,904 GPS locations collected from 7 radiocollared deer during the winter of 2002–2003 (Table 1). Our target sample of 10 marked animals was not met because 3 deer died early in the season. The RSPF included elevation, slope, and distance to well pad (Table 1). Deer selected areas with high elevations, moderate slopes, and away from well pads. Habitat units with the highest probability of use (Fig. 4) had an average elevation of 2,233 m, slope of 5 degrees, and were 3.7 km away from the nearest well pad. Predictive maps indicate probability of deer use was lowest in areas close to well

Table 1. Coefficients for population-level winter mule deer resource selection probability functions (RSPF) before and during 3 years of natural gas development in western Wyo., USA, 1998–2003.

	Predevelopment			Year 1			Year 2			Year 3		
	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Intercept	−29.649	6.637	<0.001	−84.560	21.124	0.003	−75.712	12.931	<0.001	−104.295	11.316	<0.001
Elevation	0.009	0.001	<0.001	0.031	0.008	0.005	0.027	0.005	<0.001	0.036	0.004	<0.001
Slope	0.098	0.010	<0.001	0.391	0.073	<0.001	0.258	0.046	<0.001	0.342	0.128	0.036
Slope^2	−0.004	0.001	<0.001	−0.022	0.004	<0.001	−0.017	0.003	<0.001	−0.019	0.007	0.042
Well distance	na[a]			3.129	1.899	0.134	3.375	1.264	0.018	6.712	2.394	0.031
Well distance^2	na			−0.465	0.229	0.073	−0.416	0.156	0.019	−0.719	0.289	0.047
Road density	−0.249	0.027	<0.001	−0.827	0.387	0.061	ns[b]			ns		
Aspect = NE	0.012	0.051	0.818	ns			ns			ns		
Aspect = NW	0.399	0.025	<0.001	ns			ns			ns		
Aspect = SE	−0.301	0.022	<0.001	ns			ns			ns		
Aspect = SW	0.194	0.028	<0.001	ns			ns			ns		

[a] Not applicable.
[b] Not significant.

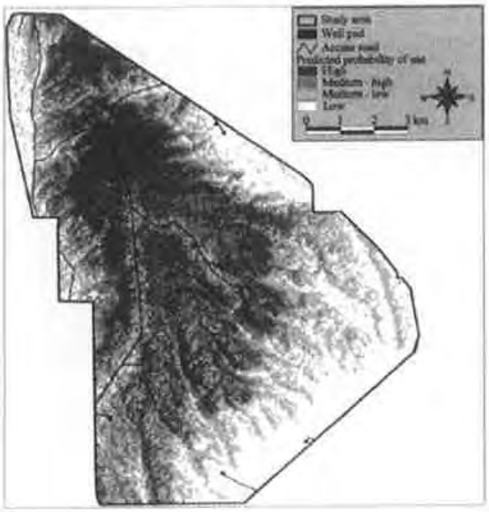

Figure 1. Predicted probabilities and associated categories of mule deer habitat use during 1998–1999 and 1999–2000 winters, before natural gas field development in western Wyo., USA.

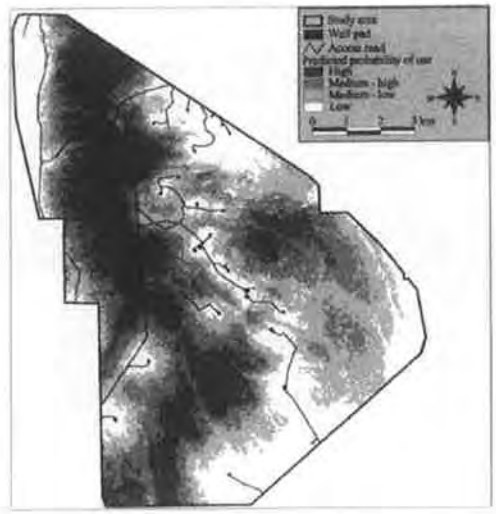

Figure 2. Predicted probabilities and associated categories of mule deer habitat use during year 1 (winter of 2000–2001) of natural gas development in western Wyo., USA.

pads (Fig. 4). Shifts in deer distribution between predevelopment, year 1, year 2, and year 3 of development were evident through the changes in the 4 deer-use categories (Table 2). Of the habitat units classified as high deer use before development, only 37% were classified as high deer use during year 3 of development (Table 2). Of the areas classified as low deer use before development, 41% remained classified as low deer use during year 3 of development (Table 2).

Discussion

Our statistical analysis differs from the typical methods used in the study of habitat selection (Manly et al. 2002) in several important ways. First, our sample size was the number of radiocollared deer during each winter, and our objective was to make statistical inferences to the corresponding population in the study area. Thus, we assumed that our radiocollared deer represented a simple random sample from the population each winter. Second, our response variable was an empirical estimate of the probability of use of a habitat unit, or the volume under an animal's utilization distribution surface. And third, we used a stepwise model-building procedure to develop a population-level model from individual deer models, where the average of the coefficients across deer comprised the population-level model for each winter period.

We recognize that other techniques may be used to estimate population-level models. Random-coefficients or hierarchical models (Littell et al. 1996) can estimate individual and population-level coefficients; however, model convergence can be problematic. To date, we believe the most appropriate method to obtain a population-level model is to fit a GLM with negative binomial errors to each radiocollared deer and average the coefficients. Seber (1984:486) describes this estimator and notes that identical population-level coefficients can be obtained if one averages the relative frequency of use in each of the sampled habitat units and fits a single model. We prefer to estimate individual models because the variation among individuals is often of biological interest.

We would have preferred the use of GPS radio collars during all years of this study because they can systematically collect thousands of accurate deer locations, regardless of weather conditions or time of day. Although the VHF radio collar locations used for the predevelopment model were collected at irregular intervals and during daylight hours, we believe the resulting model provides a reasonable comparison to models estimated during years of development with GPS radio collar locations. Hayes and Krausman (1993) suggested diurnal use of habitats by female mule deer were representative of overall patterns of habitat use, except in areas with high levels of human disturbance. Because human activity was exceptionally low on the Mesa before development, we believe the 953 VHF locations collected from 45 radiocollared deer accurately reflect overall deer use during that time period.

We view our resource selection analysis as an objective means to document mule deer response to natural gas development and quantify indirect habitat losses through time. Although indirect impacts associated with human activity or development have been documented in elk (*Cervus elaphus*; Lyon 1983, Morrison et al. 1995, Rowland et al. 2000), data that suggest similar behavior in mule deer (Rost and Bailey 1979, Yarmaloy et al. 1988, Merrill et al. 1994) are limited and largely observational in nature. Specific knowledge of how, or whether, mule deer respond to natural gas development does not exist in the literature. Our results suggest winter habitat selection and distribution patterns of mule deer were affected by well pad development. Changes in habitat selection by mule deer appeared to be immediate (i.e., year 1 of development), and through 3 years of development, we found no evidence they acclimated or habituated to well pads. Rather, mule deer had progressively higher probability of use in areas farther away from well pads as development progressed. The nonlinear relationship between probability of deer use and distance to well pad indicates deer selected areas away from well pads, but only up to a certain distance. We believe this reflects the ability of mule

Table 2. Percent change in the 4 predevelopment deer-use categories through 3 years (2001–2003) of natural gas development in western Wyo., USA.

Predevelopment category[a]	Year of development	Deer use category: High	Medium–high	Medium–low	Low
High	Year 1	60%	23%	13%	4%
	Year 2	49%	19%	23%	9%
	Year 3	37%	22%	27%	14%
Medium–high	Year 1	31%	36%	22%	11%
	Year 2	34%	23%	25%	18%
	Year 3	27%	22%	28%	22%
Medium–low	Year 1	9%	34%	31%	26%
	Year 2	16%	35%	25%	25%
	Year 3	25%	27%	25%	23%
Low	Year 1	0%	7%	34%	58%
	Year 2	1%	23%	27%	48%
	Year 3	11%	29%	20%	41%

[a] Category rows may not sum to exactly 100% because of rounding error.

deer to avoid localized disturbances and habitat perturbations without completely abandoning their home ranges.

Population-level RSPFs and associated predictive maps were useful tools for illustrating changes in habitat selection patterns through time. We recognize the 4 levels of habitat use were subjectively defined and could vary depending on study objectives or species information. Nonetheless, we believe RSPFs and associated predictive maps can provide a useful framework for quantifying indirect habitat losses by measuring the changes (e.g., percentage or area) in habitat use categories through time. Predictive maps suggest that some areas categorized as high use before development, changed to low use as development progressed, and other areas initially categorized as low use changed to high use. For example, following year 1 of development, 17% of units classified as high use before development had changed to medium–low or low use, and by year 3 of development, 41% of those areas classified as high use before development had changed to medium–low or low use. Conversely, by year 3 of development, 40% of low-use areas had changed to medium–high or high-use areas. Assuming habitats with high probability of use before development were more suitable than habitats with lower probability of use, these results suggest natural gas development on the Mesa displaced mule deer to less-suitable habitats.

Winter severity and forage availability can influence the distribution patterns of mule deer (Garrott et al. 1987, Brown 1992). However, winter conditions on the Mesa were considered relatively mild during the course of this study (1998–2003) and were unlikely to have precluded deer from using their entire winter range. Gilbert et al. (1970) reported snow depths >61 cm were required to preclude use of an area by mule deer. With the exception of isolated drifts, snow depths were <61 cm across the Mesa during all years of study. If the observed changes in deer distribution were due to severe winter conditions, we would expect deer use to shift to areas with lower elevations and south-facing slopes. Instead, deer always selected for high elevations, and aspect was never a significant predictor variable during years of development, further suggesting the observed shifts in deer distribution

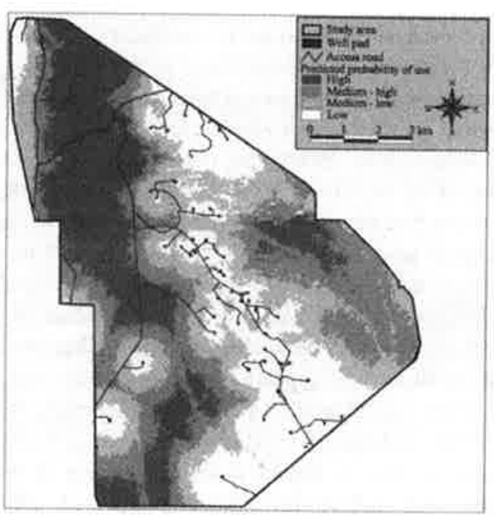

Figure 3. Predicted probabilities and associated categories of mule deer habitat use during year 2 (winter of 2001–2002) of natural gas development in western Wyo., USA.

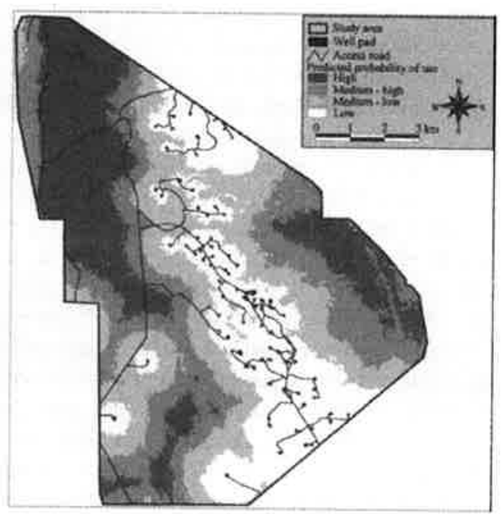

Figure 4. Predicted probabilities and associated categories of mule deer habitat use during year 3 (winter of 2002–2003) of natural gas development in western Wyo., USA.

were due to increased well-pad development and associated human activity rather than winter conditions.

A single well pad typically disturbs 3 to 4 acres of habitat; however, areas with the highest probability of deer use were 2.7, 3.1, and 3.7 km away from well pads during the first 3 years of development, respectively. There are 2 potential concerns with the apparent avoidance of well pads by mule deer. First, the avoidance or lower probability of use of areas near wells creates indirect habitat losses of winter range that are substantially larger in size than the direct habitat losses incurred when native vegetation is removed during construction of the well pad. Habitat losses, whether direct or indirect, have the potential to reduce carrying capacity of the range and result in population-level effects (i.e., survival or reproduction). Second, if deer do not respond by vacating winter ranges, distribution shifts will result in increased density in remaining portions of the winter range, exposing the population to greater risks of density-dependent effects. Consistent with Bartmann et al. (1992), we would expect fawn mortality to be the primary density-dependent population-regulation process because of their high susceptibility to overwinter mortality (White et al. 1987, Hobbs 1989).

Monitoring shifts in distribution or habitat use allows for mitigation measures aimed at reducing impacts to be evaluated and for timely, site-specific strategies to be developed. The current mitigation measure is focused on seasonal-timing restrictions, where drilling activity is limited to nonwinter months. This type of mitigation is common across federal lands and intended to reduce human activity and, presumably, the associated stress to big game during the winter months, typically 15 November to 30 April. Major shifts in the distribution of mule deer on the Mesa occurred even though drilling on federal lands was largely restricted to nonwinter months. Our findings suggest current mitigation measures may not be achieving desired results. Winter-timing restrictions are only imposed on leases that occur in areas designated as crucial winter range, and then, only through the development phase of the well. Consequently, variable levels of human activity may occur throughout the field during winter as producing wells are serviced, and despite the recognition of the uniqueness of crucial winter range, roads may cross or abut these areas, exposing them to human disturbances as well.

Management Implications

In deep-gas fields like the PAPA, where well densities range from 4 to 16 pads per section (2.58 km^2), the number of producing well pads and associated human activity may negate the potential effectiveness of timing restrictions on drilling activities as a means of reducing disturbance to wintering deer. Mitigation measures designed to minimize disturbance to wintering mule deer in natural gas fields should consider all human activity across the entire project area and not be restricted to the development of wells or to crucial winter ranges. Reducing disturbance to wintering mule deer may require restrictions or approaches that limit the level of human activity during both production and development phases of the wells. Directional-drilling technology offers promising new methods for reducing surface disturbance and human activity. Limiting public access and developing road management strategies may also be a necessary part of mitigation plans. Future research and monitoring efforts should evaluate how different levels of human activity (e.g., traffic or noise) at developing and producing well pads influence mule deer distribution. Understanding mule deer response to different levels of human activity and types of well pads would allow mitigation measures to be properly evaluated and improved.

Assuming there is some level of increased energy expenditure required for deer to alter their winter habitat-selection patterns (Parker et al. 1984, Freddy et al. 1986, Hobbs 1989), the apparent displacement of deer from high-use to low-use areas has the potential to influence survival and reproduction. This relationship, however, needs to be documented. Accordingly, we recommend appropriate population parameters (i.e., adult female survival, overwinter fawn survival, recruitment) be monitored in areas with large-scale gas development so that changes in reproduction or survival can be detected. The major shortcoming of efforts to evaluate the impacts of disturbances on wildlife populations is that they seldom are addressed in an experimental framework but, rather, tend to be short-term and observational. Brief, postdevelopment monitoring plans associated with regulatory work generally result in little or no information that allow agencies and industry to assess impacts on wildlife or to improve mitigation measures. We encourage long-term (>5 years) studies that identify habitat-selection patterns and that measure population characteristics in control and treatment areas before and during gas-development projects that occur in sensitive mule deer ranges.

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Literature Cited

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121.

Brown, C. B. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management 56:246–253.

Bureau of Land Management. 2000*a*. Record of decision: environmental impact statement for the Pinedale Anticline natural gas field exploration and development project prepared for Pinedale field office, Wyoming. Pinedale, Wyoming, USA.

Bureau of Land Management. 2000*b*. Record of decision: environmental impact statement for Continental Divide/Wamsutter II natural gas project, Sweetwater and Carbon Counties, Wyoming. Rawlins and Rock Springs field offices. Rawlins, Wyoming, USA.

Bureau of Land Management. 2002. Oil and gas activity on public lands in the United States and Wyoming. USDI-BLM, Wyoming State Office, Cheyenne, USA.

Bureau of Land Management. 2003. Final environmental impact statement

and proposed plan amendment for the Powder River Basin oil and gas project. Buffalo field office. Buffalo, Wyoming, USA.
Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York, New York, USA.
Di Orio, A. P., R. Callas, and R. J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. Wildlife Society Bulletin 31:372–379.
Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kern. 2001. Statistical issues in resource selection studies with radio-marked animals. Pages 209–242 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations, Academic, San Diego, California, USA.
Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63–68.
Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634–643.
Gilbert, P. F., O. C. Wallmo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. Journal of Wildlife Management 34:15–23.
Glenn, E. M., M. C. Hansen, and R. G. Anthony. 2004. Spotted owl home-range and habitat use in young forests of western Oregon. Journal of Wildlife Management 68:33–50.
Hayes, C. L., and P. R. Krausman. 1993. Nocturnal activity of female desert mule deer. Journal of Wildlife Management 57:897–904.
Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101.
Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.
Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.
Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.
Lyon, J. L. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 81:592–594.
Manly, B. F., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Boston, Massachusetts, USA.
Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411–1427.
McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62:793–801.
McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, Boca Raton, Florida, USA.
Merrill, E. H., T. P. Hemker, K. P. Woodruff, and L. Kuck. 1994. Impacts of mining facilities on fall migration of mule deer. Wildlife Society Bulletin 22:68–73.
Morrison, J. R., W. J. Devergie, A. W. Alldredge, A. E. Byrne, and W. W. Andree. 1995. The effects of ski area expansion on elk. Wildlife Society Bulletin 23:481–489.
Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition. McGraw-Hill, Boston, Massachusetts, USA.
Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.
Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.
Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43:634–641.
Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.
SAS Institute. 2000. SAS/STAT user's guide: statistics. Version 8. SAS Institute, Cary, North Carolina, USA.
Sawyer, H., and F. Lindzey. 2001. The Sublette mule deer study. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.
Sawyer, H., D. Strickland, and L. McDonald. 2002. Summary of 2002 project results and scope of long-term monitoring plan to assess potential impacts of energy development on mule deer in the Pinedale Anticline project area. Western Ecosystems Technology, Cheyenne, Wyoming, USA.
Seber, G. A. F. 1984. Multivariate observations. John Wiley and Sons, New York, New York, USA.
Thompson, S. K. 1992. Sampling. John Wiley and Sons, New York, New York, USA.
U.S. Geological Survey. 1999. Thirty-meter national elevation data set (tiled for Wyoming): U.S. Geological Survey EROS data center, Sioux Falls, South Dakota, USA.
White, G. C., R. A. Garrott, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Survival of mule deer in northwest Colorado. Journal of Wildlife Management 51:852–859.
White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. Ecology 77:2549–2557.
Yarmaloy, C., M. Bayer, and V. Geist. 1988. Behavior responses and reproduction of mule deer does following experimental harassment with all-terrain vehicle. Canadian Field-Naturalist 102:425–429.

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ENERGY DEVELOPMENT GUIDELINES FOR MULE DEER

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TABLE OF CONTENTS

PREFACE

The geographic scope, intensity, and pace of domestic energy development have potential to impact fish and wildlife habitats on a large scale. The capability of habitat to sustain wildlife into the future will depend on effective project planning and mitigation developed through constructive collaboration among federal land management agencies, state, provincial, and tribal wildlife management agencies, private landowners, industry, and other conservation partners.

This document establishes guidelines that will enable energy development to proceed in a manner reasonably compatible with habitat requirements of mule and black-tailed deer. These *Energy Development Guidelines for Mule Deer* will help resource managers focus on pre-project risk assessments, appropriate project designs, effective mitigation and reclamation, and adequate monitoring to better conserve mule deer habitats through adaptive management. Historically, the federal process of energy leasing and development has been too inflexible to apply best technology and information currently available. These guidelines represent the state of our knowledge at the time of publication, but it is the intent of the Mule Deer Working Group that they be promptly updated with all subsequent and pertinent research that becomes available to decision makers.

Photo courtesy of George Andrejko/AZGFD

INTRODUCTION

Black-tailed and mule deer (collectively mule deer, *Odocoileus hemionus*) are icons of the North American West. Perhaps no animal better symbolizes the region in the minds of the American public. Because of their popularity and broad distribution, mule deer are one of the most economically and socially important animals in western North America. In a 2006 survey of wildlife-related recreation, the U. S. Fish and Wildlife Service (USFWS) reported nearly 3 million people hunted in the 19 western states (USFWS 2007). In 2006 alone, hunters were afield almost 50 million days and spent more than $7 billion on lodging, gas, and hunting-related equipment. Although the survey encompassed all forms of hunting, mule deer have traditionally been one of the most important game animals in the West. According to the same survey, 25.6 million residents in 19 western states spent more than $15.5 billion "watching wildlife" in 2006. The value of abundant wildlife populations cannot be overemphasized. Because mule deer are inextricably tied to the history, development, and future of the West, the species is one of the true barometers of ecological conditions in western North America.

Mule deer are distributed throughout western North America from the coastal islands of Alaska, to southern Baja Mexico and from the northern border of the Mexican state of Zacatecas to the Canadian provinces of Saskatchewan, Alberta, British Columbia, and the southern Yukon Territory. Within these broad latitudinal and geographic gradients, mule deer have developed incredibly diverse behavioral and ecological adaptations enabling the species to occupy a diversity of climatic regimes and vegetation associations.

Federal land management agencies regulate surface disturbing activities, including energy development, throughout much of the mule deer range in the West. In the eastern portions of mule deer range, private landowners control how habitat is managed. Mule deer habitats are increasingly vulnerable to unprecedented threats from a range of anthropogenic developments. If mule deer habitats are to be conserved, it is imperative that government agencies and private conservation organizations elevate their awareness of the species' key habitat requirements, engage in habitat restoration initiatives, and fully integrate effective habitat protection and mitigation practices into all land use decisions.

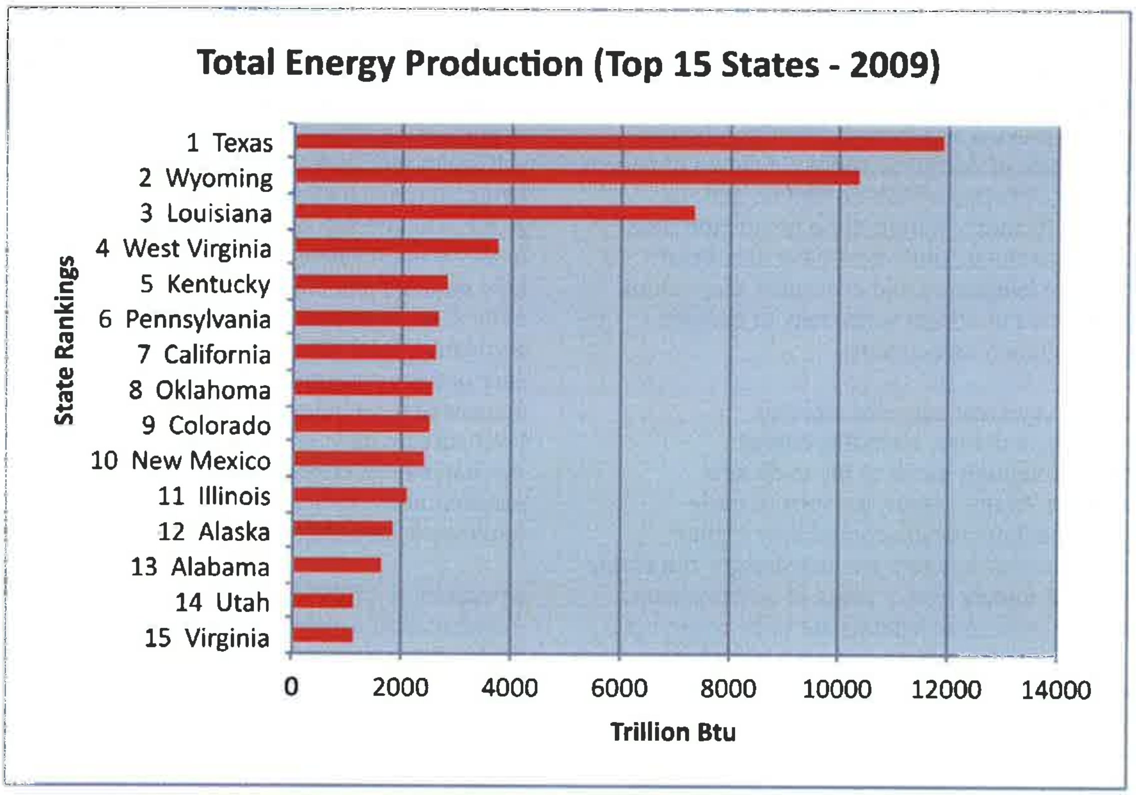
State wildlife agencies manage and regulate wildlife populations that are dependent on those habitats managed by the Federal land management agencies and private landowners. The Western Governors' Association (WGA) recognized the need to coordinate efforts to protect and maintain wildlife migration corridors and crucial habitats (WGA 2008). They approved Policy Resolution 07-01 to work "in partnership with important stakeholders, to identify key wildlife corridors and crucial wildlife habitats in the West and make recommendations on needed policy options and tools for preserving those landscapes." The WGA's *Wildlife Corridors Initiative*, is a multi-state and collaborative effort to improve knowledge and management of wildlife corridors and crucial habitat. The primary objective was to develop a tool for policy makers to integrate wildlife corridor and crucial habitat values into planning decisions, and promote best management practices for development to reduce harmful impacts on wildlife.

Energy consumption and production continue to be the focus of the nation's energy policy. According to the National Energy Policy (2001), "...if energy production increases at the same rate as during the last decade our projected energy needs will far outstrip expected levels of production. This imbalance, if allowed to continue, will inevitably undermine our economy, our standard of living, and our national security." As pressure mounts to locate and develop additional sources of domestic energy in the western states, careful attention must be given to how industry can maintain effective habitat conditions for mule deer. To best do that, rigorous research to determine population level effects of energy development on mule deer needs to continue as many questions remain unanswered. Hebblewhite (2011) observed many population level surveys have identified important changes, but the mechanisms of change remain speculative. He concludes research needs to occur to better achieve an evidence-based framework for mitigating development.

Sawyer et al. (2002) suggested habitat loss and fragmentation caused by extensive energy development could pose a serious threat to mule deer and pronghorn (*Antilocapra americana*) populations in western Wyoming. The national focus on energy independence should, at the same time, recognize the importance of maintaining intact wildlife habitats supporting diverse economic, recreational, social, and aesthetic values.

Areas of known or potential energy resources overlap much of what is considered important mule deer habitat. Development of those resources brings about habitat disturbance or loss due to construction of well pads, roads, pipelines, mine facilities, wind and solar farms, and other features. In addition, disturbances from vehicle traffic, noise, and human activities often displace mule deer to areas farther away from well pads (Sawyer et al. 2006). Presumably this displacement is to areas of less suitable habitat. This disturbance and displacement diverts time and energy away from foraging, resting, and other activities that improve physiological condition (Gill et al. 1996, Frid and Dill 2002). Therefore, there is the potential to decrease mule deer survival and recruitment rates and ultimately lead to population-level effects. Activities associated with energy exploration and development often preclude or inhibit use of winter ranges that are critically important to mule deer (Lutz et al. 2003, Sawyer et al. 2006). Roads and traffic also limit mule deer use of important habitats (Sawyer et al. 2009c). The impact of roads has been increasingly recognized in the past decade (Forman et al. 2003). In fact, highway-associated impacts are one of the most prevalent and widespread stressors affecting natural ecosystems in the U.S. (Noss and Cooperrider 1994, Trombulak and Frissell 2000, Farrell et al. 2002). These impacts are especially severe in the western states where oil and gas, and more recently wind and solar energy, are being developed rapidly at a time when mule deer populations are depressed (Heffelfinger and Messmer 2003, Lutz et al. 2003, Hebblewhite 2008).

While other energy sources such as nuclear and woody or cellulosic biomass conversion could present some issues or concerns, their impact on mule deer or mule deer habitat is not considered significant and therefore not addressed here. For purposes of this document we focus guidelines on the forms of energy development having significant effect on mule deer and their habitat.



Nine of the top 15 energy producing states are in the West and provide habitats for black-tailed or mule deer (U.S. Energy Information Administration, http://www.eia.doe.gov/state/state_energy_rankings.cfm?keyid=89&orderid=1)

OIL AND GAS ENERGY DEVELOPMENT

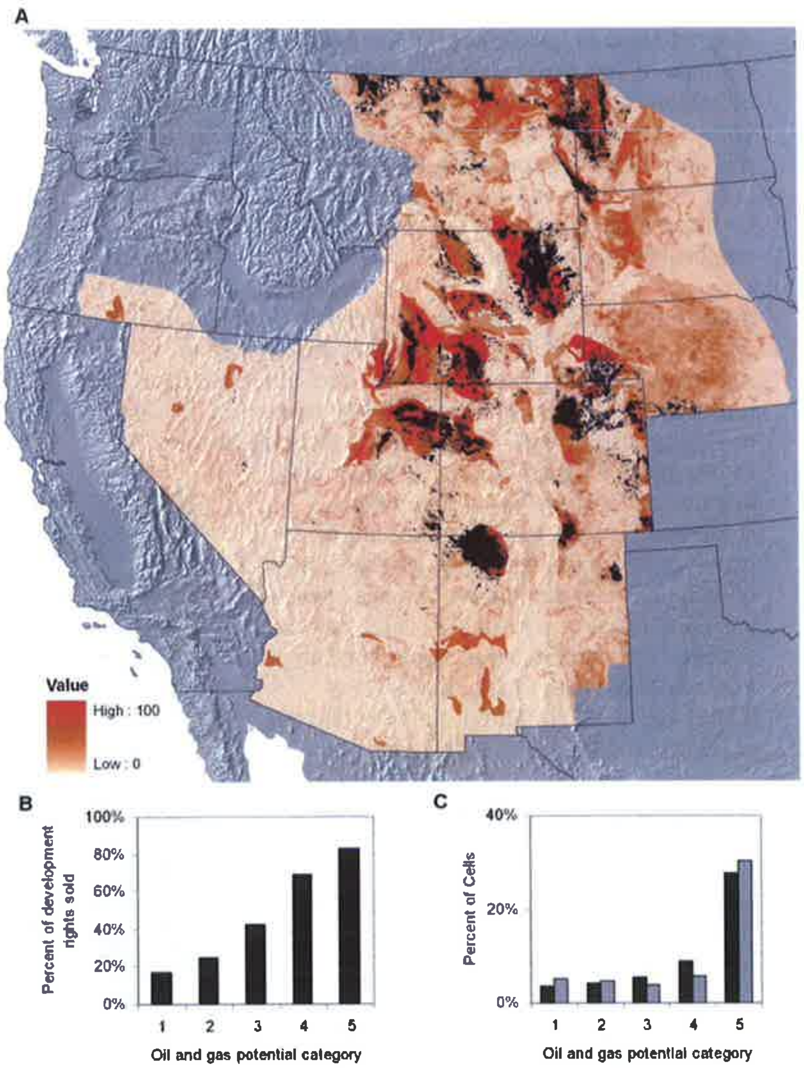
BACKGROUND

Exploration and extraction of oil and gas resources continue to have a range of effects on mule deer habitats. Some types of disturbance can be positive if they improve vegetative structure or nutritional content. However, activities associated with extraction of energy resources often have adverse effects on mule deer. The severity of impact depends upon the amount and intensity of the disturbance, specific locations and arrangements of disturbance, and ecological significance of habitats affected. In Colorado, it has been demonstrated most mule deer populations are ultimately limited by habitat (Bartmann et al. 1992, White and Bartmann 1998, Bergmann et al. 2007, Bishop 2007, Watkins et al. 2007). Thus, small isolated disturbances within non-limiting habitats are of minor consequence within most eco systems. However, larger-scale developments within habitats limiting the abundance and productivity of a mule deer population are a significant concern. Both direct and indirect impacts associated with energy and mineral development have the potential to affect ungulate population dynamics, especially when impacts are concentrated on winter ranges (Sawyer et al. 2002).

In order to meet their nutritional and energy needs, mule deer throughout most of North America depend on distinct seasonal ranges for summer (high elevation forests) and winter (low elevation shrub and grasslands). Migratory mule deer rely on networks of migration routes to transition between these critical areas (Sawyer et al. 2005). Oil and gas development not only removes habitats from these ranges, but may also displace deer from other preferred habitats (Sawyer et al. 2006) and create barriers that hinder migration and use of remaining habitats (Sawyer et al. 2009a). In some cases, construction activities might remove decadent vegetation and provide the opportunity to reclaim the area with improved forage.

Throughout the West, reservoirs of oil and gas commonly overlie important mule deer habitats, including winter ranges (Sawyer et al. 2006). Freddy et al. (1986) demonstrated that mule deer exhibit an alert-flight response at distances up to 0.08 and 0.12 mile from sources of noise and activity from snowmobiles and people afoot, respectively. Sawyer et al. (2006, 2009a, b) showed that high-use deer areas on winter range consistently occurred 1.2 to 1.8 miles away from well pads. Additionally, Sawyer et al. (2009a) found mule deer avoided all types of well pads, but selected areas farther from well pads with greater levels of human disturbance (i.e., traffic). They also concluded liquid gathering systems and directional drilling are effective practices to reduce human activity and surface disturbance during development. They suggested indirect habitat loss to mule deer may be reduced approximately 38-63% when liquids are collected in pipelines rather than stored at well pads and hauled away with tanker trucks. In western Wyoming, surface disturbance was reduced by 70-80% using directional drilling (Sawyer et al. 2009b).

A relatively new area of significant interest has been development of natural gas from coal beds. Depending on depth of the coal seam, coal bed natural gas (CBNG) production and coal mining activities can occur in the same general area, thus raising concerns about possible cumulative effects on mule deer and other wildlife. Development and extraction activities associated with CBNG,



Oil and gas resource potential in the Intermountain West (Copeland et al. 2009)

coal, and deep-well natural gas have potential for profound and long-term impacts on the environment. For the purpose of this discussion, oil and gas development includes those activities used to extract all hydro-carbon compounds such as natural gas, crude oil, coal bed methane, and oil shale.

Drilling operations during winter months (15 Nov – 30 Apr) causes measurably greater impact on mule deer compared to production and maintenance activities. Sawyer et al. (2009a) cautioned wintering mule deer are sensitive to drilling disturbance and that indirect habitat loss may increase by a factor of > 3 when seasonal wildlife protection restrictions are waived. Wildlife managers should expect considerable short-term displacement of wintering mule deer if wide-spread, year-round drilling is permitted in crucial winter range and long-term displacement depending on the level of disturbance during well field operation.

Impact Thresholds

Impact thresholds are levels of development and disturbance that impair key habitat functions by directly eliminating habitat; disrupting wildlife access to, or use of habitat; or causing avoidance and stress (WGFD 2010a). Impact thresholds, appropriate management, and mitigation will vary depending on habitats affected. Our most pressing need is to address the species and habitat functions affected by impending, large-scale developments primarily in sagebrush-steppe ecosystems.

Impact thresholds are based on 2 quantitative measures: density of well pad locations and cumulative area of disturbances/mile^2. The cumulative area of disturbance represents direct loss of habitat. While evaluating impacts to sage-grouse, Naugle et al. (2006) concluded density of well pads is highly correlated with other features of development and therefore comprises a suitable index representing the extent of development. Although the density of well pads and cumulative acreage serve as a general index to well-field development and activities, thresholds based upon these alone may under-represent the actual level of disturbance (WGFD 2010a). Relative degrees of impact are described as follow:

Low Impact— One well pad location with total disturbance not exceeding 20 acres/mile^2. Habitat effectiveness is reduced within a zone surrounding each well, facility, and road corridor through human presence, vehicle traffic, and equipment activity.

Moderate Impact— Two to 4 well pad locations with total disturbance not exceeding 60 acres/mile^2. At this range of development, impact zones surrounding each well pad, facility and road corridor begin to overlap, thereby reducing habitat effectiveness over much larger, contiguous areas. Human, equipment and vehicular activity, noise, and dust are also more frequent and intensive and will impair the ability of animals to use critical areas (winter range, parturition grounds, etc.) and impacts will be much more difficult to mitigate. It may not be possible to fully mitigate impacts caused by higher well densities, particularly by developing habitat treatments on site. Habitat treatments will then generally be located in areas near, rather than within well fields to maintain the function and effectiveness of critical areas.

High Impact— Greater than 4 well pad locations or 60 acres of disturbance/mile^2. At this level of development, the function and effectiveness of habitat becomes compromised. Long-term consequences would likely include continued fragmentation and disintegration of habitat leading to decreased survival, productivity, and ultimately, loss of carrying capacity for the herd. This will result in a loss of ecological functions, recreation opportunity, and income to the economy. An additional consequence may include permanent loss of migration memory from large segments of unique, migratory mule deer herds.

Issues and Concerns

For purposes of these guidelines, impacts to mule deer from oil and gas development can be divided into the following general categories: 1) direct and indirect loss of habitat; 2) physiological stress, 3) disturbance and displacement; 4) habitat fragmentation and isolation; and 5) other secondary (offsite) effects.

The presence of well pads, roads, pipelines, compressor stations, and out buildings directly removes habitat from use (Photo courtesy of New Mexico Department of Game and Fish [NMDGF]).

Direct and Indirect Loss of Habitat

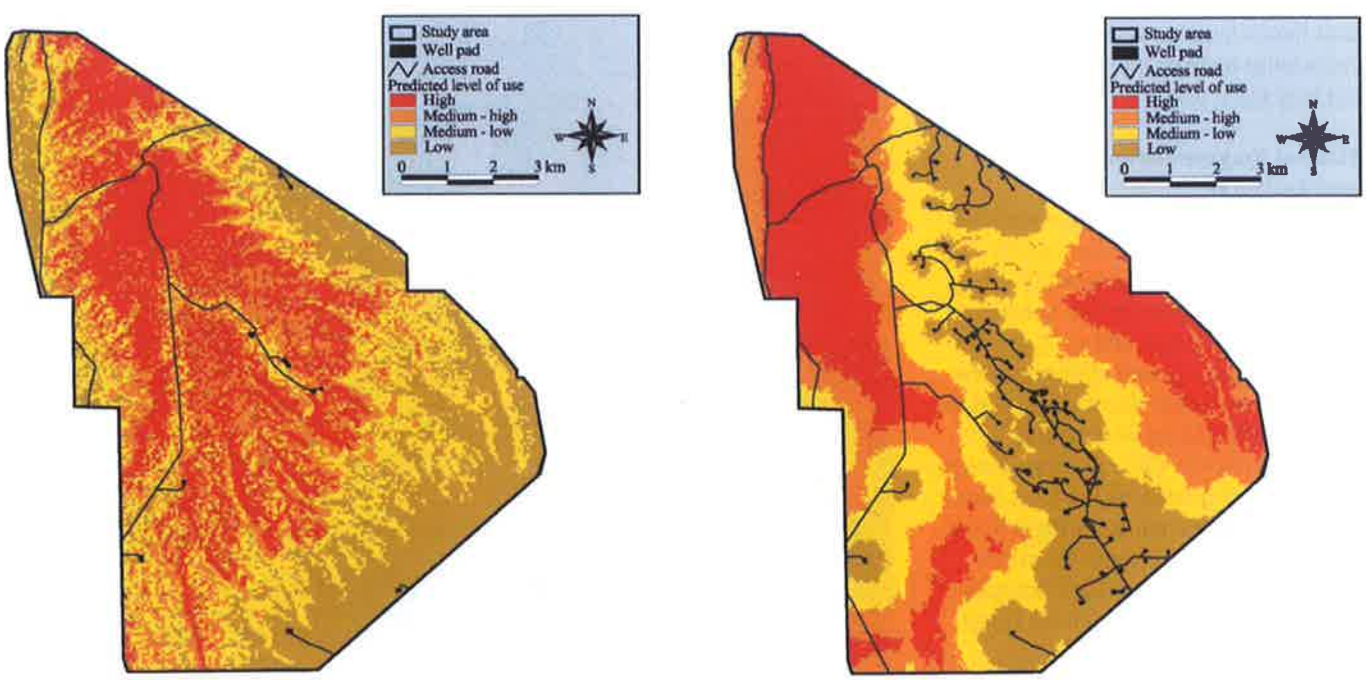
Direct loss of habitat results primarily from construction and production phases of development. The construction and subsequent presence of well pads, roads, pipelines, compressor stations, and out buildings directly removes habitat from use. Production activities require extensive infrastructure and depending upon scale, density, and arrangement of the developed area, indirect loss of habitat can be extensive (USDI 1999). As an example, within the Big Piney-LaBarge oil and gas field in Wyoming, the actual physical area of structures, roads, pipelines, pads, etc. covers approximately 7 miles^2. However, because of the arrangement of these structures, the entire 166 mile^2 landscape is within 0.5 mile of a road, and 160 miles^2 (97% of the landscape) is within 0.25 mile of a road or other structure (Stalling 2003).

Generally, it is possible to reclaim 50% of a disturbed area to minimal cover standards within 3-5 years after construction. However, re-establishing suitable habitat conditions (appropriate native species composition, diversity, structure, and age) may take 30–40 years (Young and Evans 1981, Bunting et al. 1987, Winward 1991), or may take well over 100 years (Baker 2006, Cooper et al. 2007). The remaining 50% of the disturbed area consists of the working surfaces of roads, well pads, and other facilities, and represents a much longer term loss of habitat (USDI 1999). Successful reclamation of sagebrush communities is difficult at best, as success is highly dependent upon amount and timing of precipitation. Sagebrush seed remains viable in salvaged topsoil for a comparatively brief period and reseeding is usually required if reclamation is conducted > 1 year post-disturbance. Restoration of shrub habitats important to wintering deer is critical, but reclamation of these vegetation types in dry regions may not occur quickly (Baker 2006) and therefore any disturbance will likely represent a longer-term habitat loss.

Physiological Stress

Animals become physiologically stressed when energy expenditures increase due to alarm or behavioral avoidance. These responses are generally attributed to interactions with humans or activities associated with human presence such as traffic, noise, pets, and etc. Physiological stress diverts time and energy away from critical activities such as foraging and resting important to maintain or improve fitness (Gill et al. 1996, Frid and Dill 2002). This seems especially critical to wintering deer whose nutritional condition is closely associated with survival (Sawyer et al. 2009a).

During winter months, additional stress can be particularly harmful because a deer's energy balance is already operating at a deficit (Wallmo et al. 1977). In addition, the diversion of energy reserves can be detrimental to other vital functions during the life cycle such as gestation and lactation. An environmental assessment of oil and gas development in the Glenwood Springs (CO) Resource Area expressed concern these impacts could ultimately have population effects through reduced production, survival, and recruitment (USDI 1999).



Predicted levels of mule deer use before and after natural gas development in western Wyoming. Avoidance of well pads can create indirect habitat losses that are considerably larger than direct habitat loss (from Sawyer et al. 2006)

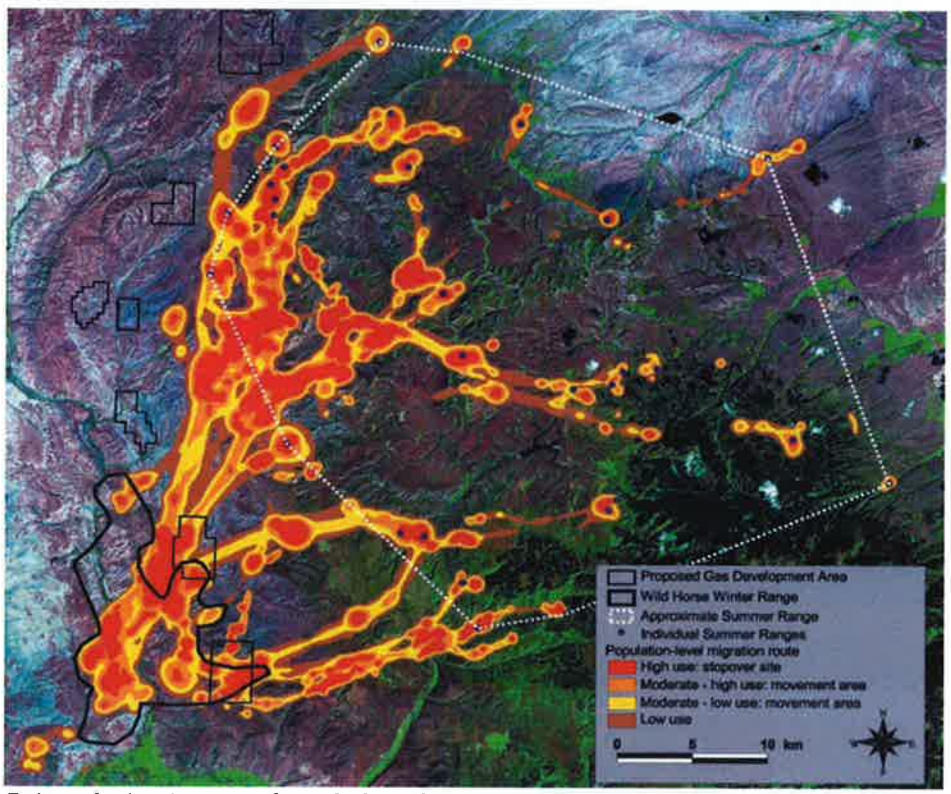
Disturbance and Displacement
Increased human presence and activity, equipment operation, vehicle traffic, and noise related to wells and compressor stations, etc. are primary factors leading to avoidance of a developed area by wildlife (Barber et al. 2010). The avoidance response by mule deer (indirect habitat loss) extends the influence of each well pad, road, and facility to surrounding habitats. In winter ranges of western Wyoming, mule deer were shown to prefer habitats 1.2 to 1.8 miles away from well pads (Sawyer et al. 2006, 2009b).

During all phases of well field development and operation, roads tend to be the most significant concern because they often remain open to unregulated use. This contributes to noise and increased human presence within the development area. Rost and Bailey (1979) documented an inverse relationship between habitat use by deer and elk and distance to roads. Sawyer et al. (2009a) found mule deer selected areas farther from well pads associated with higher levels of traffic, primarily heavy truck traffic used to remove condensate from producing wells. This 'displacement' effect can result in the under use of otherwise suitable habitats near infrastructure and disturbances and over use of habitats in more distant locations. Displacement also adds to the potential for depredation problems within nearby agricultural properties. Some other consequences of increased human presence include, but are not limited to, mortality and injury due to vehicle collisions, illegal hunting, and harassment from a variety of increasing recreational activities such as OHV use.

Habitat Fragmentation and Isolation
Human caused habitat fragmentation creates landscapes fundamentally different from those shaped by natural processes to which species have adapted (Noss and Cooperrider 1994). Human caused changes often manifest as altered plant composition, often dominated by weedy and invasive species. This, in turn, changes the type and quality of the food base as well as the structure of the habitat. When the ability to move between important daily or seasonal habitats (e.g., parturition areas, winter range, etc.) is severely disrupted, abandonment of habitat ultimately could result.

When planning developments, it is critical to consider these corridors and how to avoid or mitigate impacts in order to sustain deer migration corridors (Merrill et al. 1994). Sawyer et al (2009c) recently developed a framework to identify and prioritize mule deer migration routes for landscape-level planning. Such a framework may improve

The Rosa gas field in northwestern New Mexico shows an example of extreme impact. (Photo courtesy of NMDGF)



Estimated migration routes for mule deer relative to proposed gas development in southwest Wyoming. High-use areas represent stopover sites presumably used as foraging and resting habitat, whereas moderate-use areas represent movement corridors (from Sawyer et al 2009c).

both management and planning and ensure potential impacts to mule deer migration routes are minimized. In much of the Southwest, mule deer do not engage in predictable migrations, but may make long-distance "nomadic" movements based on seasonal variation in water and food availability. Flexibility in movement across ranges can be ultimately reflected in the survival and productivity of the deer population and likely enhances their ability to recover from population declines.

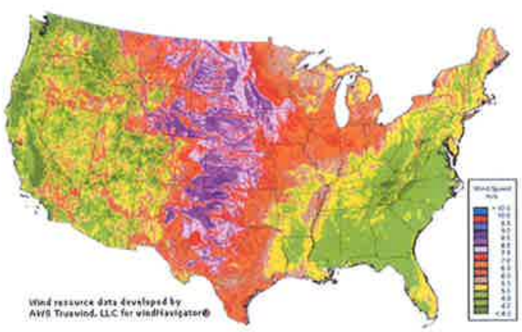
Secondary Effects

The severity of activities associated with support or service industries linked to development often equals or exceeds that of the direct effects described above. These impacts are similar to those that occur during construction and operations. Additional human presence from increased support industries and community expansion will contribute to human-wildlife interactions and declines in mule deer habitat availability and quality.

Roads, pipelines, and transmission corridors not only remove habitat, but also have the potential to contaminate ground and surface water supplies. Noxious weeds introduced by equipment can infiltrate roadside impact zones and cause additional negative impacts such as non-native bacteria, viruses, insect pests, or chemical defense compounds with toxic or allergenic properties (NMDGF 2007). In addition, these invasive species can spread to adjoining native plant communities.

Impervious roads and disturbed pipeline corridors increase surface water runoff which can reduce infiltration, lower the water table, and result in lower rangeland productivity. This problem will increase if the nation's energy infrastructure is expanded as recommended in the Energy Policy Act of 2005.

Activities occurring at the well site (drilling, pumping, etc.) or associated with product transportation to other destinations via pipeline or vehicle may lead to the release of a variety of toxic hydro-carbon based compounds. These compounds are common by-products and can pose serious health risks to not only employees, but also the environment and mule deer in the surrounding area. All these events can decrease the amount of area available to mule deer and other wildlife. Finally, potential exists for rendering an area useless to wildlife for an indeterminable amount of time unless careful consideration is given to planning and implementing quality mitigation and reclamation programs.



Wind energy resource potential in the U. S. (U.S. Department of Energy, Natural Renewable Energy Laboratory)

Construction of wind turbines can create habitat disturbances similar to other forms of energy development. (Photo by J. Heffelfinger/AGFD

WIND ENERGY DEVELOPMENT

Background

Wind-energy development is a component of the nationwide effort to reduce dependence on foreign oil and minimize carbon emissions associated with energy derived from oil, gas, and coal. At the end of 2007 the U. S. had the second highest cumulative wind capacity globally. In 2009, the U.S. wind industry installed 10,010 megawatts (MW) of generating capacity, breaking U.S. installation records for the third year in a row. Wind power represented 39% of all U.S. electric generation capacity additions for the year (USDOE 2010). This rate of development is expected to continue, and perhaps to accelerate, as U.S. energy policy emphasizes independence from foreign oil and reduction of carbon emissions. The USFWS and members of the Wind Turbine Guidelines Advisory Committee (USFWS 2010) recognize wind-generated electrical energy is renewable, and is considered to be generally environmentally friendly. The U.S. Department of Energy (DOE) estimates that a single 1.5 megawatt (MW) wind turbine displaces 2,700 metric tons of CO_2/year compared with the current U.S. average utility fuel mix. Wind energy development is proceeding without basic fact-finding research on the environmental consequences and impacts to mule deer.

Although fossil fuel consumption and carbon emissions are largely confined to the manufacture, construction, and maintenance aspects of wind power generation, wind farms themselves are an intensive, industrial-scale use of the land and have the potential to impact mule deer habitats throughout the West. With current technology, individual turbines typically generate in the range of 1.5-2.0 megawatts each. Towers range from 212 to >260 feet tall with blade sweeps of 328 to >400 feet above ground level. For maximum generating efficiency, tower strings are separated by approximately 10 rotor diameters, and individual towers within strings are separated by 3 rotor diameters. Wind farms incorporate a road network to facilitate access for turbine maintenance. In addition, power lines provide connection to transfer stations that connect to nearby transmission lines. Based on other wildlife energy research (Sawyer et al. 2006, 2009a), associated infrastructure has potential to affect mule deer.

The open areas mule deer occupy usually have high potential for wind energy development. (Photo by S. Gray, TPWD)

Issues and Concerns

Little is known about the effect of wind power development on mule deer. Although research on avian species and bats has received much attention in recent years, very little research has been done to evaluate impacts on larger mammals. The USFWS (2011) states siting of a wind energy project is the most important element in avoiding effects to wildlife and their habitats. The direct impact from surface disturbance may be relatively small in scope as turbines and roads typically constitute a small total acreage within a development area (WGFD 2010b). However, indirect impacts affecting habitat use by ungulates may be much larger. Due to the acreages that large-scale wind projects encompass (10,000- to 100,000-acre project areas), the potential exists to displace mule deer from important seasonal habitats. If displacement does occur, it may affect migration routes, parturition areas and important summer ranges, all of which provide essential seasonal habitat components to maintain mule deer populations. Other indirect effects identified by the USFWS (2011) include introduction of invasive vegetation that result in alteration of fire cycles; increase in predators or predation pressure; decreased survival or reproduction; and decreased use of the habitat as a result of habitat fragmentation.

The transmission corridors that transfer energy production to electrical grids may represent a greater impact than the actual siting of wind turbines. Transmission corridors and any associated roads can cause direct mortality and remove habitat, but they also have the potential to fragment important habitat components. These corridors can also facilitate the spread of invasive species not native to that area (Gainer 1995, NMDGF 2007). The impact of associated corridors must be considered along with the area chosen for turbine placement when evaluating impacts (Kuvlesky et al. 2007).

Mule deer crucial habitats, especially winter ranges, are often characterized by open landscapes comprised of sagebrush-steppe or sagebrush-grassland habitat types. These areas often provide accessible lands with high potential for wind-energy development. Potential impacts to mule deer include direct and indirect habitat loss, displacement, and cumulative impacts associated with other nearby energy developments.

Mule deer have been observed to maintain populations in conjunction with coal mine development where the pace of development is slow and dependent upon bond release after successful reclamation (Medcraft and Clark 1986, Gamo and Anderson 2002). However, Sawyer and Nielson 2010) found mule deer numbers declined by 40-60% following intensive gas development of the winter range. Over a 9-year period, they found no evidence of similar mule deer declines in winter ranges adjacent to the gas field (Sawyer and Nielson 2010).

Wind energy development, like other forms of development, does include a certain amount of construction and resulting infrastructure (WGFD 2010b). Temporary and permanent roads are constructed, maintenance activities occur, and the landscape becomes fragmented. It is expected that mule deer will be displaced from habitats during construction. The impacts of long-term facility operation are unclear.

SOLAR ENERGY DEVELOPMENT

Background

Solar energy development is also a component in the nationwide effort to secure a free fuel source and reduce carbon emissions associated with energy derived from oil, gas, and coal. Solar energy development in the U. S. is viewed as a source of "green" energy. Where solar energy is being developed, habitat loss for mule deer approaches 100% within the footprint of the project. Currently, identified solar projects in Arizona alone range in size from 2,000 to >25,000 acres and, in totality, encompass an estimated potential 800,000 acres resulting in significant habitat loss for wildlife (AGFD 2010).

Photovoltaic

Photovoltaic (PV) solar systems are a series of small cells made of crystalline silicon or a thin film layer that are assembled into a panel of cells, and in turn several panels can be clustered into an array. These PV cells convert sunlight directly into electricity when the sun's photons agitate electrons in the PV cell, and electrons are then channeled directly as DC electrical current. The DC output may be converted to AC output. Photovoltaic systems have mainly been used to power small and medium-sized applications, such as supplementing energy for individual homes or facilities not connected to a main power grid. Recently, multi-megawatt PV plants are becoming more common. A proposed 550 MW power station in southern California encompassing 4,245 acres is characteristic of the trend toward larger PV stations throughout the country and world. Photovoltaic solar-energy development sites are an intensive, industrial-scale use of the land and have the potential to significantly impact mule deer and their habitats throughout the West. The advantage of PV systems from a wildlife perspective is that they use much less water than other solar technologies. No water is used to collect, transfer, or store energy; water is only needed to wash the PV panels. Although efficiency is increasing, the disadvantage is their lower productivity and greater land area required to produce the same amount of energy as more efficient systems.

Nellis Air Force Base in Nevada is home to a PV system with 72,000 solar panels that produce 14 MW of electricity. (U.S. Air Force photo by Airman 1st Class N. Y. Barclay)

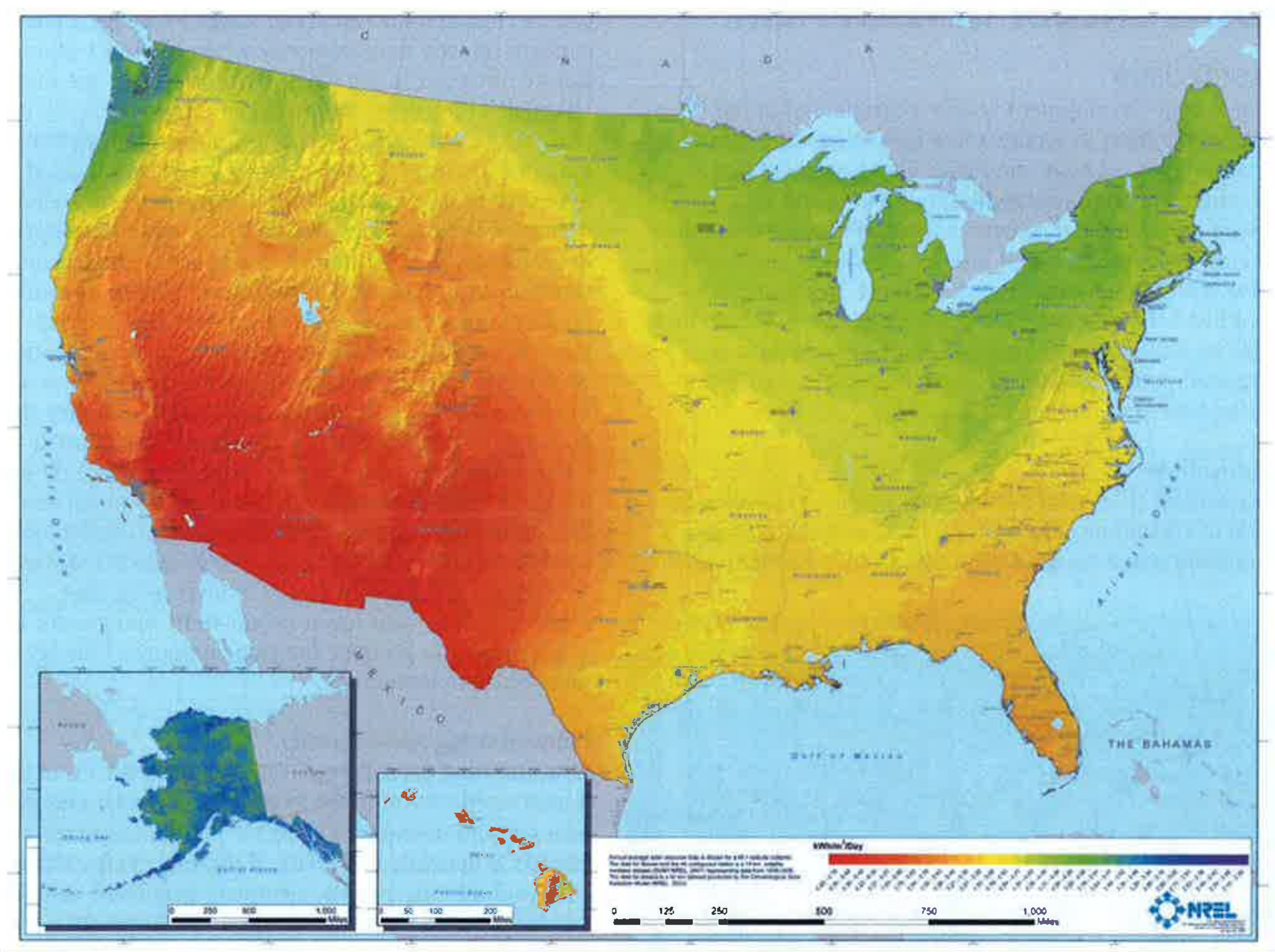
Each of these Dish/Engine units produces 10 kW of power. (Photo courtesy of Sandia National Laboratory)

Concentrating Solar Power

Concentrating Solar Power (CSP) differs from PV in that it uses a reflective surface to concentrate solar energy to heat a liquid medium to generate steam that drives a turbine to generate electricity. If thermal energy storage is included in the system, electricity generated with CSP can be supplied to an electrical grid or stored for peak usage times, nighttime, or cloudy days. This is unlike PV which does not store energy. The Southwest holds potential to generate significant amounts of electricity with this technology. However, CSP technology requires more water for energy production and washing of mirrors.

Dish/Engine Systems

Dish/Engine systems consist of a solar collector (usually a mirrored dish) that concentrates solar energy into a central power conversion unit (Stirling engine) in front of the dish. The concentrated sunlight heats a thermal receiver in the engine made of tubes filled with liquid such as helium or hydrogen. This heated gas (1,400° F) then moves pistons in the engine to directly generate electricity (DOE 2007). The dishes are designed to track movements of the sun throughout the day to assure maximum exposure. These units are well-suited for more dispersed applications because they generate relatively small amounts of energy (1-25 kW, DOE 2007). Of all the CSP technologies, Dish/Engine systems require the least amount of water, therefore minimizing impact to local hydrologic resources. However, these units can be installed on uneven ground and that could result in more solar development in important mule deer habitat.



Solar PV energy potential in the United States. (National Renewable Energy Laboratory, http://www.nrel.gov/gis/solar.html)

Parabolic Trough Systems

These CSP systems use parallel rows of long trough mirrors to reflect sunlight onto a linear receiver containing a liquid (usually an organic oil). That liquid is then superheated (about 750°F) and used to create steam which turns turbines to generate electricity. Most Parabolic Trough Systems use long parabolic troughs to simply reflect light onto the oil filled tube, but a variation called the Fresnel Reflector system uses linear mirrors to reflect sunlight onto a linear receiver suspended above the mirrors. These linear structures are oriented north-south and tilt to track the sun across the sky throughout the day. Concentrating Solar Power technology can also be combined with natural gas, resulting in hybrid systems that can provide power at any time. Currently, the largest solar trough facility in the world is being constructed near Gila Bend, Arizona and has the potential to generate 250 MW of electricity.

Power Tower Systems

Power Tower systems consist of a tall tower supporting a thermal receiver surrounded by a large field of flat "heliostat" mirrors that track the sun's movement and keep solar energy focused on the receiver. The heat concentrated (1,050° F) in the receiver is used to generate steam, which turns turbines to generate electricity. The heat can be collected and transported by water, but newer designs are incorporating molten salt because of its superior thermal energy storage properties. Individual commercial plants can produce up to 200 MW of electricity. Both parabolic trough and power tower systems can be engineered with molten salt thermal storage so that the heat can be stored and then used later to generate electricity. Molten salt integrated in a tower system allows for significantly higher power plant operating temperatures and therefore higher generation efficiencies (i.e., lower cost of electrical generation) compared with direct steam towers or trough systems.

Issues and concerns

Primary impacts to mule deer from solar energy development can be summarized into the following general categories: 1) direct loss of habitat; 2) habitat fragmentation; and 3) hydrologic changes. Each of these,

Comment Letter I9

A Parabolic Trough System uses a reflective trough to heat a tube filled with oil to produce steam to drive a turbine to generate electricity. (Photo courtesy of Sandia National Laboratory)

Compact Linear Fresnel reflectors and linear receiver. (Photo courtesy of Areva Media Department)

Abengoa's PS10 and PS20 power towers near Seville, Spain use reflectors that track the sun to concentrate the sun's energy to a focal point in the tower where liquid is heated to > 1,000° F and used to generate electricity.

alone or in conjunction with others, has the potential to significantly influence whether deer can maintain robust or depressed populations in the developed area or abandon it altogether.

Direct Loss of Habitat

Wildlife habitat loss may result from construction of large-scale solar facilities. The largest contiguous loss of habitat would occur within the perimeter of the facility's security fence. Additional habitat loss may take place through the construction of new or expansion of existing substations, new transmission lines, and associated access roads (AGFD 2010). In addition, drainages are re-routed around large facilities eliminating critical desert dry wash woodlands used as refuge and spring foraging habitats. Finally, conversion of irrigated agriculture areas to solar facilities is eliminating important water sources in some areas, although water consumption for power generation is generally comparatively lower than for agricultural use.

Habitat Fragmentation

Solar development will potentially disturb and fragment mule deer habitat during and after construction of a facility. The development of utility-scale solar fields and associated infrastructure including substations, transmission lines, and access roads will likely affect mule deer movement and habitat use (AGFD 2010). In California, several utility-scale facilities may be built adjacent to one another and are completely fenced which may impede mule deer movement over large areas. It is imperative wildlife movement corridors to and from crucial habitats are identified during pre-construction planning. These data could be used to establish the location of sensitive resources and recommend the most appropriate locations of roads, fences, and other infrastructure to minimize habitat fragmentation and disturbance.

Hydrology

Much of the Southwest, where solar energy development potential is highest, also lacks abundant water resources. In this region, water is a very crucial component that can limit mule deer populations. Any changes to hydrologic resources, ground or surface water, have the potential to affect mule deer distribution and abundance. Solar energy development can impact hydrologic resources through development of the project footprint (e.g., land disturbance, erosion, changes in runoff patterns, and hydrological alterations), project emissions (e.g., sediment runoff, chemical spills, herbicide use, and water releases), and resource use (e.g., water extraction, diversion, or change in use; AGFD 2010). Though evaporation ponds are typically located within the fenced solar facility, mule deer are attracted to any form of open water and therefore are susceptible to inadvertent poisoning due to concentrated salts and other minerals.

Because of their thermal processes, Parabolic Trough and Power Tower systems may require large amounts of water to collect and transfer heat, cool and condense steam, and also to clean mirrored surfaces. A typical wet-cooled coal or nuclear power plant consumes 500 gallons of water per megawatt hour (gal/MWh), which is similar to the amount used by a Power Tower system (DOE 2007). A water-cooled parabolic trough plant consumes approximately 800 gal/MWh, and of this, 2% is used for mirror washing (DOE 2007). Recent advances in cooling technology have shown water usage in these plants can be reduced by up to 90% with a resultant increase in energy costs of 2-10% by using dry cooling or a hybrid of wet and dry cooling technologies (DOE 2007).

GEOTHERMAL ENERGY DEVELOPMENT

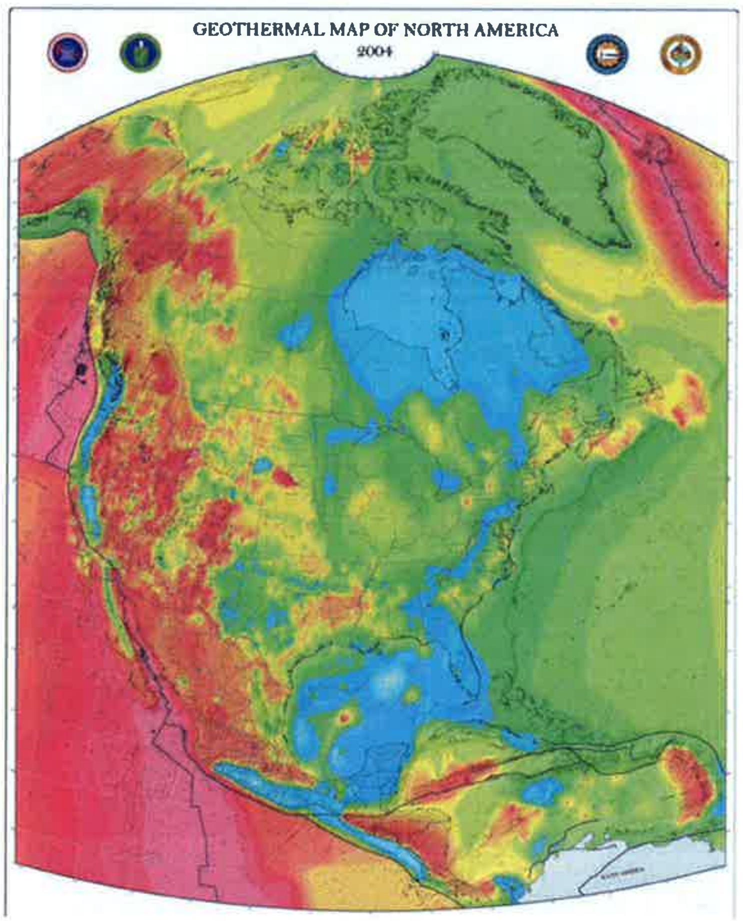
Background

Geothermal energy development has increased 20% worldwide in the last five years (Holm et al. 2010). The 2010 figures reflect 10,715 MW on line, generating 67,246 gigawatt hours (GWh) of power with a projected growth to 18,500 MW by 2015. Seventy countries currently have geothermal power projects proposed or under development. Geothermal capacity increased by 530 MW in the U.S. over the past 5 years, the largest growth logged by any single country. From a continental perspective, the largest growth occurred in Europe and Africa. Although the growth is encouraging, overall the resource as a whole is under-utilized. Some countries are developing only a small amount of the geothermal resources available and a number of countries with resources are not developing them to any significant degree. World-wide, most of the new development is for use in direct heating or other direct use application.

In North America, development is concentrated in the western third of the continent from Alaska to southern Mexico. Some lesser resource potential occurs in the southeastern U. S.. In the U. S., the increase in geothermal development is primarily to supply off-site electrical grids. The increase in activity in the U.S. is tied to increased financial support and other incentives for development, such as the Renewable Energy Tax Credit. It is unknown how long this support will be sustained. Mexico continues to be a significant developer of geothermal power production and is currently ranked fourth in the world for installed capacity. Although Canada has not developed geothermal resources for power production, a number of projects are under consideration.

The DOE maintains a website listing incentives available in the U. S. (http://www.dsireusa.org/). A growing number of states are developing requirements (Renewable Portfolio Standards) for energy providers to include renewable energy as a percent of the power provided to their customers. This mix could include geothermal-sourced energy. A list of state standards is maintained by the DOE (http://apps1.eere.energy.gov/states/maps/renewable_portfolio_states.cfm).

In Section 225 of the Federal Energy Policy Act of 2005, the Secretaries of Interior and Agriculture were charged with developing a program to reduce (by 90 percent) the backlog of geothermal lease applications. In 2008, the Bureau of Land Management and U.S. Forest Service drafted a Programmatic Environmental Impact Statement (USDI and USDA 2008) addressing this issue. The EIS addresses alternatives that identify opportunities for development and areas with sensitive resources that should be avoided. Site-specific documentation is still required, but the programmatic EIS allows for the streamlining of the leasing process. Two primary



Geothermal resources are concentrated primarily in western North America (Blackwell and Richards 2004). Energy potential ranges from very little (blue) to high (red).

A flow test in progress at the Blue Mountain Geothermal site. The initial drilling of the wells may occupy only 2-3 acres, but this is the phase where most disturbance occurs. Photo courtesy of Bureau of Land Management, Nevada State Office.

After drilling, a fenced well casing and control equipment is left in place like this structure at the Salt Wells Geothermal well site near Fallon, Nevada (operated by ENEL North America, Inc.). Photo courtesy of Bureau of Land Management, Nevada State Office.

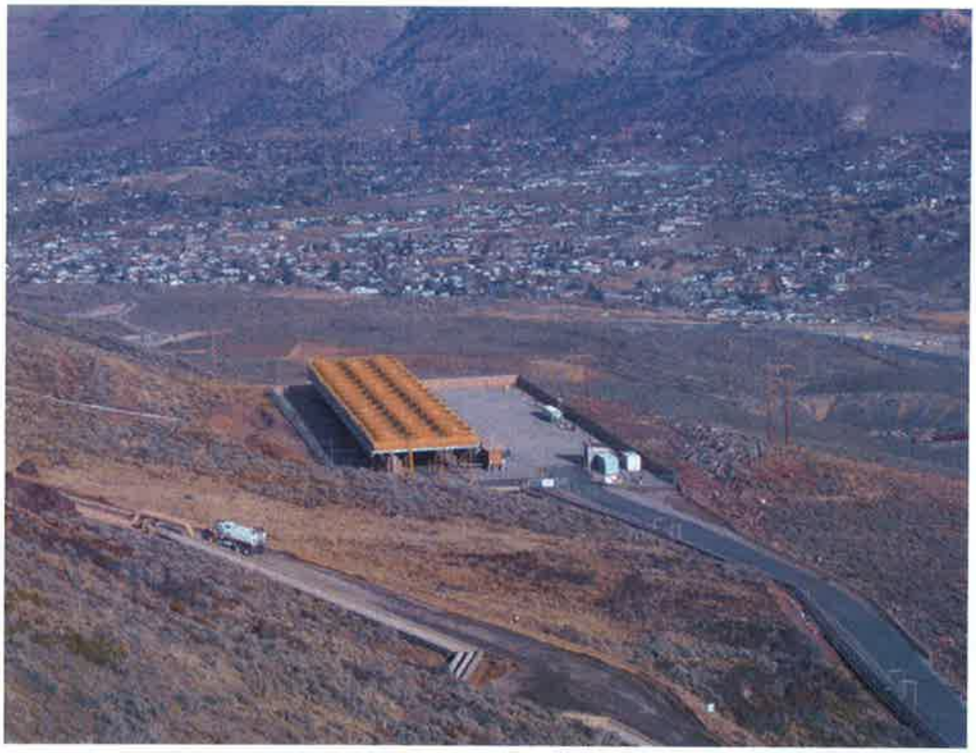
considerations determine whether a geothermal resource is suitable for development; the temperature of the resource and its extent or size. The temperature will determine how the resource could be used and the size will determine the longevity. A large amount of capital is needed to develop a resource, so developers must fully evaluate the overall value and potential before proceeding.

Depending upon its quality, a geothermal resource may produce steam (most desirable), hot water, or warm water (least desired). Current protocols are to reinject used geothermal fluids to replenish the resource, enabling it to last longer. This also allows for safe disposal of brine or high concentrations of dissolved and suspended solids, which had been a site management issue before reinjection became the standard procedure.

Geothermal resources have a range of uses, including power generation, domestic or industrial heating, recreation, fish farming and other types of aquaculture, greenhouse operation, commercial food processing, and others. Some geothermal resources have incorporated a clean surface water component which provides habitat for shorebirds and waterfowl and a source of drinkable water for larger game species and livestock.

Five components of geothermal development should be considered when assessing impacts: exploration, well drilling, power production or on-site use, transmission lines, and facility operation. Exploration usually involves site visits, drilling by a truck-mounted auger, some minimal site disturbance and noise. The effects at this early phase are short-term and temporary in nature. Well drilling results in moderate site disturbance and may include the construction of a flat well pad that could occupy 2-3 acres or more. A well casing and some apparatuses to control the well are left in place, usually within a fenced facility. Site disturbance should be temporary if the area is not needed for the development of facilities. The well site is usually connected to a primary use area by above-ground insulated piping. Existing access roads may be utilized or new roads constructed if no other access exists.

The construction of the power production or resource use facility (on-site heating, vegetable drying, electricity production, etc.) may permanently occupy ≥10 acres depending on the geothermal resource use and size of the facility. This area will represent a permanent loss of habitat (unless constructed in an area of low value initially, as recommended). Construction activity is relatively short-term, but has the potential to disturb wildlife through noise, human and vehicle presence, and habitat loss. These temporary use areas are generally reclaimed if not needed for operational activities.



The Ormat Steamboat power station at the southern edge of Reno, NV with a large brown heat exchanger, above-ground piping, and access road visible. Photo courtesy of Bureau of Land Management, Nevada State Office.

Habitat Loss, Disturbance, and Fragmentation

Impacts of geothermal energy exploration, development and extraction in mule deer habitat can be similar to those caused by oil and gas development, albeit at a smaller scale. Although pertinent to this section, there is no need to reiterate similar issues and concerns related to the direct loss of habitat, physiological stress on deer, disturbance and displacement from important habitat, fragmentation and isolation of important habitat components, and secondary effects.

It is important to consider the total impact of the project, not only at the well site and power production area, but also from the transmission corridors and access roads used in construction and operation of facilities. These linear components are more likely to fragment habitat and could present a greater concern than the core facilities. These effects will not likely be as severe or extensive as experienced from oil and gas development, but should still be evaluated by resource managers on a case by case basis.

Associated linear project components such as power lines, pipelines, and roads create additional permanent impacts to mule deer habitat if existing linear disturbances are not followed. Depending upon where the facilities are sited and how they are constructed, they can result in temporary disturbance during construction as well as permanent habitat loss and fragmentation.

Site activity is greatly diminished during facility operation. The operation phase entails periodic human presence including intermittent noise and vehicle use. Depending upon the technology employed, if resources are captured and re-injected there may be a decrease in the amount of surface water available. Also, a portion of the facility may be fenced which may impede deer movements across the site.

Issues and Concerns

In general, geothermal resource development has minimal impact on mule deer. Sites are usually compact in contrast with other forms of energy development such as wind, solar, or fossil fuels. All temporary disturbance is reclaimed and long-term disturbance at the site (human presence, vehicles, or noise) should be minimal. There can be a few potential impacts to mule deer such as above ground pipelines and elevated noise levels (USDI and USDA 2008).

Related Concerns

The Programmatic EIS for geothermal leasing (USDI and USDA 2008) identified several related concerns that may be an issue in some phases of geothermal energy development. Although direct habitat loss, disturbance, and fragmentation are the most obvious impacts of geothermal projects, invasive vegetation, fire, direct mortality, noise, and chemical contaminants warrant additional vigilance of managers.

Spread of invasive vegetation could result from construction activity, especially ground disturbance, vehicle traffic, or creation of new access routes. Once established, some invasive species have proven difficult or impossible to control. As demonstrated by several cases in the West, invasive plant species can alter entire vegetative communities, resulting poorer quality mule deer habitat on a landscape scale.

Fires accidentally ignited during construction or maintenance activities can alter the natural fire regime and produce undesirable changes in plant communities. An increase in fire frequency provides opportunities for invasive plants to become established and may result in loss of desirable vegetation for many years. Once invasive species such as cheatgrass become established, the fire cycle and natural plant community may be permanently altered, especially in native shrub-dominated communities.

Additional issues include: 1) direct mortality of mule deer from vehicle collisions, open trenches or ditches, fencing and above-ground piping, 2) intermittent noise associated with construction activity and some operational activities (e.g., steam venting), and 3) infrequent exposure to contaminants such as vehicle fuels, herbicides, or accidental spills (USDI and USDA 2008).

Photo courtesy of Tom Newman

CONSOLIDATED GUIDELINES

General guidelines and additional mitigation recommendations (Habitat Mitigation Options) are provided to minimize impacts of energy development on mule deer and their habitat. Recommendations are also categorized according to impact thresholds. When energy development is proposed on public lands, federal permitting agencies have the dual responsibility of authorizing the development while conserving surface resources, including wildlife and other environmental values.

A. GENERAL GUIDELINES

1. Consult the appropriate wildlife and land management agencies at least 2 years prior to submitting project permit applications to allow time for appropriate studies and inventories to be conducted and site-specific recommendations developed (TWS 2008a).
2. Identify minimum quality and quantity of information necessary for analysis before a lease or annual permit for construction can be issued (WAFWA 2010).
3. Develop a map of important habitats and potential conflict areas. Developers should use the map as one of the first steps in pre-development planning to identify important, sensitive, or unique habitats and wildlife in the area (TWS 2008b).
4. Utilize the Decision Support System developed by the Western Governor's Association to coordinate planning.
5. Use the most current wildlife data and applicable plans to identify important wildlife habitat resources that should be conserved (WAFWA 2010).
6. Design configurations of energy development to avoid or reduce unnecessary disturbances, wildlife conflicts, and habitat impacts. Where possible, coordinate planning among companies operating in the same area to minimize the footprint of development (e.g., negotiate unitized field development plans, co-locate power lines and pipe lines in existing corridors).
7. Implement timing stipulations that minimize or prohibit activities during critical portions of the year.
8. At a minimum, construction activities should be suspended from November 15-April 30 on areas designated as crucial winter range. If project features will be sited within identified parturition areas, activities should be suspended from 1 May – 15 June. Minimize disturbances and activities within producing well fields during the same timeframe. Include provisions in subcontractor agreements requiring adherence to the same seasonal use restrictions observed in company operations.
9. Avoid placing facilities in locations that bisect major migration corridors and other important habitats. Also, avoid unstable slopes and local factors that can cause soil instability (groundwater conditions, precipitation, seismic activity, slope angles, and geologic structure).
10. Plan the pattern and rate of development to avoid the most important habitats and generally reduce extent and severity of impacts (TWS 2008a). Implement phased development in smaller increments with concurrent reclamation of abandoned wells.
11. Disturb the minimum area (footprint) necessary to efficiently develop and operate the facility.
12. Design and implement habitat treatments sufficient to maintain habitat functions on-site. In cases where offsite mitigation would provide greater benefits than onsite mitigation, the offsite mitigation should be located within the same landscape unit indentified in consultation with the state or provincial wildlife agency. Habitat treatments should include appropriate options from Habitat Mitigation Options, selected through consultation with the state or provincial wildlife agency.
13. Mitigation should be planned to offset the loss of habitat effectiveness throughout the areas directly and indirectly affected by energy project development. Management practices identified in Habitat Mitigation Options may reduce the extent of habitat treatments needed to offset or mitigate the effect.
14. When it is not possible to avoid, minimize, or effectively mitigate impacts through other means create a Mitigation Trust Account. The operator would contribute funding to a mitigation trust account based on the estimated cost of habitat treatments or other mitigation needed to restore the functions and effectiveness of impacted habitats.
15. For mitigation planning purposes the acreage basis for mitigation will be the amount of surface that is directly disturbed plus the additional area on which habitat functions are impacted by noise, activities, and other disturbance effects. Mitigation recommendations may be refined and possibly standardized as habitat treatments are implemented and their effectiveness monitored.

Oil, Gas, & Geothermal General

16. When geological substrate and hydro-carbon resource types lend themselves to directional technologies, drill multiple wells from the same pad.
17. Utilize mats to support drill rigs in order to eliminate top-soil removal.
18. Locate drill pads, roads, and facilities in the least sensitive areas or cluster these features in locations already impacted.
19. Locate drill pads, pipelines, roads, and facilities below ridgelines or behind topographic features, where possible, to minimize visual and auditory effects, but away from streams, drainages, and riparian areas as well as important sources of forage, cover, and habitats important to different life cycle events (reproduction, winter, parturition, and rearing).

Additional Guidelines for Moderate Impact Developments (2-4 well pad locations/mile^2 with no more than 60 acres of total disturbance).

20. Apply all general guidelines prescribed above to retain as much effective habitat as possible.
21. Develop multiple wells from single pads by employing directional or horizontal drilling technologies and unitized development. The highest management priority within crucial winter range is to recover oil and gas resources with the least possible infrastructure and associated disturbance. Where several companies hold smaller, intermingled leases, the cumulative impact could be reduced substantially if the companies enter a cooperative agreement (called unitization) to directional drill from common well pads.
22. Use clustered development configurations. Locate well pads, facilities and roads in clustered configurations within the least sensitive habitats. Clustered configurations are a geographical and not necessarily a temporal (i.e., "phased development") consideration.
23. Install a liquid gathering system to convey liquids from producing wells to a centralized collection point. If fluids cannot be piped off site, enlarge storage tank capacity to minimize truck trips to ≤1/month and to eliminate trips during sensitive times of year. If the potential for production of liquids is unknown, but exceeds 1 truck trip/month after production begins, consider retrofit the field with pipelines or larger storage.
24. Install telemetry to remotely monitor instrumentation and reduce or eliminate travel required to manually inspect and read instruments.
25. Develop a travel plan that minimizes frequency of trips on well-field roads. Include provisions in subcontractor agreements requiring adherence to the same travel plan provisions observed in company operations.
26. As appropriate, gate and close newly constructed roads to public travel during sensitive times of year.
27. Implement a robust wildlife monitoring program such as the Before-After Control-Impact (BACI) research design to detect and evaluate ongoing effects such as mortalities, avoidance responses, distribution shifts, habituation, evidence of movement or migration barriers, and depressed productivity (e.g., low fawn:doe ratios), and to assess the effectiveness of mitigation. Monitor vegetation utilization within and outside the well field.
28. If it is not possible to maintain habitat effectiveness within or immediately adjacent to the well field, off-site and off-lease mitigation should be considered on a case-by-case basis. The primary emphasis of off-site or off-lease mitigation is to maintain habitat functions for the affected population or herd as close to the impacted site as possible and within the same landscape unit. Off-site and off-lease mitigation should only be considered when feasible mitigation options are not available within or immediately adjacent to the impacted area, or when the off-site or off-lease location would provide more effective mitigation than can be achieved on-site.

Additional Guidelines for High Impact Developments (>4 well pad locations/mile^2 or disturbance exceeding 60 acres).

29. Adhere to all general guidelines and those applicable to "Moderate Impact Developments."
30. Develop the well field in smaller incremental phases (phased development) to reduce the overall impact of a high-density field. Although complex geological, technical, and regulatory issues may constrain the use of this strategy, it should be considered where feasible.
31. Opportunities may exist to partially offset the loss of crucial winter range by completing habitat rehabilitation and enhancement projects in appropriate locations outside the well field (off-site mitigation). This type of mitigation is difficult and should never be looked upon as a prescriptive solution to authorize high-density well fields in crucial winter range. The most effective solution is to avoid high-density developments. If avoidance is not feasible, plan effective habitat treatments in locations selected to minimize the loss of habitat function for the affected herd or population, within the same landscape unit.

Wind and Solar

32. Site wind and solar energy developments within areas already affected by other forms of development (e.g., urban areas, agricultural land, oil and gas fields, and existing or reclaimed mines). Avoid further fragmentation of intact native habitats.
33. Avoid locating wind and solar energy facilities within crucial mule deer winter ranges.

B. ROADS

1. Use existing roads, no matter how primitive, where they exist in areas that do not impact wildlife habitat and are not within environmentally sensitive areas.
2. If new roads are needed, close unnecessary roads that impact important mule deer habitat.
3. Roads should not bisect or run immediately adjacent to any water feature, or prevent mule deer from reaching adjacent habitat.
4. Construct the minimum number and length of roads necessary.
5. Coordinate road construction and use among companies operating in the same area.
6. Design and construct roads to a minimum standard to accommodate their intended purpose.
7. Design roads with adequate structures or features to discourage off-road travel.

Comment Letter I9

C. TRANSMISSION CORRIDORS

1. Use existing utilities, power lines, roads, and pipeline corridors to the extent feasible.
2. Site new corridors in areas of already disturbed or poor quality mule deer habitat or adjacent to other linear disturbances.
3. Bury power lines whenever possible. All trenching should occur with concurrent back filling. All buried power lines should be placed in or adjacent to roads or other existing utility rights-of-way.
4. If fence construction is necessary, consult with the state or provincial wildlife agency to determine appropriate locations and designs based on wildlife resources of the site.
5. Construct above ground pipelines conveying geothermal fluids with sufficient ground clearance to allow adequate mule deer passage.
6. Conduct concurrent backfilling with trenching operations to minimize the amount of trench left open.

D. NOISE AND LIGHTING

1. Minimize noise to the extent possible. All compressors, vehicles, and other sources of noise should be equipped with effective mufflers or noise suppression systems (e.g., "hospital mufflers").
2. Wind turbines and other non-motorized structures should be designed to minimize noise.
3. Whenever possible, use electric motors instead of diesel engines to power compression equipment.
4. Use topography to conceal facilities and reduce noise disturbance in areas of known importance.
5. Manage on-site lighting to minimize disturbance to mule deer.

E. TRAFFIC AND HUMAN DISTURBANCE

1. Develop a travel plan that minimizes the amount of vehicular traffic required to monitor and maintain wells and other facilities (USDI 2005).
2. Limit traffic to the extent possible during high wildlife use hours (within 3 hours of sunrise and sunset).
3. Use pipelines (liquid gathering systems) to transport condensates off site.
4. Transmit instrumentation readings from remote monitoring stations to reduce maintenance traffic.
5. Post speed limits on all access and maintenance roads to reduce wildlife collisions and limit dust (30-40 mph is adequate in most cases).
6. Employees should be instructed to avoid walking away from vehicles or facilities into view of wildlife, especially during winter months.
7. Prohibit employees from carrying firearms in development fields or sites.
8. Institute a corporate-funded reward program for information leading to conviction of poachers, especially on winter range.

F. HYDROLOGIC RESOURCES (AGFD 2010)

1. Prepare a water management plan in those regions and for those operations that discharge surplus water of questionable quality (e.g., Coal Bed Methane).
2. Develop a contingency plan to prevent potential groundwater and surface water contamination.
3. Develop a storm water management plan to ensure compliance with state, provincial, and federal regulations and prevent off-site migration of contaminated storm water or increased soil erosion.
4. Spread excess excavated soil to match surrounding topography or dispose of in a manner to minimize erosion and leaching of hazardous materials.
5. Incorporate best management practices for addressing hydro-modification impacts (e.g., retention basins for treatment of water from runoff and infiltration and recharge of the groundwater basin).
6. Refuel in a designated fueling area that includes a temporary berm to contain the spread of any potential spill.
7. Use drip pans during refueling and under fuel pump and valve mechanisms of any bulk fueling vehicles parked at the project site to contain accidental releases.
8. Identify sustainable yields of groundwater and nearby surface water bodies.
9. Limit the withdrawal of water at the facility so it does not exceed the sustainable yield in order to preserve natural discharge sites (springs), ponds, and wells that may provide sources of water and enhanced forage for mule deer.
10. Avoid streams, wetlands, and drainages where possible. Locate access roads to minimize stream crossings and cause the least impact where crossings cannot be avoided. Where access roads would cross a dry drainage, the road gradient should be 0% to avoid diverting surface waters from the channel. Cross water bodies at right angles to the channel and in locations producing minimum impact.
11. Develop a Stormwater Pollution Plan. The Environmental Protection Agency (EPA) website contains templates for such a plan: http://cfpub.epa.gov/npdes/stormwater/swppp.cfm.
12. Locate contaminated ponds in places wildlife tend to avoid, such as areas of high human use or highly disturbed areas.
13. Waste water contaminant ponds should be fenced to prevent mule deer access.
14. Monitor ponds to detect wildlife mortalities. Develop a contingency plan to handle wildlife mortality incidents (e.g., if a waterfowl die-off is observed contact state, provincial, or federal agencies as soon as possible and have a contingency plan to handle the situation).
15. Maintain existing surface waters that mule deer use as a water source. Consider constructing freshwater ponds or wetlands nearby to attract wildlife away from

potentially toxic evaporation ponds. Water sources should not be placed in areas where increased wildlife-vehicle collisions could occur.

16. Monitor toxicity of the ponds and prepare a mitigation plan to address any rise in toxicity levels. The plan should include short- and long-term measures to deter wildlife from the area.
17. Rely on "dry cooling" technology to reduce water consumption at solar facilities. If this is not feasible, the hybrid parallel wet-dry cooling method should be used.

G. POLLUTANTS, TOXIC SUBSTANCES, DUST, EROSION, AND SEDIMENTATION

1. Avoid spilling or dumping oil or fuel (synthetic or hydrocarbon) or molten salts. Oil spills should be contained and all contaminated soil removed. Oil pits should not be used, but if absolutely necessary, they should be enclosed in netting and small-mesh fence. All netting and fence must be maintained and kept in serviceable condition.
2. Produced water from oil, gas, and geothermal facilities should not be pumped onto the surface except when beneficial for wildlife, provided water quality standards for wildlife and livestock are met. Produced water of suitable quality may also be used for supplemental irrigation to improve reclamation success.
3. Re-injection of water into Coal Bed Methane or geo-thermal sites should be considered when water quality is of concern.
4. Hydrogen sulfide should not be released into the environment.
5. If inorganic salts are spilled in solar operations, the molten material should be immediately cooled to a solid, contained within concrete dikes and curbing, and removed or recycled back into the system (AGFD 2010).
6. To contain hazardous materials such as arsenic, cadmium, or silicon, create a protocol for responsible disposal of decommissioned PV solar panels. Prior to facility construction, determine whether PV panel manufacturers provide an Extended Producer Responsibility (EPR) service which requires the manufacturer to take back their product, thus ensuring panels are recycled safely and responsibly, or recycle PV panels at existing responsible electronic waste recycling facilities or at facilities that recycle batteries containing lead and cadmium.

H. MONITORING AND ENVIRONMENTAL RESPONSE

1. Monitor conditions or events that may indicate environmental problems (e.g., water quality in nearby rivers, streams, wells, etc.). Such conditions or events can include any significant chemical spill or leak, detection of multiple wildlife mortalities, sections of roads with frequent and recurrent wildlife collisions, poaching and harassment incidents, severe erosion into tributary drainages, migration impediments, wildlife entrapment, sick or injured wildlife, or other unusual observations.
2. Immediately report observations of potential wildlife problems to the state or provincial wildlife agency and, when applicable, federal agencies such as USFWS or EPA.
3. Apply GIS technologies to monitor the extent of disturbance annually and document the progression and footprint of disturbances. Use this spatial data to evaluate the cumulative effects of existing and proposed impacts. Release compilations and analyses of this information to resource management agencies at least annually.

I. PUBLIC RECREATION AND ACCESS

1. Prior to finalizing development and travel management plans, state or provincial wildlife agencies should be consulted to ensure adverse impacts to hunting opportunity are prevented, minimized, or mitigated.
2. As projects are constructed, there is a possibility projects located over established roads may impede or restrict access to public lands. To guard against the creation of illegal roads and maintain access to public lands, coordinate with the appropriate landowners to create alternate travel routes. These alternate routes must be created in close proximity to the project and should be similar in function to the original routes. Signs should be installed to indicate public travel routes while project construction takes place and remain in place after project completion (AGFD 2010).
3. Hunting access should continue within developments on public lands and on private land with landowner permission.

Comment Letter I9

J. RESEARCH AND SPECIAL STUDIES

1. Where there are questions or uncertainties regarding cumulative impacts, the degree of impact to specific resources, or effectiveness of mitigation, industries and companies should fund special studies to collect data for evaluation and documentation.
2. Conduct research to better understand wind-energy development impacts. Research should primarily investigate deer distribution pre- and post-development, abundance, and demography. Research on habitat should document vegetation species composition, utilization rates, location of migration corridors, location of important seasonal habitats, and changes in habitat use and distribution of deer.
3. Use the Before-After Control-Impact (BACI) research design. Data should be collected ≥2 years prior to development and 3 years post-development to provide a quantitative basis for estimating development impacts.
4. Evaluate alteration of vegetation and micro-climate adjacent to energy development.
5. Evaluate movement and behavior patterns of mule deer pre- and post-construction, especially the impact on movement corridors.
6. More research is needed on population-level effects of energy development on mule deer.

K. NOXIOUS WEEDS

1. Control noxious and invasive plants that appear along roads and at development sites and ancillary facilities (USDI 2005).
2. Designate specific areas to clean and sanitize all equipment brought in from other regions. Seeds and propagules of noxious plants are commonly imported by equipment and mud clinging to equipment.
3. Request employees to clean mud from footwear before traveling to the work site, to prevent importation of noxious weeds.

L. INTERIM RECLAMATION

1. Establish effective, interim reclamation on all surfaces disturbed throughout the operational phase of the development.
2. Reclaim abandoned or decommissioned development sites concurrently with development of new sites.
3. Salvage topsoil from all construction and re-apply during interim reclamation.
4. Approved weed-free mulch application should be used in sensitive areas (dry, sandy, steep slopes).
5. A variety of native grasses, shrubs, and forbs endemic to the site should be used for revegetation. Non-native vegetation is discouraged and should not be used unless native forbs and grasses are not available or are ineffective in quickly recovering the site.
6. Continue to monitor and treat reclaimed surfaces until satisfactory plant cover is established.
7. Solar facilities need not be fenced. Native and preferred non-native forbs and grasses should be established to sustain use by wildlife during energy production.

M. FINAL RECLAMATION

1. Develop a comprehensive reclamation plan addressing vegetation and hydrology considerations, which includes specifically measurable objectives for wildlife and habitat so success can be achieved during the production phase of development (WAFWA 2010).
2. Salvage topsoil during decommissioning operations and reapply to reclaimed surfaces.
3. All buildings, well heads, turbines, solar arrays, and ancillary facilities should be removed.
4. Replant a mixture of forbs, grasses, and shrubs that are native to the area and suitable for the specific ecological site.
5. Restore vegetation cover, composition, and diversity to achieve numeric standards commensurate with the ecological site.
6. Do not allow grazing on re-vegetated sites until the plants are established and can withstand herbivory as noted through monitoring.
7. Reevaluate the existing system of bonding. Bonds should be set at a level adequate to cover the company's liability for reclamation of the entire development project.

HABITAT MITIGATION OPTIONS

The habitat enhancements suggested in this section are largely based on a similar document used successfully in Wyoming (WGFD 2010a). These represent options for companies and resource agencies to consider in designing an integrated mitigation plan to sustain mule deer habitat functions potentially affected by energy developments. The list is not exhaustive; many additional options and practices could also provide effective mitigation. Regional biologists, company personnel, and others may have alternative suggestions to address specific circumstances.

Corporate-owned Lands under Conservation Management – Management of corporate-owned or -controlled lands may be one of the best alternatives to achieve effective, long-term mitigation of energy development impacts. Availability of corporate-owned lands can provide managers with increased options and flexibility to mitigate impacts and potentially provide increased recreational access.

Conservation Easements – This concept includes numerous options and practices for mitigating impacts to the most crucial habitats. These options and practices include maintaining open space, excluding subdivisions, keeping an agricultural base of operations compatible with wildlife, excluding fencing or other developments that are restrictive to wildlife migration and movement, grazing management systems, etc. Where appropriate, conservation easements could be established through the formation of a land trust, or by earmarked contributions to an existing land trust. Depending upon the amount of property rights acquired, costs range from 35% to 95% of fee title acquisition. The mitigation would be in effect as long as the easement is held and monitored by the assignee. The intent is to maintain the easements at least throughout the time habitat functions are disrupted, including the time required for reclamation to mature.

Grazing or AUM Management Program – This practice could include many options, with the owner's or permittee's concurrence, to improve habitat quality for wildlife. Some options might include: 1) paying for private grazing AUMs to provide rest or treatments on public lands; 2) paying for a portion of the AUMs within an allotment; 3) providing for rest or treatments and once completed, turning the land back to grazing use; 4) purchase of AUMs to reduce grazing use on important habitats; or 5) establishing forage reserves (grass banks) to provide management flexibility for habitat treatments and livestock grazing. Other grazing management options include electric fencing to provide pasture systems, herding, water developments, etc. These could all be utilized to better manage grazing animals to improve range and habitat conditions.

Habitat Improvements – Several states and NGOs are currently implementing programs to acquire, protect, and improve to recover mule deer populations. The same habitat management practices could be applied as off-site mitigation where important habitats could potentially be improved to restore habitat functions impacted in other areas. Before habitat treatments are applied, qualified personnel should evaluate the prospective site to determine its condition, improvement potential, and ecologically appropriate treatments. Practitioners are encouraged to consult the Mule Deer Habitat Guidelines in their respective ecoregion for recommended practices (www.muledeerworkinggroup.com). Early consultation with the state or provincial wildlife management agency and land management agencies can greatly assist with the planning of effective habitat work and selection of appropriate treatments.

LITERATURE CITED

Arizona Game and Fish Department (AGFD). 2010. Guidelines for solar development in Arizona. Arizona Game and Fish Department, Phoenix, USA.

Baker, W. L. 2006. Fire and restoration of sagebrush ecoystems. Wildlife Society Bulletin 34:177-185.

Barber, J. R., K. R. Crooks, and K. M. Fristup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology and Evolution 25:180-189.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:1-39

Bergman, E. J., C. J. Bishop, D. J. Freddy, and G. C. White. 2007. Evaluation of winter range habitat treatments on over-winter survival and body condition of mule deer. Wildlife Research Report, Colorado Division of Wildlife, Fort Collins, USA.

Bishop, C. J. 2007. Effect of enhanced nutrition during winter on the Uncompahgre Plateau mule deer population. Dissertation, Colorado State University, Fort Collins, USA

Blackwell, D. D., and M. Richards. 2004. Subset of geothermal map of North America. American Association of Petroleum Geologists, Tulsa, Oklahoma, USA. <http://www.smu.edu/geothermal> Accessed 1 September 2010.

Bunting, S. C., B. M. Kilgore, and C. L. Bushey. 1987. Guidelines for prescribed burning sagebrush-grass rangelands in the northern Great Basin. U.S. Forest Service General Technical Report INT-231, Ogden, Utah, USA.

Cooper, S. V., P. Lesica, and G. M. Kudray. 2007. Post-fire recovery of Wyoming big sagebrush shrub-steppe in central and southeast Montana. Report to the U.S. Department of the Interior, Bureau of Land Management, State Office. Montana Natural Heritage Program, Helena, USA.

Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009. Mapping oil and gas development potential in the U.S. Intermountain West and estimating impacts to species. PLoS ONE 4(10): e7400. doi:10.1371/journal.pone.0007400

Energy Policy Act of 2005. 2005. Energy policy act of 2005. <www.epa.gov/oust/fedlaws/publ_109-058.pdf> Accessed 17 Dec 2010.

Farrell, J. E., L. R. Irby, and P. T. McGowen. 2002. Strategies for ungulate-vehicle collision mitigation. Intermountain Journal of Sciences 8:1-18.

Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63-68.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.

Gainer, R. S. 1995. Range extension of white-tailed deer. Alberta Naturalist 25:34-36.

Gamo, R. S., and S. H. Anderson. 2002. Use of reclaimed minelands by pronghorn and mule deer. Intermountain Journal of Sciences 8:213-222.

Gill, J. A., W. J. Sutherland, and A. R. Watkins. 1996. A method to quantify the effects of human disturbance for animal populations. Journal of Applied Ecology 33:786-792.

Hebblewhite, M. 2008. A literature review of the effects of energy development on ungulates: implications for central and eastern Montana. Report prepared for Montana Fish, Wildlife and Parks, Miles City, USA.

Hebblewhite, M. 2011. Effects of energy development on ungulates. Pages 71–94 in D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington D.C., USA

Heffelfinger, J. R., and T. A. Messmer. Introduction. Pages 1-11 in J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Holm, A., L. Blodgett, D. Jennejohn, and K. Gawell. 2010. Geothermal energy: international market update. Geothermal Energy Association, Washington, D.C., USA.

Kuvlesky, W. P., Jr., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and opportunities. Journal of Wildlife Management 71:2487-2498.

Lutz, D. W., M. Cox, B. F. Wakeling, D. McWhirter, L. H. Carpenter, S. Rosenstock, D. Stroud, L. C. Bender, and A. F. Reeve. 2003. Impacts to changes to mule deer habitat. Pages 13-61 in J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Medcraft, J. R., and W. R. Clark. 1986. Big game habitat use and diets on a surface mine in northeastern Wyoming. Journal of Wildlife Management 50:135-142.

Merrill, E. H., T. P. Hemker, K. P. Woodruff, and L. Kuck. 1994. Impacts of mining facilities on fall migration of mule deer. Wildlife Society Bulletin 22:68-73.

National Energy Policy. 2001. Reliable, affordable, and environmentally sound energy for America's future. Report of the National Energy Policy Development Group. U.S. Government Printing Office, Washington, D.C.

Naugle, D. E., B. L. Walker, and K. E. Doherty. 2006. Sage-grouse population response to coal-bed natural gas development in the Powder River Basin: interim progress report on region-wide lek-count analysis. Unpublished report, University of Montana, Missoula, USA.

New Mexico Department of Game and Fish (NMDGF). 2007. Oil and gas development guidelines: conserving New Mexico's wildlife habitats and wildlife. <http://www.wildlife.state.nm.us/documents/oilandgasguidelines.pdf> Accessed 8 July 2010.

Noss, R. F., and A. Y. Cooperrider. 1994. Saving nature's legacy. Island Press, Washington, D.C., USA.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43:634-641.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009a. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052-1061.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009c. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016-2025.

Sawyer, H., F. Lindzey, D. McWhirter, and K. Andrews. 2002. Potential effects of oil and gas development on mule deer and pronghorn populations in western Wyoming. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:350-365.

Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266-1273.

Sawyer, H., and R. Nielson. 2010. Mule deer monitoring in the Pinedale Anticline project area: 2010 annual report. Western Ecosystems Technology, Inc. Cheyenne, Wyoming, USA.

Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403.

Sawyer, H., R. Nielson, and D. Strickland. 2009b. Sublette mule deer study (phase II): final report 2007 - long-term monitoring plan to assess potential impacts of energy development on mule deer in the Pinedale Anticline project area. Western Ecosystems Technology, Inc. Cheyenne, Wyoming, USA.

Stalling, D. 2003. Gas and oil development on western public lands; impacts on fish, wildlife, hunting, and angling. A report produced by Trout Unlimited's Public Lands Initiative.

The Wildlife Society. 2008a. Impacts of wind energy development on wildlife and wildlife habitat, final position statement. The Wildlife Society, Bethesda, Maryland, USA.

The Wildlife Society. 2008b. Oil and gas development in the Rocky Mountain West, final position statement. The Wildlife Society, Bethesda, Maryland, USA.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

U.S. Department of Energy (DOE). 2007. Concentrating Solar Power commercial application study: reducing water consumption of Concentrating Solar Power electricity generation. Report to Congress. U.S. Department of Energy, Washington, DC, USA.

U.S. Department of Energy (DOE). 2010. Wind and water power program: wind power today 2010. USDOE, DOE/GO-102010-3011 May 2010. http://www1.eere.energy.gov/windandhydro/wind_pubs.html. Accessed 17 May 2011.

U.S. Department of the Interior, Bureau of Land Management (USDI). 1999. Glenwood Springs Resource Area; oil and gas leasing and development: final supplemental environmental impact statement, Bureau of Land Management. Glenwood Springs Field Office, Colorado, USA.

U.S. Department of the Interior, Bureau of Land Management (USDI). 2005. Record of decision: implementation of a wind energy development program and associated land use plan amendments. Washington, D.C., USA.

U.S. Department of the Interior, Bureau of Land Management (USDI) and U.S. Department of Agriculture, U.S. Forest Service (USDA). 2008. Programmatic Environmental Impact Statement for geothermal leasing in the Western United States. FES 08-44, U.S. Government Printing Office. Washington, D.C., USA.

U.S. Fish and Wildlife Service (USFWS). 2007. 2006 national survey of fishing, hunting, and wildlife-associated recreation. <http://library.fws.gov/Pubs/nat_survey2006_final.pdf>. Accessed 7 Dec 2009.

U.S. Fish and Wildlife Service (USFWS). 2010. Wind Turbine Guidelines Advisory Committee recommendations. <http://www.fws.gov/habitatconservation/windpower/wind_turbine advisory_committee.html>. Accessed 29 Oct. 2010.

U.S. Fish and Wildlife Service (USFWS). 2011. U.S. Fish and Wildlife Service draft land-based wind energy guidelines: recommendations on measures to avoid, minimize, and compensate for effects to fish, wildlife, and their habitats. <http://www.fws.gov/habitatconservation/wind.html>. Accessed 17 May 2011.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122 – 127.

Watkins, B. E., C. J. Bishop, E. J. Bergman, B. Hale, B. F. Wakeling, A. Bronson, L. H. Carpenter, and D.W. Lutz. 2007. Habitat guidelines for mule deer: Colorado Plateau shrubland and forest ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

Western Association of Fish and Wildlife Agencies (WAFWA). 2010. Resolution on energy development, Western Association of Fish and Wildlife Agencies, USA.

Western Governor's Association. 2008. Wildlife corridors initiative. <http://www.westgov.org>. Accessed 17 Dec 2010.

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. Journal of Wildlife Management 62:214-225.

Winward, A. H. 1991. A renewed commitment to management of sagebrush grasslands. Pages 2-7 in Management in the sagebrush steppe. Oregon Agricultural Experiment Station Special Report 880. <oregonstate.edu/dept/eoarc/sites/default/files/researchhome/documents/360a.pdf >. Accessed 17 May 2011.

Wyoming Game and Fish Department (WGFD). 2010a. Recommendations for development of oil and gas resources within important wildlife habitats. Wyoming Game and Fish Department, Cheyenne, USA.

Wyoming Game and Fish Department (WGFD). 2010b. Wildlife protection recommendations for wind energy development in Wyoming. Wyoming Game and Fish Department, Cheyenne, USA.

Young, J. A., and R. A. Evans. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34:501-506.

Comment Letter I9

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Comment Letter I9

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WESTERN ASSOCIATION OF FISH & WILDLIFE AGENCIES

"Delivering conservation through information exchange and working partnerships"

Comment Letter I9

A Literature Review of the Effects of Energy Development on Ungulates: Implications for Central and Eastern Montana

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Table of Contents

List of Figures

List of Tables

Executive Summary

A literature review of >160 scientific and technical reports was conducted to review the effects of energy development ungulates, separated by important seasonal and habitat types. Effects of energy development and human activity in general were assessed for elk, mule deer, pronghorn antelope, moose, bighorn sheep and woodland caribou. Weaknesses of the existing literature in addressing and providing guidelines for the management of energy development are presented. A recommended course of action for management oriented research is presented. Finally, a searchable electronic database is developed of the literature including abstracts and digital copies to aid in evaluating future energy development on ungulates.

The current management policy for energy development makes two untested assumptions regarding the effects of energy development on wildlife. First, it assumes that negative impacts of energy development on wildlife can be mitigated through small-scale stipulations that regulate the timing and duration of activity, but not the amount. This current policy also assumes that wildlife populations can withstand continued, incremental development. Neither of these two assumptions are supported or refuted by evidence reviewed in the scientific literature as part of this review. Regardless, adaptive experiments to explicitly test these management hypotheses are needed.

There is currently no rigorous scientific evidence that energy development will have population-level impacts on pronghorn, mule deer or elk in eastern or central Montana. However, this is because there have been no properly designed, thoughtful, rigorous tests of the population-level impacts conducted to date. Instead, a host of observational studies on small-scale and short-term responses provides limited guidance to managers in search of the crucial question of population impacts. While theoretically justified, relying on the precautionary principle to restrict energy development will likely be unsuccessful as an energy development policy.

Short-term and small-scale impacts of energy development have been relatively well described in previous reviews and studies, albeit most often in poorly designed observational studies. GPS collar studies have aided attempts to document small-scale responses to development, and will continue to be useful in the future in this correlational framework. Ungulates predictably avoid areas during active exploration and drilling, moving to denser cover and areas farther from human activity. Recommendations from previous studies still hold, namely timing and seasonal restrictions for critical habitats and resources. Across studies, ungulates showed avoidance responses to human development an average of 1000m from the human disturbance.

Scaling up from small-scale/short-term studies to population-level impacts will be difficult. One of the key difficulties is scaling up responses of ungulates at low development densities to high densities present in heavily developed oilfields (e.g. Upper Green River Basin). Preliminary analyses suggest that thresholds for significant impacts on ungulates will occur between densities of 0.1 to 0.5 wells/km^2 and 0.2 to 1.0 linear km/km^2 of roads and linear developments. However, these results are preliminary, and more formal meta-analyses are suggested.

Building on the strong example of the Montana Cooperative Elk-Logging study that ran through the 1970's and 1980's, a series of research and management recommendations are made. First, a formal meta-analyses of the existing energy literature is recommended to allow scientifically defensible quantitative estimates of the effects of energy development on behavior, habitat and population dynamics.

Second, building on this meta-analysis, a power analysis of the optimal experimental design, level of replication, and duration of a energy-impact study design should be conducted to reveal the best approach for both short-term (behavior, habitat) and long-term impact assessment.

Third, a series of large-scale, population-level and long-term experimental comparisons similar to the Montana Cooperative Elk-Logging study should be initiated in eastern and central Montana on elk, mule deer and pronghorn. The study design should be replicated ideally across three levels of development; none – control, initial phases – low densities of wells/roads, and after at least a decade of intensive development, to allow a rigorous test of the population effects of energy development on wildlife. Partnerships with existing studies occurring in other developed areas should be developed (e.g., Upper Green River Basin studies), but control areas in Montana should be developed (e.g., Charles M. Russell Wildlife Refuge).

Fourth, implement an adaptive management experiment (in conjunction with the third point above) to test whether the current energy policy is sustainable from a wildlife population perspective. The de-facto energy policy being implemented in Montana (and elsewhere) makes a number of assumptions that may in fact be incorrect. However, no valid alternatives have been developed or put forward as serious contenders that could be compared in large management experiments to test whether different models for energy development are required. If the bleak situation for Alberta caribou is any suggestion, alternative energy development policies are sorely needed.

1.0 INTRODUCTION

Increased energy consumption and the perception of over-reliance of the United States on foreign oil deposits to meet domestic energy requirements lead to a national level policy to: increase energy efficiency, develop new energy resources, improve efficiency and extraction of energy from existing resources, and improve the efficiency of key international energy consumers (American Gas Association 2005). This national policy manifested in Montana in October of 2005 when Governor Brian Schweitzer revealed the Schweitzer Energy Policy (Governors Office of Economic Development 2005). This Montana Energy Policy emphasized the following energy development themes in Montana, calling for diversification, a commitment to renewable and cleaner development (including clean coal), increased energy efficiency and conservation, increasing supportive infrastructure and adherence to environmental laws and community acceptance. Within the Department of Commerce, the Division of Energy Infrastructure, Promotion and Development's (DEIPD) mission statement is to:

> *"The Division's mission centers around promoting and developing additional energy distribution capacity so that potential jobs become actual jobs and Montana's tax base is further enhanced for the benefit of its citizens. Increased distribution capacity also paves the way for clean, green energy creation and utilization. We will work to facilitate the promotion and development of energy infrastructure that will allow the responsible development of Montana's abundant energy resources including wind, bio-fuels, geothermal, biomass and clean coal gasification, liquefaction and power production which use carbon sequestration technologies when possible." (DEIPD, Dept.of Commerce, Government of Montana, 2008)*

The effects of this government policy on energy development have been felt strongly in the energy sector. In Montana since 2005 oil production has increased 50% and a state renewable energy portfolio tax and incentive program to increase the growth and production of renewable energy was adapted. The state has increased tax incentives for energy development, earning itself recognition as one of the most favorable and lowest taxed places to develop energy in the world (Business Facilities Magazine 2007); initiated the Montana Alberta Tie electrical energy transmission project, and developed proposals to increase both renewable and non-renewable energy resources throughout eastern and central Montana in conjunction with federal land management agencies such as the Bureau of Land Management (BLM). Between 2002 and 2006, oil production has increased 213% (barrels production), the number of oil wells 17%, and the number of natural gas wells 34% while production increased by 17% (Montana Board of Oil and Gas Conservation 2006). While this relative growth is impressive, comparison to the heavily developed oil and gas fields of Alberta (40% larger in area to Montana) reveals Montana production is <10% of currently active oil and gas wells in Alberta, which is also undergoing similar rates of growth (10-20%, Alberta Energy 2008). Thus, from an energy development perspective, Montana is just getting started.

This increase in development in Montana closely matches the nearly 60% increase in the number of permit applications throughout the Rocky Mountain West in the last decade (American Gas Association 2005), with much of it focused on Montana, Wyoming and Colorado. Montana is touted as having amongst the greatest undeveloped natural gas and oil fields in the country (American Gas Association 2005), much of it in the Montana Thrust Belt (north-east Montana), Powder River basin (south-central Montana), and East Front deposits. Despite the focus on renewable energy development by Montana's Schweitzer Energy Policy, however, federal-state policies will ensure that traditional, non-renewable energy development will constitute the bulk of the growth in energy development in Montana, especially in these key energy deposits.

For example, within the Powder River Basin region (~16,000 km^2) within the state of Montana (BLM 2003a, b), as many as 18,000 coal bed natural gas (CBNG) wells have been approved for drilling on federal lands by the Bureau of Land Management (BLM, 2003a, b). This massive increase in oil and gas development will be associated with similar increases in infrastructure and development. For example, each CBNG wellsite is accompanied by construction of 2-7 km of access roads and 7-22 km of power lines per km^2, as well as compressor stations, pipelines, holding ponds, etc. (Bureau of Land Management 2003a, b). Other types of energy development, such as traditional oilfield drilling, natural gas development, coal bed methane, and new renewable energy developments such as wind power are also associated with extensive road, power line and pipeline developments. Throughout Montana, similar resource management plans focusing on energy development have been developed by the BLM, a key federal regulating agency on federal lands, ensuring the future expansion of energy development in eastern and central Montana, especially the Billings, Big Dry, Headwaters, Powder River Basin, and Judith Valley Phillips resource management planning areas administered by the BLM (BLM 2008, see Fig. 3 below).

Increased energy development, and the infrastructure associated with well sites, has the potential to have profound impacts on natural ecosystems in eastern and central Montana. Given this backdrop on intensive energy development, the Montana Department of Fish, Wildlife and Parks faces a huge policy, administrative and technical challenge to meet its goals to:

> *"Sustain our diverse fish, wildlife and parks resources and the quality recreational opportunities that are essential to a high quality of life for Montanans and our guests (MTFWP, 2008)."*

Energy development has been shown to impact almost all natural resources including surface and subsurface hydrological processes, natural disturbance regimes such as fire, wildlife habitat, soil erosion processes, and wildlife population dynamics themselves (e.g., BLM 2003 a,b; (Naugle et al. 2004, Bayne et al. 2005)). While regulatory processes are in place that can provide some effective mitigation for key wildlife species, such as the potentially threatened Greater Sage Grouse (*Centrocercus urophasianus*) (Aldridge and Brigham 2002, Naugle et al. 2004), mitigation strategies are usually implemented on a site-by-site basis at the scale of the individual well site, or at intermediate scales across several wellsites or adjacent oil fields. Regardless, with petitioning, even small-scale mitigation at the site of the individual wellsite can also be waived by federal agencies. And the situation is even less regulated on private lands, where a substantial portion of energy development is occurring; few to no guidelines exist to minimize the impacts of energy development to wildlife. Regardless of the small-scale regulations often applied to individual well site permits, the impacts of energy development on wildlife especially are most often felt through cumulative effects of not just one wellsite at a time, but across large landscape scales in the order of 1000's km^2 (Kennedy 2000, Schneider et al. 2003, Aldridge et al. 2004, Johnson et al. 2005, Frair et al. 2007, Walker et al. 2007). Thus, MTFWP faces the difficult task of sustaining populations of wildlife at large landscape scales across Montana despite the regulatory and policy challenge of relatively small scale and piecemeal environmental impact assessment.

To aid the mission of MTFWP, a series of reviews of the effects of energy development on key wildlife species was initiated in 2007. This review constitutes part of this process and focuses on reviewing the effects of energy development on ungulates throughout the Rocky Mountain western with particular attention towards habitats in eastern and central Montana including sagebrush, grassland and pine-breaks habitats. The following ungulate species are considered the focus of this review, bighorn sheep (*Ovis canadensis*), American pronghorn (*Antilocapra antilocapra*), elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*), although effects of energy development on the large mammal community in which these key ungulate species reside will also be considered. Moreover, given the extensive literature on the effects of energy development on woodland caribou (*Rangifer tarandus*), particularly in Alberta, I review the impacts of energy development there with a focus on providing key insights to Montana in terms of developing effective mitigation and cumulative effects assessment strategies. Given the vast difference between both the means of energy development and wildlife present in the arctic (e.g., National Research Council 2003), I do not review the effects of energy development on arctic ungulates, but discuss where appropriate. The objectives of this literature review are:

1) Review the effects of energy development (including oil, gas, and wind development) on ungulates, separated by important seasonal and habitat types.
2) Review the weaknesses of the existing literature in addressing and providing guidelines for the management of energy development.
3) Provide a conceptual framework for understanding the effects of energy development on ungulates
4) Recommend a course of action for management oriented research on the effects of energy development on ungulates.

5) Develop a searchable electronic database of the literature including abstracts and research summaries, where possible, that will be useful in evaluating future energy development on ungulates.

2.0 LITERATURE REVIEW METHODS AND SCOPE

Recent comparisons of literature reviews in ecology vs. those in the medical field revealed that ecological literature reviews often lack details of the methods used to search for studies, thus increasing potential bias in literature reviews, and made fewer efforts to review unpublished literature (potentially showing no effect because of the bias against negative results). Ecological reviews were also less likely to assess the relevance of the study in terms of quality of experimental design and made fewer efforts to quantitatively synthesize results using methods like meta-analyses (Roberts et al. 2006).

I follow the recommendations of Roberts et al. (2006) herein, by describing the methods used to conduct the literature review on the effects of energy development on bighorn sheep, elk, mule deer and pronghorn (as well as woodland caribou). I also assess rigor of study design following methods described below.

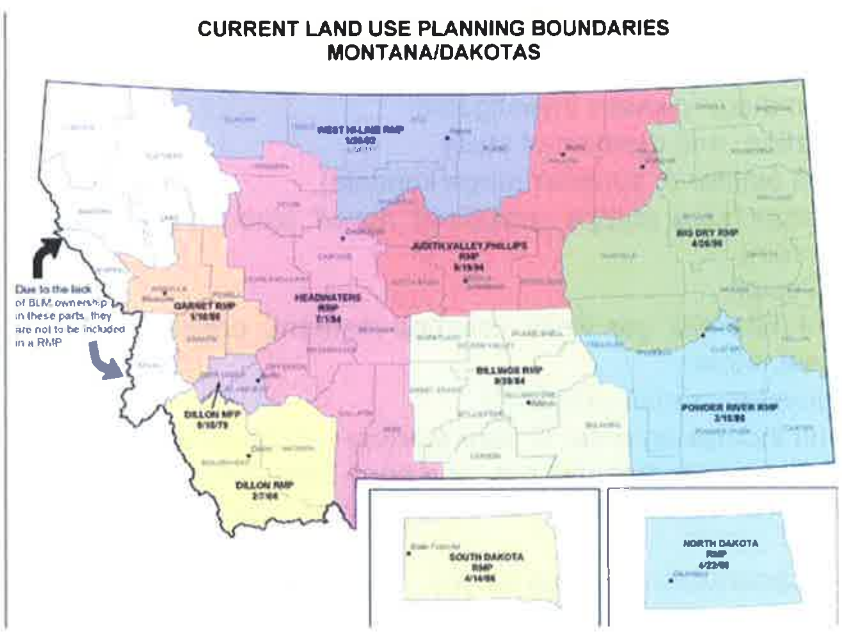


Fig. 1. Study area for the literature review of the effects of energy development on ungulates, BLM (2003a,b). This review focuses on areas in the Powder River Resource Management planning (RMP) area, the Big Dry RMP, the Judith Valley/Phillips RMP, the West-Hi Line RMP, Billings RMP, Headwaters RMP, and Garnet and Dillon RMP's.

2.1 Literature Review

I conducted a literature search of energy-ungulate impact studies using a variety of electronic, on-line databases, personal communications, and management reports from the period from 1970 to the present. Databases included: ISI web of science, Google scholar, Absearch, BIOABSTRACTS, Biological Abstracts, Environmental Sciences, Dissertation Abstracts, Government resources, Geology abstracts and Forestry abstracts. I searched databases using combinations of the following keywords: bighorn sheep, elk, mule deer, pronghorn, energy development, petroleum development, oil development, gas development, wildlife, ungulate, and the western states (e.g., Wyoming, Montana, Idaho, Colorado, Utah) as well as Alberta and British Columbia. From this list of potential scientific literature, I screened studies to include at least one large ungulate species preferably within the same types of habitats as present in eastern and central Montana. I focused on studies applicable to the BLM resource management planning areas identified in Fig. 3. See appendix A for a summary of the types of literature reviewed.

To facilitate synthesis and review, from each study, I recorded information in the following categories: study area; methods, results, recommendations and implications. For each category I recorded the following variables:

Study area

- focal species, sex- and age-classes investigated
- study area size, location, and duration of study
- seasonal information (winter or summer range impacts),
- vegetation communities (sage steppe, grassland, mixed, pine breaks, forests – foothills and mountain)

Methods & Experimental Design

- type of development (oil wells, gas wells, coal bed methane, coal bed natural gas, wind power, coal, other)
- density of human developments (units/km^2)
- study design type (in increasing order of rigor starting with observational, correlative, comparative, experimental, pre- and post- data, before after control impact design (Underwood1997,Krebs1989)) and degree of replication (if any);
- field methods (e.g., observational, aerial survey, pellet surveys, snow track surveys, telemetry)
- response variables (e.g., group size, vigilance, habitat selection, population demography), and

- statistical methods

Results
- general results
- effect size(s) (see meta-analysis section below),
- sample size, and
- measures of variation in the effect size;

Conclusions
- imitations, both identified by the authors, and this review
- management recommendations
- conclusions of each study

I revisit concepts of experimental design in the discussion with recommendations for future adaptive management experiments about energy impacts on wildlife in Montana.

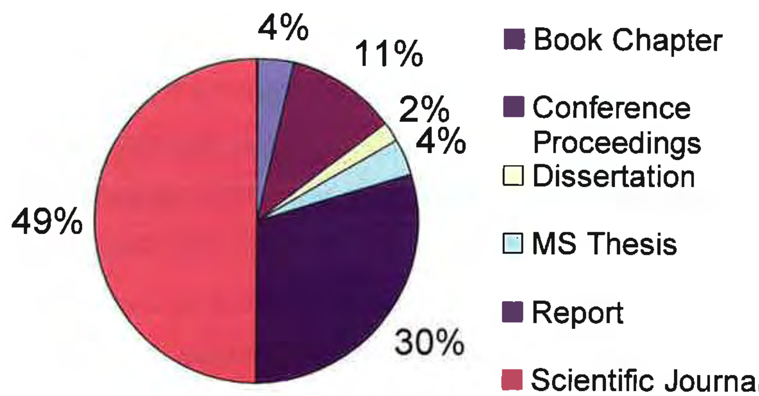
Furthermore, because of the importance of roads, and the avoidance of them by ungulates in the literature (Lyon 1983, Rowland et al. 2004,Frair et al. 2007,Edge and Marcum 1985,McCorquodale et al. 2003,Rost and Bailey 1979), I report the mean distance or distance classes avoided by ungulate species in each study for observational and experimental studies. The effects of roads in general are a huge subject and have been the target of dozens of ecological reviews (Forman and Alexander 1998,Trombulak and Frissell 2000), which similarly classify impacts of roads as direct (mortality) or indirect (avoidance). Moreover, human recreation associated with roads is a huge management topic with many excellent reviews even in Montana (Joslin and Youman 1999), so I do not attempt to review this literature. In this review, I only focus on synthesizing quantitative studies about the distance at which ungulates avoided roads in habitats similar to eastern Montana. Broad recreational and road impacts are discussed, but only in the context of potential impacts of energy development.

3.0 RESULTS

3.1 Literature Review Summary

3.1.1 Species and publication type

I found 120 publications that met the search criteria and that I was able to locate for this review. However, not all of the literature was species specific or relevant to energy development, and are included in the literature database only for background reading. For example, studies of the cumulative effects of energy development on caribou in Alberta are included (Schneider et al. 2003), but not reviewed in detail here because the focus was on studies on the four main ungulate species. Literature reviews themselves were also not included in the literature review, often because we were reviewing the same limited literature, ironically. Finally, modeling or theoretical studies, while useful in the context of interpreting the results of field studies, were not included in the literature review of field studies that documented the effects of energy development on wildlife. Thus, of the 120 or so studies assembled, 70 were direct field studies that investigated aspects of energy



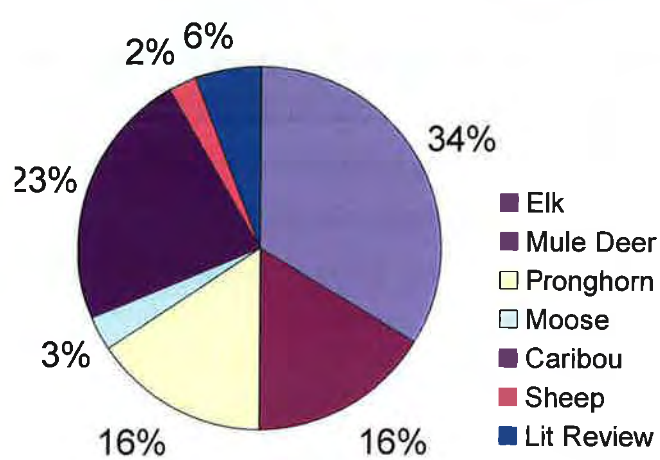


Fig. 2 & 3. Proportion of the studies that directly studied aspects of energy development on wildlife (n=70) by 2) publication type and 3) species, including literature reviews as a category.

development or more broadly human development or disturbance, on wildlife in habitats relevant to eastern Montana.

Of the 70 studies, almost 50% were peer reviewed scientific publications in the primary literature (Fig. 2). The second largest category were reports, 30% of all literature reviewed. Conference proceedings, specifically the Thorpe conference series prominent in the 1980's, constituted 11% of all literature, and a combination of book chapters, and graduate theses (MS, PhD) made up the rest of the sample. Considering graduate theses as peer reviewed, but conference proceedings, book chapters and reports as not, 53% of all literature was peer reviewed. While other authors consider graduate theses as unpublished, I disagree with this view, especially in contrast to management reports that undergo variable and undocumented peer review during the design, implementation, and analysis of the impacts of energy development. Peer review within a University department for a graduate thesis greatly exceeds the level of peer review for reports.

Elk were the most common ungulate in the literature reviewed the subject of study in 45 studies. Woodland caribou were the subject of 29 studies. Mule deer and pronghorn had a similar number of studies, 20 and 21, respectively, followed by Moose (4) and Bighorn Sheep (3). On average, each study examined the responses of 1.4 species to energy development (Table 1), with the most common ungulate combinations being mule deer and pronghorn, or mule deer, pronghorn and elk. A surprising number of literature reviews have been conducted on this scanty literature, and these constituted ~12% of all studies considered here.

3.1.2 Study design, methods, sample size

From a study design perspective, most studies (n=27, 47%) used a weak observational approach where the impacts of the development were inferred from correlations between human use activity levels and measures of ungulate responses to treatments. I defined comparative studies as those that compared ungulate responses to development by comparing effects before and after development, but without a suitable control, obviously a weaker design than with a control. Comparative designs were used in 19% (n=11) of the studies. I defined experimental designs where effects were compared between an impacted and control group at the same time, so that the control was contemporaneous. However, in this design, effects of development before and after development are not discernable. To tease apart impacts before and after an energy development, only 10 studies (18%) used the most powerful experimental design, a before-after-control impact design (Underwood1997,Krebs1989). Half of both the comparative and experimental studies utilized a before-during-after study design, where the effects of the energy development phase was contrasted with both pre- and post- data. This was the most powerful design for determining the short term impacts of development on ungulates. **No studies were replicated at the level of impact type: all studies used only 1 replicate.** I return to the issue of experimental design in the discussion with recommendations for MTFWP.

A review of the most common methods used to evaluate the impacts of energy show a higher frequency of telemetry studies compared to other methods; 51% of all studies were conducted using radio telemetry, and most of these (95%) were with conventional VHF telemetry, GPS collars the other 5%. Approximately 51% of all studies used radio telemetry, collaring a total of 1537 animals throughout their duration, the most common of which were elk (48%), followed by pronghorn (26%), mule deer (18%), and lastly, caribou (4%). There were no published studies of moose or bighorn sheep responses to energy development using radiotelemetry. The most common alternate methods to assess effects of humans on ungulates were aerial surveys (15%) and pellet or sign/track surveys (20%).

The average sample size (n) used in energy-wildlife studies was 57.5, the median 39.5, and this did not differ much from the sample size of only telemetry studies, where sample size in

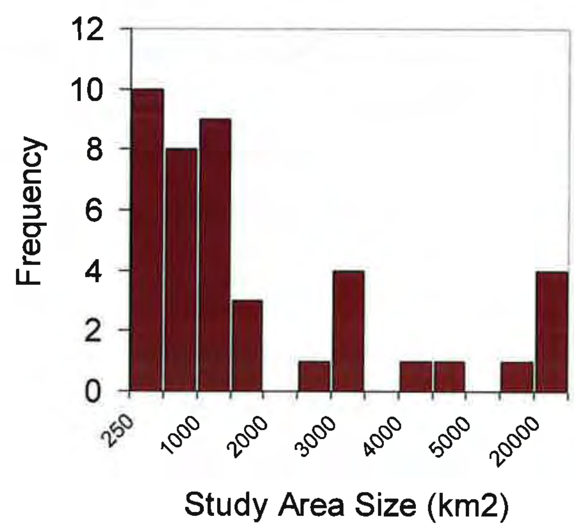


Fig. 4. Frequency distribution of study area sizes for studies on the effects of energy development on ungulates (n=44).

this case correctly represents the individual animal sample unit (Gillies et al. 2006,Otis and White 1999), not the number of sub-sample telemetry locations. However, considering the number of telemetry locations per individual animal, these were often quite low for VHF collared animals, with an average of only 22 VHF telemetry locations obtained per animal per study; for seasonal (winter, calving, summer) this sample size is even smaller. Across all studies, over 2000 ungulates were radiocollared to evaluate impacts of energy development, with mortality rates that ranged between 0% and 15% (mean 4% reported from n=10 studies, or approximately 80 mortalities).

Psuedoreplication (Hurlbert 1984) was a common problem in all studies. Approximately 30% of all studies committed psuedoreplication where enough data was presented (i.e., clear experimental design, sample sizes, etc.) were sullied somehow with pseudoreplication issues. Common pseudo replication occurred when authors confused the number of telemetry locations with the true sample unit, the individual animal. Other common instances of pseudoreplication were with pellet surveys or track count surveys.

Oddly, studies often failed to report the study area size, a key parameter in ecological studies– for example, study area size influences ungulate densities, spatial scale, and the density of disturbance. In the discussion I review this critical problem of scale. Where study area size was reported (n=56), study area size ranged from 26km^2 to 190,000 km^2. Studies of boreal woodland caribou populations were the largest, averaging 28,000 km^2 (range 225 – 190,000km^2), and were statistically larger than all other ungulate species study areas (ANOVA P-value <0.01). Not including caribou, the largest study area size in the lower 48 was 15,000km^2 in Wyoming (Sawyer et al. 2005b), and there were no differences amongst species (ANOVA, P>0.3). However, mean study area size was strongly left-skewed; while the mean study area size appears large, 3382km^2, the median was significantly smaller, only 798km^2, shown in Fig 4. This area is equivalent to a 15km^2 radius circle.

Table 1. Summary statistics for literature on the effects of energy development and human disturbance on ungulates, n= 126 studies.

Metric	Mean	Median	Range	StDev
Sample size	57.5	39.5	4-223	53.6

No. of collared animals in telemetry studies	58.7	34.2	4-223	60
Number of telemetry locations/animal	22	17	1-55	??
Population size	3950	1000	35-48000	22058
Study area size	3882 km^2	798	26-20000	5924
Study duration	2.7 years	2.1	0.15 - 11	2.28

The population size of inference for ungulates affected by energy development in the studies reviewed averaged 3950 animals, again, with a left-skewed distribution resulting in a much lower median of 1000 animals. The range of population sizes of ungulates impacted ranged from 35 to 48000, for mule deer in the Upper Green River valley of Wyoming (Sawyer et al. 2005b,Sawyer et al. 2002). From a sampling perspective, then, the average telemetry-based study sampled a mean of 1.5% of the population present, or a median of 4% of the study population of inference.

Study duration was also summarized across studies. Almost all studies were of extremely short, most often for the duration of active drilling activities, exploration, or mining development. Mean study duration was 2.6 years, and median duration 2.2 years. The range was basically 2 months to 11 years. The longest running study, consisting of annual aerial surveys by (Hayden-Wing 1990), ran from 1979 to 1990 in the Riley Ridge area of Western Wyoming: the study is no longer running. The earliest study reviewed occurred in 1969, when (Bruns 1977) conducted an observational study on pronghorn in SE

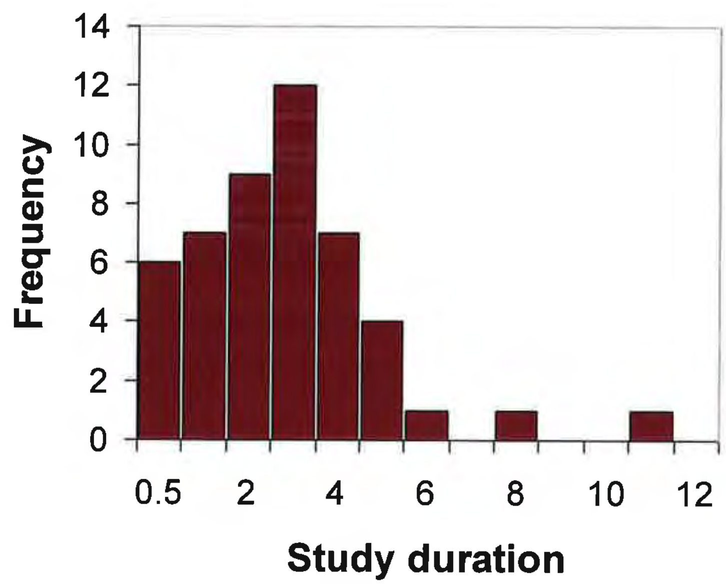


Fig. 5. Frequency distribution of study area duration for studies on the effects of energy development on ungulates where duration was reported (n=56).

Alberta. Altmann's (1958) classic study was not strictly on the effects of energy development on ungulates. The majority of studies were conducted in two peaks, the second of which we are in now, and the first, during the 1980's (Fig. 5). These two peaks in studies correspond closely with the peaks in energy exploration and development in the last three decades (American Gas Association 2005, Oil and Gas Conservation Division 2006).

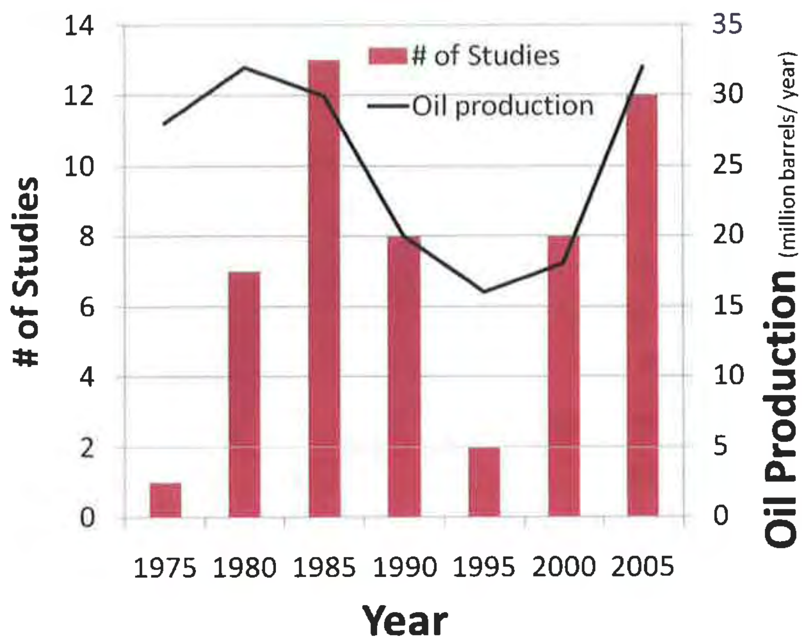


Fig. 6. Frequency distribution of study date for studies (n=60) on the effects of energy development on ungulates plotted against peak oil production in Montana (in millions of barrels of oil/year; source Oil and Gas Conservation Division (2006).

3.1.3 Types of Energy Development

Of the types of energy development studied, by far the most frequently studied activity was the effects of active seismic exploration or well drilling on an ungulate species (n=25, 31%). The next most frequent studies examined the effects of roads associated with oil and gas or forestry development on wildlife, followed by oil or natural gas well impacts on ungulates. There was an even mix of studies that investigated the effects of human activity in general, mining, logging, and military overflights on ungulates. There were 4 studies specifically designed to be pre-development studies, or in areas specifically at the beginning of energy development (e.g., Sawyer et al. 2002, Amstrup 1978, Ihsle 1981), but either development has not occurred, or no follow up studies have been conducted yet (to the best of my knowledge).

Moreover, careful reading revealed that of just the studies designed to investigate effects of energy development activities (n=56, nearly 70%) were reactionary and designed largely as consultancies to monitor and mitigate the environmental concerns of the development as a condition of the drilling or exploration permit (e.g., van Dyke and Klein 1996, Irwin 1984, Johnson 1980, Johnson 1987,Morgantini 1885, Horesji 1979). The remainders of the studies were designed to investigate the impacts of development on ungulates after the fact on an ad-hoc manner. **There was not a single case of energy development and management-oriented research proceeding in an adaptive framework in a manner to directly feedback into management of energy development (see discussion).**

Finally, from a vegetation community perspective, most studies were conducted in shrub-steppe vegetation communities and ecosystems (n=21, Fig. 7), followed by mountains (15), grasslands (11), and then pine breaks (e.g., Douglas Fir), boreal forest (caribou), foothills forests (e.g., Alberta), and other habitats such as present in Michigan.

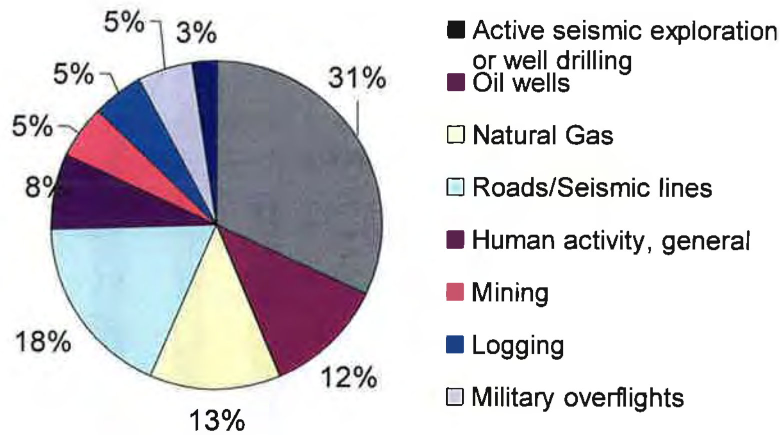


Fig. 6. Types of human disturbance and energy development studies that investigated impacts on ungulates (n=49).

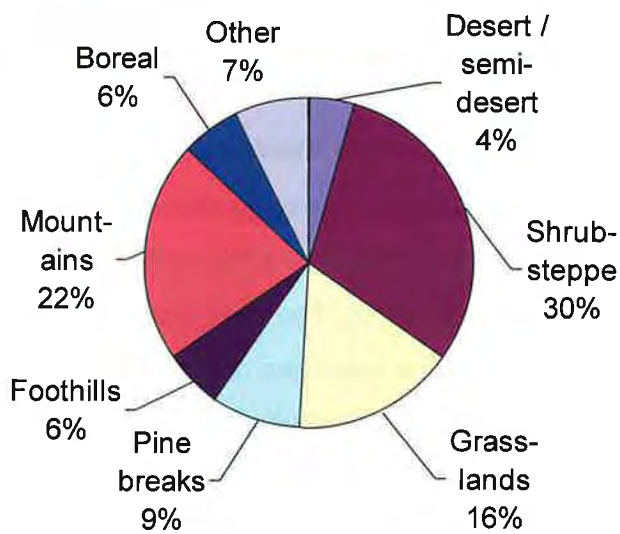


Fig. 7. Vegetation communities in which studies on the impacts of energy development on ungulates were conducted (n=69).

3.2 Elk *(Cervus elaphus)*

I now summarize, by species, the results of individual studies reviewed, commenting on their location, species, study designs, methods, and general conclusions and especially, limitations. Results by species are then summarized in a table at the end of each of the main species reviewed in this review.

3.2.1 Sagebrush Steppe and Grasslands

In perhaps the longest conducted surveys of ungulate response to natural gas field development (Hayden-Wing 1990) summarized results of 11 years of aerial survey monitoring of elk populations on two elk ranges in southwestern Wyoming (Snider Basin and Graphite Hollow) that were developed for oil/gas wells. Vegetation types included sage-steppe, grassland, pine breaks and mixed communities. They surveyed elk annually on winter range and spring calving ranges pre construction, during, and afterwards, with no control sites for comparison. Elk avoided areas during the construction phase on both the winter and calving ranges, but reoccupied these areas after intense construction ended, although variation in the degree of avoidance was high over time. Also in the Snider basin area of Wyoming, in 1978-80, (Johnson 1980) conducted an observational study of the effects of natural gas well development on elk using photo cameras, pellet surveys, and aerial and ground surveys. Elk were affected by activity on the access road, avoiding the area; cows moved calves at earlier age; elk were displaced away from drilling rig in 1979. However, a lack of pre-drilling data hampered interpretation, and the study was reactively designed in response to development.

Similarly, elk avoided roads, active gas and oil wellsites the most during summer months in the sage-steppe ecosystem of the Jack Marrow Hills, WY (Powell 2003), strongly selecting habitats greater than 2000m from these features. Avoidance of roads and wellsites declined in the fall, winter and spring when elk only avoided areas <500m surrounding human development. During calving (15 May – 30 June), elk avoided areas <1000m from roads and wellsites. This study was observational, and only examined responses of elk following development, but makes the important observation that elk continued to show avoidance of wellsites long after the construction phase had been completed.

In Colorado, (Johnson 1986) conducted an experimental (n=1 replicates) study of the effects of coal mine development on elk over a 5-year period from 1981-1984. Vegetation types were a mix of sage steppe, grassland, shrub, aspen and conifer. Johnson (1986) compared calving home ranges, site fidelity, habitat use/selection, noise tolerance and cow/calf ratios between a treatment mining area and control areas within 20 miles of the mining development, and reported no statistical differences between any variables, and concluded that coal mine development did not influence elk. However, there was some evidence that elk near the coal mine displayed lower fidelity (5796m between successive home range centroids between years) than control elk (3723m). These results are consistent with displacement by the coal mine. Potential limitations of the study are confounding between the putative control and treatment locations which were close together and between which radiocollared elk mixed throughout the study (Johnson 1986). Regardless of these problems, elk selected reclaimed coal mine sites in proportion to their availability in the landscape, neither selecting nor avoiding reclaimed areas, emphasizing the importance of reclamation activities.

Ward (1986) conducted another observational, non-experimental, study on the effects of seismic exploration on elk in the known recoverable coal resource area of south central Wyoming over 4 years from 1981-84. Vegetation types were sagebrush steppe and grasslands. Ward (1986) used ground telemetry from an unreported number of elk with an unreported number of telemetry locations combined with an unreported number of ground and aerial surveys to examine the distance of elk to development. Ward (1986) also measured sound levels (dbA) at various distances from seismograph equipment. Elk were affected most by foot traffic; distance of elk displacement depended on line-of-sight of the elk to the disturbance. In places with no topological barriers, elk displaced about 3.2 km, but where terrain yielded topological barriers, elk displaced 800 m. Following the cessation of seismic exploration, elk returned to areas of disturbance a few days after activity was concluded. Ward (1986) concluded that elk in this study did not seem to be affected detrimentally. However, where winter range habitat is limited, these disturbances have the potential to have major effects on elk. Limitations of this study are obvious; the number of collared elk, details of aerial or ground surveys, and statistical tests were all absent.

Hiatt (1981) conducted an observational study of the effects of drilling a single well on Crooks Mountain in Wyoming during late winter 1981 in response to concerns over drilling effects on ungulates in winter range. Hiatt (1981) used track counts, ground and aerial surveys and time-lapse camera's to quantify the response of elk and mule deer to development. The study was putatively a before-after comparative study, but was critically limited by only 9-days pre-development monitoring – the report gives the impression that this was an extremely reactionary study conducted at the 11th hour to ensure something was done to address environmental concerns. Hiatt (1982) concluded that both elk and mule deer shifted their ranges away from the well site, and that there was no evidence of avoidance of the access road by either species. Limitations of this study are obviously the scanty pre-treatment data, lack of control, and lack of replication. Remote cameras were of limited utility, collecting few observations and being limited by the small number of cameras deployed. Moreover, statistical analyses were psuedoreplicated at the level of the individual track-count, which were collected along transects – the true sample unit. Therefore, it is unclear whether the conclusions from this study are warranted, although it is consistent with previous literature that shows a decline in ungulate use during drilling operations.

Van Dyke and Klein (1996) also studied the effect of active drilling operations on elk in the grassland and shrub-steppe communities near Line Creek Plateau in Montana by comparing seasonal an annual home range characteristics and use of cover for 10 VHF collared elk from which they obtained 474 telemetry locations over the period from 1988 to 1991. They assumed this represented the population of 120 elk that used the entire study area. Van Dyke and Klein (1996) compared home range size, home range centroid, and coarse grain habitat use by elk before, during, and after development, each phase lasting 1 year. Elk in both the study site and the control site had significantly different distributions within the ranges, suggesting a normal seasonal change rather that effects of drilling. In terms of resource selection, elk at the study site were rarely found outside of forested areas during the day while activity was taking place at the well sites. Elk responded to disturbances by shifting their use of the range, centers of activity, and use of habitat. Elk maintained a physical barrier between themselves and the well site during active drilling, and the authors concluded that elk do not abandon their home ranges during well site development, and quickly return to pre-development conditions following development.

Unfortunately, limitations of this study are many; 1) small sample sizes per elk to accurately estimate seasonal and annual home ranges – with only 474 locations/10 elk/ 2 seasons (winter/summer) over the ~4 years of the study yields approximately 6 locations, naively, per elk per season-year – woefully low for reliable home range and centroid estimation (Powell 2000); 2) scale – this study evaluated the effect of a single oil well in an approximately 500km^2 area (note study area size was not presented, but is estimated from figures in the paper), a density of 0.003 wells/km^2, a trivially low density for such a huge area!; 3) the choice of large-scale home range analysis methods to evaluate the results of a single small-scale concentrated development also limits the strength of inference. The utility of this study to current oilfield development, where multiple, often dozens of simultaneous wells are being drilled in an existing matrix of developed oil fields is questionable, and future studies should pay particular attention to this issue of scale.

In a recent and well designed observational telemetry study of elk resource selection in a grassland/shrub-steppe ecosystem in southwestern Wyoming, Sawyer et al. (2007) examined the response of elk in open habitats to distances to roads. This study system is important because while the area has low densities of oil and gas development at present, this region is considered to have moderate to high oil and gas development potential (see Sawyer et al. 2007). Thus, this study represents a well designed pre-treatment study if development proceeds in the future, and is a valuable insight into elk resource selection in shrub-steppe ecosystems under relatively low development. Sawyer et al. (2007) developed resource selection function (RSF, Boyce and McDonald 1999, Manly et al. 2002,Boyce 2006) using telemetry locations from 33 GPS collared female elk during both winter and summer. Models were validated against 55 VHF collared elk telemetry locations. Elk selected for summer habitats with higher elevations in areas of high vegetative diversity, close to shrub cover, northerly aspects, moderate slopes, and away from roads. These results were generally consistent with the results of McCorquodale et al. (1986) in the shrub steppe of eastern Washington. Winter habitat selection patterns were similar, except elk shifted to areas closer to roads than in summer, indicating a strong response of road avoidance during summer. Results suggest that large (1,000) hunted elk populations can meet their year round forage and cover requirements in nonforested regions with low traffic, a range of elevations and shrub communities. They conclude that management of roads and related human disturbance is an important consideration for managing elk populations, especially in open habitats.

3.2.2 Mixed communities

In the mixedwood forests of Upper Peninsula of Michigan, (Knight 1981) studied the effects of initial seismic exploration and oil well development on reintroduced elk before and during development using radiotelemetry. This was the initial phase of oil well development and the study had very little previous energy development. Elk of all ages and sexes moved significantly greater distances in the presence of seismic exploration than when no disturbance was present; i.e. there was a significant negative correlation between distance to disturbance and mean daily movements of elk. Terrain and vegetation type was not a significant factor in elk movements. There was no significant difference in elk home ranges with/without seismic disturbance. Once wellsites were installed, there was no correlation found between distance to disturbance and mean daily movements. Elk appeared to become habituated to the stationary well sites, but not to the unpredictable seismic exploration activities. Knight (1981) concluded that seismic activity significantly affects the movements but not the distribution of elk; oil well activity does not significantly affect the movements nor the distribution of elk.

The effect of hydrocarbon development on elk and other wildlife in Northern Lower Michigan was further studied by Bennington et al. (1981) for 1 year from 1979 to 1980 using aerial surveys and ground track surveys. Wellsite densities were among the higher reported in the literature, approximately 0.22/km^2 (exception being Frair et al. 2005), and most wells were active and in production. Despite a regional increasing population "trend" over previous 5 years, the subregional trend was a short-term decrease in elk activity following oil drilling, as revealed by significantly lower number of tracks at drilling vs. nondrilling sites. At each wellsite, Bennington et al. (1981) found temporary (2-4 wk.) relocation after development. Overall, Bennington et al. (1981) concluded there was no significant difference between pre-drilling and post-drilling activity at the given well density has only short-term relocation effects. Limitations of the study are potential pseudoreplication in the number of sub-transects analyzed at each site (the correct sample unit), and that the intensity and coverage of the ground and aerial methods varied from previous Michigan government surveys. Moreover, the study was an observational-correlational study, with no replication, control, or comparative design.

3.2.3 Mountains and Foothills

In the Bridger Teton National Forest in 1983, Irwin (1984) examined the preliminary effects of seismic exploration on 18 collared elk. Seven of 18 elk were displaced from their spring range after seismic activity was conducted. The elk did not return during the activity, but instead migrated to the summer range. Four other elk stayed on the spring range, but maintained a 1-2 ridge barrier between them and the disturbance. Limitations of this study were lack of comprehensive pre-data, and unclear statistical analyses.

In a follow up study in the Bridger-Teton National Forest during summers of 1983-1985, Gillin (1989) studied the effects of multiple seismic exploration events on 21 radiocollared adult female elk in control and treatment groups. Over the spring and summer period, Gillin (1989) collected an average of 134 locations/events from 9 collared elk in the control group, and 184 locations from 10 elk in the treatment group. Elk avoided active exploration on average by 1.2km in spring and summer. They also changed their habitat selection to select closed conifers 18% more and higher slopes 70% more (away from low elevation seismic) during seismic exploration than the control period. The author concluded that elk avoid seismic exploration, but do not shift their home range during exploration, but merely redistribute use within their home range.

The impacts of seismic exploration on elk were also investigated in the Badger Creek – South Fork of Two Medicine River of north central Montana during spring, summer and fall of 1981 by Olson (1981). Olson used a limited experimental design with small numbers of animals, comparing the effects of seismic exploration on 4 collared female elk against 2 collared elk in a 'control' area. Response variables were movement distances between aerial telemetry locations. Olson (1981) found that distances moved between successive aerial locations were 50% greater for elk affected by seismic exploration, and drew firm recommendations for restrictions to be placed on development based on these findings. However, no statistical tests were conducted, and more troubling, the metric used, distance between locations, was not corrected for the amount of time between locations to a movement rate. Thus, distance between locations is really a function of both disturbance level and days between locations, and there may have been an important bias for greater frequency of relocations for the 'treated' group (mean of 2.8 locations/month) vs the 'control' group 0.5 (locations/month). Because movement rates scale inversely with relocation interval (meaning that the longer the movement interval between locations, the 'lower' the movement rate), the observed difference between the treatment and control group is almost certainly a function of sampling design, not treatment effects. Regardless, with ridiculously low sample sizes (n=6 total elk), little reliable inference can be drawn from this study.

In a simulated mining study on elk calves, Kuck et al. (1985) studied the responses of elk calves through radiotelemetry to three treatments of mining, human disturbance, and a control group. Kuck et al. (1985) captured and collared 25 elk in the Dry Ridge area of Idaho, and compared movement rates, resource selection, and calf survival between the groups during summer for 2 years. Disturbed elk moved greater distances, showed strong selection for closed conifer, had reduced fidelity, but there was no difference in survival rates between treatments for calves. The authors conclude that mining exploration will likely cause abandonment of spring calving ranges, but fell short of being able to connect these changes in behavior to demography, most likely because of small sample sizes of collared elk calves (n=25).

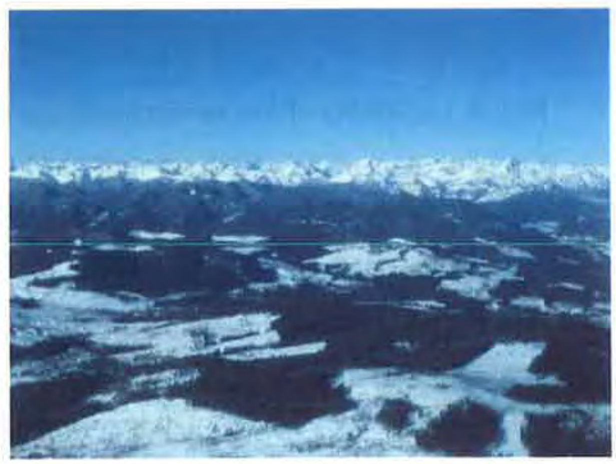
In a unique study, Morgantini and Hudson (1985) documented the effects of pipeline construction on movements of elk, moose, and deer in west-central Alberta. Using snow track surveys, Morgantini (1985) documented crossing attempts of 76 ungulate groups of the pipeline during construction. The pipeline was a barrier for 53.9% of ungulate groups that tried to cross them. Elk appeared to be the most successful, while moose were the least successful. Dirt berms did not appear to be a physical barrier to ungulates. The few encounters of ungulates and the pipeline during this study could be due to their avoidance of the development corridor at a larger spatial scale. The pipelines did not alarm the animals that did come in contact with the pipelines, but did act as a physical crossing barrier. The limitations of this study were the short duration, governed by the duration of construction, and the lack of information about the larger spatial scale and any broad-scale avoidance of the entire area (as found by many other studies) by ungulates. Regardless, Morgantini (1985) makes several practical recommendations to maintain periodic openings in pipelines under construction and even underpasses, or overpasses along pipeline to mitigate crossing barriers.

In the closed conifer forested foothills west of Rocky Mountain House Alberta, Lees (1989) studied the movements of 7 radiocollared elk along a pipeline right of way to investigate the effects of recreational disturbance (hiking, ATV's, etc) along the pipeline during winter. Lees (1989) used radiotelemetry, track counts during winter and remote camera's in an observational study design. The results of this study were largely inconclusive, due to the small sample size of collared elk (n=7) and remote cameras (n=5). However, the snow track surveys, which included a much larger sample size of track crossing locations (n=598) showed stronger avoidance by elk of areas within 350m of the pipeline right of way when human activity was high in the fall. Thus, human activity mediated the negative indirect effects of the pipeline on elk. This is the same study area of (Frair et al. 2007, Frair 2005), summarized below.

Finally, Berger (2004) did a literature review on the loss of migration amongst North American ungulates. In the Greater Yellowstone ecosystem, Berger documented 75% declines in ungulate migration for mule deer, elk, and pronghorn due to long-term human caused habitat fragmentation and overhunting. Threats to remaining long-distance migration include energy development, tourism development, sub/urban sprawl, highway mortality and habitat fragmentation.

3.2.3 A Brief Review of Related Studies on the Effects of Human Activities Not Including Energy Development on Elk

3.2.4 Elk-forestry relationships



In a now-classic series of studies in seven replicated sites in Montana, (Lyon, 1979, Lyon 1979, Lyon et al. , 1985, Edge et al. 1985, Edge and Marcum 1985) conducted long-term research into the responses of elk to logging, human recreational disturbance, and climate (Fig. 8). The management implications of these studies were summarized for MTFWP in Lyon et al. (1985), and have provided much of the basis for elk management in Montana ever since. While these studies did not specifically investigate the effects of energy development on elk, they laid the foundation of much of modern elk management in forested mountain systems in the Northwest. As such, their methodologies, approaches, and conclusions offer great insights to MTFWP for understanding the effects of energy development on ungulates in eastern Montana. Although conducted in differing habitats, as I synthesize in the discussion, the general results of avoidance of human activity demonstrated by these studies in forested mountain habitats might be expected to be greater in open habitats. Moreover, I suggest in the discussion that a similarly large scale and coordinated effort will be required to understand the effects of energy development on wildlife as these studies did for elk-forestry relationships 25 years ago.

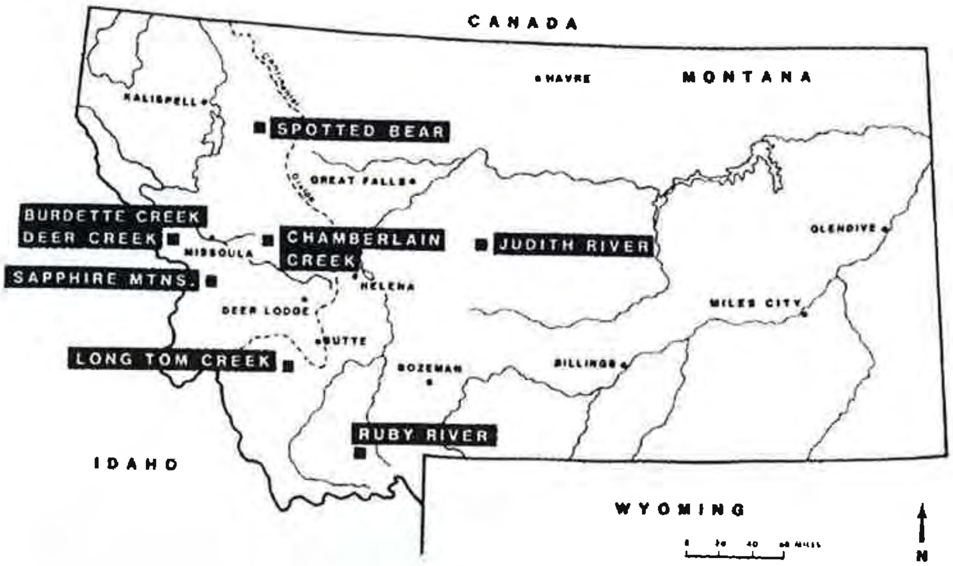


Fig. 8. Locations of the seven replicate study sites in the Montana Cooperative Elk-Logging study 1970-1985, reproduced from Lyon et al. (1985).

Over an eight year period from 1970 to 1977, Lyon (1979a,b) used extensive repeat pellet count surveys to measure the response of elk to roads, cover, and weather in one of the study sites. A total of 2.5 km/km^2 of pellet transects were sampled across the 215km^2 study every year. Elk moved away from areas during active logging operations (Lyon 1979), and avoided areas adjacent to open forest roads especially when forest cover was low such as in open habitats (Lyon 1983). Lyon (1979) recommended reducing human activity on roads to enhance security for elk, and providing elk with a line of sight barrier between disturbances and refugia.

In another Montana study area, Edge (1982) and Edge and Marcum (1985) studied the annual response of elk to logging activities using 39 radiocollared elk by investigating aspects of home range habitat selection, distance to roads and human activity and cover. In the component of the study examining elk habitat selection as a function of human activity, vegetation type and cover, Edge (1982) found elk avoided forest roads with high human activity during all seasons, especially in the absence of cover from the disturbance provided by closed conifer forests and topography. Elk avoided areas within 750m of roads and 1000-1500m of active logging operations. Even highly preferred foraging habitats were avoided within 500m of active logging operations and human activity of all types. Generalizing, Edge (1982) concluded that elk avoided a minimum of a 500m buffer from logging activity. In a unique comparison, Edge found elk were closer to active logging operations on weekends, when logging activities temporarily ceased, than during weekdays, showing a high degree of behavioral flexibility. During the hunting season, when human harvest pressure was greatest on forest access roads, elk avoidance of human activity increased to 2000m of roads. The recommended that road design avoid openings and take advantage of topography to benefit elk habitat effectiveness.

In their home range study, Edge et al. (1985) found that given increased logging disturbance, elk did not expand their home range size. In terms of home range fidelity, elk in disturbed locations were 40% more likely to shift home ranges than the control group (home range fidelity coefficient for disturbed elk = 0.58, for control elk 0.76). Although differences were not statistically significant, this was likely due to the very small sample size used in this analysis; only 10 elk that were tracked between successive years experienced disturbance (In this case, however, the exact sample size used to calculate statistical tests was unclear, to avoid pseudoreplication, sample size should be n=10 elk, but for the general coefficient of fidelity, Edge et al. (1985) used n=62 fidelity coefficients not n=39 different elk). This confusion makes it difficult to conduct meta-analysis on these data.

Other studies followed Lyon (1979) to estimate pellet densities as a function of distances to roads across the western US. In Colorado, for example, Rost and Bailey (1979) studied elk and mule deer. Rost (1979) found increasing pellet densities of elk and mule deer with increasing distance from roads in their shrub steppe ecosystem. Rost (1979) found in Colorado that elk and mule deer avoided areas up to 200m from roads. Lyon (1983) synthesized these results with the results of other studies to develop a general model of habitat effectiveness for elk that modeled % habitat effectiveness as a function of road density. Declines in habitat effectiveness were non-linear – that is, much of the loss of habitat effectiveness occurred in the first 1.6km/km^2 of increasing road densities. This habitat effectiveness model, combined with similar models for cover, formed the foundation of elk management in the western US for decades.

Recent work has started to question the generality and assumptions of the Lyon (1983) road density models, which while beneficial for elk management, have only been tested infrequently. Rowland (2000) tested the generality of the Lyon (1983) road density model by comparing observed habitat effectiveness against expected, under the model in Starkey Experimental Forest and Range in northeastern Oregon. Rowland et al. (2000) used >100,000 telemetry locations from 89 collared female elk to develop habitat selection models as a function of 0.1-km wide distance bands from roads open to human access. The predicted number of telemetry locations, however showed only weak correspondence to the Lyon (1983) habitat effectiveness models. Simulation results demonstrated that the failure of the simple habitat effectiveness models was because of the spatial patterns of roads, a covariate not considered in the original Lyon (1983) models. To be fair, recognition of the critical importance about spatially explicitly habitat models and the role of spatial dynamics in management has only emerged in the recent decade [spatial model; spatial population dynamics; habitat fragmentation], yet these results cast doubt on the generality and value of these earlier, non-spatial models. Regardless of these caveats, Rowland et al. (2000) reaffirms that the management of roads and human activity did influence elk in their study and should remain as a critical consideration in ungulate management, but that spatially explicit models are required to really

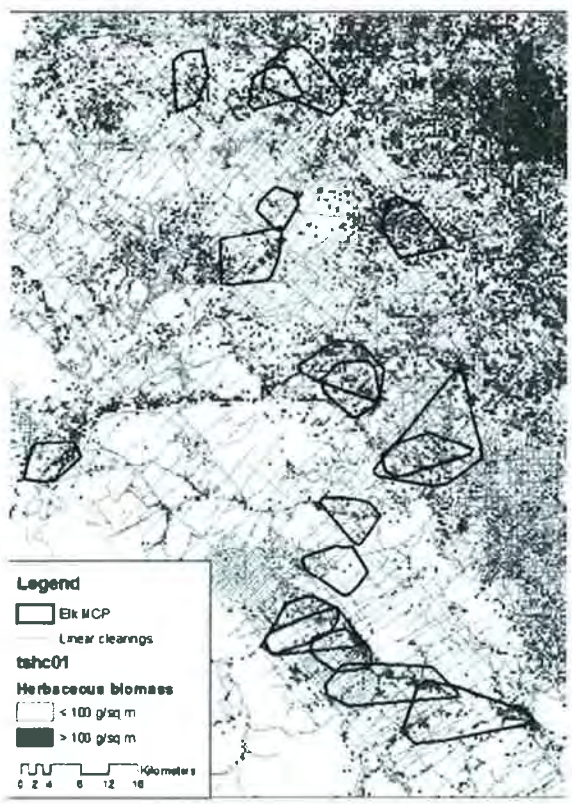


Fig. 9. Portion of the study area for Frair (2005) and Frair et al. (2007) in the central east slopes of Alberta's forested foothills. Home ranges of selected elk shown in black, against seismic cutlines (grey lines) and well sites (dots). From Frair et al. (2005).

capture the response of elk to roads at large scales.

Recent studies build on this paradigm shift in ungulate management that spatially explicit models are required to effectively mitigate the negative effects of human activity at large scales. In a follow up study also at Starkey experimental forest, Preisler et al. (2006) developed new spatially explicit methods, probabilistic flight response analysis, to analyze the effects of off-road vehicle recreation on elk movements. Consistent with previous studies, Preisler et al. (2006) found that elk responded at relatively far distances >1000m to ATV recreation, and that elk movement speeds increased when closer to trails. This study confirms the indirect effects of behavioral displacement by human activity on elk.

In the heavily developed foothills of Alberta, Frair (2005) and Frair et al. (2007) examined the responses of resident (and translocated elk, not discussed here) elk survival and movements to human activities, including seismic exploration cutlines, wellsites, and forestry. Their study area was 17,000km^2 of lower and upper foothills consisting of primarily closed conifer forests that contained over 28,000km of seismic exploration lines and 7,000 wellsites, for average densities of 1.7 km/km^2 of seismic lines and 0.4 wellsites/km^2 ,(Fig. 4) on the higher end of many of the studies reviewed in this literature review. From a movement perspective, Frair et al. (2005) found that elk were more likely to move away from linear seismic lines, and forage and bed at greater distances, respectively, from seismic lines.

To determine mechanisms driving elk movement patterns, Frair et al. (2007) studied survival of >200 radiocollared elk, detecting 104 mortalities (many of translocated elk) from 2001-2005. Elk survival decreased as a function of distance to seismic line (Frair et al. 2007), as a function of increased human caused hunting mortality and wolf predation, both of which selected to be close to roads (e.g. Hebblewhite et al. 2005b, Frair et al. 2007, Hebblewhite and Merrill 2008). But, importantly, humans and wolves use roads and seismic lines differently, roads being more heavily used by human hunters, and seismic lines being more heavily used by wolves. This trade-off likely occurred because of the indirect effect of wolf avoidance of human activity; wolves themselves being hunted by humans (see Hebblewhite and Merrill 2008, Hebblewhite et al. 2005a). From an elk perspective, however, for each

100m increase in distance from seismic lines, elk were 0.68 and 0.78 times less likely (reported as odds ratios, odds <1 are reduced) to die from wolves and humans, respectively. Thus survival increased with distance away from seismic lines. When considering roads, however, mortality risks contrasted for wolf and human hunting. For every 500m increment farther from roads, elk were 0.84 less and 1.34 times more likely to die from human hunting and wolf predation, respectively. Failing to separate out mortality sources masked the different responses to different types of mortality and how different predators (human, wolf) used the landscape differently.

3.2.5 Effects of Hunting and Recreation on Elk

The mechanism behind road avoidance by elk in the above studies was hypothesized to be due to increased hunting mortality associated with open roads. This mechanism has been corroborated by numerous studies across western North America since (Unsworth et al. 1999, Frair et al. 2007, Cole et al. 1997, McCorquodale 2000). As an example, Morgantini and Hudson (1980) studied the effects of human disturbance on elk in a montane grassland in the eastern slopes of Alberta from 1977-1979 using a combination of observations, pellet surveys, diet studies, and telemetry on radiocollared elk. Their study area contained energy development, but this study specifically focused on the effects of hunting pressure on elk. They found, similar to the studies in Montana, that elk avoided human activity more during the hunting season, shifting to denser cover farther from roads, and adapted their activity patterns to forage only during dusk and dawn.

Reasonably strong experimental evidence supports an increased mortality risk to elk from human hunters on roads. Cole et al. (1997), tested the effects of an unreplicated (n=1) experimental road closures on survival of Roosevelt elk (*Cervus* *elaphus nelsonii*) in Oregon from 1991-1995. Cole et al. (1997) determined home range size, movement rates, and survival differences between the pre- and post- road closure periods for 41 radiocollared adult female elk in a before after design without an contemporaneous control. By removing access to 128km of BLM roads (35% of roads in study area), Cole et al. (1997) documented a 12% reduction in home range size, a 18% reduction in daily movements, and a 7% reduction in mortality for elk, although the difference in survival was not statistically significant with only 6 mortalities observed during the study. Limitations of the experimental design are 1) the lack of adequate controls for the treatment period – improvements to adult survival and reductions in home range size or other variables could have been because of more favorable climatic conditions (spring precipitation, etc.) or other unmeasured variables; 2) small sample sizes for making strong population inferences. In survival estimation, the number of mortalities strongly determines the level of confidence in survival estimates, and in long-lived ungulates with high annual survival rates, determining population level impacts requires substantial sample sizes. Despite the fact that this study is often cited as compelling evidence for the beneficial effects of road closures, these two weaknesses reduce the scientific merit of this study. Similar studies in Montana and elsewhere also examined the effects of hunter road restrictions on elk, including Basile (1979), but few made the difficult but important connection to demography that Cole et al. (1997) attempted.

Human recreation besides human hunting from roads can also affect elk populations, a subject that has been the focus of numerous studies and literature reviews in itself (Bjornlie and Garrott 2001, Cassirer et al. 1992, Joslin and Youman 1999,Oliff et al. 1999). Elk and other wildlife may view human recreation as a form of predation risk even without direct mortality because of indirect behavioral mechanisms (Frid and Dill 2002,Geist 2002). For example, Millspaugh et al. (2001) showed clear physiological stress responses of elk to proximity to roads and when in areas with higher road densities. Here, I only review a few recent key studies that exemplify proper experimental design and provide a beacon of scientific rigor to biologists considering improving studies of the effects of energy development on wildlife.

In a series of exceptionally well planned studies in the Beaver Creek and Vail areas of Colorado, Phillips and Alldredge (2000) and Shivley et al. (2005) conducted a well designed experimental (albeit only n=1 replicate) test of the effects of spring/summer hiking recreational disturbance on elk on calving and summer ranges. Phillips and Alldrege (2000) and Shivley et al. (2005) maintained a total sample of 75-85 radiocollared adult female elk across both the control and treatment areas and applied hiking disturbance to the control group in a before-after-control-impact (BACI) design as follows. In 1995, no treatment was applied to the treatment area (before), and the disturbance was applied in 1996 and 1997 (see discussion), then not applied in 1998 and 1999. In the control area, no treatments were applied. They then compared the effects of hiking disturbance on calf:cow ratio's, a key indicator of population performance in ungulates and elk in particular (Raithel et al. 2007,Gaillard et al. 2000).

Calf:cow ratio's were similar before hiking disturbance was applied in 1996. Calf:cow ratio's steadily declined for the two years of treatments for an average reduction in calf:cow ratio of 0.173, or 17 calves:100 cows, (95% CI: -0.32 to -0.03). Population modeling revealed that this reduction in calf survival could reduce population growth rates from 7%/year to 0%/year, confirming the substantial negative impacts of human disturbance during spring and summer to population dynamics of elk. On the basis of this exceptionally well designed study, the authors of both studies make strong recommendations to protect spring calving habitat, concluding "to ignore potential effects of human-induced disturbance to elk during calving seasons is to risk declining reproductive success in elk populations" (Phillips and Alldredge 2000).

Extending these results to the effects of human development in general, an observational study of the effects of increased ski resort development in the Vail area of Colorado (Morrison et al. 1995) showed that during ski area development, when human disturbance was the highest, elk avoided human activity and the development site more than afterwards. Elk use after development was still lowest when human activity was highest, indicating that while elk habituated to development to some degree, there may be long term negative impacts. These two examples illustrate the benefits of conducting well designed experimental studies to guide the interpretation of less intensive observational studies.

Table 2. Review of scientific literature on the effects of energy development on Elk, summarizing study authors, location, vegetation type, species (Aa- *Antilocapra* sp., AlAl – *Alces alces*, Ce- *Cervus elaphus,* Oh- *O. hemionas*, Oc- *Ovis canadensis*), whether the study was peer reviewed or not, study area size, duration, development type, study design and sample size, general results and management recommendations.

Authors, location, Veg. type	Spp.	Peer Review	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Bennington et al. 1981 MI, Mixedwood	*Ce*	No	512 km^2 and 1.4 years	Oil drilling/well pumping	Observational, aerial surveys, track surveys, n=N/A	Short-term decrease in activity following oil drilling, temporary (2-4 wk.) relocation after development, no significant diff. between pre-drilling and post-drilling activity.	Avoid high impact habitat sites such as calving grounds; habitat mitigation required.
Cole et al. 1997 OR, Mountain	*Ce*	Yes	972 km^2 and 3 years	Roads and human hunting	Experiment, radio-telemetry, n=41*	Core area and home range size, as well as movement rates decreased and elk survival increased with experimental road closures.	Increase road removal and road management areas, decrease illegal hunting on open roads, restrict human access to roads.
Edge et al. 1982 MT, Mountain	*Ce*	Yes	Unk, 5 years	Logging	Observational, radio-telemetry, n=36*	Avoided open habitats and logging especially in areas of high human activity.	Construct roads with cover and topography in mind, manage human recreational access, greatest impact in summer.
Edge et al. 1985 MT, Mountain	*Ce*	Yes	Unk, 5 years	Logging, human recreation	Observational, radio-telemetry, n=39*	Elk did not change home range size or fidelity with logging.	Logging activities limited to unoccupied seasonal habitats & logging restrictions the minimize time and overlap with elk winter ranges.
Frair et al. 2007 AB, Foothills	*Ce*	Yes	17000 km^2 and 5 years	Siesmic, roads, wells, forestry	Comparative, GPS telemetry, n=40 resident elk	Mortality increased closer to roads by humans, closer to seismic cutlines by wolves. Landscape-scale changes from cumulative impacts in wolf and human predation risk survival.	Manage for lower human use on roads all year to improve elk survival. Impacts were cumulative with other land use changes from forestry.

Table 2. Cont.

Authors, location, Veg. type	Spp.	Peer Review	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Frair 2005	*Ce*	Yes	17000 km^2 and 5 years	Seismic, roads, wells, forestry	Comparative, GPS radio-telemetry, n=40 resident elk	Effects of roads were compounded by attraction to clearcuts associated with roads, elk avoided clearcuts within 200m of a road. Road network design became increasingly important as road density increased and accounted for as much as 30-55% of the change in mortality risk	Availability of core areas declined to 50% above road densities of 0.5-1km/km^2, and elk could not tolerate road densities >1.4km/km^2. Road network design that minimized roads and restricted human access could minimize risks to elk.
Gillin 1998 WY, Mountain	*Ce*	Yes	Unk, 2.2 years	Seismic exploration, roads	Experiment, radio-telemetry, n=21	Elk were temporarily displaced during and after seismic activity for up to two weeks, but returned later.	Seismic spaced min 2, max 7-10 days apart; designated helicopter flight corridors w/ altitudes > 150m; avoid calving areas, foraging areas and open meadows; spring impacts greatest.
Hiatt et al. 1982 WY, Mountain	*Ce, Oh*	No	101 km^2 and 0.25 years	Oil well	Comparative, radio-telemetry, Unk	Elk and mule deer shifted home ranges away from the well site, did not avoid access road.	Late winter spring were the greatest impact seasons
Hayden-Wing Associates 1991 Review	*Aa, Oh, Ce*	No		Gas, oil, seismic exploration	Review, n=N/A	N/A, Literature review	Recommend restriction of exploration on occupied winter range from Nov 15 to April 30 as a precautionary principle Winter impacts greatest
Hayden-Wing Associates 1990 WY, shrub steppe	*Ce*	No	96 km^2 and 11 years	Active wells	Comparative, aerial elk surveys, n=11	No significant difference in elk population size over 11 years in response to drilling, but changes in distribution varied widely.	Need for long-term studies; recommended putting wells in low visibility areas; avoidance of calving and winter ranges
Irwin and Gillin 1984 WY, Mountain	*Ce*	No	Unk, 1 years	Seismic exploration	Observational, radio-telemetry n=21	Elk partially avoided calving ranges after seismic, migrating to summer range. Elk avoided disturbance using topography and cover.	Restrictions on development during calving on calving ranges, road alignment should minimize visibility of the road using cover and topography.

Table 2. Cont.

Authors, location, Veg. type	Spp.	Peer Review	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Johnson 1980 WY, Mountain, sagebrush steppe	*Ce*	No	Unk, 1 years	Oil and gas wells.	Observational, aerial telemetry & aerial surveys, n=4-56	Elk were affected by activity on the access road; cows moved calves at earlier age; elk were displaced away from drilling rig in 1979.	Minimize drilling activities in spring and winter range, road mitigation required.
Johnson and Wollrab 1987 WY, sagebrush steppe	*Ce*	No	Unk, 8 years	Natural gas field	Comparative, radio-telemetry, n=16	80% of surveyed elk were on gas field prior to drilling; only 39% were on the field during drilling. Calving ground was also abandoned during the intense drilling.	Avoid drilling on calving and winter ranges.
Johnson et al. 1986 WY, mixed	*Ce*	No	25.9 km^2 and 3.25 years	surface coal mine	Experimental, radio-telemetry n=64*	All measured variables showed no significant difference between control and mine study groups, winter impacts greatest	None.
Knight 1981 MI, mixedwood	*Ce*	Yes	56 km^2 and 1 years	Seismic exploration; oil well drilling	Comparative, radio-telemetry n=12	Elk moved away from seismic: terrain and vegetation type had no effect. No significant difference in elk home ranges with/without disturbance, no correlation between distance to disturbance and mean daily movements.	Need to study effects of pipelines on wildlife, timing restrictions for seismic exploration to avoid winter range and calving.
Kuck et al. 1985 ID, Forests	Ce	Yes	350 km^2 and 2 years	Simulated mining & human disturbance	Experimental, radio-telemetry n=25	Disturbed calves moved greater distances, used larger areas, showed greater use of coniferous forest, and lacked selection for favorable physiographic parameters. Cow/calf pairs abandoned calving areas, Winter survival between groups and between years was similar.	Development restrictions during calving, spring summer greatest impacts.

Table 2. Cont.

Authors, location, Veg. type	Spp.	Peer Review	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Lees 1989 AB, Foothills	*Ce*	No	Unk, and 1.25 years	oil pipeline	Observational, n=7* collars, 5 cameras, n=568 tracks	Telemetry: inconclusive; tracks: avoidance of human impacts; cameras: inconclusive, fall impacts greatest	Control public use and access through gating, improvements to forage on pipelines.
Lyon 1979 MT, Mountain	*Ce*	No	215 km^2 and 8 years	logging; roads	Observational, pellet surveys, n= Unk	Elk consistently moved away from active logging.	Manage roads to reduce human hunting, avoid logging in winter, spatial overlap with elk winter range.
Morgantini and Hudson 1980 AB, Mountain	*Ce*	No	35 km^2 and 0.5 years	Roads and human hunting	Observational, behavioral observations, n= Unk	Elk avoided roads in day, forage closer to them at dusk and dawn. Elk avoided the open grasslands near roads.	Restrict human activity to reduce negative impacts of roads.
Morgantini 1985 AB, Foothills	*Alal, Ce, Oh, Ov*	Yes	Unk, 0.33 years	oil pipeline	Observational, Snow track surveys, n=Unk	Pipeline was a barrier for 53.9% of ungulate groups that tried to cross them. Elk were least affected, moose the most impacted by the pipeline.	Have periodic openings, underpasses, or overpasses along pipeline to mitigate it as a crossing barrier.
Olson 1981 MT, Mountain	*Ce*	No	503 km^2 and 0.5 years	Seismic exploration, natural gas	Comparative, radiotelemetry , n=4	Elk avoided visual disturbances more than auditory; movement rates increased closer to disturbance.	Winter activity should be kept to a minimum; have specified flight paths for helicopters to minimize disturbance
Phillips and Alldrege 2000 CO, Mountain	*Ce*	Yes	500 km^2 and 3 years	Human recreation on trails.	BACI, radio-telemetry n=80	Average calf production was 0.23 calves/cow lower for elk disturbed by humans than control elk, reduced population growth rate 7%.	Calving-season closures for all human activity in elk habitat.
Powell 2003 WY, sagebrush steppe	*Ce*	No	2521 km^2 and 3 years	active oil and gas wells, roads	Observational, n=40*	Elk avoided active wells and roads by 2 km in summer, showing 73% less use than expected.	Summer impacts greatest, seasonal road restrictions in summer habitat.

Table 2. Cont.

Authors, location, Veg. type	Spp.	Peer Review	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Rowland et al. 2000 OR, Starkey, Mountain	*Ce*	Yes	77.6 km^2 and 3 years	roads	Observational, radio-telemetry n=89*	Elk consistently selected areas away from open roads in both spring and summer. Model predictions of simple habitat effectiveness models corresponded only weakly with observed habitat effectiveness values.	Spatial distribution of roads must be considered for habitat effectiveness models for evaluating impacts. Summer road restrictions needed. Spring summer impacts greatest.
Sawyer et al. 2007 WY, shrubsteppe, grasslands	*Ce*	Yes	2517 km^2 and 2 years	n/a	Observational, GPS telemetry, n=33* (55 VHF collars in validation sample)	Elk selected for summer habitats with higher elevations in areas of high vegetative diversity, close to shrub cover, northerly aspects, moderate slopes, and away from roads. Winter habitat selection patterns were similar, except elk shifted to areas closer to roads.	Management of roads and related human disturbance is an important consideration for managing elk populations. Summer impacts greatest
Shivley et al. 2005 CO, Mountain	*Ce*	Yes	500 km^2 and 2 years	Human recreation.	BACI, radio-telemetry, n=145	Productivity rebounded following release from disturbance, and full recovery was achieved by the second post-disturbance year.	Selective closures, or at least restrictions on recreational activity, may be warranted during calving season, when greatest impact occurred
Van Dyke 1996 MT, grasslands	*Ce*	Yes	500 km^2 and 4years	Active oil well	BACI, n=10	Minimal effect of drilling on elk home range use in a low density drilling area. Elk used cover during drilling.	
Ward 1986 WY, sagebrush steppe, grasslands	*Ce*	No	Unk, 4years	Seismic exploration	Observational, few radio-collared elk, surveys, etc. n=Unk	Elk avoided human activity depending on line-of-sight; without topography, elk moved 3.2 km; with topography, 800 m. Elk returned to areas of disturbance a few days after activity was concluded.	Road, wellsites should be aligned in areas of low visibility in topography out of line of sight.

3.3 Pronghorn Antelope (*Antilocapra americana*)

3.3.1 Grasslands

In one of the earliest studies of pronghorn considered in this literature review, Bruns (1977) investigated general patterns of pronghorn habitat use, movements, and effects of human developments using ground and aerial observational methods including snow tracking and behavioral observations. Bruns (1977) focused on short grass prairie in south eastern Alberta from 1968-69 during an exceptionally severe winter. He found that pronghorn movements were restricted during winter months, and selected habitats that minimized snow depths during winter, had lower winds, and with softer snow that made pawing through snow to forage easier. Severe snowstorms caused rapid, long distance movements. Average herd sizes were 38 animals. Pronghorn often used plowed roads as movement corridors, but suffered effects of habitat fragmentation from fences and gates. Management recommendations included barbless wire fences, pronghorn specific designs in important migration and travel routes, and keeping gates open to facilitate movements.

Oil and gas exploration in the little Missouri grasslands have negatively impacted habitat for Mule deer, Elk, and White-tailed deer, reviewed in a study by Girard and Stotts (1986). Girard et al. (1985) summarized the effects of energy development as impacts during development and exploration phases, chemical spills that upset sensitive prairie grassland and stream ecology, and displacement of wildlife species. Approximately 1% of the entire area considered was physically lost because of energy development, and an undetermined area surrounding development was avoided by these ungulate species. Girard (et al. 1985) emphasized how critical site reclamation was for sensitive grasslands, the critical task of suppressing non-native invasive weed species, the danger of saltwater pond (associated with drilling operations) blowout on downstream systems, and the negative effects of H_2S (hydrogen sulphide) on wildlife species. I return to this important and understudied area in the discussion.

In a study that could be useful as a baseline to compare against development underway in eastern Montana, Armstrup (1978) studied the habitat use, movement patterns, and home range use of 102 pronghorns marked with VHF or visual collars on the border of Montana and Wyoming in and around the Powder River basin from 1976 to 1977. Armstrup (1978) found wide variation in selection for vegetation types seasonally, and that selection was largely a function of available vegetation. This corresponds with the concept of functional responses in resource selection that emphasize 'critical' habitat changes across regional gradients in availability (Mysterud and Ims 1998,Hebblewhite and Merrill 2008). Topography was not a big driver of pronghorn habitat selection. The most significant finding of this study was that all marked pronghorn used a completely different winter range during 1976 than in 1977 – confirming that long-term studies are required to evaluate key habitats and even to define areas of occupancy.

3.3.2 Shrub-Steppe

Approximately 10 studies on pronghorn ecology and energy impacts in sagebrush-steppe ecosystems were reviewed from a total of 4 study areas; the Northern Range of Yellowstone National Park (White et al. 2007a), the Upper Green River Basin (Berger 2004, Berger et al. 2006, 2007,Sawyer et al. 2002, 2005b,2006), in the Rattlesnake hills in Wyoming (Easterly 1991), and on a reclaimed coal mine in northeastern Wyoming (Medcraft and Clark 1986). The series of studies by Sawyer and colleagues in the Upper Green River focused on both mule deer and pronghorn, and so are summarized below in the combined section.

The series of studies by Berger and colleagues (Berger 2004, Berger et al. 2006a,b, 2007), examine the response of pronghorn to energy development in the Upper Green river basin overlapping the study area of Sawyer et al. (2002). This area is underlaid by the Jonah and Pinedale Anticline natural gas formations that are estimated to contain >10 trillion cubic feet of natural gas and coal bed methane deposits, and is undergoing rapid expansion in oil and gas development. Energy development only started in 2001, so all of the studies of Berger, Sawyer and colleagues should be considered as assessing the early impacts of energy development.

The studies of Berger and colleagues were initiated in fall 2002 as a pilot study investigating migration in pronghorn (see Berger et al. (2004, 2006) summarized below), the study was expanded in 2005 to a five-year study of the effects of natural gas development on pronghorn behavior, migration, habitat selection, and, ultimately, the population consequences of development. Methods involved collaring ~50 pronghorn/year split evenly between a control (undeveloped area) and treatment (energy development area) area. In 2007, they increase the sample size to 100 VHF collars to estimate survival rates and to provide better longitudinal data on survival. They recovered 48 GPS collars in 2005 and 42 GPS collars in 2006, and in these preliminary progress reports, compare resource selection between the control and treatment groups. In their first (Berger et al. 2006) and second-year progress reports (Berger et al. 2007), the authors emphasize that results are preliminary and subject to change given long-term responses and final analysis. Regardless, their interim results can provide some important information about pronghorn responses to increasing development on winter ranges.

Berger et al. (2006, a,b) report that the overriding natural factor influencing distribution of pronghorn on the winter range was snow depth – pronghorn selected 60% shallower snow depths than available throughout the study area (e.g., 12cm versus 19cm). In terms of resource selection, while some individual animals continued to select habitat in the energy development areas, some animals avoided developed areas. At the population level, however, the authors did not find pronghorn were avoiding developed areas at the current levels of development. Identification of core areas of use by pronghorn, dictated by patterns in resource availability, may be useful tools to identify areas that are important to pronghorn for future energy development planning. From a population perspective, the authors found no differences in survival rates or body measurements of pronghorn between the control or treatment groups. While their results suggest energy development does not influence pronghorn within the Upper Green River Basin, the authors caution that results are preliminary, winter severity has been mild during the study (impacts may be greater during deeper winters given pronghorn selection for shallower snow), the area of most intense development at present are not within prime pronghorn habitat, and responses may be expected to increase over longer periods of time for long-lived ungulates than the two year time-window reported on to date. A long-term commitment to understanding the effects of energy development on this and other populations of ungulates is required. Regardless of the equivocal results of energy development on winter ranges, these studies documented substantial potential impacts of energy development on migration both within this study area, and at the regional scale.

Berger's (2004) literature review on the loss of migration also mentions pronghorn migratory declines, especially in the GYE, where approximately 75% of all migrations have been lost. Berger (2004) illustrates the problem with a case study involving their long-term pronghorn study in the Pinedale area of WY. Both residential development and future potential energy development threatens one specific migratory corridor pinch point, the Trapper's Point bottleneck, where the migration corridor narrows to less than 800m. In a follow up study to this literature review, Berger et al. (2006) confirm that this particular migration corridor, from the Upper Green River through to Teton National Park, has likely been used for over 6000 years. Using archaeological data that confirms the presence of pronghorn in this migration corridor, Berger et al. (2006) argues that this migration route has likely persisted uninterrupted for at least 6000 years and likely since the end of the Pleistocene. Only by creating large scale migration corridors that are protected from development or managed specifically to mitigate energy development, will long-term migration, a critical ecological process that is declining across the Rocky Mountain west, persist.

The importance of migratory corridors for pronghorn is also emphasized by a recent study in Yellowstone National Park by White et al. (2007). Movements of 44 radio-collared pronghorn over 6 years revealed a similar 'pinch point' in the migration corridor between summer and fall ranges which resulted from topographic constrictions, habitat requirements of pronghorn for open habitats, and fidelity to historic migration routes. Development proposed within the park for increased tourist facilities and buildings threatens this migration corridor. White et al. (2007) also showed that this population was partially migratory with approximately 70% migratory, and 30% resident.

Migratory pronghorn showed some fidelity to summer ranges, but 20% switched between years and switched strategies from year to year from migrant to resident. This study clearly emphasizes how little we know about migration in most populations, and that migration is likely a condition dependent strategy that depends on density, population history, climate, and, potentially, disturbance regimes. Management implications of this study are that it takes a long-time to document migration patterns and that, combined with the studies of Berger (2004) above, pronghorn seem especially vulnerable to development within migration corridors.

3.3.3 Semi-desert: effects of military activities

The Sonoran pronghorn (*Antilocapra antilocapra sonoriensis*) is the most endangered subspecies of pronghorn, with population declines to <33 animals as recently as 2003 (Krausman et al. 2005). Despite being listed as an endangered species for over 30 years, reasons for the population declines are relatively unknown, but though to be linked to habitat and forage degradation, loss of water sources because of hydroelectric developments, and human development. Forty percent of identified Sonoran pronghorn habitat occurs in military lands in southwestern Arizona, and a series of studies investigated the effects of military overflights and ground activities on pronghorn habitat use, behavior, hearing, and potential population consequences (Krausman et al. 2004, 2005, Landon et al. 2003). The most comprehensive study compared behavior of pronghorn on the military base to baseline behavior of animals in the closest population of pronghorn without military activity, albeit from a different subspecies. The study primarily relied on behavioral observations of pronghorn responses to human activities. Pronghorn exposed to military activity foraged less, stood alert and moved more than pronghorn not exposed to military activity. Pronghorn did not appear to respond to military overflights, and the study found that ungulates do not hear sounds from military aircraft as well as humans do.

These results contrasted with the results of (Landon et al. 2003) that found habitat use of 31 radiocollared pronghorn tended to be in areas with lower noise levels from military activities, although this study apparently pseudoreplicated, confusing the # of locations of animals with the true sample size instead of the # of animals. Landon et al. (2003) acknowledge that more detailed habitat selection studies are certainly needed before firm conclusions could be drawn. Acting on these recommendations, Krausman et al. (2005) investigated habitat selection of Sonoran pronghorn using detailed behavioral observations (n=1203) of pronghorn collected over a 3 year period from 1999-2002. Sonoran pronghorn showed stronger selection for burned sites and sites previously disturbed by military activity (bombing ranges, fires, etc.) over undisturbed sites. They speculate that increase forage production, visibility and ease of movement all contribute to pronghorn selection for disturbed sites, and that declines in military activity that simulate natural disturbance may actually be detrimental to pronghorn. Overall, Krausman et al. (2004, 2005) found few impacts of military activities on Sonoran pronghorn, but conclude that the population remains in serious danger of extirpation and immediate conservation actions are needed.

3.4 Mule Deer (*Odocoileus hemionus*)

3.4.1Sagebrush-Steppe and Grasslands

Berger's (2004) literature review on the loss of migration amongst North American ungulates also has implications for mule deer and energy development. In the Greater Yellowstone ecosystem, Berger documented 75% declines in ungulate migration for mule deer, elk, and pronghorn due to long-term human caused habitat fragmentation and overhunting. Threats to remaining long-distance migration include energy development, tourism development, sub/urban sprawl, and highway mortality and habitat fragmentation. Large scale migration corridors that are protected from development or managed specifically to mitigate energy development are needed to protect the critical ecological process of long-term migration which is declining across the Rocky Mountain west.

In a series of studies on the effects of energy development in the same Jonah-Pinedale Anticline project area of western Wyoming, Berger and colleagues and Sawyer and colleagues conducted a series of related studies on the effects of energy development on mule deer and also pronghorn to a lesser degree (Sawyer et al. 2005a,b, 2006, 2007). This area is a winter range for large numbers of elk, mule deer and pronghorn and habitat for animals migrating from the entire Upper Green River Basin area, approximately 15,000km^2. Initial studies focused on migration of radiocollared mule deer (n=158) and pronghorn (n=32), and found seasonal migrations for 95% and 100% of all collared animals ranged an average of 84 and 177 km straight line distance between seasonal ranges. This study also noted the potential for energy development impacts on migration corridors, and documented the same narrow pinch point for the migration corridor of pronghorn migrating from the winter range to summer ranges in Grand Teton National Park that Berger et al. (2006, a,b) describe. The authors conclude, with similar recommendations as in other migratory ranges, to minimize development, remove barriers to migratory movements such as fences and pipelines, and potentially develop seasonal restrictions to avoid the peak months of migratory movements in May/June and October/November. This study echoes the results of Berger (2004), who found that impacts on migratory ranges may affect a huge area surrounding the localized development, and requires a regional-scale, cumulative effects assessment approach.

Focusing on winter range impacts was the focus of the studies by Sawyer et al. (2005b, 2006) collectively called the Sublette Mule deer study. The study was started in 1998 to examine the ecology of mule deer home range use, habitat selection, migration routes and demography during a pre-development phase that ended in 2001. From 2001-present, the study entered the second phase as a long-term study on the effects of energy development within the Pinedale area on mule deer ecology in an experimental comparison of areas with and without energy development. With the pre-data collected in phase 1 and two treatment areas in phase 2 (with, without development), this study represents a well designed before-after-control impact study, albeit unreplicated.

Before development, the Sublette Mule deer population was a healthy and productive population, with adult female survival rates (0.85, n=14) and fawn:doe ratio's (>75:100) indicative of a growing population (Unsworth et al. 1999). In 2002, mule deer densities were similar between the control and energy development treatments, but have been diverging since 2002. In the developed area, mule deer densities declined significantly by ~47% over a 4-year period ending 2005, whereas in the control area, there was no negative trend and mule deer densities were constant and similar to pre-development density on the treatment area. This trend in density is suggestive of a demographic impact of energy development, yet survival differences between adult female and overwinter fawn survival were not statistically different between the two areas, although overwinter fawn survival tended to be higher, the differences reported to date in their preliminary progress report were not statistically different. Sawyer et al. (2005) speculate that the lack of demographic difference between treatments may be because 1) small scale demographic differences could explain the differences in population trend, but are preliminary and influenced more by small sample size, and will be verified at a later date by more detailed analysis, or 2) differences were driven by emigration or dispersal from the developed areas. Migration routes were also identified, as discussed above, in this first phase.

From a habitat perspective, Sawyer et al. (2006) reported expanding energy development over a 5-year period with an increase of 95km of roads, 324 ha of well pads, and a total of ~400 ha of lands directly lost to development footprints within the study area, an increase in density of 0.12km/km^2 and ~0.3 wells/km^2 (considering the study area size just the Pinedale Anticline project area of ~800km^2). Effects of energy development are summarized in their 2006 Journal of Wildlife Management paper (Sawyer et al. 2006), where they evaluated the effects of energy development on VHF and GPS collared mule deer collared from 1998 to 2003 over the first three years of development. Sample sizes of VHF and GPS collared mule deer ranged from 7-45 / year of the study. Mule deer avoided areas close to energy development during this study, responses to development occurred rapidly within 1-year of development, and avoidance of energy development increased over the course of the 3–year study. Sawyer et al. (2006) found lower predicted probabilities of use within 2.7 to 3.7 km of an oil or gas well sites, confirming that indirect effects of habitat loss from energy development were much greater than the loss of the direct footprint of energy developments. Over the course of the study, areas that were classified as high quality habitat before development changed to low quality, and vice-versa, showing that mule deer shifted habitats away from favored high quality habitats because of energy development. Presumably, these population level habitat selection responses will eventually have important population implications to the total area of high quality habitat available in the study area. The authors recommend such demographic studies, as well as activities that reduce the footprint of energy development including; 1) directional drilling from single well pads to multiple gas sources to reduce surface impact, 2) limiting public access, 3) developing road networks with the goal of minimizing new road construction, and 4) guidelines to minimize human disturbance during the winter and on designated high quality ranges.

Several reviews of the effects of energy development, with specific focus on mule deer or pronghorn, were also reviewed. Bromley (1985) reviewed the effects of energy development in wildland environments for the USFS, and provides an annotated bibliography similar to this review, including more broadly, the effects of all human activities on wildlife. Generally, she makes the following conclusions; 1) many results are conflicting, yet few studies have quantitatively shown the effects of human activities on population dynamics of wildlife, likely because long-term demographic studies have been extremely rare in the environment; 2) It is often difficult to separate out naturally induced variation in response variables from human disturbance without adequate baseline (pre-development) data and experimental controls; 3) severity of the impacts of energy development are often site-specific and will require localized mitigation strategies in many cases; and 4) Effects of energy development may be most critical during sensitive periods including winter, spring calving, migration corridors, and for social species (no study reviewed in this review was actually replicated).

In a study on the effects of human activity on mule deer in the grassland and pine break vegetation communities in southeastern Colorado, Stephenson et al. (1996)

examined home range use and fidelity in response to military activity during ground training exercises over a three year period. Human activity during military exercises was extreme; during the seven 2-3 week military exercises, between 2624-6619 humans in 854-2397 vehicles used the 1040km^2 study area. They used a comparative design where home range dynamics and fidelity were compared between times with and without human activity for 71 radiocollared female mule deer. Mule deer female and fawn home ranges were larger during military activities during winter and summer. However, only the 50% core areas used by mule deer males were larger during military activities. Forty percent of female deer shifted home ranges between military activities. This study shows that intense human activity can have large impacts on patterns of space use. However, the limitations of this study are the extreme human activity levels observed – few energy developments even at peak construction periods, would approach these human disturbance levels. Secondly, while this study showed large changes in home range behavior, they did not investigate population impacts.

3.4.2 Mountain

Freddy et al. (1986) conducted some comparative trials (without controls) to compare the effects of human hikers and snowmobiles in Colorado from 1979 to 1980 within a mule deer winter range. They compared the responses of 7-11 mule deer to n=67 approaches to hikers and snowmobiles and documented the level of response. Mule deer took flight in response to snowmobiles at a greater distance, but showed a longer duration of response to human hikers than to snowmobiles, and showed a high response, running, more often to hikers than snowmobiles. Based on energetic calculations, each disturbance event cost between 0.2-5% of the daily metabolic requirements of mule deer. When fleeing from hikers, deer moved an average of 907m, and consumed more energy than when responding to snowmobiles. Freddy et al. (1986) concluded that human activity on winter ranges should be severely restricted to minimize negative impacts. Limitations of this relatively well thought out study include psuedoreplication and small actual sample sizes. Sample sizes for tests were considered to be individual approach trials, whereas the true sample unit was the individual radiocollared deer. Therefore, a mixed-model that accounted for deer as the sample unit should have been employed Gillies et al. (2006) and this may have affected results because of the lower effective sample size of 7 to 11 animals.

Evaluating the potential population responses of mule deer to energy development will be difficult because of broad scale declines in mule deer productivity across western North America (Gill 2001,Unsworth et al. 1999). Gill et al. (2001) reviewed the factors causing declines of mule deer populations in Colorado, and concluded declines could be caused by the following factors acting synergistically; 1) competition with increasing elk populations, 2) density dependence in vital rates caused by historic high population densities, 3) long-term declines in habitat quality for mule deer because of changes in fire history regimes in forest and shrub-steppe ecosystems, 4) overharvest in some key areas, 5) increasing predator populations, and finally, 6) diseases, such as chronic wasting disease. Co-authoring the review of causes of mule deer declines were Dr. N.T. Hobbs, Dr. G.C White and other noted experts in mule deer and population biology of ungulates. Given the difficulties of disentangling all these potentially interacting and confounding influences on mule deer population dynamics, the report concludes with a series of recommended large-scale adaptive management experiments designed to test the main hypotheses of predation and habitat change. The authors emphasize that long-term (6-8 year), large–scale (WMU scale, 1000km^2) will be required to rigorously assess reasons for mule deer declines. The recommendations of this study are particularly relevant for considering the effects of energy development on large ungulates. To rigorously link energy development to changes in demography, long-term, large-scale, and well funded adaptive management experiments will be required.

From 1980 to 1981, Ihsle (1981) worked with MTFWP and the BLM to study the population ecology of mule deer along the east slope of the Rockies west of Choteau to determine the effects of oil and gas drilling and development on mule deer. There study occurred early in development under extremely low densities of development – less than 0.003 wells/km^2 had been constructed within their 2725 km^2 study area at the beginning of the study, and their general results was almost no impacts of energy development on mule deer. They radiocollared 78 mule deer and considered home range, movement, habitat selection, migration, and fawn:doe ratio to determine the effects of energy development in an observational correlation-based study design. They found no effects of development, generally because oil wells were restricted to a small part of the study, development density was very low, and the large spatial scale of the study area. Limitations of this study were the lack of a suitable treatment effect of development given the huge study area size. Perhaps focusing just on movements or habitat selection by mule deer in the area surrounding development would have provided more relevant results with respect to energy development. Regardless, while this study was designed as a pre-development study, to my knowledge there has not been any follow up, a similar theme in the review of many studies that were putatively pre-development. Hopefully data from this earlier study can be used in the future to evaluate the effects of energy development, albeit without controls.

Five-years later, in the same study area, Irby et al. (1988) reviewed the status of energy development, created guidelines for the mitigation of energy development on wildlife, and provided recommendations for energy development. Irby et al. (1988) reiterated the results of Ihsle (1981) and Irby et al. (1988) and found no detectable response to low density oil and gas development, but emphasized that this earlier study was largely conducted during the pre- or early phases of energy development. Irby et al. (1988) recommended that continued monitoring occur throughout the increasing development phase, and recommended that mitigation should occur on the scale of entire winter ranges prior to development occurring. Irby also reviewed the guidelines used by Interagency Technical Committee 1987 guidelines for wildlife that BLM used for mule deer, which I provide in Appendix B for an important historic perspective. Importantly, however, despite the existence of best practices guidelines, Irby et al. (1988) note that BLM often violated these guidelines, and frequently issues exceptions to these stipulations for exploration and well drilling operations.

In southeastern Idaho, Merrill et al. (1994) studied the effects of mining developments on migration by mule deer between seasonal ranges in the Dry Ridge area. Using a combination of track surveys and a small number of radiocollared mule deer (n=5-7), they evaluated movements of mule deer around a phosphate mine located in a migratory corridor. The found avoidance of mining developments during migration, and recommended providing adequate forest cover, travel fences to direct movements away from development, and under or over-passes at specific locations to facilitate movements around human developments where required. They also caution that short term studies may fail to document effects in low snow winters, because migration was strongly influenced by snowfall.

In perhaps the first study on mitigating effects of highway caused habitat fragmentation on ungulates, Reed et al. (1975) studied the responses of mule deer approaching and attempting to cross a concrete highway underpass under I-70 in Colorado. The concrete underpass was not specifically designed for wildlife crossings, but observations suggested that it was being used by mule deer. Reed et al. (1975) used remote video camera's to record 4450 approaches by groups of mule deer that resulted in 1739 entrances/crossings (~40% success rate) of the structure. Sixty one percent of all individual mule deer that attempted to cross were successful, eventually. Animals that were unsuccessful at crossing were more vigilant and wary, reflecting the perceived risk of the crossing structure. This study laid a foundation for the development of the growing field of wildlife-highway mitigation (Clevenger et al. 2001,Clevenger and Waltho 2000). I do not review any additional studies of ungulate responses to roads, but summarize general results from the literature in the discussion.

3.5 Combined Studies on Mule Deer and Pronghorn

3.5.1 Sagebrush-Steppe

From 1988-91, Easterly (1991) conducted a study to examine the effects of energy development on both pronghorn and mule deer in the Rattlesnake hills of Wyoming, an area of sagebrush-steppe vegetation communities. Their study was in response to repeated violation by the BLM of the 1985 environmental impact statement

(EIS) on the Platte River Resource Area (which included the Rattlesnake hills) of their own policies regarding timing restrictions of energy development on crucial winter range for ungulates. Their policy, stated in the EIS, was that "no surface development will be allowed from Nov 15 through April 30 in critical pronghorn or mule deer winter range (BLM, 1985: 29). Despite this policy, BLM issued 18 permits in violation of this policy for drilling operations in crucial winter range between 1987 and 1991. Easterly et al. (1991) focused on testing whether violation of this policy was negatively affecting ungulates, but collected no pre-development data nor had any controls or comparison sites. Easterly et al. (1991) captured pronghorn and mule deer; they deployed 20 VHF collars, 175 neckbands, and ear tagged 28 males on pronghorn, and collared 29 mule deer all with VHF collars. They used a combination of radiotelemetry, and aerial and ground surveys to measure home range responses, densities, movements, and survival as a function of human development. Pronghorn densities were substantially lower closer to energy development and collared pronghorn avoided well sites during disturbance. Results for mule deer were more equivocal; densities of mule deer were similar close to and far from drilling activities, but mule deer were located farther from development during drilling, but not after, when they were the same distance as before development. This indicates some habituation response of mule deer to development. The authors attempted to draw some population consequences from their study, but were unable to. The prime limitation of this relatively well designed study was the lack of pre-development data on mule deer and pronghorn distribution in the region.

Medcraft and Clark (1986) studied the effects of reclamation of a 200ha coal mine on seasonal habitat use and diets over a 1 year period in northeastern Wyoming. The coal mine was reclaimed by a mix of native and non-native graminoids, forbs, and shrubs – only native shrubs were planted. Mule deer showed statistically significant selection for reclaimed lands more than expected based on availability, but pronghorn strongly avoided reclaimed lands. This difference was thought to be because mule deer selected non-native plants during summer (e.g., alfalfa), whereas pronghorn preferred native forbs which occurred at lower frequencies on reclaimed lands. Through behavioral observation, the authors also concluded that remaining mining structures such as fences and berms did not impede mule deer or pronghorn movements. The authors conclude by recommending reclamation of all disturbed sites with native species including graminoids, forbs and shrub species. To encourage shrub revegetation following development, Medcraft and Clark (1986) recommend concentrating shrub establishment efforts by patch seeding sites that are ecologically suitable such as draws, coulees, etc. Furthermore, cattle grazing of reclaimed lands should be minimized to allow re-vegetation and use by native ungulates.

Table 3. Review of scientific literature on the effects of energy development on Mule deer and Pronghorn, summarizing study authors, location, vegetation type, species (Aa- *Antilocapra* sp., Aas – *A. A. sonoranensis*, AlAl – *Alces alces*, Ce- *Cervus elaphus*, Oh- *O. hemionus*, Oc- *Ovis canadensis*), whether the study was peer reviewed or not, study area size, duration, development type, study design and sample size, general results and management recommendations.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Armstrup 1978 MT-WY, grassland, sagebrush steppe	*Aa*	No	1036 km^2 and 2years	pre-development	Pre-development study, n=27 Ce; 75 Aa	General ecology study. Select sagebrush vegetation types in winter, fed for longer periods of time in winter, largely diurnal activity patterns, movements peaked during spring and fall, naturally shift between home ranges from year to year.	Sagebrush key for winter forage for pronghorn. Variation in winter range use makes long-term studies to identify critical habitat key.
Berger, 2004. Review	*Aa, Oh, Ce*	Yes	Review	Human habitat fragmentation, oil and gas.	Literature review of radio-telemetry studies	75% of the historic migration routes for elk, mule deer, and pronghorn in the Greater Yellowstone ecosystem have been lost due to human caused habitat fragmentation. Local risks to the trapper point migration corridor in the Upper Green River basin.	Creation of network of long-distance migration corridors required to conserve existing long distance migrations. Impacts greatest during spring and fall migrations.
Berger et al. 2005, 2006a, WY, sagebrush steppe	*Aa*	No	4000 km^2 and 2years		Comparative, radiotelemetry, n>50	First and second year progress reports on the effects of gas development on pronghorn in a control and treatment area in the Upper Green River basin.	Authors did not find pronghorn were avoiding developed areas at the current levels of development, but cautioned results are preliminary and ongoing and results of development should not be expected to occur instantly.
Berger et al. 2006b	*Aa*	Yes	~15,000 and 2years		Observational, archaeology, radio-telemetry, n=10	Compared migration routes identified with telemetry to archeological sites 6,000BP. Migration route has remained the same for at least 6000 years. Migration corridor has extremely narrow restrictions.	To protect critical migration routes, energy development needs to be restricted or removed to maintain long-term ecological processes. Migration seasons impacted most.

Table 3.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Bromley 1985 Review	*Aa, Oh, Ce*	No	N/A	Gas, oil, seismic exploration	Review, n=N/A	Ungulates avoid areas during construction phases, road building, drilling, seismic. Responses to established oil field difficult to determine because of few long-term studies with adequate temporal and spatial controls.	Timing and location restrictions required to avoid conflicts with ungulates, but this requires detailed knowledge of ungulate ecology. Called for large scale, long-term studies.
Bruns 1977 Alberta, grasslands	*Aa*	Yes	2500 km^2 and 0.3years	Roads	Observational, n=N/A	Avoidance of fences and highway; graded roads appeared to be selected by pronghorn, especially in deep snow winters.	Barbless fences not higher than 46 cm; farmers leave gates open (when unoccupied); improvement of winter microhabitat. Winter impacts greatest.
Easterly 1991 WY, shrubsteppe, grasslands	*Aa, Oh*	No	632 km^2 and 4years	Oil	Observational, n=20 Aa, 29 Oh	Densities within oil fields were consistently lower than outside. The 2 most heavily used oil fields were used less than expected, but others were used in proportion to their availability.	Recommend drilling on crucial winter range during summer months only when area is less critical to ungulates.
Freddy et al. 1986, CO, mountain	*Oh*	Yes	3 km^2, 2 years	Human disturbance	Comparative, radio-telemetry, n=7	Compared flight responses of mule deer to snowmobiles and hikers. Mule deer responded more to hikers than to snowmobiles.	Human activity restrictions required on winter ranges, winter greatest impact.
Gill et al. 2001 CO, Review	*Oh*	No	N/A	oil and gas, seismic	Review	Evaluated different hypotheses for mule deer declines in Colorado, with relevance to Montana. Causes for declines could be long-term habitat changes, competition with expanding elk populations, harvest, density dependence, disease.	Large-scale replicated management experiments are required to disentangle complex interactions to understand ungulate ecology. Recommended study designs are presented that are very relevant to energy development in Montana.

Table 3.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Girard et al. 1985 ND, grassland	*Oh, Ov, Ce*	No	4068 km^2 and years	various oil/gas development	Review	Early-development literature review. 1% of landbase in ND study area impacted directly by energy development, unknown how much area lost indirectly.	Avoid wooded areas; reclamation; mitigation required. Emphasized importance of understanding effects of environmental toxins on wildlife.
Hayden-Wing Associates 1991 Review	*Aa, Oh, Ce*	No	N/A	Gas, oil, seismic exploration	Review, n=N/A	Ungulates respond the most during the construction phase, but are also displaced by human activities in the longterm, especially during winter and spring.	Recommend restriction of exploration on occupied winter range from Nov 15 to April 30 as a precautionary principle
Hiatt et al. 1982 WY, Mountain	*Ce, Oh*	No	101 km^2 and 0.25 years	Oil well	Comparative, n=	Both elk and mule deer shifted their ranges away from the well site. There was no evidence of avoidance of the access road by either species.	Minimal
Ihsle et al. 1981 MT, grasslands, pine breaks	*Oh*	No	2725 km^2 and 1.4 years	oil and gas, seismic	Observational, n=78	Impacts of gas and oil development difficult to assess because this was largely a pre-development study that has not been followed up.	None
Irby et al. 1988 MT, Review	*Oh*	No	2725 km^2 and years			No detectable response to low density oil and gas development, study largely conducted during the pre- or early phases of energy development.	Mitigation should occur on the scale of entire winter ranges prior to development occurring. Review the Interagency Technical Committee 1987 guidelines for wildlife (see Appendix B of this review).
Krausman, et al. 2004 AZ, Semi desert	*Aa, Oh*	Yes	km^2 and 2.25years	Military Operations	Experimental, n=4	No detectable difference between exposed/unexposed animals to either ambient or anthropogenic noise; no detectable difference in exposed/unexposed hearing thresholds	Reduce ground stimuli could help, but overall, drastic recovery measures beyond curtailing military activity are needed.

Table 3.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Krausman, et al. 2004 AZ, Semi desert	*Aas*	Yes	377 km^2 and 3years	Military Operations	Observational, n=UNK	Habitat use proportional to availability, but appeared to favor habitats previously disturbed by military activities.	Continued monitoring required, ; multi-species responses; coordinated military/wildife use required, may benefit from fires from military use.
Landon et al. 2003 AZ, Semi desert	*Aas*	No	km^2 and 4years	Military Operations	Observational, n=31	Radiocollared pronghorn avoided high noise areas.	Potentially reduce overflights, study human disturbance in more detail.
Medcraft et al., 1986, WY, shrub steppe	*Oh*	Yes	200ha, 1 year	Mining	Observational, diet studies, N=?	Mining site reclaimed with a mix of native and non-native plants. Deer selected reclaimed mining lands more than unmined lands, preferring non-native plants during summer.	Reclaim all mining sites including graminoids and shrub species. Need to ensure cattle cannot access reclaimed lands or benefits lost. Focus on native species recommended.
Merrill et al. 1984, ID, Mountain	*Oh*	Yes	Unk, 5 years	Mining	Observational, tracks, telemetry, n = 5	Mining operations curtailed migratory movements of mule deer.	Travel corridors with sufficient cover should be considered to mitigate disturbance caused by mines.
Reed et al. 1975. CO, Mountain	*Oh*	Yes	Unk, 1 year	Roads	Observational, video N=4450	Videotaped mule deer responses to a concrete box underpass under I-70 in Colorado. Mule deer crossed underpass 40% of time at each attempt, 60% overall.	Underpasses can be useful to mitigate negative effects of habitat fragmentation and mortality caused by roads – first study of its kind.
Rost et el 1979 MT, pine breaks	*Oh, Ce*	Yes	km^2 and 2 years	roads	Observational, n=N/A	Deer and elk avoided roads, particularly areas within 200m of a road (based on abundance and density of fecal pellets).	Range improvement projects would benefit deer and elk more if they were located away from roads.

Table 3.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Develop ment Type	Study design & size	General Results	Management Recommendations
Sawyer et al. 2002 WY, shrubsteppe, grassland	*Aa, Oh*	Yes	798 km^2 and 4years	pre-develop ment	Pre-developme nt, n=171 Oh; 35 Aa	Mule deer populations traveled 64-161 km yearly; pronghorn traveled 161-241 km.	Energy development has the potential to impact travel corridors for pronghorn and mule deer.
Sawyer et al. 2004 WY, sagebrush, grasslands	*Oh*	Yes	798, 3 years	Gas, seismic	Review, n=N/A	Review of the potential effects of oil and natural gas development on Pronghorn in Wyoming.	Recommends approach to determine the effects of energy development on wildlife that emphasizes long-term, well thought out management experiments between control and treatment areas.
Sawyer et al. 2005 WY, sagebrush, grasslands	*Oh*	No	~800 km^2 and 4 years	natural gas develop ment	BACI, n=69	Mule deer in the treatment area decreased 46% in 4 years under high densities of roads and well sites (see Table 5 below).	Higher densities of wellpads will negate the potential effectiveness of timing restrictions on drilling activities.
Sawyer et al. 2005 WY, sagebrush, grasslands	*Oh, Aa*	Yes	15,000 km^2 and 3 years	roads, housing develop ments, mineral explorati on	Observatio nal, n=171 Oh; 34 Aa	Mule deer and pronghorn migrated 20-158 km and 116-258 km respectively, between seasonal ranges. A number of significant bottlenecks were observed on migration routes.	Migration routes are important components of mule deer and pronghorn ranges. Fences, road networks, and increased human disturbance associated with energy and housing developments influences the effectiveness of mule deer and pronghorn migration routes.
Sawyer et al. 2006 WY, sagebrush, grasslands	*Oh*	Yes	~800 km^2 and 6 years	natural gas develop ment	Comparati ve, n=77	Mule deer avoided areas in close proximity to well pads. Changes were immediate (i.e., year 1 of development), and no evidence of well-pad acclimation. Lower predicted probabilities of use within 2.7 to 3.7 km of well pads.	Higher densities of wellpads will negate the potential effectiveness of timing restrictions on drilling activities.

Table 3.

Authors, location, Veg. type	Spp.	Peer Review ?	Study Area Size, Duration	Development Type	Study design & size	General Results	Management Recommendations
Stephenson et al. 1996 CO, grasslands, pine breaks	*Oh*	Yes	1040 km^2 and 3 years	Military Operations	Comparative, n=71	Mule deer in areas with active military operations (or previous activity) consistently had larger home ranges than those in areas with no activity. 40% of does shifted their home ranges and after military operations started in an area.	
White et al. 2007. MT/WY, mountain, sagebrush-steppe ecosystem	*Aa*	Yes	~750 km^2, 6 years	Tourism development	Observational, radiotelemetry, n=44	Yellowstone pronghorn were partially migratory, with 70% migrating 15-50km away to 4 different summer ranges from the same winter range. Individuals showed high fidelity to summer ranges, but 20% adopted a variable migration strategy from year to year. Migration though to be condition dependent, influenced by weather, climate and density. Migration corridor has extremely narrow restrictions.	Protection of critical migration corridors for pronghorn especially important because of threats to migration corridors in the study area and considering large scale loss of migration in the Greater Yellowstone ecosystem.

3.6 Bighorn Sheep (Ovis canadensis)

No published studies were found on the effects of energy development on bighorn sheep. Most resource conflicts between development and bighorn sheep appear to be cause by mining, not energy development *per se*. A number of studies have been conducted on the effects of human development and recreation. Therefore, I focus on reviewing the effects of mining and energy development in general on bighorn sheep.

In general, bighorn sheep avoided habitats disturbed by human activities (hiking, etc) in Arizona (Etchberger et al. 1989), roads and highway traffic in Rocky Mountain National Park (Keller and Bender 2007), construction activities in Nevada (Leslie and Douglas 1980), human activities including vehicles, mountain bikers and hikers in Canyonlands National Park (Papouchis et al. 2001) and to human hikers or humans with dogs in Alberta (MacArthur et al. 1982). Sheep in Canyonlands avoided areas within ~500m of human development, a loss of access to 15% of high quality habitat. Dall sheep (*Ovis dalli nelsonii*) also showed responses to human activities, especially females, who rested less and foraged more when disturbed by humans. One of the most common forms of human disturbance investigated was the effects of aircraft overflights (helicopter, fixed-wing) on bighorn sheep. Studies on the effects of aircraft on bighorn and Dall sheep (Bleich 1990, Stockwell 1991, Frid 2003) as well as Mountain Goats (*Oreamnos oreamnos*) consistently show an impact on bighorn sheep at distances from 250-750 meters straightline distance (above ground level) for sheep, and even greater distances for mountain goats (Cote 1996), who responded to aerial disturbance at distances of up to 2000m. Based on these studies, clear recommendations to avoid overflights on mountain sheep and goat habitat were presented by all authors.

In terms of bighorn sheep response to mining development, results were equivocal. Jansen et al. (2006, 2007) showed behavioral differences in and out of a copper mine in Arizona, where sheep fed less and bedded more within the mine site, controlling for the effects of age-class. However, despite these minor differences, Jansen et al. (2006, 2007) concluded that bighorn sheep may readily habituate to mining activity, and that reclamation was needed following mining activities. In contrast, Oehler et al. (2007) found that at a mine in the semi-desert mountains of California, Desert bighorn were negatively impacted by mining activities, suffering reduced forage quality, increased signs of disturbance during summer, and potentially important population effects. They concluded that where water was limiting for desert bighorns, mines should avoid areas near permanent water sources for bighorn sheep. In Alberta, a large open-pit mine was reclaimed following coal extraction using planting of native plants combined with extensive post-mining soil grading, seeding, and fertilization (MacCallum and Geist 1992). Sites were successfully reclaimed with native legume species (e.g., Astragalus spp. Smyth 1997), and forage biomass increased for sheep dramatically from 1700kg/ha on native grasslands to 4100kg/ha on reclaimed lands. bighorn sheep apparently responded at the population level, with higher local densities, increased horn growth, and lower lungworm counts. Therefore, sheep seem able to respond to reclamation very well.

3.7 Moose

There have been few studies of the impacts of energy development or human activity on moose in the regions considered as part of this literature review. In a classic study of the effects of human disturbance on moose, Altmann (1958) studied the effects of moose sex, age, reproductive status and season on the flight response of moose to human observers. Flight response measures the perceived risk of ungulates to disturbance; as flight response increases, i.e., ungulate flee an approaching human at a greater distance, the perceived risk imposed by the disturbance are thought to also increase. Altmann (1956) found that female moose with calves at heel fled human disturbance at a farther distance than other age-classes, and that moose fled sooner during the hunting season because of increased risk of human caused mortality during this period. Flight responses varied seasonally, declining the most during the rut, and for moose females with <1 month old neonate calves at birthing sites. This study laid the foundation for research investigating flight response of ungulates, and provides an important foundation for understanding the potential population implications of development.

In the Kakwa River valley of Alberta's forested foothills Horesji (1979) conducted a brief observational study using snow track surveys of ungulate crossings of a seismic line before, during, and after the construction phase in winter. Four species, in order of track abundance, were recorded; Moose, Elk, Mule Deer and Woodland Caribou. Despite very small sample sizes for all species (n=26 total track crossings), Horesji (1979) concluded that Moose avoided the seismic line only during construction, use before and after did not appear affected, though inferences are weak at best because of the limited duration, scope, and sample size. Conclusions about other species could not be drawn because of low numbers of samples.

In the only other study of human activities on moose I review, Berger (2007) showed that the responses of moose to human activity were complex and mediated by predation risk by grizzly bears in Grand Teton National Park, WY. Over a nine-year study, Berger (2007) documented selection by moose for distance to roads within the park, and showed that as the density of grizzly bears increased over this 9 year study, moose increased their selection for areas for calving close to roads within the study area. Because grizzly bears are an important predator of neonatal moose calves, and because grizzly bears avoided human activity, Berger (2007) argues that moose were selecting areas near human activity because grizzly bears avoided human activity. Thus, human caused refugia in predation risk by a natural predator emerged as an indirect effect of human activity on roads in this National Park ecosystem. This phenomenon, whereby human activity repels carnivores such as wolves and grizzly bears, thereby providing are refuge for ungulate prey, has been documented in other systems in North America. In Banff National Park, wolf avoidance of human activity created a refuge for elk, which benefited from increased adult and calf survival in areas where wolves avoided people. This refuge effect lead to a trophic cascade on vegetation, beavers, and other competitors with elk inside the refuge (Hebblewhite et al. 2005).

These studies emphasize the important consequences of human development on ungulates will often be mediated through the indirect effects of changes of the distribution of predators in response to roads and human activity. In Montana, where natural predators such as coyotes, wolves, and mountain lions coexist with ungulate species, the responses of ungulates to energy development will often be mediated by human-induced changes to carnivore distribution and habitat use.

3.8 Woodland Caribou (*Rangifer tarandus tarandus*)

In this review I focus my efforts on studies on the effects of energy development on Boreal woodland caribou (*Rangifer tarandus tarandus*). I exclude, in the large, effects of energy development on Barrenground caribou (*Rangifer tarandus grantii*), focusing here mainly on the effects of development on Alberta woodland caribou populations. Energy impacts on migratory arctic caribou have been summarized by numerous authors, and focus on the effects of development of the Alaska north slope oil reserves (National Research Council 2003,Cronin et al. 2000,Cronin et al. 1998), although more recent efforts focus on impacts in the Canadian Arctic (Johnson et al. 2005). While I do not review them in detail in the text, I summarize Arctic caribou herd studies in Table 4.

Research on the effects of energy development on woodland caribou has progressed largely in these three phases; 1) studies on the effects of construction or seismic activities during exploration, 2) studies on altered ecosystem dynamics that influence caribou population viability, and 3) regional, cumulative effects assessment approaches that address caribou population viability at large regional scales. In the discussion I draw parallels between caribou research in Alberta and ungulate-energy impacts in the lower-48 states, where research is largely being conducted at the first or second step.

Studies that examined the impacts of well-site development or seismic exploration confirmed the negative impacts of these phases of energy development on caribou. Initial development restrictions in Alberta were similar to those put in place in the 1970's and 1980's in Montana for wildlife (e.g., Appendix B) – namely that it was the disturbance during development which posed the most significant impact on caribou. This formed the basis for early regulations designed to minimize the timing of development overlap with key 'calving seasons' and late winter seasons. In effect, this policy is a formulation of the hypothesis that the main impacts of development are behavioral only, and that through avoidance of key behavioral periods, development impacts can be minimized. This policy was tested in a series of experimental and modeling studies. Bradshaw et al. (1997, 1998) showed the negative impacts of disturbance caused by seismic exploration explosions increased caribou movement rates, habitat shifts, and reduced feeding times. These behavioral changes resulted in potential loss of body mass and reduced reproduction, linking avoidance to population declines. Yet the magnitude of observed impacts in these simulation studies was less than the rate of declines of some caribou herds, suggesting the next round of studies that investigated dynamics at the level of the individual caribou herd.

A series of studies across the boreal forest now confirm that amongst the main reason caribou populations are declining through large-scale changes to predator-prey dynamics as a result of forestry and oil and gas development (Alberta woodland caribou recovery team2005, COSEWIC2002). Historically, caribou coexisted at large spatial scales with moose and wolves by adopting a spatial separation strategy whereby they selected large contiguous patches of habitats unsuitable for wolves and their primary prey, such as peatland bogs or large patches of old growth conifers (James et al. 2004). Increased forestry produces early-seral stands with abundant food for primary prey, moose, which increase in population density with increasing forestry. This in turn increases wolf population densities (Fuller et al. 2003), which, when they exceed a density of approximately 7 wolves/1000km^2 exert enough secondary predation influence on caribou to reduce survival rates and drive population declines (Stuart-Smith et al. 1997, McLoughlin et al. 2003, Alberta woodland caribou recovery team 2005, James and Stuart-Smith 2000). Oil and gas development exacerbates changes from forestry by providing high densities of oil and gas seismic exploration lines upon which wolves have been shown to have the following negative ecological impacts. Wolves travel at higher speeds on seismic lines (James et al. 2004), which increases kill rates on large ungulate prey species (Mckenzie 2006, Webb et al. In Press), and increases overlap of wolves and caribou (Neufeld 2006). As a result, caribou show strong avoidance of human development near roads and seismic lines, as well as well sites (Dyer et al.

2001, 2002). Dyer et al. (2001) documented maximum caribou avoidance of areas 250m from roads and seismic lines and 1000m from wells, which, when extrapolated to the entire study area, impacted from 22-48% of available caribou habitats with potential road avoidance effects. Dyer et al.'s (2000) results presented the first clues that human development impacts were operating cumulatively and at large spatial scales.

During the next phase, scientists began studying population dynamics of impacted caribou herds across Alberta, confirming that the majority were declining (Mcloughlin et al. 2003, Alberta woodland caribou recovery team 2005) due to the mechanisms described above (Mcloughlin et al. 2005). Both empirical (McLoughlin et al. 2005) and modeling research at this stage confirmed the grim predictions of the cumulative effects of landscape change on caribou (Lessard et al. 2005,Weclaw and Hudson 2004, Sorenson et al. 2008) – aggressive and dramatic changes to the status quo energy development policy and/or aggressive interim measures such as landscape restoration, core protected areas, and large-scale energy development restrictions may be necessary to recover this federally threatened species (Alberta woodland caribou recovery team 2005). Unfortunately, efforts to restore seismic lines using experimental line blocking experiments failed to achieve any measureable reduction in travel by wolves, and Neufeld (2006) concluded that seismic line restoration at the scale necessary to reduce predation risk on caribou was unfeasible.

Finally, cumulative effects assessment at large scales confirms the grim picture facing caribou conservation in the face of energy development in Alberta. Using data from the previously mentioned studies, Schneider et al. (2003) developed cumulative effects assessment scenario's for caribou herds in Alberta, and showed that even under optimistic scenario's in development rates, which that have been exceeded within the 5 years since Schneider et al. (2003), available caribou habitat would decline from 42% of the study area (59,000km^2) at present to around 6% within 100 years. Empirical cumulative effects models also confirm the dire straits caribou face. By comparing population growth rates of caribou populations against the total amount of industrial development within caribou ranges and the total amount of caribou ranges burned by fire, a management model was developed that predicted expected caribou population growth rate simply as a function of % industrial development and % area burned

(Sorenson et al. 2008, Fig. 10). **Therefore, from a simple management perspective, the key variables after decades of research boiled down to the amount of habitat lost, which disproves the policy hypothesis that energy development can be mitigated with timing or seasonal restrictions, and also refutes the hypothesis that incremental continued energy development is consistent with caribou persistence.**

Today, caribou are listed as a threatened species both federally and provincially, with over 60% of identified herds in Canada declining because of some form of industrial human development (Alberta woodland caribou recovery team 2005). Drastic recovery actions are being proposed, and the federal government is presently developing critical habitat designation that will undoubtedly result in recommendations for restrictions on the amount of industrial development allowed within caribou ranges (Alberta woodland caribou recovery team 2005). In summary, these studies emphasize several key points; 1) short-term disturbances from energy development are not necessarily the most significant population level impacts; 2) by the time population-level impacts were detected, it was almost too late to recover many populations, or the level of restoration activities required are not feasible; 3) it is the amount of habitat disturbed by humans, not habitat fragmentation effects per se, that drove caribou population declines, 4) the sample size is effectively the population of caribou both for statistical, biological, and planning reasons, 5) cumulative impacts were not always evident from individual studies, and required scaling up to regional scales.

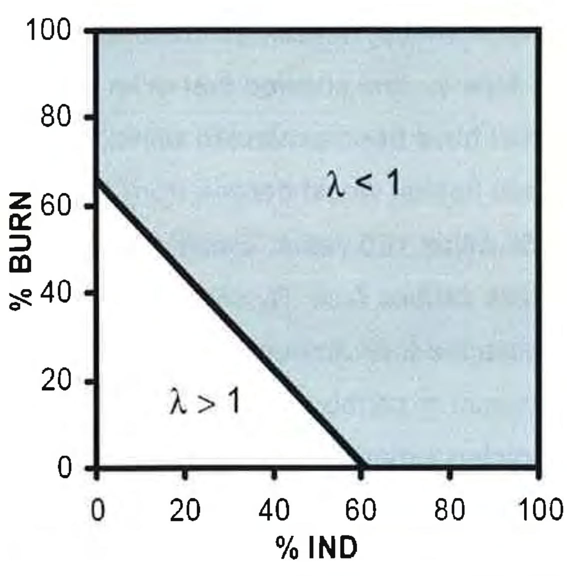


Fig. 10. Meta-analysis model for woodland caribou population growth rate as a function of the % of the boreal caribou range that was burned and the % of the caribou range converted to non-habitat through industrial development. The regression model was developed using n=6 woodland caribou population ranges across a 20,000km^2 area in Northern Alberta, and is described by λ= 1.191 - (0.314 * IND) - (0.291 *BURN) (R^2 = 0.96, n = 6, P = 0.008) [Sorenson et al. 2008].

Table 4. Review of scientific literature on the effects of energy development on Moose, Bighorn Sheep, and Caribou, summarizing study authors, location, vegetation type, species (AlAl – *Alces alces* (Moose), Oc- *Ovis canadensis*, Rtc – *Rangifer tarandus caribou* (Newfoundland subspecies), Rtg – *Rangifer tarandus grantii* (Barrenground caribou), and Rtt- *Rangifer tarandus taranuds* (Woodland caribou), whether the study was peer reviewed or not, study area size, duration, development type, study design and sample size, general results and management recommendations.

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
<u>Moose</u>							
Altmann 1958 WY, various	*AlAl*	Yes	Unk, 3years	Human recreation / hunting	Observational	Hunting pressure increased flight response, and cows with calves were easily disturbed. Flight distance declines during rut, and with newborn calves. Both sexes became habituated to some degree to human disturbance.	Effects of human disturbance on moose could be great enough to affect population dynamics.
Berger 2007, WY Mountains	*AlAl*	Yes	~500km^2, 9 years	Human activities	Comparative radiotelemetry, n= 192	Evaluated effects of predation by grizzly bears on selection by moose for roads. Moose selected to be closer to human activity as grizzly bear predation increased. Grizzly bears avoided human activity, providing a human-caused refugia from predation.	Effects of human activities on wildlife can be counter-intuitive in the presence of human-caused refugia from predation. Considering indirect effects of trophic interactions to gauge development impacts key.
Horesji 1981 Alberta, foothills	*AlAl, Oh, Rtt, Ce*	No	and 0.15years	Seismic exploration	Comparative (BDA), n=26		Moose only species with enough data, crossed less during than before/after exploration

Table 4. Bighorn Sheep

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Bighorn Sheep							
Etchberger et al. 2007, AZ, semi desert	*Oc*	Yes	250km^2, 2 years	Human disturbanc e	Observation al	Compared landscape covariates between areas currently occupied by bighorn sheep in the Coronado forest vs. areas unoccupied. Habitats used by bighorn sheep have less human disturbance, and higher forage biomass.	Fire is important and restoration of fire could enhance sheep habitat. Reducing human activity in the abandoned areas could enhance restoration of this population.
Frid (2003)	*Oc*	Yes	Unk, 1 year	Helicopter & aircraft disturbanc e	Experimenta l, n=56 experimenta l overflights	Aircraft approaches that were more direct (relative to the sheep) were more likely to cause sheep to flee or disrupt resting, and latency to respond was longer. Sheep had a 10% chance of fleeing when aircraft were as close as 750m, and a 10% chance of disrupting rest as far as 1.5km away.	Recommend avoiding known sheep ranges by as much as 1.5 km based on disturbance to resting behavior instead of fleeing behavior – the most costly response.
Jansen et al. (2006, 2007), AZ, semi-desert	*Oc*	Yes	Unk, 2 years	Mining disturbanc e	Observation al, radioteleme try, n=12	Minor differences in sheep behavior inside and outside the mining area; Sheep spent more time feeding and less bedding inside the mine.	Sheep appeared to habituate to mining activity rapidly. Emphasis placed on restoration, especially in desert or semi-desert environments.
Keller & Bender (2007), CO, mountain	*Oc*	Yes	~500km^2, 2 years	Human recreation al disturbanc e, roads	Observation al, behavioral observation	The number of sheep groups visiting a key mineral lick adjacent to a road declined as human disturbance increased, and the time and number of attempts required by bighorn to reach Sheep Lakes was positively related to the number of vehicles and people present at Sheep Lakes.	Negative effects of road and human avoidance may affect population dynamics. Recommended seasonal human use restrictions to maintain sheep populations..

Table 4. Bighorn Sheep

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Leslie & Douglas (1980), NV, semi-desert	*Oc*	Yes	Unk, 1 year	Human disturbance, Construction	Observational, telemetry, n=17	Construction caused a significant shift in use of artificial water sources by 9 of 17 female marked sheep. Productivity during construction did not depart from the long-term population mean; however, lamb survival may have been affected.	Particular care should be given to water sources for bighorn sheep during development, habituation may ameliorate long-term negative effects to some degree, but population declines could occur.
Loehr et al. (2005), YT, Subarctic mountains	*Oc dalli*	Yes	Unk, 1 year	Human disturbance by hikers	Observational, n =35	Females rested less and foraged more under human disturbance and were more vigilant, but not males.	None.
MacArthur & Geist (1982), AB, Mountain	*Oc*	Yes	Unk, 2 years	Human disturbance, hikers and dogs	Observational, heart rate monitors, n=5	Cardiac and behavioral responses were greatest to humans and humans with dogs or approached sheep from over a ridge. Reactions to road traffic were minimal, and no reactions to helicopters or fixed-wing aircraft were observed at distances exceeding 400 m from sheep.	Responses to disturbance were detected using HR telemetry that were not evident from behavioral cues alone.
MacCallum & Geist (1992), AB, Mountain	*Oc*	Yes	Unk, 1 year	Mining disturbance & restoration	Observational	Sheep seasonal movements were similar to those found on native ranges. They used the reclaimed areas as winter range and for the mineral licks exposed during mining. Two thirds of all sightings were confined to 1.3 km of reclaimed grassland; its average productivity (4190 kg/ha) exceeded native ranges (1700 kg/ha). Infestation with lungworms was moderate. Lamb production and survival were high.	Design criteria should be: feeding areas should be dry and lie within 300 m of escape terrain, which should have a slope of 40% and contain at least three benches. Rock piles should be placed on grazing areas. Mineral licks, a vital welfare factor, already existed within the high walls created by strip mining.

Table 4. Bighorn Sheep

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Oehler et al. (2005), CA, semi-desert, mountain	*Oc*	No	Unk, 3 years	Mining disturbance	Comparative, treated vs. treated area, radiotelemetry n = 19	Size of annual home ranges, composition of diet, and ratios of young to adult females did not differ between female sheep inhabiting mined and nonmined areas. Nonmined areas had higher forage biomass than mined sites, and in spring, female sheep had lower forage quality. Sheep were reliant on water adjacent to the mine which influenced results.	Greatest impacts were observed in the summer, recommended either providing alternate water sources away from the mine to mitigate negative impacts or ceasing mining activities during the summer.
Papouchis et al. (2001), UT, semi-desert	*Oc*	Yes	Unk, 2 years	Human disturbance, hiking	Comparative, behavioral avoidance	Hikers caused the most severe responses in desert bighorn sheep (animals fled in 61% of encounters), followed by vehicles (17% fled) and mountain bikers (6% fled). Bighorn sheep were avoided around 39% farther from roads (490 +/- 19 m vs. 354 +/- 36 m) than in the low-use area.	We recommend managers confine hikers to designated trails during spring lambing and the autumn rut in desert bighorn sheep habitat.
Smyth (1997)	*Oc*	Yes	Unk, 2 years	Mining, reclamation	Observational	Survival and success of high elevation legumes varied as a function of drought stress, root exposure by frost-heaving, and elevation.	Native Astragalus spp. species can be used for mining reclamation.
Stockwell (1991)	*Oc*	Yes	Unk, 1 year	Helicopter & aircraft disturbance	Observational	Bighorn were sensitive to disturbance during winter (43% reduction in foraging efficiency) but not during spring (no significant effect. Further analyses indicated a disturbance distance threshold of 250-450 m.	Restrictions on helicopter overflights are recommended for National Parks, recommended >500m linear distance between sheep and aircraft.

Table 4. Cont' Caribou

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Caribou							
Alberta Caribou Recovery Team 2005, AB, boreal forest and foothills	*Rtt*	No	>100,000 km^2, endangered species recovery plan	Oil, gas, seismic, forestry, linear development	Review	Caribou populations declining across the province because of cumulative effects of energy development	Aggressive energy development restrictions and restoration activities required including reduced logging, road removal, rehabilitation of seismic lines, protected areas with no development, predator and ungulate control
Bradsaw et al. 1998, AB, boreal	*Rtt*	Yes	20,000 km^2 and 5years	Petroleum exploration	Modeling, n=N/A	Potential loss of mass and increased energy costs	Model may serve as a template for future research
Bradsaw et al. 1997, AB, boreal	*Rtt*	Yes	20,000 km^2 and 1years	Simulated Seismic explosions	Experimental, n=23	Exposed animals showed higher mean movement rate; no effect of distance from animal to canon vs. movement; exposed animals showed higher habitat patch change; exposure to sound reduced feeding time.	Total avoidance of winter petroleum exploration rather than shorter activity restrictions
Cameron et al. 2005, Alaska, arctic	*Rtg*	Yes	8,000 km^2 and 22years	Petroleum development	Review	calving caribou avoided roads and caribou exposed to petroleum development may have consumed less forage during the calving period.	Assessments of cumulative effects of petroleum development on caribou must incorporate the complex interactions with a variable natural environment.
Cronin et al. 1998, 2000 Alaska, arctic	*Rtg*	Yes	17,000 km^2 and 20years	Oil fields, roads, well pads, infrastructure	Review	Herd-level impacts of the Prudhoe Bay oil fields are not apparent on the Central Arctic caribou herd.	Resource extraction and wildlife populations can be compatible when managed properly.

Table 4. Cont' Caribou

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Dyer et al. 2000, AB, boreal	*Rtt*	Yes	6,000 km^2 and 1years	roads, seismic lines, pipelines	Observational, n=36	Seismic lines were semipermeable barriers to caribou movements, roads were barriers with high traffic. Caribou avoided human development by 250 – 1000 meters (seismic vs wells). 22% - 48% of study area impacted by roads.	Semi-permeable barrier effects may exacerbate functional habitat loss through avoidance behavior. Effects great year round.
Dyer et al. 2001, AB, boreal	*Rtt*	Yes	6,000 km^2 and 1years	new/old well pads; roads; seismic	Observational, n=36	traffic indices inconclusive; disturbance sites showed bias towards habitat type;	Fewer human-used/created corridors; less industrial development; effects greatest during summer.
Haskell et al. 2006, Alaska, arctic	*Rtg*	Yes	700 km^2 and 3years	Oil fields, roads, well pads	Observational, n=up to 12,000	Caribou are able to habituate to active oilfield infrastructure during and after the calving period depending on the timing of the spring snowmelt. Groups with calves were on average distributed farther from infrastructure than groups without calves.	Development of calving period-specific mitigation measures that are effective and flexible is important because annual rehabituation is correlated with timing of spring snowmelt.
James et al. 2005	*Rtt*	Yes	20,000 km^2, 4 years	Oil and gas, seismic lines	Observational	Caribou avoided habitats selected by wolves and moose, but moose preferred habitats impacted by forestry.	Limit overlap of energy and forestry development with spatial refuge areas for caribou.
James & Stuart-Smith 2000, AB, boreal	*Rtt*	Yes	20,000 km^2 and 7years	roads, trails, seismic lines, pipelines	Observational, n=98	Caribou mortalities attributed to wolf predation were closer to linear corridors.	Development of new corridors within caribou habitat should be minimized. Existing corridors should be made unsuitable as travel routes to reduce impacts.
Johnson et al. 2006, NWT, arctic	*Rtg*	Yes	190,000 km^2 and 5years	Energy exploration, hunting, mines.	observational, n=28	Mines had the largest negative effect on species. During post-calving caribou had a 37% reduction in the area of the highest quality habitats and an 84% increase in the area of the lowest quality habitats.	Regional cumulative effects analyses serve as the coarsest framework for understanding the impacts of human developments on wide-ranging animals.

Table 4. Cont' Caribou

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Joly et al. 2006, Alaska, arctic	*Rtg*	Yes	Ukn and 23 years	Oil field, roads, infrastructure	review	Calving caribou gradually abandoned the oilfield with a drop in abundance by at least 72% in spite of the fact that the total herd increased 4-5 fold.	
Mahoney et al. 2002, Newfoundland, boreal	*Rtc*	Yes	12,000 km^2 and 7 years	Hydroelectric development	Observational before, during, after development, n=51	Hydroelectric development caused a disruption of the migration timing during construction and longer-term diminished use of the range surrounding the project site.	Long-term studies of individually marked animals can aid in environmental assessments for migratory animals.
McLoughlin et al. 2005, AB, boreal	*Rtt*	Yes	Unk and 11 years		Observational, n=195	Uplands present caribou with higher than expected levels of predation risk. Caribou should max selection of peatlands.	Linking fitness measures to multivariate resource selection will enable us to ask questions of evolutionary ecology once restricted to only the finest ecological scales.
McLoughlin et al. 2003, AB, boreal	*Rtt*	Yes	Ukn and 10 years	human development	Observational, n=332	Wolf predation most common cause of death. Calf production 75-95%, mean annual recruitment was ~20 calves per 100 cows. 4 of 6 herds declining.	New land-use guidelines to promote caribou conservation
Nellemann et al. 2001, Norway, arctic	*Rtt*	Yes	2900 km^2 and 12 years	Roads, railroads, power lines	Observational, n=2500	Density of reindeer was 79% lower within 2.5 km from power lines compared with background areas. Areas within 5km of development were avoided in all years.	Construction of roads, power lines and cabin resorts endanger the available winter ranges of reindeer in southern Norway.
Nellemann et al. 2003, Norway, arctic	*Rtt*	Yes	1350 km^2 and 10 years	Hydroelectric development	Observational, before, during, after development n=>2000	Reindeer densities within a 4km radius to infrastructure declined during winter and summer with a 217% increase in use of the few remaining sites located >4km from infrastructure.	Controlling piecemeal development in infrastructure is critical for the survival of the remaining European populations of wild mountain reindeer.

Table 4. Cont' Caribou

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Neufeld 2006, Boreal forest, foothills	*Rtt*	Yes	~3500 km^2, 3 years	Oil and gas, seismic lines	Observational & Experimental	Experimental rehabilitation of seismic lines using logging equipment failed to elicit any reduced use of cutlines by wolves. Spatial overlap between wolves and caribou was enhanced by seismic lines.	Managers should not assume long-term impacts of oil and gas development can be restored or reclaimed. Cutline restoration will require large investment in funding to be successful. Better approach to reduce footprint initially.
Noel et al. 2004, Alaska, arctic	*Rtg*	Yes	225 km^2 and 23 years	Oilfield development, roads	Observational, n=up to 1,259	Caribou density after road construction was not lower < 1km of roads than pre-road. # calving caribou in the study area has declined since road construction. Distribution of caribou was not strongly influence by presence of the road.	
O'Brien et al. 2006, Manitoba, Boreal forest	*Rtc*	Yes	900 km^2 and 4 years	forestry and road development	Modeling, n=11	Strong relationship between large clusters of high-quality winter habitat patches and winter GPS telemetry locations from two herds in Manitoba	Results highlight importance of accounting for the spatial configuration of habitat on the landscape and the intervening land cover types when assessing range quality for woodland caribou.
Schaefer & Mahoney 2007, boreal	*Rtc*	Yes	2700 km^2 and 9 years	clearcut logging	Observational,68 years, n=237 animal-years	Females avoided cutovers and maintained an average of 9.2km from active cutovers, males had no response to clearcuts.	Long-term investigations are needed to enhance our capacity to evaluate anthropogenic habitat changes.
Schneider et al. 2003, AB, boreal	*Rtt*	Yes	59,000 km^2 and model dependent	energy and forestry development	Modeling	Model predicts caribou habitat availability will decline from present levels of 43 to 6% in 40 years.	Substantial improvement in ecological outcomes can be achieved through alternative management scenarios while still maintaining a sustainable flow of economic benefits.

Table 4. Cont' Caribou

Authors, location, Veg. type	Spp.	Peer Rev-iew?	Study Area Size, Duration	Develop-ment Type	Sample design & size	General Results	Management Recommendations
Sorenson et al. 2008, Boreal forest	*Rtt*	Yes (In Press)	50,000 km^2, 10 years	Oil and gas developm ent, forestry	Comparative , n=6 caribou herds	Compared the cumulative amount of all industrial development and natural disturbance (fire) against caribou population growth rates (Lambda) in 6 different herds. Lambda well predicted by % industrial development.	5 of 6 caribou herds declining in study because industrial development exceeded thresholds of a maximum of about 40-60% of the range impacted by industrial development. Recommend planning at the range level (~8,000km^2) scale.
Stuart-Smith et al. 1997, AB, boreal	*Rtt*	Yes	20,000 km^2 and 4years	n/a	Observation al, n=65	Adult survival averaged 0.88, calf survival was 18 calves/100 cows. Lambda was 0.92. Lower calf survival and smaller home ranges in landscape with less fen patches and a higher proportion of upland.	n/a
Vors et al. 2007, Ontario, boreal	*Rtc*	Yes	n/a and 15years	roads, utility corridors, mines, pits and quarries, trails, rail lines	Modeling	Forest cutovers were the best predictor of caribou occupancy with a tolerance threshold of 13 km to nearest cutover and a time lag of 2 decades between disturbance by cutting and caribou extirpation.	Buffers should be incorporated around habitat and range of occupancy should be monitored.
Weclaw & Hudson 2004, AB, boreal	*Rtt*	Yes	20,000 km^2	roads, infrastruct ure	Modeling	The most detrimental factor is the loss of habitat due to avoidance of good habitat in proximity of industrial infrastructure.	Wolf control is not a practical solution. Development thresholds to maintain habitat required.
Weir et al. 2007, Newfoundland , boreal	*Rtc*	Yes	195 km^2 and 6years	gold mine developm ent	Observation al, before, during developmen t, n=~8000	Caribou avoided areas within 4km of the site in most seasons. Group size and number decreases as mine activity progressed in late winter, pre-calving and calving seasons.	Importance of evaluating the year-round impact of human-induced environmental change.

4.0 DISCUSSION

Wildlife managers, environmental planners, wildlife consultants, and energy developers who had hoped that this review would provide clear recommendations for approaches to mitigate the effects of energy development on wildlife populations are likely to be disappointed. A number of reviews have already been conducted on the impacts of energy development on wildlife, nearly 10% of all studies reviewed in this effort were previously conducted literature reviews on exactly the topic covered here (e.g., Hayden-Wing 1991,Berger 2004, Bromley 1985). If the preponderance of reviews on the subject is any indication, then there is a large demand for information about the effects of energy development on wildlife such as ungulates. Many of these previous reviews provide information about mitigation strategies for small-scale effects of energy disturbance on ungulate behavior, yet most conclude their reviews admonishing managers to conduct more long-term, population-oriented studies. Unfortunately, my conclusions from reviewing the literature are that, at least for ungulates, there still remains no clear or effective management recommendations that will definitively mitigate the impacts of energy development on ungulate ***populations*** (emphasis added) in the habitats present in eastern and central Montana.

I draw this conclusion for the following main reasons. First, to date, there has not been one rigorously conducted study (e.g., a replicated experiment) of the effects of energy development on ungulates for a ***sufficient duration*** of both study and energy impact to be able to draw firm conclusions about the population impacts of development on ungulates species present in eastern and central Montana. The average duration of studies was very short (2.5 years) when compared to the lifespan of ungulates that may live for over 20 years. Few studies actually measured adult female survival, and *not one* study reported population growth rate for pronghorn, mule deer, elk or bighorn (caribou being the exception). The studies that did measure adult female survival failed to show any impact of energy development by and large, but were only conducted for a short time period, consistent with the low statistical power (Gerrodette 1987) expected for species with high and constant adult survival rates (Gaillard et al. 2000). For long-lived species such as ungulates, impacts of changes to the environment may take up to decades to manifest through cohort effects, compensatory reproduction by adult females, resilience in the adult age-cohort, and because ungulates in general have extremely high and constant adult survival, even despite large-scale changes in environmental conditions (Albon et al. 2000, Coulson et al. 2005, Festa-Bianchet et al. 2003, Gordon et al. 2004). Following from Gaillard et al. (2000) and Eberhardt (2002), energy impacts are expected to manifested first on the least sensitive, but most variable population vital rates such as calf survival and recruitment, not the most important, but least variable adult survival rates. In fact, ungulate life-history in general makes it extremely difficult, or almost impossible, to determine the effects of energy development on population parameters within a short 2-3 year study. Recent recommendations of reviews of ungulate demography studies suggest that a minimum of 50-60 marked adult female ungulates monitored over at least 5-years (Gordon et al. 2003, 2004) are required to gain a mechanistic understanding of changes in adult survival rates linked to environmental changes such as energy development. While population level surveys are capable of picking up important changes (Sawyer et al. 2005), without detailed demographic data, mechanisms driving changes will be cause for speculation. Thus, long-term changes in the way in which agencies and industry engage in research on energy impacts on wildlife need to occur.

My second major reason for why I conclude that impacts of energy development on populations are not possible at this point in time is because of the timing of many studies during early development phases. Following from the arguments above that the effects of energy development may take years to manifest on long-lived ungulates, most studies reviewed were conducted either during the pre- or first 1-5 years of development. This does not give populations long-enough to equilibrate to development and loss of habitat. A major additional problem with studying impacts of development only early during development is that density of development is confounded with duration of development – again confusing clear cause and effect relationships because of the period of equilibration that might be required for long-lived ungulates. An extreme example of this is the study by Van Dyke and Klein (1996) who investigated the impacts of the first oil well constructed in a nearly undeveloped area on elk behavior with a hope to estimate population-level impacts. At such low densities, population level responses for a large bodied mobile herbivore would not be expected to occur because, as this review confirmed, ungulates can habituate to responses at low enough development thresholds.

Regardless of these conclusions about the **population-level** impacts of energy development, the review provides some conclusions about the behavior-level impacts of energy development on ungulate species that will be useful to planners at the site-level of the individual wellsite or road alignment. Many of these behavior-level impacts were already summarized by previous literature reviews (Bromley 1985, Hayden-Wing 1991, National Research Council 2003,Girard and Stotts 1986). However, the real question is whether such small-scale mitigations, referred to as 'death by a thousand cuts' (e.g., Lustig 2002) are useful to scale up to population level responses.

At the small scale, most ungulates displayed behavioral responses that weakly to strongly avoided energy development activities during the development phase (seismic blasting, road construction, mining construction, forest operations, and well drilling), although responses varied. Pronghorn, elk, and mule deer generally showed the strongest avoidance responses, in that order, while bighorn sheep were equivocal in their responses to the construction phases of energy development (Table 2, 3, 4). Seasonal impacts were variable, and occurred year round during winter ranges, calving ranges, migratory corridors, and summer ranges. Early studies tended to focus on effects of development on winter ranges, and restrictions on 'crucial' winter ranges are still enforced as small-scale mitigation measures to minimize the impacts of energy development on wildlife. However, recent studies seem to show increasing effects of energy development on spring calving ranges of ungulates, during summer, and especially in migration corridors (discussed below). This may reflect the growing appreciation within the literature of the importance of summer nutrition to ungulate demography (Cook et al. 2004, Parker et al. 2005). Regardless, clear recommendations for timing restrictions on spring calving ranges and critical winter ranges were echoed by a majority of studies for all species, especially elk, mule deer and pronghorn. Therefore, timing restrictions already developed to minimize the effects of development on ungulates during these key times should probably be kept in place and continued to be monitored for effectiveness (see below).

Also at the small-scale, energy development had impacts on ungulates through the effects of roads and the amount of development, which I review next.

4.1 Effects of Roads

Roads are one of the most pervasive impacts of human development on natural landscapes (Forman and Alexander 1998), and by far, their greatest impact lies in the indirect effects of habitat fragmentation and avoidance by wildlife. By current estimates of wildlife-road relationships, the lower continental USA has around 10-20% of available habitats impacted to some degree or another by wildlife. Impacts of roads on wildlife are not all or nothing, and extend in some continuous function of distance from roads that differ in the overall avoidance buffer size across species (Forman and Alexander 1998). In a preliminary attempt to extract information about ungulate responses to roads associated with energy development for this review, I summarized those studies that presented analyses of the effects of distance to energy development (road, wellsite) on measures of ungulate resource selection.

It is important to note that this zone of influence does not imply 100% avoidance (Schneider et al. 2003,Harron 2007), yet from the information presented in many of the studies reviewed, actual effective reductions in habitat use was not presented. For example, Dyer et al. (2001) found on average 40% reduction within 100m of a seismic line, and declines up to 250m away. Powell (2003) reported 73% reductions in use within 2000m of energy development, but other studies did not usually present enough information. In the 8 or so studies that did report some sort of avoidance effect of roads that was quantifiable, the average 'zone' of influence extended approximately 1000m from both roads and wells, though responses varied within seasons and between species (Table 5). In general, ungulates avoided roads more during the summer months than during winter, when they were often constrained to be closer to roads because of increased snow depths, etc. Regardless, even considering an effective loss of habitat of 50% within this zone of avoidance and a modest buffer size of 500m reveals that 10% of a study area can be effectively lost due to indirect avoidance of roads under optimistic assumptions. The role that overlap between well sites and roads plays on the effects of habitat loss due to avoidance is important and should be investigated in detail in the kinds of habitats present in eastern Montana because of the importance of spatial configuration of habitats in determining road impacts (Rowland et al. 2000,Frair 2005).

Table 5. Summary of ungulate studies showing avoidance of roads and well sites, averaging results across seasons and habitat types.

Author	Species	Avoidance Buffer (m) Roads	Wells
Gillan (1981)	Elk	1200	500
Edge (1982)	Elk	500	1000
Rost (1988)	Elk	200	
Dyer et al. (2000)	Caribou	250	1000
Sawyer et al. (2005)	Mule deer	2700	
Powell (1988)	Elk	2000	2000
Frair (2005)	Elk	200	
Ward (1986)	Elk	2000	
	Average	1131	1125

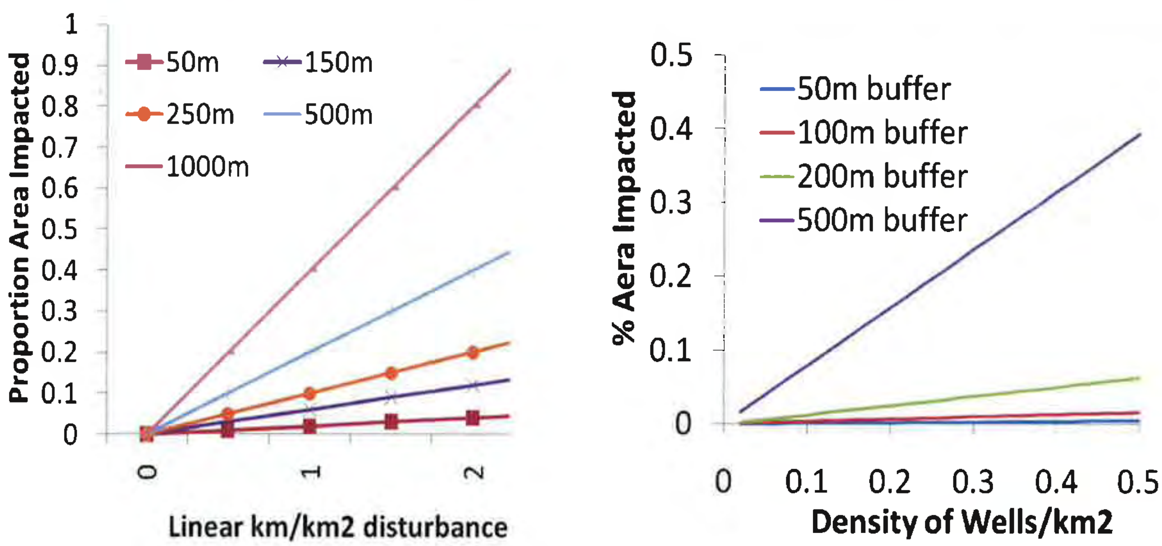


Fig.11. Simple algebraic models for the effects of increasing wildlife buffer avoidance size as a function of linear disturbance and the density of wells, assuming no overlap of buffers of disturbances – an unlikely biological scenario. However, these are useful as guidelines because the actual effects of overlap will be landscape specific, although they will tend to cause the relationships to decline asymptotically to a lower % total area impacted. Studies of the effects of road and wellsite distribution in grassland and sage-steppe habitats are needed.

4.2 Amount of Development

I extracted the density of oil and gas development from studies where possible. Unfortunately, from the n=70 or so studies that investigated the direct impacts of development on wildlife, only a handful (n=12) presented sufficient information to be able to estimate either the density of wellsites or the density of linear disturbance (road, seismic Table 6). Undoubtedly, with additional research and perhaps change detection remote sensing studies, densities of development during the actual study could be backcast for meta-analyses (see below). For these 12 studies, I attempted a simple univariate meta-analysis of development densities for studies that reported a significant statistical effect of energy development on some response variable against those studies with no effect. I present these results only as preliminary results of univariate meta-analyses as an example what additional investment in meta-analyses of existing data could yield. Caveats of this simple summary are many; scale effects of study area size and determination were not accounted for, study duration was also not included, and sample size of the original study, and its variance, were not considered. Regardless, studies that showed a significant impact of energy development tended to have a much higher density of both wellsites and roads, consistent with ecological theory (Forman 1998) and results of individual studies. Somewhere between 0.1 and 0.4 wells/km^2 and between 0.18 and 1.05 linear km/km^2 of development significant impacts started to manifest on ungulate species including mule deer, pronghorn and elk. Additional research is necessary, however, to disentangle effects of sample size, study duration, and impact type (behavioral, habitat effect, population) on the relationship between development density and impacts. I review formal meta-analyses below as a next step in energy-wildlife research needs.

Table 6. Summary of density of energy development disturbance in terms of density of active wellsites/km2 and linear kilometers of pipelines, seismic lines and roads / km2 from studies where such information was reported. Despite small sample sizes of studies that reported densities, ambiguities in definition of study areas, and simplification of impacts to a binary variable, densities of disturbance appears to be related to the impact of energy development.

Study	Density of Wells/km^2	Linear km of roads / pipelines / seismic / km^2	Significant Impact?[3]
Knight et al. (1981) – Ce[1]	0.088	N/A	NO
Olson (1981) – Ce	N/A	0.15	NO
Rowland et al. (2000) - Ce	N/A	0.62	YES
Sawyer (2002) - Aa, Oh	N/A	0.62	YES
Bennington (1981) – Ce	0.20	N/A	NO
Van Dyke & Klein (1996) - Ce	<0.001	N/A	NO
Sawyer (2005a, b)[2] – Oh	1.01	1.36	YES
Berger (2005, 2006)[2] – Aa	0.25	0.20	NO
Frair et al. (2005, 2007) – Ce	0.20	1.6	YES
Easterly et al. (1991) – Aa	0.27	N/A	YES
Ihlse et al. (1981) – Oh	0.003	N/A	NO
<u>Summary Statistics</u>	<u>Mean (n)</u>	<u>Mean (n)</u>	
Significant Impact – Yes	0.49 (3)	1.05 (4)	
Significant Impact – No	0.10 (4)	0.18 (2)	

1- Species are as in Tables 3-4.
2- These two sets of studies occur in approximately the same area but defined different study area sizes based on species life history.
3- Significant impact is a simple binary variable confirming whether statistically significant effects of energy development were detected on key response variables.

4.3 Limitations

4.3.1 Experimental Design

Despite the useful information provided in the reviewed studies for developing preliminary guidelines to guide energy development to minimize impacts on ungulate species, my review revealed several major problems with previous studies including 1) poor experimental design including lack of replication, controls and pseudoreplication, 2) limitations of scale, 3) and poor execution and timing with respect to energy development. Gill (2001) provide an excellent review of experimental designs for large scale adaptive management experiments required to tease apart reasons for mule deer declines in Colorado, many of which would be suitable designs for determining the effects of energy development on wildlife. I briefly touch on experimental design issues here (Krebs1989, Underwood1997, Gill 2001, Williams et al. 2002).

From a traditional scientific paradigm, reliable knowledge is generated through carefully thought out and planned replicated experiments that are designed to test a specific hypothesis, then revised once that hypothesis is accepted or rejected and a new experiment designed. In ecological systems, researchers and managers often do not have the luxury of conducting one at a time experiments just to test one hypothesis; instead, the philosophy of multiple working hypotheses is adopted (Chamberlain 1890, Burnham and Anderson 1998). Regardless, experimental controls in a replicated system provide the strongest inference.

Unfortunately, of the reviewed studies, the vast majority employed an observational or correlational-design (47%), where responses within one population to human disturbance are regressed against some covariate such as distance to roads (Fig 14). While useful, it is difficult to determine cause-and-effect relationships or mechanisms in such studies. Many observational studies were gray-literature reports designed as a mitigation strategy to permit development (which I discuss below). Reviewing these studies especially gives the impression of the following common scenario (summarized succinctly by Lustig (2002);

1) A permit for drilling a well is requested in an area defined as critical winter range for an ungulate.
2) The permit is granted with stipulations that minimize putative negative effects by minimizing temporal risks during critical times (calving).
3) Either because of violation of the stipulations, or in fact as an additional stipulation, a study is commissioned to investigate the effects of energy development activity X on wildlife species Y.
4) The correlative study is often designed hastily, with inadequate resources, sample size, temporal or spatial scope, without pre-development data, nor any commitment to monitoring beyond the intended life of the development phase.

In the course of my review, I have come to the conclusion that wildlife biologists, as a profession, are failing to live up to professional standards and guidelines of their chosen professional organization, The Wildlife Society, by agreeing to participate in these poorly-designed studies that are merely aimed at appeasing the small-scale regulatory process. The huge number of animals captured and handled (>2000), their capture-related mortality, the huge financial investments made by energy development companies, and the huge investment in personnel time do not weigh favorably against the meager conclusions about the effects of energy development on ungulate populations. Figure 6 reinforces the impression that the bulk of studies of wildlife-energy relationships have been reactive, driven by trends in oil production, not part of any pro-active adaptive management program. At the least, I hope this review convinces some of the need for better designed studies of energy-wildlife impacts.

Comparative studies provide stronger inference, for example, between the same population before and after without a control, and were employed in 19% of studies reviewed. The lack of a control makes it difficult to determine whether changes before and after development were due to the development, or some unmeasured covariate, for example, snow or weather. For this reason, comparative studies, while an improvement, will be unable to provide strong inference about the effects of development on populations.

The third kind of study design, experimental, is when effects of development on ungulates after development occurred are compared between a control and developed population, without before data on the development population (Fig. 14). Eighteen percent of studies reviewed used this design. This example was common when pre-development data were not available, usually because the study was designed as an afterthought to development or to allow violation of a stipulation for drilling during exploration. The problem with experimental comparisons of this kind is that without data on the pre-development population, it is difficult to conclude that differences between treatments were not due to some additional, unmeasured variable present in the treatment population. This is a serious concern where experimental units cannot be randomized and where replication is difficult; both conditions are prevalent in all wildlife-energy studies. Randomization is so difficult to achieve at the level of assigning treatments that I do not discuss it further here; but randomization of the assignment of control populations could conceivably occur, and randomization of animal's radiocollared within studies should also occur as possible. A good example of a strong experimental comparison amongst the studies reviewed were the Upper Green River Basin studies on pronghorn by Berger (2004, 2006) and colleagues. The study used a treatment and control group, but had limited data pre-development, although as energy development increases in the study area, the first year of the study may very well serve as pre-development conditions. If so, this would make this study design very powerful.

The most powerful design, that of a before-after-control-impact design (BACI, Underwood 1997) was employed in 18% of studies reviewed. BACI designs are amongst the most powerful experimental designs because effects of development are compared between a treatment and control simultaneously both before and after development. This design alleviates difficulties with previous designs controlling for spatial and temporal confounding. The best example of this BACI design in all the studies reviewed are epitomized by the studies on the Sublette mule deer herd because they had extensive pre-development data on mule deer survival and habitat use, compared to 5-years and running of post-development data between a control and treatment population (Sawyer et al. 2005, 2006). Priority should be given to maintaining funding for this study especially because of its relevance, large spatial scale (see below), and strong design.

Despite these compliments, a central tenant of experimental design, replication, was absent from all reviewed studies. Not one study was replicated at the level of treatment. Obviously replication at the spatial scale here is difficult to achieve, but future efforts should be made to initiate additional studies in areas with and without development to serve as meta-replicates; that is, replicates at the scale of meta-analyses between populations.

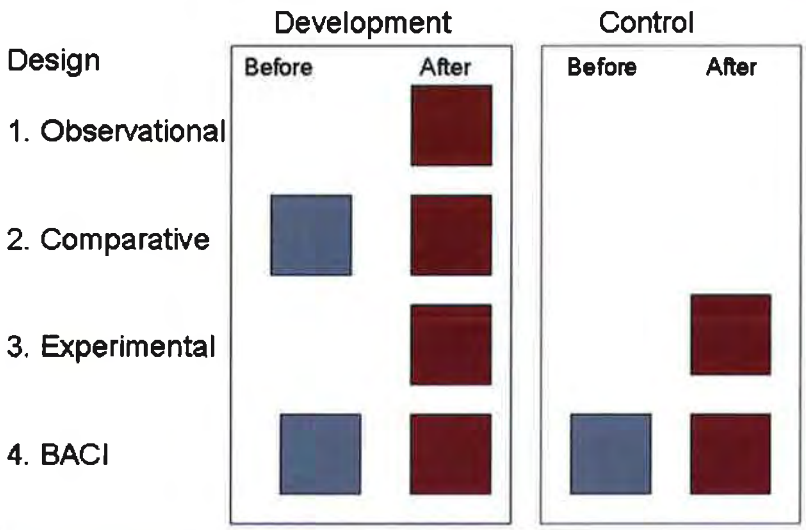


Fig. 13. Common experimental designs for studying the impacts of energy development on wildlife in increasing order of scientific rigor (Underwood 1996). 1) Observational studies simply observe relationships between a parameter and the level of development. 2) Comparative studies compare the effects of development before and after on a parameter without contemporaneous control. 3) Experimental designs compare a control and treatment group post development. 4) In a Before-After-Control Impact (BACI) design, 4 paired sites are used to compare effects of development on a parameter before development in both a control and pre-treatment site, and after development in both a control and post-development site. Note in this schematic, there is no replication.

4.3.2 Spatial Scale

A difficult problem in ecology is how to scale-up from short-term small scale behavioral decisions of animals to long-term landscape scale population and distributional responses. The difficulty in scaling up is why so few of the studies that showed short-term responses were able to measure or demonstrate these long-term or population level responses. A second scaling problem is presented by Berger et al. (2007) when discussing issues of spatial scale and habitat fragmentation, both of which are totally dependent on each other (Dale et al. 2000, Turner et al. 2001). Quantifying habitat fragmentation metrics will be completely determined by the study area size, and for this reason, many authors recommend conducting multi-scale analyses of the effects of habitat fragmentation on wildlife species (Turner et al. 2001, Harrison and Bruna 1999).

In many of the studies I reviewed, there was a third scaling problem – that of extrapolating responses. This occurred where the effects of a local point source disturbance (wellsite) was assessed at the population or at the home range scale, and results extrapolated well beyond the development densities under which the response was studied. For example, Van Dyke and Klein (1996) document the responses of elk home ranges to installation of a single well in a hitherto undeveloped grassland ecosystem in north central Montana. This was the first well to be installed in a 200km^2 area, an extremely low well density. The authors basically found few impacts of the well installation on elk home range use, and no lasting impacts on behavior or habitat use. The results of this study have been extrapolated to other wells across Montana, yet the validity of extrapolating the finding of no significant impacts to areas of higher well density, for example, is questionable. This emphasizes the need to establish thresholds for development or broad, regional scale cumulative impact assessments as the density of well sites and development increases.

Finally, there was often a scale-mismatch between the spatial scale of the study in question, most often focused on some crucial winter range, and the spatial scale of the population under investigation. Assuming the goal of an impact study is to assess the impacts of a particular development on a population, unless the study area represents the annual range occupied by the ungulate population, it will become difficult to evaluate whether the changes in the population are occurring because of energy development on the winter range, or because of undocumented changes occurring elsewhere in the populations range, for example.

One potential solution to the issue of how to determine the appropriate study scale is to use the spatial scale of migration as a guideline in migratory populations. Berger (2004) reviews long-distance migration throughout western North America and worldwide, and migration distances for ungulates in western North America are presented in Table 7. While not all populations are migratory, the reported degree of partial migration ranged from 45 to 100%. Considering the one-way migration distances as a buffer of any particular energy development suggests that the correct spatial scale to consider evaluating the effects of energy development could range from 1500km^2 for bighorn sheep to nearly 19,000km^2 for pronghorn. Notably, when compared to the scale of reported study areas in this review, these rough guidelines are much greater than reported by studies attempting to address development impacts in the literature. Surely, study area specific guidelines should be developed once migratory movements are determined, but these guidelines emphasize the large spatial scale required to understand population-level impacts.

Table 7. Summary of one-way migration distances recorded in selected reviewed studies that were mainly summarized by Berger (2004). Assuming the goal of the energy-wildlife impact study is to make inferences to the population, the study area size and spatial scale that impacts should be assessed over can be calculated as the spatial scale of migration.

Study	Species	Distance (km)	SE	% Migrant	n
Sawyer et al. 2005	Pronghorn	177	2	95	34 pronghorn
Sawyer et al. 2005	Mule deer	84	5.1	100	158 deer
White et al. 2007	Pronghorn	35	---	70%	44 pronghorn
Berger 2004	Pronghorn	137	12.1	N/A	7 pops.
Berger 2004	Mule deer	73	5.2	N/A	16 pops.
Berger 2004	Elk	93	7.1	N/A	7 pops.
Berger 2004	Bighorn	39	4.1	N/A	5 pops.
Berger 2004	Caribou	71	7.9	N/A	4 pops.
Berger 2004	Moose	85	4.3	N/A	13 pops.
Hebblewhite et al. 2006	Elk	55	8.9	45%	60 elk
	Summaries				
	Species	**Study area size required to contain migratory movements**			
	Elk	8,464 km^2			
	Mule Deer	5,423 km^2			
	Pronghorn	18,769 km^2			
	Bighorn	1,521 km^2			
	Caribou	5,041 km^2			

4.4 Potential Toxicological Impacts

Girard and Stotts (1986) are the only studies in this review that specifically mention the potential negative effects of H_2S (hydrogen sulphide) on wildlife species. Yet recent studies have demonstrated the potential negative effects of H_2S emitted from sour gas wells (natural gas fields) on domestic cattle in Alberta (Waldner et al. 2001a,b, Scott et al. 2003a), although results are equivocal at this point (Scott et al. 2003b).

Moreover, there is increasing interest in investigating the human health consequences of sour gas emissions from natural gas wells, with recent studies potentially linking H_2S emissions to human health and increased risk of cancer, cardiovascular disease, and endocrine dysfunction (Saadat et al. 2006, Roth and Goodwin 2000, Waldner et al. 1998) and even real estate prices. A recent government sponsored study in Alberta emphasizes that H_2S should be considered a broad-spectrum toxicant, and that repeated exposure may result in cumulative health impacts on the brain, lung, and heart (Roth and Goodwin 2000), although the report calls for increased medical research to establish cause-and-effect relationships. Regardless of the uncertainty regarding the effects of emissions from energy development on wildlife, it is surprising that no studies have investigated the effects of increased exposure to toxic chemicals emitted from oil and gas wells. Collaboration with ecotoxicologists is recommended as a future area of potentially important research

4.5 Conceptual Approach for Understanding the Effects of Energy Development on Wildlife

One of the conclusions from this review is that the effects of energy development on ungulate species will be manifested through changes in the ecological communities of species, including humans, in which they exist. As such, impacts of energy development on ungulates can be classified into direct impacts and indirect impacts. Distinguishing between *direct* effects and *indirect* effects and between species is critical to understanding the mechanisms of energy development impacts on ungulates, and to providing effective mitigation strategies to ensure the sustainability of energy development. In community ecology, *direct effects* between species (e.g., human, energy development, and elk) occur when there are no intermediary species between two interacting species, for example, through direct mortality associated with energy development (road kills, poaching, destruction of nests, etc Estes et al. 2004). Most direct effects are classified as either predation (energy development directly kills wildlife species) or habitat destruction, where the population size of wildlife is directly reduced because of the reduction in available forage as a result of development (area of habitat directly lost by well sites, roads, compressor stations, etc).

In contrast, *indirect effects* of energy development are where impacts on a wildlife species are mediated by an intermediate species. As an example of indirect effects, Fig. 12 illustrates the indirect effect of energy development on sage grouse and kit foxes (*Vulpes macrotis*) mediated by human caused changes in the densities of important predators in this terrestrial grassland community, such as coyotes (*Canis latrans*) or red-tailed hawks (*Buteo jamaicensis*, e.g., Fig. 12). In this example, raptors have increased predation rates on sage grouse because of increased perching habitat near attractive sink habitat near road ditches for sage grouse (Aldridge and Boyce 2007, Fletcher et al. 2003). Similarly, coyote populations increase following human development because of habitats associated with human development supports higher densities of small mammals, causing increased predation by coyotes on kit foxes (Haight et al. 2002a).

Effects of energy development will likely go far beyond direct impacts purely based on community ecology theory (Estes et al. 2004). Recent reviews have reminded ecologists that direct effects are but a fraction of the potential species interactions possible in even a simple food-web (Estes et al. 2004, Bascompte et al. 2005). For example, in Fig. 13, the total number of direct interactions (such as direct mortality) between the six species is 30, whereas the number of indirect species interactions is 1,920! (see Estes et al. (2004) for calculations). This emphasizes that wildlife managers should be very concerned about indirect effects of energy development in Montana and

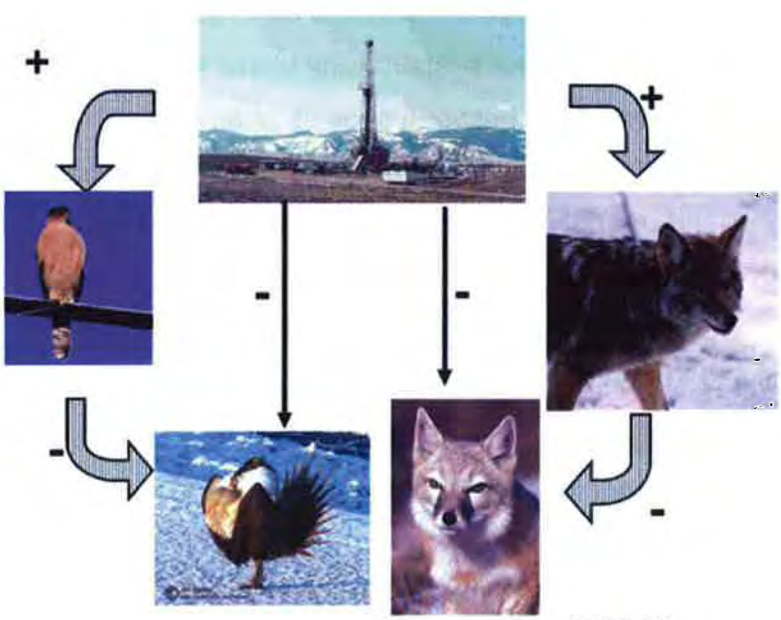


Fig. 12. Conceptual trophic food web illustrating direct (solid lines) and indirect effects (dashed). Interaction strength of one trophic level on another is shown by the thickness of the arrow, and the magnitude of the effect by the sign whether positive (+) or negative (-). In this example, energy development benefits predators such as raptors and coyotes with additional foraging habitat, causing stronger negative indirect effects than direct effects on vulnerable Sage grouse and Kit fox.

design effective strategies to mitigate them.

Indirect effects of energy development can also arise because of behavioural changes by ungulates in response to energy development such as avoidance of roads and wellsites. These results have been corroborated across systems and at larger scales in ungulates confirming the importance of indirect behavioural effects, such as the avoidance of predation risk and human disturbance (i.e., energy development) by ungulates on ecosystem dynamics (Fortin et al. 2005, Rothley 2001, Hebblewhite et al. 2005).

Despite the theoretical support for the importance of indirect effects, a cursory review of the literature on the subject of impacts of energy on wildlife reveals a seemingly myopic focus of mitigation strategies on reducing direct effects such as road mortality and direct habitat destruction (BLM 2003a,b). A renewed focus on the indirect effects of energy development mediated by community level changes in species will underscore the influences of indirect effects in the cumulative impacts of energy development. In this literature review, I will test the hypothesis that indirect effects are more prevalent than direct effects of energy on ungulate species. If indirect effects are more common than direct effects, I expect to find evidence that the impacts of energy development on wildlife are mediated by changes in community dynamics of other species (i.e., increased human access during hunting season, increased coyote abundance, etc.,) or through behavioural changes of ungulates in response to energy development.

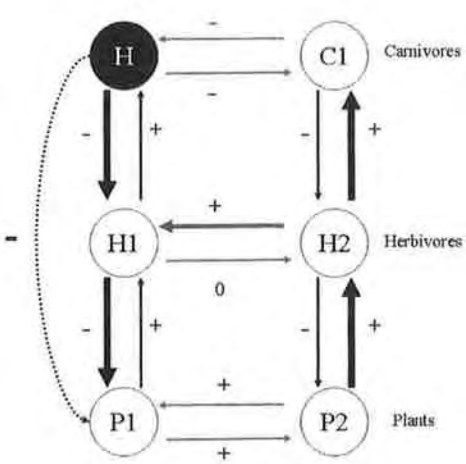


Fig.14 . Conceptual diagram illustrating the importance of indirect species interactions in understanding the effects of energy development on wildlife. A conceptual three-trophic level food web illustrating direct (solid) and indirect (dashed) interactions between human energy development, carnivores, herbivores, and plants is shown. Predation and other direct interactions (competition, etc) are illustrated by black and gray lines, respectively. Fourteen of 30 direct species interactions are shown, whereas only 1 of 1920 potential indirect effects are shown, in this case, the indirect effects of human energy development on plant species 1 mediated via changes in the abundance of herbivore 1.

4.6 Recommendations for Future Energy Development Impact Studies on Ungulates in Eastern Central Montana

4.6.1 Meta Analyses

Meta-analysis is the most rigorous form of synthesis and review in the scientific literature, and is used to combine results of analyses into one synthetic framework to test broad hypotheses in science (Hobbs and Hilborn 2006, Osenberg et al. 1997, Hedges et al. 1999, Arnqvist and Wooster 1995). Great advances have been made in the recent decade in ecology in particular by synthesizing results of single studies to test broad ecological hypotheses, for example about the effects of predators on ecosystems (e.g., Schmitz et al. 2000, Shurin et al. 2002). In its simplest form, each study becomes one replicate in the meta-analysis, thus, meta-analysis is extremely useful for augmenting statistical power in hypothesis testing because multiple small-scale studies are combined effectively as a series of replicated studies.

Meta-analysis of the effects of energy development is the next logical step to take to quantify the impacts of energy development on ungulates following standard meta-analysis. Three basic pieces of information from published studies are required to conduct meta-analysis; the mean treatment effect, the sample size (n), and the standard deviation in the response (Schmitz et al. 2000, Gurevitch and Hedges 1999, Arnqvist and Wooster 1995). For advanced meta-analysis, extraction of more detailed information from each study area; such as road density, well density, date of initiation of development, etc., could help elucidate responses of wildlife to energy development in formal meta-analyses. For each study, the mean values are extracted for response variables from the experimental (energy development) treatment ($\overline{X}_j^E$ where E is experimental) and the control treatment ($\overline{X}_j^C$ where C is control). The difference between two treatments for the j^{th} study, or the effect size, is calculated by the difference of the means following:

$$E_j = \overline{X}_j^E - \overline{X}_j^C \qquad \text{(equation 1).}$$

While effect size is an intuitive metric, it is difficult to compare across studies and different response variables because of scaling issues (Hedges et al. 1999); how does one compare the magnitude of the difference in survival which may be small, especially with ungulates (e.g., 0.1) with the magnitude of flight response between studies? A better measure is the log response ratio, L_j, for several reasons (see Oseberg 1999 for details). Meta-analyses uses the response-ratio to estimate the effect size of the energy development between the treatment and control (Hedges et al. 1999,Gurevitch and Hedges 1999) following:

$$L_j = \log(\overline{X}_j^E / \overline{X}_j^C) \qquad \text{(equation 2)}$$

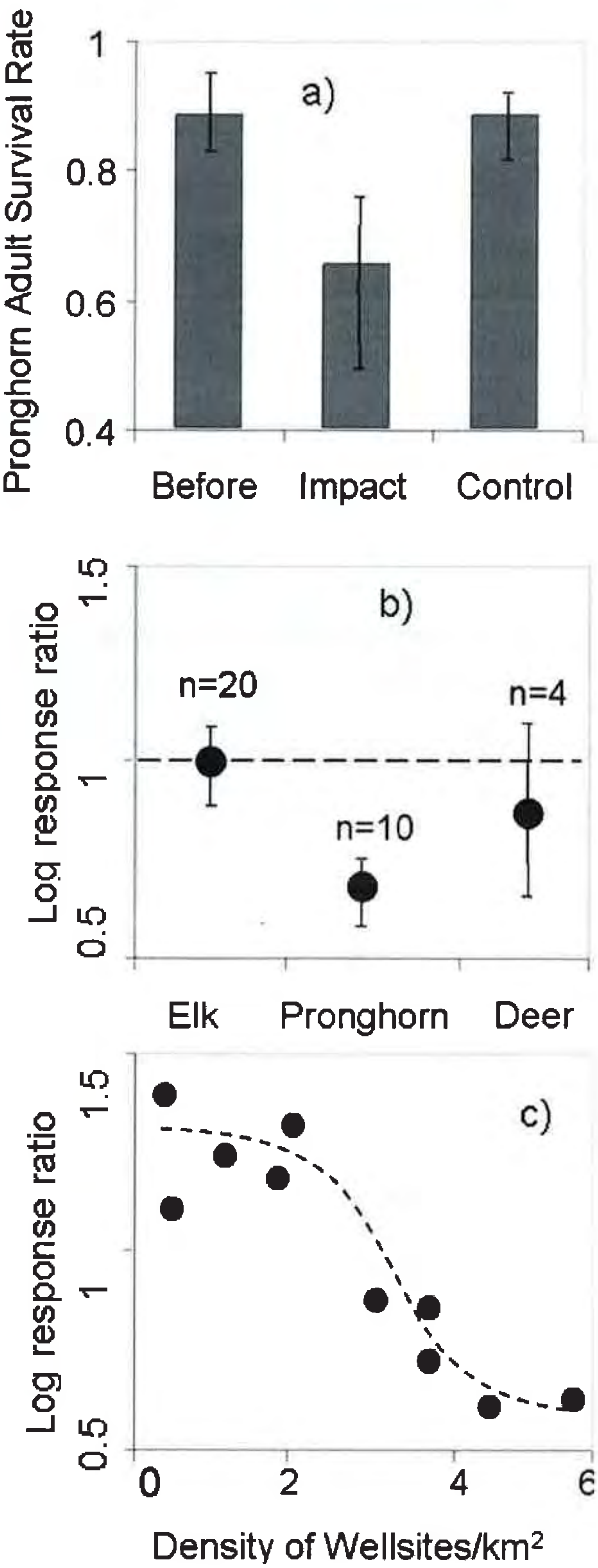
Response ratios less than 1 represent the hypothesis that energy development has a negative impact on the response variable, and vice versa for values greater than 1. For parameters that may be changing over the duration of energy development (i.e., as the ungulate population equilibrates to the new disturbance, lost habitat, changed predator-prey regimes, etc), it is important to consider trends over time in the response ratio (Osenberg et al. 1997). If effects are not constant, it is important to report the trend in effects. Variance in log response ratios are calculated following Hedges et al. (1999). As an example, I illustrate meta-analysis using a hypothetical example of a review of the effects of energy development on survival of adult female pronghorn, elk and mule deer (Box 1). Meta-analysis of the literature reviewed in this study would help formalize the tantalizing syntheses presented in Tables 4 and 5 that are suggestive of thresholds in responses of wildlife to the amount of energy development, and calculate averaged responses of wildlife avoidance of roads associated with human development.

Box 1. Meta-analysis illustrated with a hypothetical example of a review of the effect of energy development on survival rates of adult female pronghorn, elk and mule deer.

The first figure (a) shows a well designed, replicated (see section 4.4) study on the effects of energy development on survival of adult pronghorn in a before-after-control impact design (BACI). The magnitude of the difference in survival between the control/before treatment and the impacted treatment (0.85-0.63 = 0.22) is termed the **effect size** of the treatment (see equation 1 above), in this case, energy development. Sample size is the number of collared animals, and the wider confidence intervals in the impact represent the common situation of greater variation in the treatment response, emphasizing the importance of sufficient sample size.

In the second figure (b) **the log response ratio** (see equation 2) from a number of different studies on ungulate survival have been summarized. Response ratio's greater than zero represent a net positive impact of energy development and values less than zero represent a net negative impact of the treatment across studies (n is now # of studies). Effect sizes are standardized with respect to the sample size and variance of the data in figure (a) for each study. Deer illustrate the case where too few studies were likely conducted to draw concrete conclusions.

In the final figure (c) the response ratio is now regressed against some consistent spatial measure of habitat fragmentation (in this case density of wellsites/km^2) to test for thresholds in the cumulative effects of development on, in this example, ungulate survival rates. In this example, if the standardized effect size, Z, corresponding to the maximum decrease in ungulate survival was -0.2 (which could correspond to a survival rate of 0.75), then the threshold for wellsite density would be approximately 3 wells/km^2.



4.6.2 Habitat-linked cumulative effects assessment

Johnson et al. (2005) and Johnson and Boyce (2005) provide a template for the assessment of regional cumulative environmental effects on 4 species of wildlife in the central Canadian Arctic in a region of rapidly increasing diamond mine (and oil) exploration and development. The area in which regional development impacts were assessed was a huge area, over a 190,000km^2 area for four wildlife species; caribou, grizzly bears, wolves and wolverines. Lack of adequately sized spatial or temporal controls, the sheer size and difficulty of collecting wildlife data in the study area,

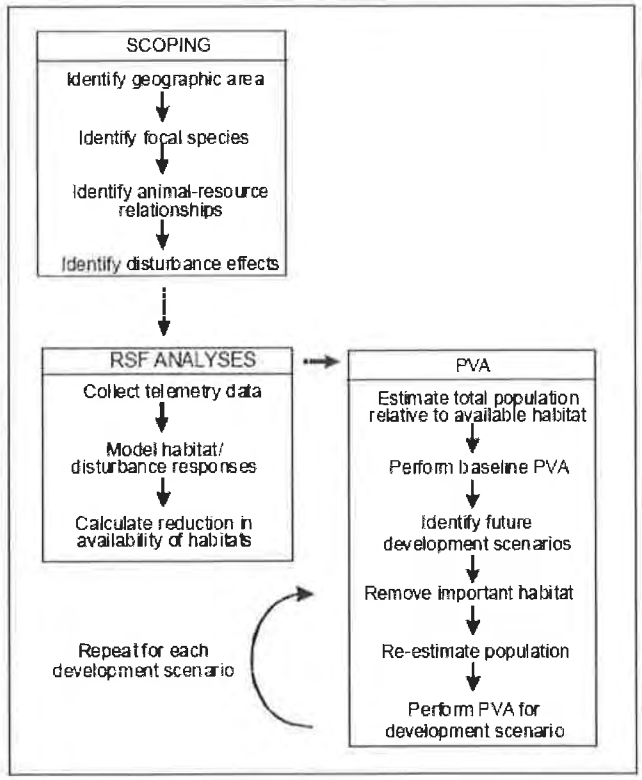


Fig.15. From Johnson & Boyce (2005). Analytical framework for the development of habitat linked PVA analysis to assess the impact of wildlife within a population undergoing energy development.

and the availability of existing wildlife telemetry data lent themselves to a habitat-modeling based assessment of development impacts. Under the assumption that resource selection ultimately dictates population demography of wildlife species (Boyce and McDonald 1999, Manly et al. 2002), Johnson et al. (2005) developed habitat-based population viability model based on Resource Selection Functions (RSF). Briefly, once focal species are identified, RSF models that quantify the relationship to human activity are developed. Next, potential habitat disturbance caused by energy development is modeled as a function of future landscape scenarios (Johnson et al. 2005, Schneider et al. 2003), and the area of effective habitat loss is measured using the RSF model. The assumption that habitat quality predicted by RSF models relate to population sizes has been recently supported in several studies on caribou (Seip et al. 2007) and grizzly bears (Ciarniello et al. 2007, Boyce and Waller 2003). Then, given a reduction in habitat quality revealed by the RSF model, a habitat-linked population viability model (Haight et al. 2006, Carroll et al. 2003) can be developed to evaluate the effects of competing energy development scenarios on wildlife. I agree with recent authors (Carroll and Miquelle 2006, Morris and Doak 2002) that caution against treating the predictions of such PVA as quantitative. Rather, recent studies show that habitat-linked PVA provides relative comparisons between alternate development scenarios. As such, habitat linked PVAs could be a useful modeling tool for adaptive management (see below). The limitations of this approach is the fundamentally correlative nature within one population undergoing energy development; whether relationships hold over future development patterns need to be assessed through continued monitoring, and whether the link between resource selection and fitness is necessarily held in wildlife populations impacted by human development (e.g., Mcloughlin et al. 2005) needs to be tested. A comparative study design between populations that are and are not impacted by development would be a stronger approach.

4.6.3 Large-scale, replicated experimental tests of the impact of energy development on ungulates.

As this literature review summarizes above, the current state of knowledge about the impacts of energy development on wildlife is woefully lacking on several critical fronts. First, knowledge of the effects of long-term impacts on wildlife population parameters is essentially absent – study duration averaged <3 years, an inadequate timeframe to assess the impacts of energy development on long-lived ungulates. With dozens of short-lived studies, we literally have almost no idea what population responses to energy development will be.

Second, by and large, studies conducted to date have suffered from extremely poor experimental design, lack of controls, and lack of replication, and when present, pseudoreplication; mismatches between the scale of the problem and the scale of investigation, and a general tendency to be reactive, post-hoc designed studies developed as part of a mitigation strategy to allow continued development instead of an a-priori designed adaptive management process. These difficult problems provide managers little guidance on how to minimize the negative effects of continuing energy development at the population level.

Fortunately, Montana Fish Wildlife and Parks, along with other key partners, including industry, have a successful history of working together to assess the impacts of human development on ungulates at large scales. The Montana Cooperative Elk Forestry study epitomizes the cutting edge of forestry-wildlife relationships at its time, with 6 replicated studies across the state of Montana (Fig. 8). The study monitored the results of different management treatments on elk response to human activity across different spatial scales. This time, the stakes of development will be higher, with the projected impacts of energy development potentially exceeding impacts of logging in the western half of the state.

Clearly, designing long-term replicated studies across several locations in eastern and central Montana (potentially even replicated across states such as in the Upper Green River Basin of Wyoming) represents the next step in developing a scientific assessment of the effects of energy development on ungulates. Basic principles of experimental design should be followed, with control and replicate treatment populations monitored across similar habitats for a sufficient duration (10-years) to determine population level responses. Gill (2001) provides useful recommendations for large scale, population-level experiments in their review of the underlying causes of mule deer declines in Colorado. Building on the meta-analysis of the effects of energy development on wildlife, power-analyses (Gerrodette 1987) could be conducted to determine the appropriate study duration to ensure that population level responses are documented a-priori. This would alleviate the problem of uncertainty over impacts where ongoing studies fail to show any population responses in initial years of the study (Berger et al. 2007,Sawyer et al. 2006) – if a-priori power analysis confirmed that it will take 10 years to determine even small changes in adult female survival of ungulates (e.g., 4%), then preliminary analyses would be interpreted within the limits of statistical power. In that case, based on the expected treatment responses and appropriate scales of investigation of the population (see migration section above), well designed, replicated experiments between developed and undeveloped areas could be implemented that would allow MTFWP to rigorously test for the effects of energy development on wildlife.

However, this approach will ultimately fail if the current policy for energy development is incompatible with wildlife conservation. Some have criticized the current policy as an incremental energy development policy where development is approved on a piecemeal and uncoordinated basis in a linearly increasing fashion (Lustig 2002, Nelleman et al. 2003). From a policy perspective, we are currently operating under the hypothesis that wildlife and continued incremental development are sustainable. If we really want to advance wildlife conservation under energy development, we should endeavor to test this hypothesis by comparing this policy against alternative policies. **To advance our understanding of how to mitigate energy-wildlife conflicts two things are required; 1) innovative new policies for large-scale energy development, and 2) an adaptive management approach.**

4.6.4 An Adaptive Management Framework for Assessing the Cumulative Impacts of Energy Development on Ungulates

Walters (1986) defined the adaptive management process as follows: "the central tenet that management involves a continual learning process that cannot conveniently be separated into functions like research' and ongoing regulatory activities,' and probably never converges to a state of blissful equilibrium involving full knowledge and optimum productivity." Adaptive management has often been co-opted by management agencies to mean "learning by doing," but Walters (1997) criticizes many management agencies for missing the critical point of adaptive management – experimentation, controls, and adequate monitoring – without these key steps, there is no difference between adaptive management and 'regular' management that seeks only to satisfy short-term objectives without ensuring that long-term problems are adequately addressed. Walters (1986) describes the adaptive management process of:

1. Bounding management problems and recognizing constraints;
2. Representing existing knowledge in models of dynamic behavior that identify assumptions and predictions so experience can further learning;
3. Representing uncertainty and identify alternate hypotheses;
4. Designing policies to provide continued resource productivity and opportunities for learning in experimental comparisons of policies. (Fig. 16)

Adaptive management has been applied previously to large scale environmental problems in the United States with great success. Bormann et al. (1998) proposed an adaptive management process for the Pacific Northwest in response to concerns sparked by the spotted owl controversy - the Northwest Forest plan that affected a huge geographical area. The plan proposed 10 adaptive management areas with different management policies for forest management, and developed a framework for managers, scientists, and industry to determine improvements to policies that would allow societal goals for resource extraction to be met while minimizing negative environmental effects.

An adaptive management experiment on the effects of energy development on ungulates in Montana would help address proposed changes to energy regulation that are hypothesized to minimize negative effects of development. At present, the policy for energy development could be described as "incrementalist', where gradually, phased development increases at regional scales in incremental steps until the entire area is brought into energy development. Under this policy, the % area affected by development will increase continually over time. Impacts are only assessed at small, local scales, usually at the scale of individual wellsite developments. Small scale timing restrictions (i.e., no drilling on winter ranges, calving ranges, etc.) represent the policy hypothesis that the main impacts of development are behavioral only, and that through avoidance of key behavioral periods, development impacts can be minimized.

Moreover, management policies designed to minimize development impacts at these small scales are hypothesized to mitigate impacts at the larger, regional scale. Both the small and large-scale predictions of this management hypothesis are as yet untested. This model of development is the current favored policy alternative amongst federal and state energy regulators by default.

An alternate policy that has been proposed could be called 'phased' or spatially concentrated development where energy development is concentrated geographically to maximize extraction rates of resources, minimize the % area developed, and localize impacts. Under this policy, rehabilitation of the developments would be encouraged as policy before additional sites were developed, and the overall population level impacts on key wildlife species is hypothesized to be ameliorated compared to incremental development. The predicted area impacted would be expected to increase non-linearly to some asymptotic threshold determined by the rate of new phases coming on-line and cycling through the development and restoration phase.

A third policy could be described as a protected area policy that identifies core areas for multiple species (e.g., pronghorn, mule deer, sage grouse, sage brush) that are protected from oil and gas development to provide critical habitat for threatened or (potentially) endangered species, and the ecosystems on which they depend (i.e., sagebrush steppe). This would ensure viable populations at some large, landscape scale that maintained populations and connectivity while allowing incremental development outside of these protected core areas. This is a model that is gaining support for threatened boreal caribou based on the scientific evidence that present levels of industrial development in many herds exceeds critical thresholds, causing populations to decline. Predicted area impacted under this policy would be expected to asymptotically increase to some threshold similarly to the phased policy, but the threshold would be set by the % of the landscape protected under core areas.

Under adaptive management, these 'simplified' policy alternates could be scientifically evaluated by encouraging development under the three hypothetical policies in two ecologically similar areas, and by monitoring responses of key wildlife (ungulate) populations at these two sites, and a similar experimental control population, over the duration of the energy development project (10-20 years long-term), in a replicated design. Whether these policy alternatives are indeed, reasonable is beyond the scope of this review. The critical point is that under adaptive management, resource extraction would be permitted to continue in a controlled fashion, embedded within an adaptive management framework that would ensure that 20 years from now, additional reviews on the effects of energy development on wildlife have something to report, and not just review another batch of poorly designed studies that fail to address the pressing policy decisions facing wildlife and land managers.

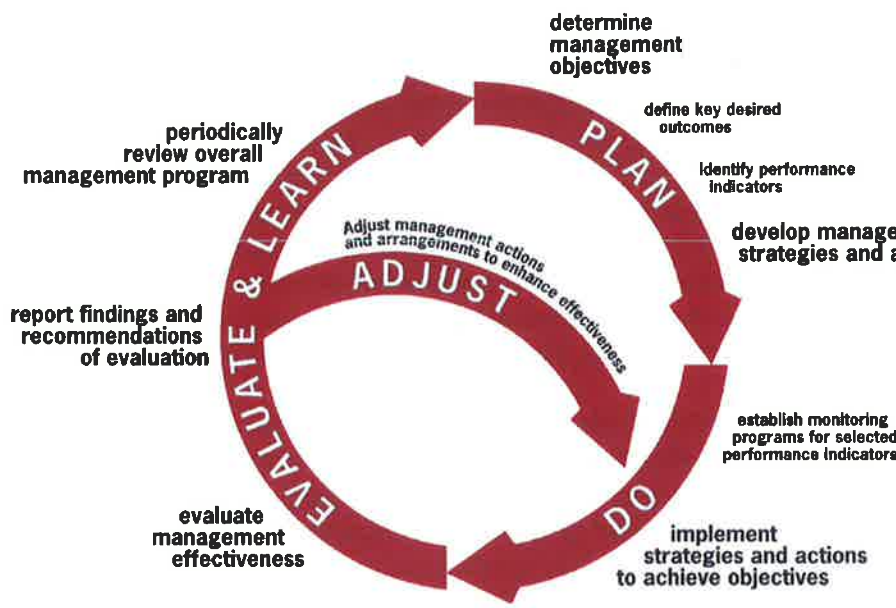


Fig.16 . Conceptual diagram of adaptive resource management as defined by Walters (1986, adapted from http://www.cmar.csiro.au/research/mse). Critically, management experiments are designed that contrast results of management experiments on key ecological indicators between control and treatment areas.

5.0 MANAGEMENT IMPLICATIONS

Based on this review, I draw the following conclusions regarding the impacts of energy development on wildlife populations.

1) **The current management policy for energy development makes two untested assumptions regarding the effects of energy development on wildlife.** First, it assumes that negative impacts of energy development on wildlife can be mitigated through small-scale stipulations that regulate the timing and duration of activity, but not the amount. This current policy also assumes that wildlife populations can withstand continued, incremental development. Neither of these two assumptions are supported or refuted by evidence reviewed in the scientific literature as part of this review. Regardless, adaptive experiments to explicitly test these management hypotheses are needed.

2) **There is currently no rigorous scientific evidence that energy development will have population-level impacts on pronghorn, mule deer or elk in eastern or central Montana.** However, this is because there have been no properly designed, thoughtful, rigorous tests of the population-level impacts conducted to date. Instead, a host of observational studies on small-scale and short-term responses provides limited guidance to managers in search of the crucial question of population impacts. While theoretically justified, relying on the precautionary principle to restrict energy development will likely be unsuccessful as an energy development policy.

3) **Short-term and small-scale impacts of energy development have been relatively well described in previous reviews and studies, albeit most often in poorly designed observational studies.** GPS collar studies have aided attempts to document small-scale responses to development, and will continue to be useful in the future in this correlational framework. Ungulates predictably avoid areas during active exploration and drilling, moving to denser cover and areas farther from human activity. Recommendations from previous studies still hold, namely timing and seasonal restrictions for critical habitats and resources. Across studies, ungulates showed avoidance responses to human development an average of 1000m from the human disturbance.

4) **Scaling up from small-scale/short-term studies to population-level impacts will be difficult.** One of the key difficulties is scaling up responses of ungulates at low development densities to high densities present in heavily developed oilfields (e.g. Upper Green River Basin). Preliminary analyses suggest that thresholds for significant impacts on ungulates will occur between densities of 0.1 to 0.5 wells/km^2 and 0.2 to 1.0 linear km/km^2 of roads and linear developments. However, these results are preliminary, and more formal meta-analyses are suggested.

5) Building on the strong example of the Montana Cooperative Elk-Logging study that ran through the 1970's and 1980's, a series of research and management recommendations are made.

a. First, a formal **meta-analyses** of the existing energy literature is recommended to allow scientifically defensible quantitative estimates of the effects of energy development on behavior, habitat and population dynamics.

b. Second, building on this meta-analysis, a **power analysis** of the optimal experimental design, level of replication, and duration of a energy-impact study design should be conducted to reveal the best approach for both short-term (behavior, habitat) and long-term impact assessment.

c. Third, a series of **large-scale, population-level and long-term experimental comparisons** similar to the Montana Cooperative Elk-Logging study should be initiated in eastern and central Montana on elk, mule deer and pronghorn. The study design should be replicated ideally across three levels of development; none – control, initial phases –low densities of wells/roads, and after at least a decade of intensive development, to allow a rigorous test of the population effects of energy development on wildlife. Partnerships with existing studies occurring in other developed areas should be developed (e.g., Upper Green River Basin studies), but control areas in Montana should be developed (e.g., Charles M. Russell Wildlife Refuge).

d. Fourth, implement an **adaptive management experiment** (in conjunction with the third point above) to test whether the current energy policy is sustainable from a wildlife population perspective. The de-facto energy policy as being implemented in Montana (and elsewhere) makes a number of assumptions that may in fact be incorrect. However, no serious alternatives have been developed or put forward as serious contenders that could be compared in large management experiments to test whether different models for energy development are required. If the bleak situation for Alberta caribou is any suggestion, alternative energy development policies are sorely needed.

6.0 LITERATURE REVIEW

Alberta woodland caribou recovery team. 2005. Alberta woodland caribou recovery plan, 2004/05 - 2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, AB, Canada.

Albon, S.D., T.N. Coulson, D. Brown, F.E. Guinness, J.M. Pemberton, and T.H. Clutton-Brock. 2000. Temporal Changes in Key Factors and Key Age Groups Influencing the Population Dynamics of Female Red Deer. Journal of Animal Ecology **69**:1099-1110.

Aldridge, C.L. and M.S. Boyce. 2007. Linking Occurrence and Fitness to Persistence: Habitat-Based Approach for Endangered Greater Sage-Grouse. Ecological Applications **17**:508-526.

Aldridge, C.L., M.S. Boyce, and R.K. Baydack . 2004. Adaptive Management of Prairie Grouse: How Do We Get There? Wildlife Society Bulletin **32**:92-103.

Aldridge, C.L. and R.M. Brigham. 2002. Sage-Grouse Nesting and Brood Habitat Use in Southern Canada. Journal of Wildlife Management **66**:433-444.

Altmann, M. the flight distance in free-ranging big game. The Journal of Wildlife Management 22(2), 207-209. 1958.

American Gas Association. 2005. Natural gas: balancing supply, demand and the environment. White paper delivered at the Natural Gas: Balancing Supply, Demand and the Environment Forum, May 24, 2005, Washington DC, USA.

Amstrup, S.C. 1978. Activities and Habitat Use of Pronghorns on Montana-Wyoming Coal Lands. *in* Anonymous, Proceedings of the Eighth Biennial Pronghorn Antelope Workshop. U.S. Fish and Wildlife Service.

Arnqvist, G. and D. Wooster. 1995. Metaanalysis - Synthesizing Research Findings in Ecology and Evolution. Trends in Ecology & Evolution **10**:236-240.

Bascompte, J., C.J. Melian, and E. Sala. 2005. Interaction Strength Combinations and the Overfishing of a Marine Food Web. Proceedings of the National Academy of Sciences of the United States of America **102**:5443-5447.

Basile, J. V. vehicle restrictions influence elk and hunter distribution in montana. Journal of Forestry 77, 155-159. 1979.

Bayne, E.M., S. Boutin, B. Tracz, and K. Charest. 2005. Functional and Numerical Responses of Ovenbirds (*Seiurus aurocapilla*) to Changing Seismic Exploration Practices in Alberta's Boreal Forest. Ecoscience **12**:216-222.

Berger, J.. 2004. The Last Mile: How to Sustain Long-Distance Migration in Mammals. Conservation Biology **18**:320-331.

Berger, J.. 2007. Fear, human shields, and the re-distribution of prey and predators in protected areas. Biology Letters 3: 620-623.

Berger, J., K.M. Berger, and J. Beckmann. 2006. Wildlife and Energy Development: Pronghorn of the Upper Green River Basin - Year 1 Summary. Wildlife Conservation Society, Bronx, NY.

Berger, J., S.L. Cain, and K.M. Berger. 2006. Connecting the Dots: an Invariant Migration Corridor Links the Holocene to the Present. Biology Letters **2**:528-531.

Berger, K. M., Beckman, J., and Berger, J. wildlife and energy development: pronghorn of the upper green river basin - year 2 summary. Report . 2007. Bronx, NY, Wildlife Conservation Society.

Bernard T. Bormann, Patrick G. Cunningham, Martha H. Brookes, Van W. Manning, and Michael W. Collopy, 1994, Adaptive Ecosystem Management in the Pacific Northwest, Pacific Northwest Research Station, General Technical Report PNW-GTR-341, Forest Service, U.S. Department of Agriculture. Further development of the adaptive management process outlined in FEMAT.

Bjornlie, D. and A. Garrott. 2001. Effects of Winter Road Grooming on Bison in Yellowstone National Park. Journal of Wildlife Management **65**:560-572.

Bleich, V.. 1990. Responses of mountain sheep to helicopter surveys. California Fish and Game 76: 197.

Boyce, M.S.. 2006. Scale for Resource Selection Functions. Diversity and Distributions **12**:269-276.

Boyce, M.S. and J.S. Waller. 2003. Grizzly Bears for the Bitterroot: Predicting Potential Abundance and Distribution. Wildlife Society Bulletin **31**:670-683.

Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in ecology and evolution 14: 268-272.

Bradshaw, C., S. Boutin, and D. Hebert. 1998. Energetic Implications of Disturbance Caused by Petroleum Exploration to Woodland Caribou. Canadian Journal of Zoology-Revue Canadienne De Zoologie **76**:1319-1324.

Bradshaw, C.J.A., S. Boutin, and D.M. Hebert . 1997. Effects of Petroleum Exploration on Woodland Caribou in Northeastern Alberta. Journal of Wildlife Management **61**:1127-1133.

Bromley, M. wildlife management implications of petroleum exploration and development in wildland environments. 1985. Ogden, UT, USFS.

Bruns, E. winter behavior of pronghorns in relation to habitat. The Journal of Wildlife Management 41(3), 560-571. 1977.

Bureau of Land Management [BLM]. 2003*a*. Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project. http://www.blm.gov/wy/st/en/info/NEPA/bfodocs/prb-feis.html. Accessed 18 March2007.

Bureau of Land Management [BLM]. 2003*b*. Montana Statewide Final Oil and Gas EIS Amendment of the Powder River and Billings Resource Management Plans.http://www.mt.blm.gov/mcfo/cbm/eis/index.html. Accessed 18 March 2007.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carroll, C. and D.G. Miquelle. 2006. Spatial Viability Analysis of Amur Tiger Panthera Tigris Altaica in the Russian Far East: the Role of Protected Areas and Landscape Matrix in Population Persistence. Journal of Applied Ecology **43**:1056-1068.

Carroll, C., R.F. Noss, P.C. Paquet, and N.H. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. Ecological Applications 13: 1773-1789.

Cassirer, F., Freddy, D., and Ables, E. elk responses to disturbance by cross-country skiers in yellowstone national park. Wildlife Society Bulletin 20(4), 375-381. 1992. Allen Press.

Chamberlain, T.C.. 1890. The method of multiple working hypotheses. Science 15: 93.

Ciarniello, L.M., N.S. Boyce, D.C. Heard, and D.R. Seip. 2007. Components of Grizzly Bear Habitat Selection: Density, Habitats, Roads, and Mortality Risk. Journal of Wildlife Management **71**:1446-1457.

Clevenger, A.P., B. Chruszcz, and K. Gunson. 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. Wildlife Society Bulletin 29: 646-653.

Clevenger, A.P. and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14: 47-56.

Cole, E., Pope, M., and Anthony, R. effects of road management on movement and survival of roosevelt elk. The Journal of Wildlife Management 61(4). 1997.

Cook, J.G., B.K. Johnson, R.C. Cook, R.A. Riggs, T. Delcurto, L.D. Bryant, and L.L. Irwin. 2004. Effects of Summer-Autumn Nutrition and Parturition Date on Reproduction and Survival of Elk. Wildlife Monographs 1-61.

COSEWIC. 2002. COSEWIC assessment and update status report on the Woodland Caribou, *Rangifer tarandus* caribou, in Canada. Committee on the status of endangered wildlife in Canada, Environment Canada, Ottawa, Ontario, Canada.

Cote, S.D.. 1996. Mountain Goat Responses to Helicopter Disturbance. Wildlife Society Bulletin **24**:681-685.

Coulson, T., J.M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the Variation in Population Growth Into Contributions From Multiple Demographic Rates. Journal of Animal Ecology **74**:789-801.

Cronin, M.A., W.B. Ballard, J.D. Bryan, B.J. Pierson, and J.D. McKendrick. 1998. Northern Alaska oil fields and caribou: a commentary. Biological Conservation 83: 195-208.

Cronin, M.A., H.A. Whitlaw, and W.B. Ballard . 2000. Northern Alaska Oil Fields and Caribou. Wildlife Society Bulletin **28**:919-922.

Dale, V.H., S. Brown, R.A. Haeuber, N.T. Hobbs, N. Huntly, R.J. Naiman, W.E. Riebsame, M.G. Turner, and T.J. Valone. 2000. Ecological principles and guidelines for managing use of the land. Ecological Applications 10: 639-670.

Dyer, S., J. O'Neill, S. Wasel, and S. Boutin. 2001a. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65: 531-542.

Dyer, S.J., J.P. O'Neill, S.M. Wasel, and S. Boutin. 2001b. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65: 531-542.

Dyer, S.J., J.P. O'neill, S.M. Wasel, and S. Boutin. 2002. Quantifying Barrier Effects of Roads and Seismic Lines on Movements of Female Woodland Caribou in Northeastern Alberta. Canadian Journal of Zoology-Revue Canadienne De Zoologie **80**:839-845.

Easterly, T.A.A.W.T.L. 1991. Responses of Pronghorn and Mule Deer to Petroleum Development on Crucial Winter Range in the Rattlesnake Hills. Wyoming Game and Fish Department, Cheyenne.

Eberhardt, L.L.. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83: 2841-2854.

Edge, W..1982. Distribution, Habitat Use, and Movements of Elk in Relation to Roads and Human Disturbances in Western Montana. University of Montana. Missoula, MT.

Edge, W., Marcum, C., and Olson, S. effects of logging activities on home-range fidelity of elk. The Journal of Wildlife Management 49(3), 741-744. 1985.

Edge, W.D. and C.L. Marcum. 1985. Movements of Elk in Relation to Logging Disturbances. Journal of Wildlife Management **49**:926-930.

Estes, J.A., E.M. Danner, D.F. Doak, B. Konar, A.M. Springer, P.D. Steinberg, M.T. Tinker, and T.M. Williams. 2004. Complex Trophic Interactions in Kelp Forest Ecosystems. Bulletin of Marine Science **74**:621-638.

Etchberger, R. C., Krausman, P. R., and Mazaika, R. 1989. Mountain sheep habitat characteristics in the pusch ridge wilderness, arizona. The Journal of Wildlife Management 53(4). 1- 14.

Festa-Bianchet, M., J.M. Gaillard, and S.D. Cote. 2003. Variable Age Structure and Apparent Density Dependence in Survival of Adult Ungulates. Journal of Animal Ecology **72**:640-649.

Fletcher, Q.E., C.W. Dockrill, D.J. Saher, and C.L. Aldridge. 2003. Northern Harrier, *Circus Cyaneus*, Attacks on Greater Sage-Grouse, *Centerocercus urophasianus,* in Southern Alberta. Canadian Field-Naturalist **117**:479-480.

Forman, R.T.T. and L.E. Alexander. 1998. Roads and Their Major Ecological Effects. Annual Review of Ecology and Systematics **29**:207-+.

Fortin, D., H. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, and J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86: 1320-1330.

Frair, J., E. Merrill, J. Allen, and M. Boyce. 2007. Know thy enemy: experience affects elk translocation success in risky landscapes. Journal of Wildlife Management **71**:541-554.

Frair, J.L..2005. Survival and movement behaviour of resident and translocated wapiti (*Cervus elaphus*): implications for their management in west-central Alberta, Canada. University of Alberta. Edmonton, Alberta, Canada.

Frair, J.L., E.H. Merrill, J.R. Allen, and M.S. Boyce. 2007. Know Thy Enemy: Experience Affects Elk Translocation Success in Risky Landscapes. Journal of Wildlife Management **71**:541-554.

Frid, A. and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6: 11.

Frid, A. dall's sheep responses to overflights by helicopter and fixed-wing aircraft. Biological Conservation 110(3), 387-399. 2003.

Fuller, T.K., Mech, L.D., and Cochrane, J.F. 2003. Wolf population dynamics. Pages 161-190. *in* L. D. Mech and L. Boitaini editors. Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, IL, USA.

Gaillard, J.-M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31: 367-393.

Gaillard, J.M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort Effects and Deer Population Dynamics. Ecoscience **10**:412-420.

Geist, V. 2002. Adaptive behavioral strategies. Pages 219-277. *in* J. W. T. D. E. Thomas editor., Elk of North America - ecology and management. Stackpole books, Herrisburg, Penn.

Gerrodette, T.. 1987. A power analysis for detecting trends. Ecology 68: 1364-1372.

Gill, R. B. declining mule deer populations in colorado: reasons and responses. 2001. Denver, CO, Colorado Division of Wildlife.

Gillies, C., M. Hebblewhite, S.E. Nielsen, M. Krawchuk, C. Aldridge, J. Frair, C. Stevens, D.J. Saher, and C. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887-898.

Gillin, C..1989. Response of elk to seismograph exploration in the Wyoming range, Wyoming. University of Wyoming. United States -- Wyoming.

Girard, M. and Stotts, B. 1986. Managing Impacts of Oil and Gas Development on Woodland Wildlife Habitats on the LIttle Missouri Grasslands, North Dakota. Pages 128-130. *in* Anonymous, Proceedings II: Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute, Boulder, CO.

Gordon, I.J., A.J. Hester, and M. Festa-Bianchet. 2004. The Management of Wild Large Herbivores to Meet Economic, Conservation and Environmental Objectives. Journal of Applied Ecology **41**:1021-1031.

Governors Office of Economic Development. 2006. Tapping Montana's Power Potential: The Schweitzer Energy Policy. Government of Montana. [available at URL http://commerce.mt.gov/energy/energypolicy.asp]

Gurevitch, J. and L.V. Hedges. 1999. Statistical Issues in Ecological Meta-Analyses. Ecology **80**:1142-1149.

Haight, R.G., B. Cypher, P.A. Kelly, S. Phillips, H.P. Possingham, K. Ralls, A.M. Starfield, P.J. White, and D. Williams. 2002b. Optimizing Habitat Protection Using Demographic Models of Population Viability . Conservation Biology **16**:1386-1397.

Harrison, S. and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22: 225-232.

Harron, D.E.. 2007. Assumptive error and overestimation of effects of in wildlife model output. Ecology and Society 12: [Online].

Hayden-Wing Associates. 1990. Response of Elk to Exxon's Field Development in the Riley Ridge Area of Western Wyoming, 1979-1988. Exxon Company, U.S.A., Wyoming Game and Fish Department,

Hayden-Wing Associates. 1991. Review and Evaulation of the Effects of Geophysical Exploration on Some Wildlife Species in Wyoming. Geophyisical Acquisition Workshop, Rawlins, WY.

Hebblewhite, M. and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology Accepted October 2007.

Hebblewhite, M., E. Merrill, and T. McDonald. 2005a. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk system. Oikos 111: 101-111.

Hebblewhite, M., C.A. White, C. Nietvelt, J.M. McKenzie, T.E. Hurd, J.M. Fryxell, S. Bayley, and P.C. Paquet. 2005c. Human activity mediates a trophic cascade caused by wolves. Ecology 86: 2135-2144.

Hedges, L.V., J. Gurevitch, and P.S. Curtis. 1999. The meta-analysis of response ratio's in experimental ecology. Ecology 80: 1150-1156.

Hiatt, G. and D. Baker. 1981. Effects of Oil/Gas Drilling on Elk and Mule Deer Winter Distributions on Crooks Mountain, Wyoming. Wyoming Game and Fish Department, Cheyenne.

Hobbs, N.T. and R. Hilborn. 2006. Alternatives to Statistical Hypothesis Testing in Ecology: a Guide to Self Teaching. Ecological Applications **16**:5-19.

Horesji, B. 1979. Seismic operations and their impacts on large mammals: results of a monitoring program. 1979. Calgary, Alberta, Western wildlife environments.

Hurlbert, S.H.. 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs **54**:187-211.

Ihsle, H..1981. Population Ecology of Mule Deer with Emphasis on Potential Impacts of Gas and Oil Development along the East Slope of the Rocky Mountains, Northcentral Montana. Montana State University. Bozeman, MT.

Interagency Technical Committee. 1987. Management guidelines for seleted species: Rocky Mountain Front Studies. Bureau of Land Management, publication BLM-MT-PT-87-003-4111. Great Falls, MT, 71pp.

Irby, L., Mackie, R., Ihsle Pac, H., and Kasworm, W. 1988. Management of Mule Deer in Relation to Oll and Gas Development in Montana's Overthrust Belt. Pages 113-121. *in* Anonymous, Issues and Technology in the Management of Impacted Wildlife; Proceedings of a National Symposium. Thorne Ecological Institute, Boulder, CO.

Irwin, L. and C. Gillian. 1984. Response of Elk to Seismic Exploration in the Bridger-Teton Forest, Wyoming. The University of Wyoming,

James, A., S. Boutin, D. Hebert, and A. Rippin. 2004. Spatial Separation of Caribou From Moose and Its Relation to Predation by Wolves. Journal of Wildlife Management **68**:799-809.

James, A. and Stuart-Smith, A. distribution of caribou and wolves in relation to linear corridors. The Journal of Wildlife Management 64(1), 154-159. 2000. Allen Press.

Jansen, B.D., P.R. Krausman, J.R. Heffelfinger, and J.C. De Vos. 2007. Influence of Mining Influence, on Behavior of Bighorn Sheep. Southwestern Naturalist **52**:418-423.

Jansen, B.D., P.R. Krausman, J.R. Heffelfinger, and J.C. Devos. 2006. Bighorn Sheep Selection of Landscape Features in an Active Copper Mine. Wildlife Society Bulletin **34**:1121-1126.

Johnson, B. 1980. Response of Elk During Calving to Oil Gas Drilling Activity in Snider Basin, Wyoming. Wyoming Game and Fish Department,

Johnson, B. and L. Wolrab. 1987. Response of Elk to Development of a Natural Gas Field in Western Wyoming. Wyoming Game and Fish Department, Cheyenne.

Johnson, C., Boyce, M., Case, R., Cluff, H., Gau, R., Gunn, A., and Mulders, R. culmulative effects of human developments on arctic wildlife. 160(1), 1-36. 2005.

Johnson, T. 1986. Impacts of Surface Coal Mining on Calving Elk. Pages 255-269. *in* Anonymous, Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute, Glenwood Springs, CO.

Joslin, G. and Youman, H. effects of recreation on rocky mountain wildlife: a review for Montana. 1999. Committee on the effects of recreation on wildlife, Montana Chapter of the Wildlife Society.

Keller, B.J. and L.C. Bender. 2007. Bighorn Sheep Response to Road-Related Disturbances in Rocky Mountain National Park, Colorado. Journal of Wildlife Management **71**:2329-2337.

Kennedy, A.J. 2000. Cumulative environmental effects management: tools and approaches. Hignell Printing, Calgary, Alberta.

Krausman, P., Harris, L., Blasch, C., Koenen, K., and Francine, J. effects of military operations on behavior and hearing of endangered sonoran pronghorn. Wildlife Monographs (157), 1-41. 2004. Allen Press.

Krausman, P., Harris, L., Haas, S., Koenen, K., Devers, P., Bunting, D., and Barb, M. 2005. Sonoran pronghorn habitat use on landscapes disturbed by military activities. Wildlife Society Bulletin 33(1), 16-23.

Krebs, C.J. 1989. Ecological Methodology. Harper Collings Publishers, New York.

Kuck, L., Hompland, G., and Merrill, E. elk calf response to simulated mine disturbance in southeast idaho. The Journal of Wildlife Management 49(3), 751-757. 1985. Allen Press.

Landon, D., Krausman, P., Koenen, K., and Harris, L. pronghorn use of areas with varying sound pressure levels. The Southwestern Naturalist 48(4), 725-728. 2003. Southwestern Association of Naturalists.

Leslie, D. and Douglas, C. human disturbance at water sources of desert bighorn sheep. Wildlife Society Bulletin 8(4), 284-290. 1980.

Lessard, R.B., S.J.D. Martell, C.J. Walters, T.E. Essington, and J.F. Kitchell. 2005. Should ecosystem management involve active control of species abundances? Ecology and Society 10: 1-21.

Lustig, T. 2002. Where would you like the holes drilled into your crucial winter range? Transactions of the 67th North American Wildlife and Natural Resources Conference **67**:317-325.

Lyon, J. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 22: 592-595.

Lyon, L. 1979. Habitat Effectiveness for Elk as Influenced by Roads and Cover. Journal of Forestry **77**:658-660.

Lyon, L. 1979. Influences of Logging and Weather on Elk Distribution in Western Montana. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Lyon, L. road density models describing habitat effectiveness for elk. Journal of Forestry 81, 592-613. 1983.

Lyon, L., T. Lonner, J. Weigand, C. Marcum, D. Edge, J. Jones, D. McCleerey, and L. Hicks. 1985. Coordinating Elk and Timber Management. Montana Department of Fish, Wildlife, and Parks, Bozeman, MT.

MacArthur, R., Geist, V., and Johnston, R. cardiac and behavioral responses of mountain sheep to human disturbance. The Journal of Wildlife Management 46(2), 351-358. 1982. Allen Press.

MacCallum, B.N. and V. Geist. 1992. Mountain restoration: soil and surface wildlife habitat. GeoForum 27: 23-46.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, USA.

McCorquodale, S., Raedeke, K., and Taber, R. elk habitat use patterns in the shrub-steppe of washington. The Journal of Wildlife Management 50(4), 664-669. 1986. Allen Press.

McCorquodale, S.M., R. Wiseman, and L. Marcum. 2003. Survival and harvest vulnerability of elk in the Cascade range of Washington. Journal of Wildlife Management 67: 248-257.

McCorquodale, S.M..2000. Habitat ecology and vulnerability to hunting mortality of elk in the southcentral Washington Cascades . Wildlife Biology Program, School of Forestry, University of Montana. Missoula, MT .

Mckenzie, H..2006. Linear features impact predator-prey encounters: analysis with first passage time. University of Alberta. Edmonton, AB.

Mcloughlin, P.D., J.S. Dunford, and S. Boutin. 2005. Relating Predation Mortality to Broad-Scale Habitat Selection. Journal of Animal Ecology **74**:701-707.

Mcloughlin, P.D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in Populations of Woodland Caribou. Journal of Wildlife Management **67**:755-761.

Medcraft, J. and Clark, W. big game habitat use and diets on a surface mine in northeastern wyoming. The Journal of Wildlife Management 50(1), 135-142. 1986. Allen Press.

Merrill, E., Hemker, T., Woodruff, K., and Kuck, L. impacts of mining facilities on fall migration of mule deer. Wildlife Society Bulletin 22(1), 68-73. 1994. Allen Press.

Millspaugh, J., Woods, R., Hunt, K., Raedeke, K., Brundige, G., Washburn, B., and Wasser, S. fecal glucocorticoid assays and the physiological stress response in elk. Wildlife Society Bulletin 29(3), 899-907. 2001. Allen Press.

Montana Board of Oil and Gas Conservation. 2006. Annual Review 2006, volume 50. Board of Oil and Gas Conservation, Department of Natural Resources and Conservation, State of Montana Oil and Gas Conservation Division. Accessed 1/1/2008, [URL http://bogc.dnrc.mt.gov/PDF/AR_2006.pdf].

Morgantini, L. 1885. Ungulate Encounters with Construction Materials (Pipe, Berms, etc.) During the Building of an Underground Gas Pipeline in Western Alberta, Canada. Alces **21**:215-230.

Morgantini, L.E. and R.J. Hudson. 1985. Changes in diets of wapiti during a hunting season. Journal of Range Management 38: 77-79.

Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Morrison, J., de Vergie, W., Alldredge, A., Byrne, A., and Andree, W. the effects of ski area expansion on elk. Wildlife Society Bulletin 23(3), 481-489. 1995. Allen Press.

Mysterud, A. and R.A. Ims. 1998. Functional Responses in Habitat Use: Availability Influences Relative

Use in Trade-Off Situations. Ecology **79**:1435-1441.

National Research Council. 2003. Cumulative Environmental Effects of Oil and Gas Activities on Alaska's North Slope. The National Academic Press, Washington, D.C.

Naugle, D.E., C.L. Aldridge, B.L. Walker, T.E. Cornish, B.J. Moynahan, M.J. Holloran, K. Brown, G.D. Johnson, E.T. Schmidtmann, R.T. Mayer, C.Y. Kato, M.R. Matchett, T.J. Christiansen, W.E. Cook, T. Creekmore, R.D. Falise, E.T. Rinkes, and M.S. Boyce. 2004. West Nile Virus: Pending Crisis for Greater Sage-Grouse. Ecology Letters **7**:704-713.

Neufeld, L..2006. Spatial dynamics of wolves and woodland caribou in an industrial forest landscape in west-central Alberta. University of Alberta. Edmonton, AB.

Oliff, T., Legg, K., and Kaeding, B. 1999. Effects of winter recreation on wildlife of the greater yellowstone area: a literature review and assessment. Yellowstone National Park, Wyoming, National Parks Service . Report to the greater Yellowstone coordinating committee.

Olson, G. 1981. Effects of Seismic Exploration on Summering Elk in the Two Medicine - Badger Creek Area, Northcentral Montana. Montana Department of Fish, Wildlife, and Parks.

Osenberg, C.W., O. Sarnelle, and S.D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. American Naturalist 150: 798-812.

Otis, D.L. and G.C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63: 1039-1044.

Papouchis, C.M., F.J. Singer, and W.B. Sloan . 2001. Responses of Desert Bighorn Sheep to Increased Human Recreation. Journal of Wildlife Management **65**:573-582.

Parker, K.L., P.S. Barboza, and T.R. Stephenson. 2005. Protein Conservation in Female Caribou (Rangifer Tarandus): Effects of Decreasing Diet Quality during Winter. Journal of Mammalogy **86**:610-622.

Phillips, G. and Alldredge, A. reproductive success of elk following disturbance by humans during calving season. The Journal of Wildlife Management 64(2), 521-530. 2000. Allen Press.

Powell, J..2003. Distribution, Habitat Use Patterns, and Elk Response to Human Disturbance in the Jack Marrow Hills, Wyoming. University of Wyoming. Laramie, Wyoming.

Powell, R.A. 2000. Animal home ranges and territories and home range estimators. *in* L. Boitani and T. K. Fuller editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York.

Preisler, H., A. Ager, and M. Wisdom. 2006. Statistical Methods for Analyzing Responses of Wildlife to Human Disturbance. Journal of Applied Ecology **43**:164-172.

Raithel, J.D., M.J. Kauffman, and D.H. Pletscher. 2007. Impact of Spatial and Temporal Variation in Calf Survival on the Growth of Elk Populations. Journal of Wildlife Management **71**:795-803.

Reed, D., Woodard, T., and Pojar, T. behavioral response of mule deer to a highway underpass. The Journal of Wildlife Management 39(2), 361-367. 1975. Allen Press.

Roberts, P.D., G.B. Stewart, and A.S. Pullin . 2006. Are Review Articles a Reliable Source of Evidence to Support Conservation and Environmental Management? A Comparison With Medicine. Biological Conservation **132**:409-423.

Rost, G. and Bailey, J. distribution of mule deer and elk in relation to roads. The Journal of Wildlife Management 43(3), 634-641. 1979. Allen Press.

Roth, S. and Goodwin, V. health effects of hydrogen sulphide. 2000. Edmonton ,Alberta, Alberta Ministry of the Environment.

Rothley, K.D.. 2001. Manipulative, Multi-Standard Test of a White-Tailed Deer Habitat Suitability Model. Journal of Wildlife Management **65**:953-963.

Rowland, M., Wisdom, M., Johnson, B., and Kie, J. elk distribution and modeling in relation to roads. The Journal of Wildlife Management 64(3), 672-684. 2000. Allen Press.

Rowland, M., M. Wisdom, B. Johnson, and M. Penninger. 2004. Effects of Roads on Elk: Implications for Management in Forested Ecosystems. Transactions of the Sixty-ninth North American Wildlife and Natural Resources Conference **69**:491-508.

Rowland, M.M., M.J. Wisdom, B.K. Johnson, and J.G. Kie. 2000. Elk Distribution and Modeling in Relation to Roads. Journal of Wildlife Management **64**:672-684.

Saadat, M., Z. Zendeh-Boodi, and M.A. Goodarzi. 2006. Environmental Exposure to Natural Sour Gas Containing Sulfur Compounds Results in Elevated Depression and Hopelessness Scores. Ecotoxicology and Environmental Safety **65**:288-291.

Sargeant, G.A. and M.W. Oehler. 2007. Dynamics of Newly Established Elk Populations. Journal of Wildlife Management **71**:1141-1148.

Sawyer, H., Lindzey, F., and McWhirter, D. mule deer and pronghorn migration in western wyoming. 33(4), 1266-1273. 2005.

Sawyer, H., F. Lindzey, and D. Mcwhirter. 2005b. Mule Deer and Pronghorn Migration in Western Wyoming. Wildlife Society Bulletin **33**:1266-1273.

Sawyer, H., F. Lindzey, D. McWhirter, and K. Andrews. 2002. Potential Effects of Oil and Gas Development on Mule Deer and Pronghorn Populations in Western Wyoming. Trans. of the 67th NA Wildlife and Natural Resources Conference **67**:350-365.

Sawyer, H., Nielson, R., Lindzey, F., Keith, L., Powell, J., and Abraham, A. habitat selection of rocky mountain elk in a nonforested environment. Journal of Wildlife Management 71(3), 868-874 . 2007.

Sawyer, H., Nielson, R., Lindzey, F., and Mcdonald, L. winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70(2), 396-403. 2006.

Sawyer, H., R. Nielson, D. Stickland, and L. McDonald. 2005. Mule Deer Study (Phase II): Long-term Monitoring Plan to Assess Potential Impacts of Energy Development on Mule Deer in the Pinedale Anticline Project Area . Western Ecosystems Technology, Inc., Cheyenne, WY.

Sawyer, H., R.M. Nielson, F. Lindzey, and L.L. Mcdonald. 2006. Winter Habitat Selection of Mule Deer Before and During Development of a Natural Gas Field. Journal of Wildlife Management **70**:396-403.

Sawyer, H., R.M. Nielson, F.G. Lindzey, L. Keith, J.H. Powell, and A.A. Abraham. 2007. Habitat Selection of Rocky Mountain Elk in a Nonforested Environment. Journal of Wildlife Management **71**:868-874.

Schmitz, O.J., P.A. Hämback, and A.P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. The American Naturalist 155: 141-153.

Schneider, R.R., J.B. Stelfox, S. Boutin, and S. Wasel. 2003. Managing the cumulative impacts of land uses in the western Canadian sedimentary basin: a modeling approach. Conservation Ecology 7: 8.

Scott, H.M., C.L. Soskolne, K.D. Lissemore, S.W. Martin, M.M. Shoukri, R.W. Coppock, and T.L. Guidotti. 2003a. Associations Between Air Emissions From Sour Gas Processing Plants and Indices of Cow Retainment and Survival in Dairy Herds in Alberta. Canadian Journal of Veterinary Research-Revue Canadienne De Recherche Veterinaire **67**:1-11.

Scott, H.M., C.L. Soskolne, S.W. Martin, J.A. Basarab, R.W. Coppock, T.L. Guidotti, and K.D. Lissemore. 2003b. Lack of Associations Between Air Emissions From Sour-Gas Processing Plants and Beef Cow-Calf Herd Health and Productivity in Alberta, Canada. Preventive Veterinary Medicine **57**:35-68.

Seip, D.R., C.J. Johnson, and G.S. Watts. 2007. Displacement of Mountain Caribou From Winter Habitat by Snowmobiles. Journal of Wildlife Management **71**:1539-1544.

Shivley, K., A.W. Alldredge, and G.E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. Journal of Wildlife Management 69: 1073-1080.

Shurin, J.B., E.T. Borer, E.W. Seabloom, K. Anderson, C.A. Blanchette, B. Broitman, D. Cooper, and S. Halpern. 2002. A cross-system comparison of the strength of trophic cascades. Ecology Letters 5: 785-791.

Smyth, C.R.. 1997. Native Legume Transplant Survivorship and Subsequent Seedling Recruitment on Unammended Coal Mine Soils in the Canadian Rocky Mountains. Mountain Research and Development **17**:145-157.

Sorenson, T., McLoughlin, P., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. determining sustainable levels of cumulative effects for boreal caribou: a management model. Journal of Wildlife Management (In Press). 2008.

Stephenson, T., Vaughan, M., and Andersen, D. mule deer movements in response to military activity in southeast colorado. The Journal of Wildlife Management 60(4), 777-787. 1996.

Stockwell, C.A.. 1991. Conflicts in National Parks: a case-study of helicopters and bighorn sheep time budgets at the grand canyon. Biological Conservation 56: 317-325.

Stuart-Smith, A.K., C.J.A. Bradshaw, S. Boutin, D.M. Hebert, and A.B. Rippin. 1997. Woodland Caribou Relative to Landscape Patterns in Northeastern Alberta. Journal of Wildlife Management **61**:622-633.

Trombulak, S. and Frissell, C. review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14(1), 18-30. 2000. Blackwell Publishing.

Turner, M.G., R.H. Gardner, and R.V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag, NY, NY.

Underwood, A.J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance/. Cambridge University Press, Cambridge, UK.

Unsworth, J.A., D.F. PAc, G.C. White, and R.M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63: 315-326.

U.S. Departments of Interior, Agriculture, and Energy. 2003. Energy policy and conservation act report: scientific inventory of onshore federal lands' oil and gas resources and reserves and the extent and nature of restrictions or impediments to their development. <http://www.doi.gov/epca> (26 April 2004).

van Dyke, F. and Klein, W. response of elk to installation of oil wells. Journal of Mammalogy 77(4), 1028-1041. 1996.

Waldner, C.L., C.S. Ribble, and E.D. Janzen. 1998. Disaster Medicine - Evaluation of the Impact of a Natural Gas Leak From a Pipeline on Productivity of Beef Cattle. Journal of the American Veterinary Medical Association **212**:41-48.

Waldner, C.L., C.S. Ribble, E.D. Janzen, and J.R. Campbell. 2001a. Associations Between Oil- and Gas-Well Sites, Processing Facilities, Flaring, and Beef Cattle Reproduction and Calf Mortality in Western Canada. Preventive Veterinary Medicine **50**:1-17.

Walker, B.L., D.E. Naugle, and K.E. Doherty. 2007. Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. Journal of Wildlife Management **71**:2644-2654.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology, 2:1. [Online].

Walters, C. 1986. Adaptive Ecosystem Management. Toronto, ON, Canada.

Ward, L. 1986. Displacement of Elk Related to Seismograph Activity in South-central Wyoming. Pages 246-254. *in* Anonymous, Proceedings II: Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute, Glenwood Springs, CO.

Webb, N., M. Hebblewhite, and E.H. Merrill. In Press. Statistical methods for identifying wolf kill sites in a multiple prey system using GPS collar locations. Journal of Wildlife Management

Weclaw, P. and R.J. Hudson. 2004. Simulation of Conservation and Management of Woodland Caribou. Ecological Modelling **177**:75-94.7

White, P. J., Davis, T. L., Barnowe-Meyer, K. K. , Crabtree, R. L., and Garrott, R. A. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation 135(4), 502-510.

Williams, E.S., M.W. Miller, T.J. Kreeger, R.H. Kahn, and E.T. Thorne. 2002. Chronic Wasting Disease of Deer and Elk: a Review With Recommendations for Management. Journal of Wildlife Management **66**:551-563.

Appendix A: Electronic Database

Ungulate Energy Development Literature Citation Database

This searchable electronic database contains literature and research summaries on all aspects of the effects of energy development on ungulates. This exhaustive database contains all journal papers, conference proceedings, M.S. and Ph.D. theses, government reports, and other unpublished manuscripts concerning ungulates (Bighorn Sheep (*Ovis canadensis*), American pronghorn (*Antilocapra antilocapra*), Elk (*Cervus elaphus*), Mule deer (*Odocoileus hemionus*), woodland caribou (*Rangifer tarandus*)). The database was made using multiple search methods and bibliographic sources.

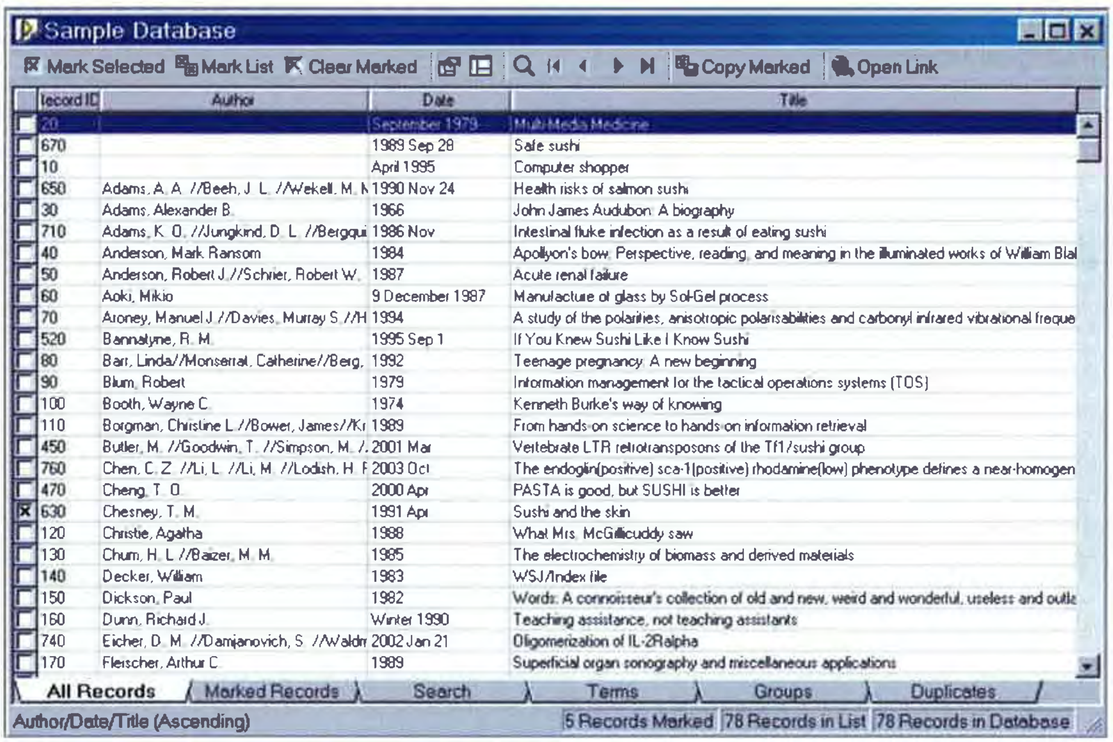
The database utilizes ProCite 5, a commercial reference management software.

To open the Wild Energy database:

1. Start ProCite

2. A file **Open** dialog displays for you to locate and open a database. If not, go to the **File** menu and choose **Open.**

The database window displays a record list of abbreviated records. By default the first Author field, Title field and Date field are shown from each record.

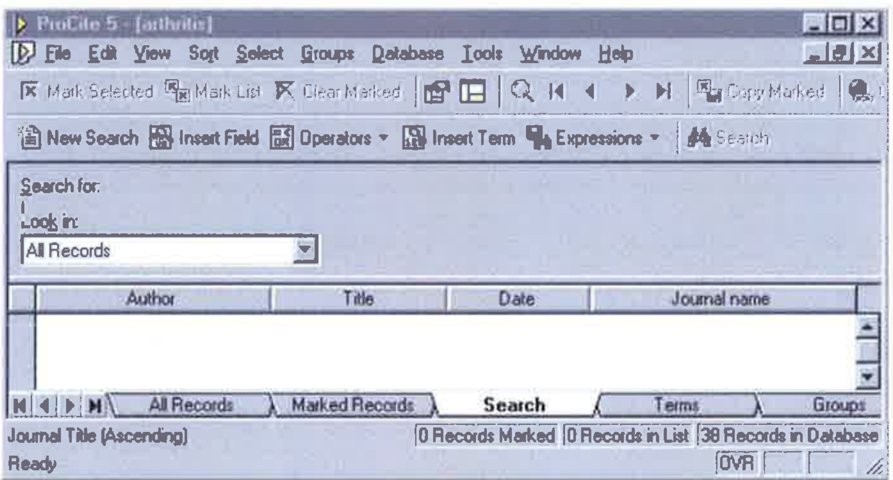


A status line at the bottom of the window indicates the sort order (Author/Title/Date in ascending order by default), the number of records marked, the number of records displayed in the current list and the total number of records in the database.

Double click on a specific reference to view the detailed data record.

Searching the database:

1. Click on the **Search** tab at the bottom of the window.



You can enter search terms, use Boolean operators, and limit your search to certain fields. All records that fit your search will be presented as a group in the results box at the bottom of the screen.

To launch a PDF found in ProCite's Location/URL field:

1. Double-click a record to display the full record.

2. Locate the *Location/URL (38)* field.

3. If there is a file path location in the field, the PDF is linked to the record.

4. From the **Tools** menu, choose **Open File/URL** or click the toolbar icon. ProCite launches the application that opens the PDF.

Note: You are not required to display the full record. You can launch a URL from a record list by highlighting the record and using the Open File/URL toolbar icon.

Assistance with ProCite:

1. ProCite Web Site - http://www.procite.com

The ProCite web site has a great deal of useful information on using ProCite, including a frequently asked questions page, a user email discussion list, and a free demo version of ProCite.

2. Using ProCite 5: A Guided Tour - http://www.procite.com/support/docs/ProCite%205%20Guided%20Tour-2005.pdf

This tour contains detailed information on how to manipulate and utilize the ProCite database.

Appendix B: Management Guidelines

Management guidelines developed to minimize the impacts of oil and gas development in north-central Montana (Interagency Technical Committee 1987) cited in Irby et al. (1988).

Table 3. Management guidelines developed to minimize the impacts of oil and gas development in north-central Montana (Interagency Technical Committee 1987).

GENERAL GUIDELINES

1. Identify and evaluate for each project proposal the cumulative effects of all activities, both existing uses and other planned projects.

2. Evaluate human activities, combinations of activities, or the zones of influence of such activities that occur on seasonally important wildlife habitats and avoid those which may adeversely impact the species or reduce habitat effectiveness.

3. Space concurrent active seismograph lines at least 9 miles apart to allow an undisturbed corridor into which wildlife can move when displaced.

4. Establish helicopter flight patterns of not more than 1/2 mile in width along all seismographic lines ....

5. Helicopters will maintain a minimum altitude of 600 feet above ground level between landing zones and work areas....

6. Designate landing zones for helicopters in areas where helicopter traffic and associated associated human disturbance will have minimum impact on wildlife populations.

7. The use of helicopters instead of new road contruction to accomplish energy exploration and development is encouraged.

8. Base road construction on a completed transportation plan ....

9. Use minimum road and site construction specifications based on projected transportation needs. Schedule construction to avoid seasonal use periods for wildlife ....

10. Locate roads, drill sites, landing zones, etc. to avoid important wildlife components ...

11. Insert "doglegs" or visual barriers on pipelines and roads built through dense vegetation to prevent open, straight corridors >1/4 mile.

12. Roads which are not compatible with area management objectives and are no longer needed .... will be closed and reclaimed.

13. Keep roads which are in use during oil and gas exploration and development activity closed to unauthorized use.

14. Impose seasonal closures or vehicle restrictions based on wildlife or other resource needs on roads which remain open.

15. Bus crews to and from drill sites to reduce activity on roads.

16. Keep noise levels to a minimum by muffling such things as engines, generators, and energy production facilities.

17. Prohibit dogs during work periods.

18. Prohibit firearms during work periods or in vehicles traveling to and from work locations.

19. Seismographic and exploration companies should keep a daily log of activities.

SPECIFIC GUIDELINES FOR MULE DEER

1. Avoid disturbance related to human activities on ....
   - A. Primary and secondary winter ranges - December 1 - May 15
   - B. Transitional ranges - October 15 - December 31
   - C. Migration corridors - May 15 - June 15.

2. Population units should be monitored to detect changes in population size, productivity, mortality, and distribution associated with changes in land use. Intensive monitoring should be initiated if gas/oil well density exceeds 1 well/section on 25% of secondary winter/transition range or 10% of a primary winter range supporting high mule deer densities.

Chapter 5

Effects of Energy Development on Ungulates

MARK HEBBLEWHITE

Increased energy consumption and overreliance of the United States on foreign energy has led to an increase in development of domestic resources. This national policy manifested in western North America especially through the late 1990s and 2000s. For example, between 2002 and 2006 in Montana, oil production increased by 213 percent, the number of oil wells by 17 percent, and the number of natural gas wells by 34 percent (Montana Board of Oil and Gas Conservation 2006). Increases are similar to the nearly 60 percent increase in the number of permit applications throughout the West in the last decade (American Gas Association 2005). Although this relative growth is impressive, comparison with the heavily developed oil and gas fields of Alberta reveals that Montana production is less than 10 percent of currently active oil and gas wells in Alberta. Thus, from an energy development perspective, energy impacts on wildlife in the conterminous United States are just getting started.

Energy development can affect almost all natural resources, including surface and subsurface hydrological processes, natural disturbance regimes such as fire, soil erosion processes, wildlife habitat, and wildlife population dynamics (Naugle et al. 2004; Bayne et al. 2005a, 2005b). Limited regulatory mechanisms may be in place for a few key wildlife species, including greater sage-grouse (*Centrocercus urophasianus*; chap. 4), but mitigation is typically implemented on a site-by-site basis. Regardless of small-scale regulations often applied to individual well site permits, impacts of development are most often felt through cumulative effects of not just one well site at a time but across large landscape scales on the order of thousands of square kilometers (Kennedy 2000; Schneider et al. 2003; Aldridge et al. 2004; Johnson et al. 2005; Frair et al. 2008; Walker et al. 2007a). Thus, management agencies face the difficult task of sustaining wildlife populations at large landscape scales in the face of small-scale and piecemeal environmental impact assessment (chap. 11).

In this chapter, I review effects of energy development on large mammals, with a focus on ungulates in western North America. I emphasize ungulates because of recent interest by the public and management agencies on effects of development on these focal species. Ungulates also provide a useful entry point to understanding energy impacts on wildlife because as herbivores, they must balance risk of being killed by predators with changes in forage availability (Hebblewhite and Merrill 2008), and energy development can influence the entire food web in which ungulates live (DeCesare et al. 2009). Indeed, often the indirect effects of food web dynamics influence focal species after development (chap. 3). Objectives of this chapter are to synthesize the literature about the effects of energy development on ungulates, identify weaknesses of existing research to provide guidelines for the management of energy development, and propose a conceptual framework for understanding effects of development on ungulates. Given substantial shortcomings in the existing approaches used to study the effects of energy on large mammals, I conclude with recommendations to improve the science of energy impacts on wildlife.

Effects of Energy Development on Ungulates

I conducted a literature search of energy–ungulate impact studies using searches of electronic databases from 1970 to the present, including ISI Web of Science, Google Scholar, Absearch, Bioabstracts, Biological Abstracts, Environmental Sciences, Dissertation Abstracts, government resources, Geology Abstracts, and Forestry Abstracts. I searched databases using combinations of the keywords *elk*, *mule deer*, *pronghorn*, *woodland caribou*, *energy development*, *petroleum development*, *oil development*, *gas development*, *wildlife*, and *ungulate in western North America*. I recorded information on each study regarding study area, methods, results, recommendations, and implications. I found 120 publications that met search criteria. Seventy were field studies that investigated aspects of energy development on ungulates. Of those seventy studies, almost half were peer-reviewed scientific publications, 30 percent were unpublished reports, 11 percent conference proceedings, and a combination of book chapters and graduate theses made up the remainder. Elk were the most common ungulate studied in forty-five studies, followed by woodland caribou (twenty-nine), mule deer (twenty), and pronghorn (twenty-one). A surprising number of literature reviews (ten) have been conducted on this scant literature.

From a study design perspective, most studies (N = 27, 47 percent) used a weak observational approach in which impacts of development were inferred from correlations between levels of human activity and measures of ungulate responses to treatments. Comparative designs, where responses were evaluated before or after development, but without a control, were used in 19 percent (N = 11) of the studies. Only ten studies (18 percent) used the most powerful experimental design, a before–after control–impact design (BACI) (Krebs 1989; Underwood 1997). Three studies were specifically designed to be predevelopment studies conducted at or before the beginning of development (Amstrup 1978; Ihsle 1982; Sawyer et al. 2002). None of the studies were replicated. Approximately 51 percent of studies used radio telemetry, collaring more than 2,000 animals. The most common alternative methods were aerial surveys (15 percent) and pellet or sign and track surveys (20 percent). Average sample size (N) used in energy–wildlife studies was 57.5, the median 39.5, considering the sample unit as the individual animal (Gillies et al. 2006; Otis and White 1999) (table 5.1).

Size of the ungulate population affected by development averaged 3,950 animals, with a median of 1,000 (table 5.1). From a sampling perspective, then, the average telemetry-based study sampled a mean of 1.5 percent or a median of 4 percent of the population. In radio telemetry studies,

TABLE 5.1. Summary statistics for literature on the effects of energy development and human disturbance on ungulates (N = 126 studies).

Metric	*Mean*	*Median*	*Range*	*SD*
Sample size	57.5	39.5	4–223	53.6
Number of animals marked in telemetry studies	58.7	34.2	4–223	60
Number of telemetry locations per animal	22	17	1–55	
Population size	3,950	1,000	35–48,000	22,058
Study area size (km^2)	3,882	798	26–20,000	5,924
Study duration (years)	2.7	2.1	0.15–11	2.28

only twenty-two VHF locations were obtained per animal per study. Pseudoreplication (Hurlbert 1984) occurred in 30 percent of studies, most commonly where telemetry locations were considered the sample unit.

Oddly, studies often failed to report the size of the study area, a key parameter influencing magnitude of impacts, spatial scaling, and density of disturbances. Where size was reported ($N = 56$), it ranged from 26 to 190,000 square kilometers. Studies of boreal woodland caribou populations had the largest study areas, averaging 28,000 square kilometers (range 225–190,000 square kilometers), and were statistically larger than those for other species (ANOVA; $P < .01$). Excluding caribou, the largest study area in the lower forty-eight states was 15,000 square kilometers in Wyoming (Sawyer et al. 2005b), with no other differences between species ($P > .30$). Although the average size of study areas appeared large (3,382 square kilometers), the median was only 798 square kilometers, a 15-square-kilometer radius (table 5.1).

Studies were short, paralleling the duration of active energy development. Average and median duration were 2.7 and 2.1 years, respectively. Most studies were conducted in two time periods, the first in the 1980s and the second of which we are currently experiencing (hence this book; fig. 5.1).

Two peaks in the number of studies correspond closely ($r = .57$, $P = .09$) with peaks in energy exploration and development in the last 30 years (American Gas Association 2005; Montana Board of Oil and Gas Conservation 2006). Careful reading revealed that of just the studies designed to

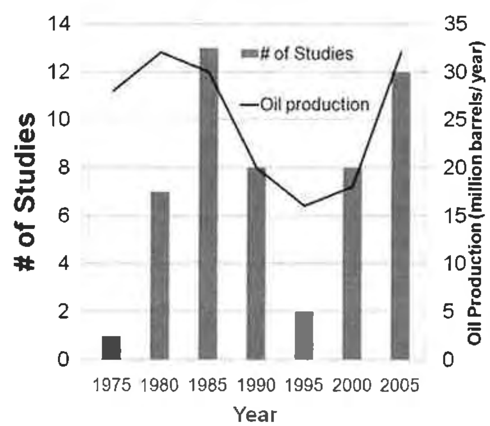


FIGURE 5.1. Frequency of study date for studies ($N = 60$) of the effects of energy development on ungulates plotted against peak oil production in Montana (Montana Board of Oil and Gas Conservation 2006).

investigate effects of energy development activities, nearly 70 percent (*N* = 56) were reactionary and designed largely as consultancies to monitor and mitigate environmental concerns about the development as a condition of the drilling or exploration permit (e.g., Horesji 1979; Irwin and Gillian 1984; Johnson and Wollrab 1987; Morgantini 1985; van Dyke and Klein 1996).

Next, I briefly review effects of development on the main ungulate species, drawing parallels between species-specific effects. I start with woodland caribou; although they are unfamiliar to readers in the lower forty-eight states, I begin with these endangered species because more long-term and large-scale research concerning effects of energy development has involved caribou than other ungulates. Research on caribou can be explained in part by the accelerated rate of development of the boreal forest in Alberta, Canada, and because woodland caribou are sensitive to anthropogenic changes to community dynamics.

Woodland Caribou (Rangifer tarandus tarandus)

I focus on effects of development on boreal woodland caribou rather than those on barren-ground caribou (*R. t. grantii*), which have been summarized elsewhere (Cronin et al. 1998, 2000; National Research Council 2003; Johnson et al. 2005). Research on woodland caribou has progressed largely in three phases: studies on (1) initial effects of exploration; (2) altered ecosystem dynamics that influence caribou population processes (e.g., survival, growth); and (3) regional, cumulative effect assessments that address population viability at regional scales. In subsequent sections on elk and other species, I draw parallels between caribou research and ungulate–energy impacts in the lower forty-eight states, where I argue research is being conducted largely at the first or second step.

A consilience of findings across studies of the boreal forest confirms that the decline in caribou populations is attributable to large-scale changes to predator–prey dynamics as a result of forestry and energy development (Committee on the Status of Endangered Wildlife in Canada 2002; Alberta Woodland Caribou Recovery Team 2005). Historically, caribou coexisted at large spatial scales with moose and wolves. Caribou adopted a spatial separation strategy whereby they selected large contiguous tracts of habitat such as peat bogs and old-growth conifer that were unsuitable for wolves and moose, the wolves' primary prey (James et al. 2004). Increased forestry produced early seral stands, which provided an abundance of forage, which in turn increased moose populations. Higher wolf populations soon followed (Fuller et al. 2003), which upon exceeding a density of about seven wolves per 1,000 square kilometers exerted enough secondary predation on caribou to reduce their survival rate and drive population declines (Stuart-Smith et al. 1997; James and Stuart-Smith 2000; McLoughlin et al. 2003; Alberta Woodland Caribou Recovery Team 2005).

Energy development exacerbates impacts from forestry by adding to the landscape high densities of seismic exploration lines. Studies that examined the impacts of well site development or seismic exploration confirmed the negative impacts of exploration on caribou. This formed the basis for early regulations designed to minimize the timing of development overlap with key calving seasons and late winter seasons. In effect, this policy is a formulation of the hypothesis that the main impacts of development are behavioral only and that through avoidance of key behavioral periods, development impacts can be reduced. This policy was tested in a series of experimental and modeling studies. Bradshaw et al. (1997, 1998) showed that the negative impacts of disturbance caused by seismic exploration explosions increased caribou movement rates and habitat shifts and reduced feeding times. Behavioral changes resulted in potential loss of body mass and reduced reproduction, linking avoidance to population declines. Also, wolves travel at higher speeds on seismic lines (James et al. 2004), which increases kill rates on large ungulate prey species (Webb et al. 2008; McKenzie et al. 2009) and increases overlap of wolves and caribou (Neufeld 2006). As a result, caribou show strong avoidance of human development near roads and seismic lines, as well as well sites (Dyer et al. 2001, 2002). Dyer et al. (2001) documented maximum caribou avoidance of areas 250 meters from roads and seismic lines and 1,000 meters from wells, which, when extrapolated to the entire study area, affected 22–48 percent of available caribou habitats with potential road avoidance effects. Dyer et al.'s (2001) results presented the first clues that human development impacts were operating cumulatively and at large spatial scales. Yet the magnitude of observed impacts in these simulation studies was less than the rate of declines of some caribou herds, suggesting the next round of studies that investigated dynamics at the level of the individual caribou herd.

During the next phase, scientists began studying population dynamics of affected caribou herds across Alberta, confirming that the majority were declining (McLoughlin et al. 2005; Alberta Woodland Caribou Recovery Team 2005) for the reasons described earlier. Empirical (McLoughlin et al. 2005) and modeling research at this stage confirmed the grim predictions of the cumulative effects of landscape change on caribou (Weclaw and Hudson 2004; Lessard et al. 2005; Sorensen et al. 2008). We now know that dramatic changes in energy development policy and aggressive measures such as landscape restoration, core protected areas, and development restrictions may be necessary to recover this federally threatened species (Alberta Woodland Caribou Recovery Team 2005). Unfortunately, small-scale mitigation efforts to restore seismic lines using experimental line blocking experiments failed to achieve any measurable reduction in travel by wolves. Neufeld (2006) concluded that seismic line restoration at the scale necessary to reduce predation risk on caribou was unfeasible and that large-scale mitigation is a key to conservation.

Cumulative effect assessment at large scales confirmed the grim picture facing caribou conservation in the face of energy development in Alberta. Schneider et al. (2003) developed cumulative effect assessment scenarios for caribou herds in Alberta and showed that even under optimistic scenarios in development rates, available caribou habitat would decline from 42 percent of the study area (59,000 square kilometers) at present to about 6 percent within 100 years. Empirical cumulative effect models also confirm the dire straits caribou face. Sorensen et al. (2008) compared the caribou population growth rate with the total amount of industrial development within caribou ranges and the total amount of caribou ranges burned by fire. This simple management model successfully predicted the expected caribou population growth rate as a function of percentage industrial development and percentage area burned (Sorensen et al. 2008; fig. 5.2).

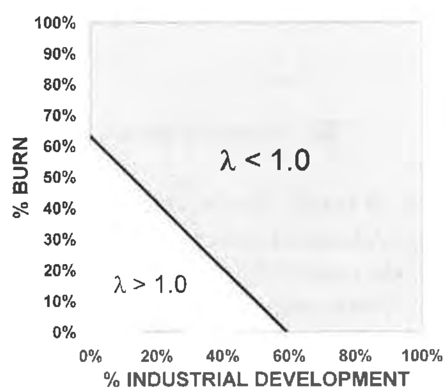


FIGURE 5.2. Meta-analysis model for woodland caribou population growth rate as a function of the percentage of the boreal caribou range that was burned and the percentage of the caribou range converted to nonhabitat through industrial development. The regression model was developed using six woodland caribou population ranges across a 20,000-square-kilometer area in northern Alberta, and is described by $\lambda = 1.191 - (0.314 * \text{IND}) - (0.291 * \text{BURN})$ ($R^2 = .96$, $N = 6$, $P = .008$) (modified from Sorensen et al. 2008).

Therefore, from a simple management perspective, the key variables after decades of research boiled down to the amount of habitat lost, which disproves the implicit policy hypothesis that energy development can be mitigated with timing or seasonal restrictions and also refutes the hypothesis that incremental continued energy development is consistent with caribou persistence.

Today, caribou are listed as a threatened species both federally and provincially, with more than 60 percent of identified herds in Canada declining because of some form of industrial human development (Alberta Woodland Caribou Recovery Team 2005). Drastic recovery actions are being proposed, and the federal government is developing critical habitat designations that will undoubtedly result in recommendations for restricting the amount of industrial development allowed within declining caribou ranges. In summary, we have learned the following conservation lessons from the caribou–energy development story in Alberta: Short-term disturbances from energy exploration phases were not necessarily the most significant population-level impacts; by the time population-level impacts were detected, it was almost too late to recover many populations, or the level of restoration activities needed was unfeasible; it was the amount of habitat destroyed by humans, not habitat fragmentation effects per se, that caused declines; the sample size was effectively the population of caribou for statistical, biological, and planning reasons; and cumulative impacts were not always evident from individual studies, and scaling up to regional scales was needed.

Elk (Cervus elaphus)

Studies of the effects of energy development on elk have largely investigated impacts during exploration, with few studies focusing on population-level impacts and almost none examining cumulative effects. For example, van Dyke and Klein (1996) studied the effect of active drilling on elk near Line Creek Plateau in Montana by comparing seasonal and annual home range characteristics and use of cover for ten VHF-collared elk from 1988 to 1991. They compared home range size, home range centroid, and coarse-grain habitat use by elk before, during, and after development, with each phase lasting 1 year. Elk in the study site and the control site had significantly different distributions, suggesting a normal seasonal change rather than effects of drilling. Elk were rarely found outside the forest during the day while activity was taking place at the well sites. Elk responded to disturbances by shifting their use of the range, centers of activity, and use of habitat, and the authors concluded that elk do not abandon their home ranges during well site development, and they quickly return to predevelopment conditions after development. Unfortunately, limitations of this study are many, including small sample sizes; only 474 locations, ten elk, and two seasons (winter and summer) over approximately 4 years of the study yields approximately six locations, per elk per season-year, which is woefully low for reliable home range and centroid estimation (Powell 2000). A second problem was scale: This study evaluated the effect of a single oil well in an approximately 500-square-kilometer area, a density of 0.003 wells per square kilometer, a trivially low density for such a large area. The utility of this study to current development, where dozens of wells are being drilled simultaneously in an existing matrix of developed oil fields, is questionable.

Other studies used radio telemetry to examine the effects of seismic exploration on elk (Johnson and Lockman 1979; Hiatt and Baker 1981; Irwin and Gillian 1984; Gillin 1989; Hayden-Wing Associates 1990; Olson 1981; van Dyke and Klein 1996). By and large, these were observational studies with poor experimental design, with few or no predevelopment data, of short duration, or with ridiculously small sample sizes (e.g., $N = 6$; Olson 1981). As an exceptional example of weak experimental design, Hiatt and Baker (1981) evaluated effects of drilling a single well on elk in Wyoming by comparing track counts in a 9-day period before development with track counts after development. Despite weak inference, results of these studies generally support the conclusion that elk move away from active exploration areas, altering their habitat selection, movement rates, and use of areas in their seasonal home ranges but do not shift or change home ranges and merely redistribute within their home ranges.

In a unique study, effects of pipeline construction on movements of elk, moose, and deer were evaluated in west-central Alberta (Morgantini 1985). Using snow track surveys, crossing attempts through the pipeline during construction were documented for seventy-six ungulate groups. The pipeline was a barrier for 53.9 percent of ungulate groups that tried to cross them. Several practical recommendations are provided to maintain periodic openings in pipelines under construction and even underpasses or overpasses along pipeline to mitigate crossing barriers.

There were few examples of well-designed comparative or experimental studies on elk habitat selection and indirect loss of habitat from energy development. In a recent study, Sawyer et al. (2007) examined the response of elk in open habitats to distances to roads in a system with low densities of oil and gas development at present but with moderate to high development potential. Sawyer et al. developed seasonal resource selection functions (Boyce and McDonald 1999) using telemetry locations from thirty-three Global Positioning System (GPS)-collared female elk and validated them against fifty-five VHF-collared elk. Elk selected for summer habitats with higher elevations in areas of high vegetative diversity, close to shrub cover, with northerly aspects and moderate slopes, away from roads. Winter habitat selection patterns were similar, except elk shifted to areas closer to roads than in summer, indicating a strong response of road avoidance during summer. Results suggest that elk can meet their year-round needs with low traffic. Similarly, elk avoided roads and active gas and oil well sites the most during summer in the Jack Marrow Hills, Wyoming (Powell 2003), strongly selecting for habitats more than 2,000 meters from these features. Avoidance of roads and well sites declined in fall, winter, and spring, when elk avoided only areas less than 500 meters from human development. During calving (May 15–June 30), elk avoided areas less than 1,000 meters from roads and wells. These studies make the important observation that elk continued to avoid energy development long after exploration was completed, and findings open the door to examine potential population-level impacts if areas continue to be developed. Unfortunately, no studies of elk examined population-level impacts.

Pronghorn (Antilocapra americana)

Studies of energy development and pronghorn have focused less on the effects of exploration and more on disruption of migration routes, changes in habitat selection, and population-level impacts. Foci represent marked improvements over most studies on elk. Given that most pronghorn studies are quite recent, they seem to capture the same phenomenon as caribou studies in that by the time impacts are detected, populations may have already started to decline.

The series of studies by Berger and colleagues (Berger 2004; Berger et al. 2006a, 2006b, 2007) examined the response of pronghorn to energy development in the Upper Green River as a 5-year project (still ongoing), overlapping the study area of Sawyer et al. (2002). This area is underlain by the Jonah and Pinedale Anticline natural gas formations, which are estimated to contain more than 283 billion cubic meters of natural gas and coal bed methane deposits and is undergoing rapid expansion. Energy development started here in 2001, so studies by Berger, Sawyer, and colleagues assess only early impacts of development. Goals were to investigate the effects of natural gas development on pronghorn behavior, migration, habitat selection, and, ultimately, population consequences. Study design was strong, with GPS collaring of about fifty pronghorn per year and 100 VHF collars per year in a control and energy development area.

Berger et al. (2006a, 2006b) reported that the overriding natural factor influencing distribution of pronghorn on the winter range was snow depth. Despite avoidance by some individuals, at the population level, authors did not find that pronghorn avoided infrastructure at current levels of development. From a population perspective, they also found no difference in pronghorn survival in undeveloped and developed areas. Findings suggest that development does not influence pronghorn, but the authors caution that results are preliminary, winters have been mild during the study (impacts may be greater during harsh winters with deeper snow), the area of most intense development is not prime pronghorn habitat, and responses may be expected to increase over longer periods of time for long-lived ungulates than the 2-year time window reported on to date. Regardless of the equivocal results of energy development on pronghorn winter ranges, the studies by Berger et al. (2006a, 2006b, 2007) showed dramatic effects of development on migration at the regional scale, which we return to later in discussion.

In a particularly illustrative example, Easterly et al. (1991) conducted a study to examine the effects of energy development on both pronghorn and mule deer in the Rattlesnake Hills of Wyoming. Their study was in response to repeated violation by the Bureau of Land Management of the 1985 environmental impact statement on the Platte River Resource Area of their own policies regarding timing restrictions of development on crucial winter range. Despite a federal policy of no surface development between November 15 and April 30, the Bureau of Land Management issued eighteen permits for drilling operations in crucial winter range between 1987 and 1991. Easterly et al. tested whether violation of this policy was negatively affecting ungulates, but they collected no predevelopment data and had no controls or comparison sites. They used a combination of radio telemetry and aerial and ground surveys to measure home range responses, densities, movements, and survival as a function of human development. Pronghorn densities were substantially lower closer to energy development, and radio-marked pronghorn avoided well sites during disturbance. The prime limitation of this well-designed study was the lack of predevelopment data on mule deer and pronghorn distribution in the region.

Mule Deer (Odocoileus hemionus)

More studies have focused on reasons for population declines of mule deer, in part because of broad scale declines in mule deer productivity across western North America (Unsworth et al. 1999; Gill 2001). Factors resulting in declines of mule deer populations in Colorado included competition with increasing elk populations, density dependence in vital rates caused by historic high population densities, long-term declines in habitat quality for mule deer because of changes in fire history regimes, overharvest, increasing predator populations, and disease including chronic wasting disease (Gill 2001). Energy development can now be added to the list throughout much of mule deer range. Long-term (6- to 8-year) and large-scale studies (e.g., wildlife management units; about 1,000 square kilometers) are needed to rigorously assess causes for mule deer declines (Gill 2001). Their recommendations are relevant for considering the effects of energy development on large ungulates.

Early studies on mule deer paralleled those of elk in their evaluation of early phases of development. For example, Ihsle (1982) and Irby et al. (1988) worked in the same study area, conducting an observational (without a control) study over a 10-year period during oil field development on the east slope of the Rocky Mountains in Montana. Early on, development was minimal, with less than 0.003 wells per square kilometer. Phase I findings showed almost no impacts of development on mule deer home range, movement, habitat selection, migration, and fawn-to-doe ratios (Ihlse 1982). They found no effects of development because oil wells were restricted to a small part of the study, development density was very low, and the spatial scale of the study area was large. Similarly, Easterly et al. (1991) found equivocal effects of development on mule deer. Densities of mule deer were similar close to and far from drilling activities, but mule deer were located farther from development during drilling, but not after, when they were the same distance as before development. This indicates some habituation response of mule deer to development.

More recently, Sawyer et al. (2005a, 2005b, 2006, 2007) conducted a series of related studies on effects of energy development on mule deer in the Pinedale–Jonah Anticline in southwest Wyoming. Initial studies focused on migration of radio-collared mule deer (N = 158) and pronghorn (N = 32) and noted the potential for energy development impacts on migration corridors. From a habitat perspective, Sawyer et al. (2006) reported expanding development over a 5-year period with an increase of 95 kilometers of roads, 324 hectares of well pads, and a total of about 400 hectares of lands directly lost to development footprints in the study area, an increase in density of 0.12 kilometers per square kilometer and about 0.3 wells per square kilometer. Mule deer avoided areas close to development, responses to development occurred rapidly (within 1 year of development), and avoidance of development increased over the course of the 3-year study. Sawyer et al. (2006) reported lower predicted probabilities of use within 2.7 to 3.7 kilometers of well sites, confirming that indirect habitat losses far exceeded direct losses. Over the study, areas classified as high-quality habitat before development changed to low quality, and vice versa, showing that mule deer shifted their habitat use away from high-quality habitats to marginal habitats in response to development. Presumably, such responses will have population implications, but Sawyer et al. (2006) did not examine them. The authors recommend demographic studies and activities that reduce the footprint associated with development, including directional drilling from single well pads to multiple gas sources to reduce surface impact, limited public access, road networks developed with the goal of minimizing new road construction, and guidelines to minimize human disturbance during winter and on designated high-quality ranges.

In a related study, Sawyer et al. (2005b, 2006) focused on predevelopment phase mule deer ecology from 1988 to 1991 before development started from 2001 to present in the Sublette mule deer herd near Pinedale, Wyoming. With the preliminary data collected in Phase I and two treatment areas in Phase II (with and without development), this study represents a well-designed before–after control–impact study. Before development, the Sublette mule deer population was a healthy and productive population, with adult female survival rates (0.85, $N = 14$) and a fawn-to-doe ratio (more than 75:100) indicative of a growing population (Unsworth et al. 1999). In 2002, mule deer densities were similar between the control and energy development treatments, but they have been diverging since 2002. In the developed area, mule deer densities declined by about 47 percent over a 4-year period ending in 2005, whereas in the control area, there was no negative trend and mule deer densities were constant and similar to predevelopment density on the treatment area. This suggests a demographic impact of energy development, yet survival differences in adult female and overwinter fawn survival were not statistically different between the two areas. Sawyer et al. (2005b) speculate that they found no demographic difference between treatments because small-scale demographic differences could explain the differences in population trend, but they are preliminary and influenced more by small sample size and will be verified later by more detailed analysis; or differences were driven by emigration or dispersal from the developed areas. Migration routes were also identified, as discussed later, in Phase I. Results echo conclusions from caribou and pronghorn studies that the effects of energy development often take a long time to manifest on ungulate populations, if present, and detecting these effects is the biggest challenge.

Discussion

Readers who had hoped that a clear picture would emerge about how to mitigate effects of energy development on ungulates are probably disappointed, and this is perhaps the most important message from this chapter. Previous reviews provide strategies for mitigating small-scale effects of disturbance on ungulate behavior, yet most conclude by admonishing managers to conduct more long-term, population-based studies. Unfortunately, my conclusions from reviewing the literature are that, at least for ungulates, few have heeded this advice. During the current energy development rush, sadly, there are still few clear evidence-based management recommendations that will definitively mitigate impacts of energy development on ungulate populations (emphasis on populations).

A second major conclusion is that energy development studies proceed in the following manner (sensu Lustig 2002): (1) A well drilling permit is applied for on an ungulate winter range; (2) the permit is granted with stipulations that attempt to reduce impacts by applying timing restrictions at critical life stages (e.g., calving); (3) either because stipulations are knowingly violated or as an additional stipulation, a study is commissioned to investigate effects of development on ungulates; and (4) the "monitoring" study is often designed hastily, with inadequate resources, sample size, temporal or spatial scope, and experimental design such as predevelopment data, and no commitment to monitoring beyond the intended life of the development phase. Thus, I conclude that wildlife biologists, as a profession, are failing to live up to professional standards and guidelines of the Wildlife Society by agreeing to participate in poorly designed studies that are aimed merely at appeasing the small-scale regulatory process. The large number of animals captured and handled (more than 2,000), their capture-related mortality, the financial investments made by energy companies, and investments in personnel time do not weigh favorably against the meager knowledge base available on the effects of development on ungulate populations. Figure 5.1 reinforces the impression that most studies of wildlife–energy relationships have been reactive, driven by trends in energy production, and are not part of any proactive adaptive management program (chap. 12). I hope this review convinces some of the need for better-designed studies of energy–wildlife impacts.

I draw these conclusions for the following main reasons. First, to date, there has not been one rigorously conducted study (e.g., a replicated experiment) of the effects of energy development on ungulates with a sufficient duration of both study and energy impact to be able to draw firm conclusions about the population impacts of development on ungulates. The average duration of studies was very short (2.5 years) when compared with the lifespan of ungulates that may live for more than 20 years. Few studies actually measured adult female survival, and not one study reported effects of energy development on population growth rate for pronghorn, mule deer, or elk (caribou are the exception). Studies that did measure adult female survival failed to show any impact of energy development by and large and were conducted only for a short time period, consistent with effects of low statistical power due to small sample sizes (Gerrodette 1987) and for species with high and constant adult survival rates (Gaillard et al. 2000). For long-lived species such as ungulates, impacts of changes in the environment may take decades to manifest because of compensatory reproduction and resilience in the adult age cohort and because ungulates possess high and constant adult survival (Albon et al. 2000; Festa-Bianchet et al. 2003; Gordon et al. 2004; Coulson et al. 2005). Following from Gaillard et al. (2000) and Eberhardt (2002), energy impacts would be expected to manifested first on the least sensitive but most variable population vital rates such as calf survival and recruitment, not the most important but least variable adult survival rates such as adult female survival. In fact, ungulate life history in general makes it extremely difficult to determine the effects of development on populations in a 2- to 3-year study. Recent recommendations of reviews of ungulate demography studies suggest that a minimum of fifty marked adult female ungulates monitored over at least a 5-year period (Gordon et al. 2004) are needed to gain a mechanistic understanding of changes in adult survival rates linked to environmental changes such as energy development. Although population-level surveys are capable of identifying important changes (Sawyer et al. 2005a, 2005b), without detailed demographic data, mechanisms driving changes will be cause for speculation. Thus, long-term changes in the way in which agencies and industry engage in research on energy impacts on wildlife need to occur to achieve an evidence-based framework for mitigating development.

The second major reason why I conclude that impacts are poorly understood is that most studies focus only on early phases of development.

Effects of development may take years to manifest on long-lived ungulates, yet most studies were conducted either before or during the first 1–5 years of development. Short-term studies do not give populations enough years to equilibrate to development and loss of habitat. Time lags should be expected as normal and are likely to be at least one generation time for long-lived ungulate species (Gaillard et al. 2000). A major additional problem with studying impacts of development only early during development is that density of development is confounded with duration of development, again confusing clear cause–effect relationships because of the period of equilibration needed for long-lived ungulates. In an extreme example, van Dyke and Klein (1996) investigated impacts of the first oil well constructed in a nearly undeveloped area on elk behavior in hopes of estimating population-level impacts. At such low development densities, population-level responses for a large ungulate are not expected to occur because ungulates can habituate to responses at low development thresholds.

This review does provide some conclusions about behavior-level impacts of energy development on ungulate species that will be useful to planners at the level of the individual well pad or road. Many of these behavior-level impacts were already summarized in previous reviews (Bromley 1985; Girard and Stotts 1986; Hayden-Wing Associates 1991; National Research Council 2003). However, the real question is whether such small-scale mitigations, referred to as "death by a thousand cuts" (Lustig 2002), are useful to scale up to population-level responses.

At the small scale, most ungulates displayed behavioral responses that weakly to strongly avoided energy development activities during the development phase (exploratory seismic blasting, road construction, mining construction, forest operations, and well drilling). Pronghorn, elk, and mule deer, in that order, generally showed the strongest avoidance of development during the construction phase. Seasonal impacts were variable and occurred year-round in winter ranges, calving ranges, migratory corridors, and summer ranges. Early studies focused on the effects of development on winter ranges, and restrictions on crucial winter ranges are still enforced as small-scale mitigation measures to reduce impacts. However, recent studies show increasing effects of development on spring calving ranges, during summer, and especially in migration corridors. This may reflect a growing understanding of the importance of summer nutrition to ungulate demography (Cook et al. 2004; Parker et al. 2005). Regardless, recommendations for timing restrictions on spring calving ranges and critical winter ranges were echoed by a majority of studies for all species, especially elk, mule deer, and pronghorn. Unfortunately, there is little evidence that such small-scale mitigation is sufficient to mitigate effects of development at large scales. In the case of caribou, for example, we now realize that small-scale mitigation did not prevent declines resulting from large-scale cumulative impacts.

Despite this purposefully scathing critique, I draw some conclusions about impacts of development on large mammals, including the negative effects of roads, density of development, and the role of migratory movements in assessing scale of impacts.

Effects of Roads

Roads are one of the most pervasive impacts of human development on natural landscapes (Forman and Alexander 1998), and by far their greatest impact lies in the indirect effects of habitat fragmentation and avoidance by wildlife. Current estimates indicate that the lower continental United States has about 10–20 percent of habitats affected by roads. Impacts are typically most severe near the road and extend out a variable distance depending on the species of interest (Forman and Alexander 1998). Here I summarize the distances to which impacts extend from developments (e.g., roads, well sites). Readers should note that this zone of influence around roads does not imply 100 percent avoidance (Schneider et al. 2003; Harron 2007), yet from the information presented in studies, actual effective reductions in habitat use were not presented. For example, Dyer et al. (2001) reported on average a 40 percent reduction within 100 meters of a seismic line and declines up to 250 meters away. Powell (2003) reported 73 percent reductions in use within 2,000 meters of energy development, but other studies did not usually present enough information. In the eight studies that did report avoidance of roads, the average zone of influence extended about 1,000 meters from both roads and wells, although responses varied within seasons and between species (table 5.2).

In general, ungulates avoided roads more in summer than winter, when snow depth constrained animal movements away from roads. Regardless, even considering an effective loss of habitat of 50 percent within this zone of avoidance and a modest buffer size of 500 meters, 10 percent of a study area can be effectively lost due to indirect avoidance of roads. The effect of overlap between well sites and roads on habitat loss due to avoidance is important and deserves further investigation (Rowland et al. 2000; Frair 2005).

TABLE 5.2. Summary of ungulate studies showing avoidance of roads and well sites, with results averaged across seasons and habitat types.

		Avoidance Buffer (m)	
Author	*Species*	*Roads*	*Wells*
Gillin (1989)	Elk	1,200	500
Edge (1982)	Elk	500	1,000
Rost and Bailey (1979)	Elk	200	
Dyer et al. (2001)	Caribou	250	1,000
Sawyer et al. (2005b)	Mule deer	2,700	
Powell (2003)	Elk	2,000	2,000
Frair (2005)	Elk	200	
Ward (1986)	Elk	2,000	
	Average	1,131	1,125

Density of Development

I extracted density of oil and gas infrastructure (e.g., roads, wells, seismic lines) where possible, but only 17 percent of studies (twelve of seventy) that investigated direct impacts presented sufficient information (table 5.3).

Existing time-stamped datasets provide the ability to estimate densities for use in meta-analyses. I present results of a univariate meta-analysis of density of infrastructure for the twelve studies that reported an effect of development on some response variable against studies with no effect. Caveats of this simple analysis are many, and variables that could not be accounted for include size of study area, length of study, and sample size and its associated variance. Regardless, studies that reported an impact of development had higher densities of wells and roads. Impacts started to manifest on ungulate species including mule deer, pronghorn, and elk from 0.1–0.4 wells per square kilometer and 0.18–1.05 linear kilometers of roads per square kilometer. However, replicated studies are necessary to disentangle effects of sample size, study duration, and severity and type of biological response (i.e., avoidance versus population impacts) to density of development.

Migration and Identifying Appropriate Scales

A difficult problem in ecology is how to scale up from short-term and small-scale behavioral decisions of animals to long-term landscape-scale

TABLE 5.3. Summary of density of energy development disturbance in terms of density of active well sites and linear kilometers of pipelines, seismic lines, and roads from studies where such information was reported. Despite small sample sizes of studies that reported densities, ambiguities in definition of study areas, and simplification of impacts to a binary variable, densities of disturbance appear to be related to the impact of energy development.

Study	*Density of Wells (per km²)*	*Linear Kilometers of Roads/ Pipelines/Seismic (per km²)*	*Significant Impact?*[a]
Knight et al. (1981)	0.088	n/a	No
Olson (1981)	n/a	0.15	No
Rowland et al. (2000)	n/a	0.62	Yes
Sawyer et al. (2002)	n/a	0.62	Yes
Bennington et al. (1982)	0.20	N/A	No
van Dyke and Klein (1996)	< 0.001	N/A	No
Sawyer et al. (2005a, 2005b)[b]	1.01	1.36	Yes
Berger et al. (2006a, 2007)[b]	0.25	0.20	No
Frair (2005), Frair et al. (2008)	0.20	1.6	Yes
Easterly et al. (1991)	0.27	N/A	Yes
Ihsle (1982)	0.003	N/A	No
Summary Statistics	*Mean (N)*	*Mean (N)*	
Significant impact: yes	0.49 (3)	1.05 (4)	
Significant impact: no	0.10 (4)	0.18 (2)	

[a]Significant impact is a simple binary variable confirming whether statistically significant effects of energy development were detected on key response variables.
[b]These two sets of studies occurred in approximately the same area but defined different study area sizes based on species life history.

population responses. In the case of energy development, the question of scale also touches on the growing consensus that energy development negatively affects ungulate migration and large-scale processes. The difficulty in scaling up is why so few of the studies that showed short-term responses were able to measure or demonstrate these long-term or population-level responses. A second scaling problem is presented by Berger et al. (2007) when discussing issues of spatial scale and habitat fragmentation, both of which are totally dependent on each other (Dale et al. 2000; Turner et al. 2001). Quantifying habitat fragmentation metrics will be determined completely by the study area size, and for this reason many authors recommend conducting multiscale analyses of the effects of habitat fragmentation on wildlife species (Harrison and Bruna 1999; Turner et al. 2001).

In many of the studies I reviewed, there was a third scaling problem: that of extrapolating responses. This occurred where the effects of a local point source disturbance (well pad) were assessed at the population or home range scale, and results were extrapolated well beyond the development densities under which the response was studied. For example, van Dyke and Klein (1996) document weak or no responses of elk to installation of a single well in an undeveloped grassland ecosystem in north-central Montana. Results of this study have been extrapolated to other wells across Montana, yet the validity of extrapolating the finding of no significant impacts to areas with higher well densities is questionable. This emphasizes the need to establish thresholds for development or broad, regional-scale cumulative impact assessments as the density of well sites and development increases.

Finally, there was often a mismatch between the spatial scale of the study in question and the spatial scale of the population under investigation that links to impacts on migration. Assuming that the goal of an impact study is to assess the impacts of a particular development on a population, unless the study area represents the annual range occupied by the ungulate population, it will be difficult to evaluate whether the changes in the population are occurring because of energy development on the winter range or because of changes occurring elsewhere in the population's range. One potential solution to the issue of how to determine the appropriate study scale is to use the spatial scale of migration as a guideline in migratory populations. Berger (2004) reviews long-distance migration throughout western North America and worldwide. Although not all populations are migratory, the reported degree of partial migration ranged from 45 to 100 percent; and most populations in studies reviewed in this article contained some migrants. Considering the one-way migration distances (35–177 kilometers across species) as a buffer suggests that the correct spatial scale to consider in evaluating the effects of energy development could range from 5,041 square kilometers for mule deer, 5,041 square kilometers for caribou, 8,464 square kilometers for elk, or nearly 19,000 square kilometers for pronghorn (Berger 2004). Guidelines suggest much larger study area sizes than are currently used to evaluate impacts. Moreover, because one of the areas where we have seen a convergence across studies is the effects of energy development on migration, studying population impacts at the migratory scale will be critical.

For example, Berger (2004) found that in the Greater Yellowstone Ecosystem about 75 percent of all large ungulate migrations have been lost due to human development. Berger (2004) illustrates the problem with a case study involving a long-term pronghorn study in the Pinedale area of Wyoming. Both residential development and future potential energy development threaten one specific migratory corridor pinch point, the Trapper's Point bottleneck, where the migration corridor narrows to less than 800 meters. In a follow-up study to this review, Berger et al. (2006b) confirm that this particular migration corridor, from the Upper Green River to Teton National Park, has probably been used for more than 6,000 years. Sawyer et al. (2009) used GPS collars on mule deer in Wyoming to monitor migration routes between winter and summer ranges in the face of impending energy development. Unlike the simpler example where Berger (2004) showed an entire pronghorn population moving through a single corridor, Sawyer et al.'s mule deer study shows that migration routes often are varied and reticulate, making protecting migratory routes challenging, and these results have been echoed for both elk and woodland caribou (Hebblewhite et al. 2006; Saher and Schmiegelow 2006). Indeed, considering the future effects of climate change, ensuring retention of migratory behaviors in the landscape may be an effective mitigation strategy. For example, a recent molecular ecology study of woodland caribou revealed important links between energy development and potential responses to future climate change. Woodland caribou in the Canadian Rocky Mountains were a mix of boreal and barren-ground caribou, and caribou with barren-ground haplotypes had a higher probability of migrating but also a higher risk of mortality because of changes to the landscape induced by energy development. Thus, energy development may be reducing migration, and in the future migratory behavior will undoubtedly help species respond to climate changes, as caribou did during the Pleistocene interglacial. Regardless, only if we create large-scale migration corridors that are protected from development or managed specifically to mitigate energy development will long-term migration persist, a critical ecological process that is declining across the Rocky Mountain West. Fortunately, the Western Governors' Association and other government agencies have recently recognized the crucial role migratory corridors play as natural mitigation because migration enables ungulates to use seasonal resources over a much larger area. Support from political bodies will aid decision-making processes to ensure protection of migratory routes.

A Conceptual Approach for Understanding Cumulative Effects of Development

I conclude here that the effects of development on ungulates are manifested through changes in the ecological communities of species, including humans, in which ungulates exist. Therefore, impacts on populations can be classified as direct and indirect impacts. Distinguishing between these two types of effects and between species is critical to identifying mechanisms and providing effective mitigation strategies. Direct effects between species (e.g., humans, development, and elk) occur when there are no intermediary species between two interacting species, for example, through direct mortality associated with energy development (e.g., roadkills, poaching; Estes et al. 2004). Most direct effects are attributed to predation or to habitat loss, such as when a population responds negatively to a reduction in available forage where development has denuded vegetation. In contrast, indirect effects occur when impacts on a species are mediated by an intermediate species. As an example, consider the indirect effect of development on sage-grouse and kit foxes (*Vulpes macrotis*) mediated by human-induced changes in avian or mammalian predators. An increase in the number of perches available to raptors indirectly increased predation rates on breeding and nesting sage-grouse (Fletcher et al. 2003; Aldridge and Boyce 2007). Similarly, coyote populations increased after development because altered landscapes support higher densities of small mammals, causing increased predation by coyotes (*Canis latrans*) on kit foxes (Haight et al. 2002). In this case, predation is proximate to the ultimate cause of human-induced changes to landscape function. Apparent competition will be a common indirect effect of human disruption of ecosystem dynamics (DeCesare et al. 2009). Therefore, effects of energy development will probably go far beyond direct impacts based purely on community ecology (Estes et al. 2004). Recent reviews have reminded ecologists that direct effects are but a fraction of the possible interactions between species in even a simple food web (Estes et al. 2004; Bascompte et al. 2005). Indirect effects of energy development also may arise because of behavioral changes by ungulates in response to energy development, such as avoidance of roads and well sites. Such findings have been corroborated across systems and at larger scales in ungulates, confirming the importance of indirect behavioral effects, such as the avoidance of predation risk and human disturbance on ecosystem dynamics (Rothley 2001; Fortin et al. 2005; Hebblewhite et al. 2005b).

Despite theoretical support for indirect effects, a cursory review of the literature reveals a myopic focus of mitigation strategies to reduce direct effects such as road mortality and habitat loss (Bureau of Land Management 2003a, 2003b). A renewed focus on the indirect effects of development mediated by community-level changes across species would provide a more complete understanding of the cumulative impacts of development.

Conclusion

I provide five recommendations regarding the impacts of development on ungulate populations.

First, current management policies make two untested assumptions about the effects of energy development on wildlife. One is that policies assume that negative impacts can be mitigated through small-scale stipulations that regulate timing and duration but not the amount of development activity. Policies also assume that wildlife populations can withstand continued, incremental development. Neither assumption is supported or refuted by evidence. Adaptive experiments are needed to explicitly test these assumptions.

Second, little scientific evidence exists to suggest that energy development will have population-level impacts on pronghorn, mule deer, or elk because rigorous and properly designed experiments have not been conducted. Instead, a host of observational studies on small-scale and short-term responses provides limited guidance to managers in search of the crucial question of population impacts. Although it is theoretically justified, relying on the precautionary principle to restrict energy development will probably be unsuccessful as an energy policy.

Third, efforts to mitigate short-term and small-scale impacts of energy development have been well described in previous reviews, albeit most often as poorly designed observational studies with weak inference. Ungulates predictably avoid areas during exploration and drilling, moving to denser cover and to areas farther from human activity. Across studies, ungulates avoided development to an average of 1,000 meters. Recommendations from previous studies still hold, namely the continued application of timing and seasonal restrictions for critical habitats and resources. However, it is increasingly apparent that small-scale mitigation alone cannot offset impacts of large-scale development on ungulates.

Fourth, scaling up from small-scale and short-term studies to population-level impacts will be difficult. One difficulty is scaling up responses of ungulates at low development densities to high densities observed in most oil and gas fields today. Preliminary analyses suggest that thresholds of development will occur at densities of 0.1–0.5 wells per square kilometer and 0.2–1.0 linear kilometer of roads and other linear developments per square kilometer. However, these results are preliminary, and more formal meta-analyses are needed. Future studies should use large-scale approaches to test for thresholds of energy development and to otherwise replicate and extend for other species what has been learned about population viability of caribou.

Finally, an adaptive management experiment should be implemented to test whether the current energy policy provides for sustainable wildlife populations. The de facto energy policy contains untested assumptions that, if invalid, will severely affect wildlife, but no serious alternatives have been put forward as tested and proven alternatives. Alternative development policies are sorely needed if other ungulate species are to avoid the same bleak outlook as caribou in Alberta.

Comment Letter I9

University of Nevada, Reno

Conservation of Mule Deer in the Eastern Sierra Nevada

A thesis submitted in partial fulfillment of the

requirements for the degree of Master of Science in

Geography

by

Shasta P. Ferranto

Dr. Paul Starrs / Thesis Advisor

December, 2006

Comment Letter I9

University of Nevada, Reno

THE GRADUATE SCHOOL

We recommend that the thesis
prepared under our supervision by

SHASTA FERRANTO

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ABSTRACT

Although mule deer are common in the Sierra Nevada, individual herds have declined for 40 years due to wintering habitat loss, deer-vehicle collisions, wildfires, drought, and competition with cattle. Mule deer are a prey species for top predators, such as mountain lions, and a hunter-valued game species. These deer function also as an umbrella species – ultimately contributing to an overall goal of protecting biodiversity. Mule deer habitat needs protection, with herds managed accordingly. This study examines land management for important at-risk habitat of three eastern Sierra Nevada mule deer populations. Using GIS, I identified distinct mule deer distributions and determined areas most important to purchase or place under a conservation easement. I then examined other threats to mule deer persistence and land use conflicts associated with protecting mule deer habitat.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Introduction

Lovely deer, you are always in my heart, dancing down the dawn into the light. Lovely deer, you are always in my blood, dancing down the dusk into the night.

- RICHARD NELSON, *Heart and Blood*

There are many ways to examine the natural world. The biologist is concerned with the composition and structure of nature – how and why living entities exist and interact the way that they do. The environmental scientist is concerned with the changes humans make to the world – the toxins we release into the wild and the impacts of our modern society. The conservationist cares to protect the natural world – either for its intrinsic beauty or the role it may serve to future generations. The cultural geographer examines the human connection to the natural world and the interactions between nature and culture. This work does not fall under any single one of these approaches, but rather draws sustenance from all of them in an attempt to peer holistically and from all angles at the natural landscape and the modern day world. Above all, this work represents a geographical exploration into a unique western location and a fairly common western problem. Although themes that arise in my research may resonate across many western landscapes, the work is rooted deeply in place. I make no claim that I achieved my goal to unveil ALL aspects of this story – to do so would be near impossible; I hope, however, that my research can serve as a step in this direction and a testament that the natural world is inherently inter-disciplinary.

Planning for Conservation

When Rachel Carson published her seminal book *Silent Spring* in 1962, she could hardly have foreseen the widespread environmental movement her writing would inspire. The movement she engendered would eventually lead to a ban on dangerous chemicals such as DDT, enactment of legislation including the Endangered Species Act, and prompt an overall increase in public awareness and concern for the natural environment. Carson's work, however, was not the first to draw attention to the natural world, although it undoubtedly served as a catalyst for this awareness. Decades earlier, John Muir, Aldo Leopold, and Gifford Pinchot began the germination of an environmental ethic in American minds, albeit in strikingly distinct forms. Although each of these individuals had a unique perspective and philosophy, their collective work, with that of others, influenced the creation of disciplines such as conservation biology, ecology, and environmental science. The newest of these disciplines, conservation planning, is rooted heavily in the principles of these fields and the ethics of minds such as Muir, Carson, and Pinchot. Consequently, conservation planning is saturated with the same conflicts of opinion and disagreement in goals as many another environmentally-related field.

In practice, conservation as a formal practice commenced in the United States as early as the last of the 1700s (Fairfax 2005). The emergence of the heritage-model national parks and an entire agency dedicated to managing these parks demonstrates the past success of conservation efforts. Why then, has it recently become necessary to *plan* for conservation above and beyond pre-existing natural reserves? The answer to this question is complex and can vary dramatically depending on personal preferences. From a biological perspective, the determining factor is known as the biodiversity or extinction crisis – the widespread belief that the diversity of life on earth is being lost at an alarming rate, loss catalyzed by human actions. Current extinctions occur at a rate estimated to be 100 to 1000 times greater than those recorded through recent geological time (Lawton and May 1995). The underlying forces driving these extinctions are well-documented in the conservation literature and include loss and fragmentation of natural habitats, the introduction of non-native species, the direct exploitation of species, pollution, the disruption of natural ecological processes, industrial-scale agriculture and forestry, and climate change (Groves 2003). All of these factors are directly related to human presence and dominion over nature and are propelled by the physical and spatial needs of an ever-increasing human population, as by the cultural practices of many human groups. For example, the suburban sprawl that accounts for significant habitat loss in North America is not, by any strict definition, a physical requirement for North American people; rather it represents an efflorescence of wealth and a cultural tendency toward consumptive excess. Similarly, the introduction of many invasive species throughout the world was more rooted in cultural preferences or ignorance than in necessity. Until both the physical and cultural factors affecting the loss of biodiversity are sufficiently addressed, it will be necessary to designate land for conservation.

Habitat loss is the single most important factor affecting species extinctions and endangerment (Wilcove and others 1998, Czech and others 2000, Groves 2003). Important habitat, however, is rarely located uniformly across a landscape. More commonly, we see a distribution of areas that vary in importance for species viability. Protecting habitat in the face of the impending threats of urbanization and agriculture requires conservation practitioners to prioritize conservation sites, ensuring in the process that areas of greater biological importance are protected first. This is where planning for conservation becomes critically important – through various techniques, practitioners can identify geographical areas that if protected will have the most significant impact on preserving conservation targets. In the face of limited funds and resources, conservation planning ensures that biodiversity (or any other conservation or preservation goal) is protected in the most effective and efficient manner.

Beyond the scope of maintaining biodiversity, conservation planning can be based on many other important goals. These include the preservation of open space, the protection of ecosystem services or processes such as providing for clean air and water, the protection of historical working landscapes such as farms or ranches, or the protection of individual species of economic significance such as waterfowl. Successful conservation planning will often encompass several of these goals in a single comprehensive plan.

Although the intrinsic value of conservation planning is now widely accepted, the specific techniques and principles used to create conservation plans are widely debated. This dialogue of disagreement began in the 1970s with the well-known SLOSS debate (Abele and Connor 1979, Gilpin and Diamond 1980, Simberloff and Abele 1982, Soule and Simberloff 1986) in which several biologists argued over the superiority of a Single Large Or Several Small reserves (spelling out SLOSS). Despite its popularity, the SLOSS debate was never resolved, and most conservationists eventually dismissed the debate itself as impractical and overly theoretical. With the passing of this imbroglio, several new debates over means to an end quickly took its place. For example, the value in protecting movement corridors generates an on-going and heated debate that will be discussed in detail later in this chapter.

Perhaps one of the most important and pressing controversies surrounds the specific targets used to create conservation plans. In the past, plans were based solely on the geographic distributions of species. The recent advent of spatial technologies such as remote sensing using satellite imagery and Geographic Information Systems (GIS), however, has made environmental data such as vegetation or habitat types readily available at minimal cost (O'Neil and others 2005). Many conservationists advocate the use of these data as surrogates in lieu of a detailed on-the-ground survey of a site's species-by-species biodiversity (Margules and Pressey 2000).

Spelling out their reservations, Brooks and colleagues (2004) make several strong arguments against using environmental data for conservation planning. Environmental data, they note, are defined by human classification systems and therefore must be interpreted in the context of the classification system chosen to create them. If land types are protected, rather than species, then we are tacitly agreeing that land types represent "natural spatial subdivisions of biological organization" (Brooks and others 2004), though this is often not the case. What species recognize as major habitat changes may differ from the way humans define such changes. Habitat change can also vary in its effects among different species. Another problem in protecting land types occurs when there is variability within a land type. If we only protect a target percentage of that land type, then a significant amount of the variability may be lost. Blanket goals, such as the protection of 10% of every biome, may detract from the overall goal of protecting biodiversity because they create a false sense of accomplishment when in fact a considerable amount of diversity is overlooked.

A practical response to this debate is that both species and environmental data should be used, in combination, to create accurate and comprehensive conservation plans. Available species data can serve as a foundation for conservation planning, with empty gaps filled through the use of surrogates such as environmental data. In many parts of the world, comprehensive species data will never be sufficiently available. In these situations, the use of surrogates is preferred to conservation plans that are formed without any grounding in scientific data.

In the last decade, many conservation practitioners have begun to use systematic techniques for conservation site selection and design. These types of methods in sum are referred to as systematic conservation planning and typically involve the use of mathematical algorithms and decision support software to select the optimal network of reserves (Margules and Pressey 2000). The implementation of systematic techniques has been controversial and saturated with conflicting opinions. An important argument in support of systematic site selection methods holds that they provide a set of rules that efficiently helps to achieve goals and yields a product that is both repeatable and transparent in design, which adds accountability and validity to any conservation project (Williams 1998, cited in Groves 2003, p. 229). Systematic methods are based on quantitative data, making the pathway to selecting a reserve easy to document and to understand for individuals who lie outside of the core planning committee. In addition, systematic planning follows a clearly established methodology. This type of approach may appeal to planners wanting to ensure consistency in their projects.

Despite several clear advantages of systematic planning, the implementation of systematic techniques remains unrealistic. Prendergast and others (1999) identify several problems that limit the applicability of these tools in real management situations. Systematic techniques can only be applied when species distributions and the contents of potential reserves are known. These data can be expensive for managers to obtain, however, and acquisition draws on funds that could otherwise be applied to purchasing land. For many organizations, the costs of hardware, expert operators, and experimentation are too high. Algorithms cannot handle the complexity of land ownership, status, and control that exists in many countries and are often insensitive to variation in landscape and habitat scale. For these reasons, site selection algorithms are widely criticized within the conservation literature and have minimal success in applied situations. Technical flaws are only one of the issues associated with systematic reserve design – even were the techniques perfect, there is still the problem of getting land managers to implement systematic techniques. Planners and land managers do not implement systematic approaches for many reasons including (1) lack of knowledge or understanding, (2) real and perceived shortcoming in new approaches, and (3) lack of resources. Prendergast and others argue that until communication is forged between conservation theorists and land managers, reserve design techniques will remain untested theories.

In reality, effective conservation planning is likely to be a compromise between many of the controversial pillars of thought within the discipline. Systematic planning techniques may reach some goals, but they cannot be expected to provide all of the answers. Planners would be better to interpret systematic results within the context of a particular landscape; in some situations systematic methods may be better left out completely. The ideal methodology employed in the creation of a conservation plan will then depend on the unique variables and limitations that are present in every landscape.

Creating a Conservation Plan

Each conservation plan must be based on the complexities of the particular landscape; no set-in-stone guidelines can be guaranteed to fit every situation. Beginning the planning process, however, with a loose framework in mind can help to keep the plan organized and in line with major goals. In his book *Drafting a Conservation Blueprint*, Craig Groves (2003) outlines seven steps to effective conservation planning based on a blend of scientific theory and his own tested experience in conservation planning.

Step One: Identify Conservation Targets

Step Two: Collect Information and Identify Information Gaps

Step Three: Assess Existing Conservation Areas for their Biodiversity Values

Step Four: Set Conservation Goals

Step Five: Evaluate the Viability and Integrity of Conservation Targets

Step Six: Select and Design a Network of Conservation Areas

Step Seven: Assess Threats and Set Priorities within the Planning Unit

Although these steps are presented in a linear fashion, Groves indicates that several steps will occur simultaneously, creating a dynamic process. In conservation situations, these steps may apply only loosely; some steps may not apply at all. Each conservation practitioner must decide how and if this framework fits within a task-at-hand. My research loosely follows these guidelines; steps that are inapplicable or impractical, however, are omitted.

Mule Deer as a Conservation Target

The first step in planning for conservation is to choose an appropriate conservation target (Groves 2003). The target will depend heavily on the ultimate goals of the project, the resources available (such as funding, data, or technological resources), and the chosen methodology. Ideally, a conservation target should incorporate at least one to several conservation goals (for example: protection of biodiversity, open space, working landscapes, ecosystem services and processes, or species of economical significance). In addition, for a project to be successful, the conservation target should account for the cultural setting where the plan will be implemented (see chapter 5 of this thesis for a more in-depth explanation on culture and conservation). A target that fits within the cultural context will be more likely to gain local support, ultimately making the conservation goals easier and more realistic to reach.

Choosing a conservation target is critical to the success of the conservation plan. With this in mind, I chose a conservation target appropriate for this research project – mule deer (*Odocoileus hemionus*). Mule deer are undeniably tied to the western United States landscape. Over the last century, this species served as a “barometer of environmental trends” (Heffelfinger and Messmer 2003, 1). Management techniques such as predator eradication were reflected in the deer populations; the emergence of a “*let nature be*” mentality in the 1970s equally impacted deer (Baron 2004). The release of popular films such as *Bambi* (1942) shaped Americans perceptions of deer turning them into an icon symbolic of nature and wildlife (Lutts 1992). Although Bambi was a white-tailed deer, most Americans did not differentiate between species, and mule deer were also brought into the spotlight. As mule deer became popular through cinema, their widespread distribution enabled everyone to experience them firsthand. Mule deer were not a species only for the elite or well-educated, rather a common and fairly abundant species that could be seen on any family camping trip, ultimately forging a connection between the average person and nature. The social equity of this species resonates in their widespread popularity and cultural importance. In addition to their value culturally and socially, mule deer are also a species of economic significance. Hunting accrues funds for state wildlife agencies and brings money into small, rural communities through associated tourism. A survey by the U.S. Fish and Wildlife Service found that in 2001 over 4 million people hunted in the 18 western states. These hunters spent almost 50 million days in the field and over $7 billion. On average, each hunter spent $1,581 per year in local communities on gas, lodging, and hunting-related equipment (Heffelfinger and Messmer 2003, 9-10). Hunters, although not falling under the modern stereotype of "conservationist," provide widespread support for the conservation of game species and their habitat. This type of support can improve the long-term success of conservation plans.

As a game species and a charismatic large mammal, mule deer have become just as important culturally as they are biologically. Humans identify with deer; to many people deer represent wildlife – in fact, for them, deer **ARE** wildlife. The importance of this anthropomorphism cannot be overstated. For these reasons, mule deer are an ideal conservation target. In the language of conservation biology, mule deer are a flagship species – a species that appeals to the public, making them suitable for communicating conservation concerns.

Mule deer offer an effective window on conservation solely for cultural considerations. Conservation planning, however, requires that a conservation target help to achieve widespread conservation goals. The protection of a species of economic and cultural significance is a worthy goal in and of itself. The conservation of mule deer, however, can produce several other benefits. Mule deer flourish on ranchlands and agricultural lands. Protection of historical working landscapes can easily coincide with the protection of mule deer habitat if conservation is approached with both of these goals in mind. In addition, mule deer require large areas of land, contributing to a larger social goal of protecting open space.

Perhaps one of the most important and less obvious benefits of protecting mule deer habitat is the protection of overall biodiversity. As a migratory species, mule deer require a large range size and distinct seasonal ranges. These ranges typically encompass a diversity of different habitats – many of which are also used by other species. In arid regions, including the eastern Sierra Nevada, riparian areas and wetlands are extremely important for maintaining local deer herds and many other species including migratory waterfowl, songbirds, raptors, amphibians, and more (Taylor 2005). Based on their extensive spatial and habitat requirements, mule deer act as an umbrella species. Umbrella species confer some form of protective status to numerous co-occurring species (Fleishman and others 2000); oftentimes these co-existing species are lesser known and difficult to protect otherwise. It is important to note that the protection of an umbrella species, such as mule deer, may not be the ideal method to maximize biodiversity protection. Species will be encompassed in the protection of this species, but other important species may be left out. Mule deer as a flagship species, however, may make them a more successful and effective conservation target than other potential targets. The public's inclination to protect deer is a surrogate for distinct and important conservation goals.

Long Distance Migration

Although most conservation goals pertain to the protection of species, biodiversity, or specific landscapes, the conservation of ecological processes is acknowledged among conservationists as equally important. Long-distance migration is an example of an ecological process that occurs in North America at landscape scale. Although no single and clear definition of long-distance migration exists, most operational definitions classify it as "seasonal round-trip movement between discrete areas not used at other times of the year" (Berger 2004, 321). The length of the movement is species-dependent, but typically exceeds 10-12 km (Berger 2004). The necessity of vast landscapes, migration corridors, and multiple distinct ranges makes long-distance migration a process inherently prone to threat and extinction. The forces of urbanization and fragmentation can easily sever migration routes or remove important components of a migratory species' seasonal range. Nor do most migratory species fit into normal conservation plans because a portion of their range often falls outside of the planning unit. If long-distance migration is going to persist in North America, strategies that address the conservation of long-distance migration must be discussed and implemented. Berger (2004) offers several solutions to protecting long-distance migration; these include enhanced protection for highly sensitive areas, enhanced protection for bottlenecks along migration routes, and formal designation of national wildlife migration corridors.

In California long distance migration is rare among large mammals. Mule deer remain one of few migratory mammals, making them integral to the long-term persistence of this process. Using mule deer as a conservation target will help to protect the process of long-distance migration in California.

Movement Corridors

The conservation of long-distance migration is intimately connected to the protection of migration corridors. Migratory species often show high fidelity to seasonal ranges and migration routes (Loft and others 1989, Brown 1992, Kucera 1992, Nicholson and others 1997). In some situations, the movement patterns between home ranges are based on the physical limitations of the landscape; in other words, there is only one route that individuals can choose. In other situations, the physical, biological, or learned parameters that direct migration are not well understood. In fact, how migration, corridor use, and population persistence are all connected has not been well studied (Simberloff et al. 1992, Beier & Noss 1998). Considering how few studies have shed light on this subject, a surprisingly extensive dialogue has occurred within the conservation literature on movement corridors.

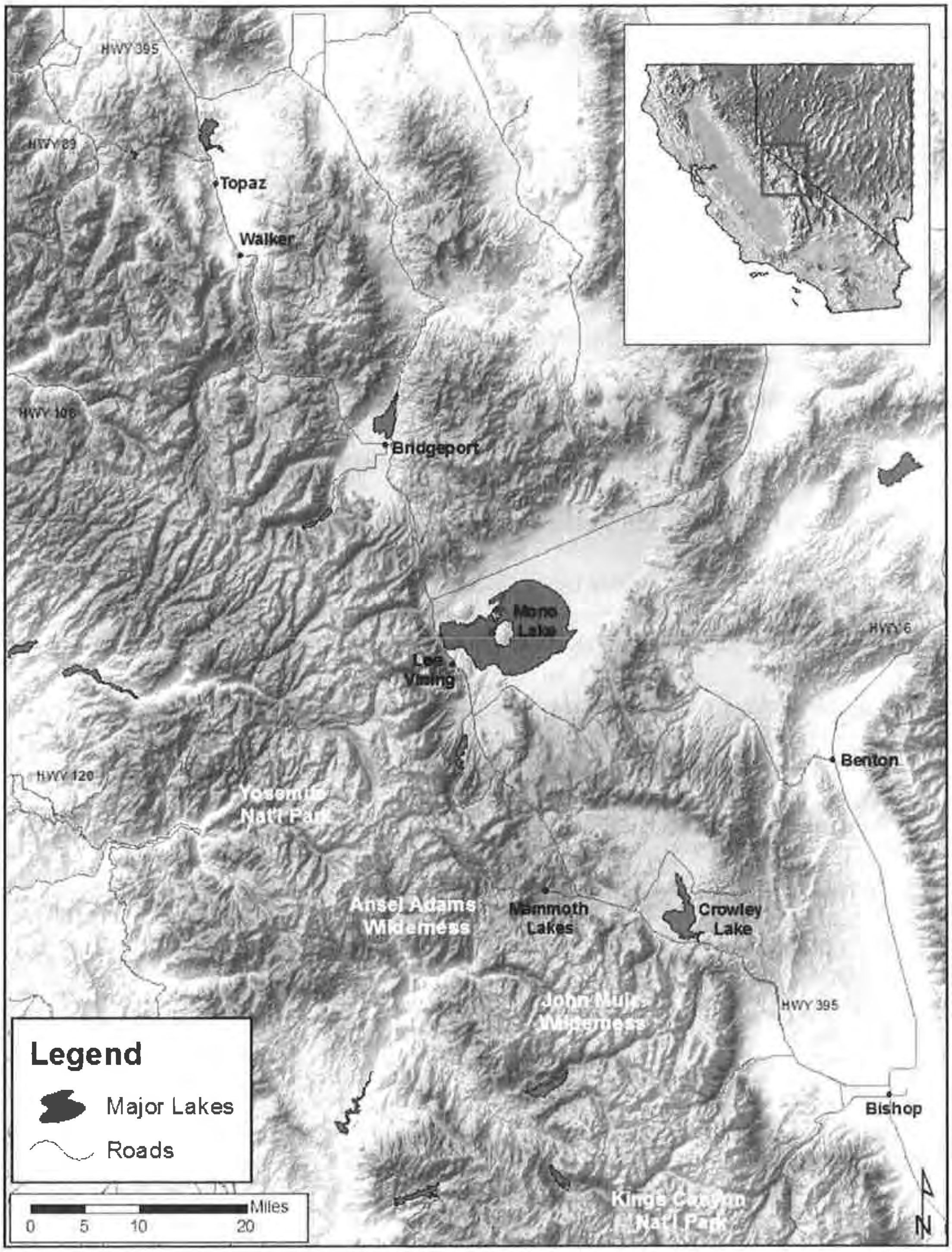
Perhaps the most confusing problem associated with movement corridors is the ambiguity in finding a steady definition of a corridor (Hess and Fischer 2001). Corridors are recognized across several disciplines, and consequently a unique definition exists within each. In landscape ecology, corridors are structural linear features. In game management, island biogeography, and meta-population literature, usage of "corridor" focuses on function, specifically the movement of flora and fauna. This function can vary from migration within a population to gene flow among populations. Because these definitions are rarely discussed, many of the arguments about corridors use different definitions. Hess and Fischer (2001) propose the abandonment of a succinct definition of 'corridors', and instead recommend explicitly identifying the functions a corridor will be expected to fulfill during the design process. This will eliminate the confusion surrounding the definition without excluding critical functions.

In addition to the ambiguity surrounding the definition of corridors, most of the studies meant to test corridor usage are of poor design and draw conclusions unsupported by the data (Simberloff and others 1992, Rosenberg and Noon 1997). Many studies document animal presence in linear habitat patches that are located between larger patches and infer that the linear patches are acting as corridors. These studies fail to demonstrate that corridors assist successful movement between patches. Researchers confuse the presence of linear habitat patches with movement passageways (Rosenberg and Noon 1997). Management or conservation decisions involving corridors are often based on these improper and non-conclusive studies. Joined with the common misuse of the definition of a corridor, the potential exists for management decisions justified by poor science.

This discussion is not meant to imply that corridors are a poor concept, but instead to argue that as a poorly understood concept it must be treated with care. This research project is unique among corridor studies in the sense that it deals solely with well-documented and well-understood *migration* corridors. These corridors are used for seasonal movement between low elevation, concentrated winter range and high elevation, dispersed summer range. The necessity of migration corridors for the persistence of mule deer herds is well-documented (Kucera 1988, Kucera and McCarthy 1988, Taylor 1988, Taylor 1991, Taylor 1997). Summer range is only available for a few months of the year, buried under snow for the remaining months. Winter range cannot support many deer year round and is impoverished by the end of each winter. The combination of these two ranges allows mule deer to take advantage of these habitats during their optimal periods but requires twice-yearly movement between them. Functional migration corridors are a necessity for the conservation of these herds.

Study Area: The Eastern Sierra Nevada

The Sierra Nevada is a northwest-southeast oriented mountain range that extends nearly 600 km from Mt. Lassen in the north to Walker Pass, east of Bakersfield, in the south (Storer and Usinger 1968 cited in Kucera 1988, p. 3). The eastern slope of the Sierra Nevada merges into the western edge of the Great Basin in a region that is commonly known as the Eastern Sierra (Smith 2000). This region lies in both eastern California and west-central Nevada and is known for its aridity and steep, dramatic slopes. As winter storms move inland off the Pacific Ocean, they deposit moisture up the western slope of the Sierra, but a rain shadow effect leaves the eastern side much more arid (Kucera 1988, Smith 2000). This, in turn, creates a flora and fauna dramatically different from the nearby western slope. In contrast to the dense pine-fir forests typically found on the west side, east side forests are sparse with little understory, vanishing into sagebrush scrub below 7000 feet (Smith 2000). The large rivers found on the west side are mirrored only by small streams that usually terminate in large alkaline sinks or shallow seasonal lakes east of the Sierra Nevada (Smith 2000). Because the eastern Sierra represents the merging of two distinct bioregions – the Sierra Nevada and the Great Basin Desert – plants and animals typical of both regions intermingle, creating an astounding diversity (Smith 2000). Desert species occur up mountain slopes, while montane species blend into the arid valley below.



HWY 395
HWY 89
Topaz
Walker
HWY 108
Bridgeport
Mono Lake
Lee Vining
HWY 6
Benton
HWY 120
Yosemite Nat'l Park
Ansel Adams Wilderness
Mammoth Lakes
Crowley Lake
John Muir Wilderness
HWY 395
Bishop
Kings Canyon Nat'l Park
Legend
Major Lakes
Roads
Miles
0 5 10 20
N

This research focuses on a portion of the south-eastern Sierra, extending from Topaz Lake in Nevada, south to Bishop, California (figure 1-1). This region overlaps almost entirely with what is commonly referred to as the High Sierra (Yosemite south to Mt. Whitney), and is characterized by extensive glaciation, deep winter snows, mild summers, and hundreds of peaks above 4000 m (Kucera 1988). The Sierra Crest sharply delineates the western slope from the eastern slope of the Sierra, and can only be crossed by a series of passes that generally increase in elevation from north to south (Kucera 1988). Eastern Sierra mule deer use these passes to migrate from winter range occurring east of the Sierra Crest to summer range on the western slopes. Although these deer spend time on both the eastern and western slopes of the Sierra Nevada, they are named and managed based on their winter range, located in the eastern Sierra.

The physical geography is not the only factor that makes this region unique. Much as the biology represents a mélange of montane and desert ecosystems, so too does the cultural landscape consist of intriguing combinations of ownership and management. The vast majority of the land in this area is in public hands, split between the US Forest Service, the Bureau of Land Management, National Parks, and state agencies. Like many places in California, land values on private land are rising dramatically. That private land within this region is limited, combined with increasing demand for second homes or retirement havens, puts significant development pressure on much of the so-far undeveloped land. Many of these private parcels are anticipated to be developed within the next 10 to 20 years (Newbry 2006). From a conservation perspective, this is a region ripe with potential and concern. Perhaps one of the most interesting land owners, however, is the Los Angeles Department of Water and Power (LADWP), a major player in the eastern

Sierra region. The LADWP owns about 314,000 acres in Mono and Inyo counties, much of it acquired in a concerted spate of effort in the 1920s and 1930s. Although this land is technically considered private, in the past it has functioned in many ways as public land. For example, public access is permitted on most LADWP land, as are grazing permits. Increasing development pressure on private land in the eastern Sierra raises questions as to how LADWP land will be treated in the future.

Figure 1-2: *Looking east over the High Sierra toward Mount Tom and Bishop, California. The base of the White Mountains may be seen in the distance. Image by William Bowen.*

Chapter 2: Research Methods

In an ideal world, conservation and management decisions would be based on accurate, current, and unbiased data collected specifically to address the situation at hand. In reality, decisions must be made regardless of data quality or availability. And, in truth, data can be too difficult or too expensive to collect and update; in the absence of good and current data, decisions have to be based on the best available resources. This does not mean that all conservation decisions are made ad hoc, lacking proper knowledge or resources, but rather, that modern-day conservation requires a certain degree of opportunism, improvisation, and innovative thought. While collecting original data in the field may be difficult, that does not mean information adequate for the drafting of a conservation plan is unavailable.

Recognizing the constraints that cost, time, and the requirements of formal field-based original data collection impose on conservation topics, I entered into this project interested in the reality of conservation planning. Rather than considering such planning in an ideal world offering unlimited financial resources and field time and funding sufficient to allow for the collection of single-site unique data in the field, I focused on the accumulation and analysis of existing data. My goal was to see how a practical, viable and credible conservation plan can be developed from existing information of an eclectic sort that might be found in a situation where a grab-bag of data exists, without its having previously undergone much formal collation and analysis.

Through the help of several individuals, a sharing of data, and the further exploration of knowledge in formal and informal interviews, I managed to compile the information necessary to draw reasonable conclusions and make what I consider to be informed recommendations. The variety of techniques used in this project represents the opportunism and innovation necessary for successful — and cost-effective — conservation.

Delineation of Herd Boundaries

This research is based on three Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) herds that winter in the eastern Sierra: the West Walker herd, the Casa Diablo herd, and the Round Valley herd (figure 2-1). Each of these particular herds presents a distinct opportunity for conservation. Their current status raises concern about continued success without intervention; in addition, these three herds spend a portion of their winter or migration in areas that are both biologically important and likely to be developed in the future.

Two additional herds that occur in this region, although originally taken into consideration, were omitted from closer examination – the East Walker herd and the Mono Lake herd (figure 2-2) (Taylor 1991). After careful evaluation, the conservation status of these two additional herds appears stable in comparison to the three herds documented in this research. Threats causing concern for other herds, such as urban development, are less significant for the East Walker or Mono Lake herds, at least under current conditions. In addition, herd numbers have not declined in recent years, such as in the Round Valley and West Walker herds. It is important that these two herds continue to be monitored, but currently they will not be considered a priority for conservation efforts.

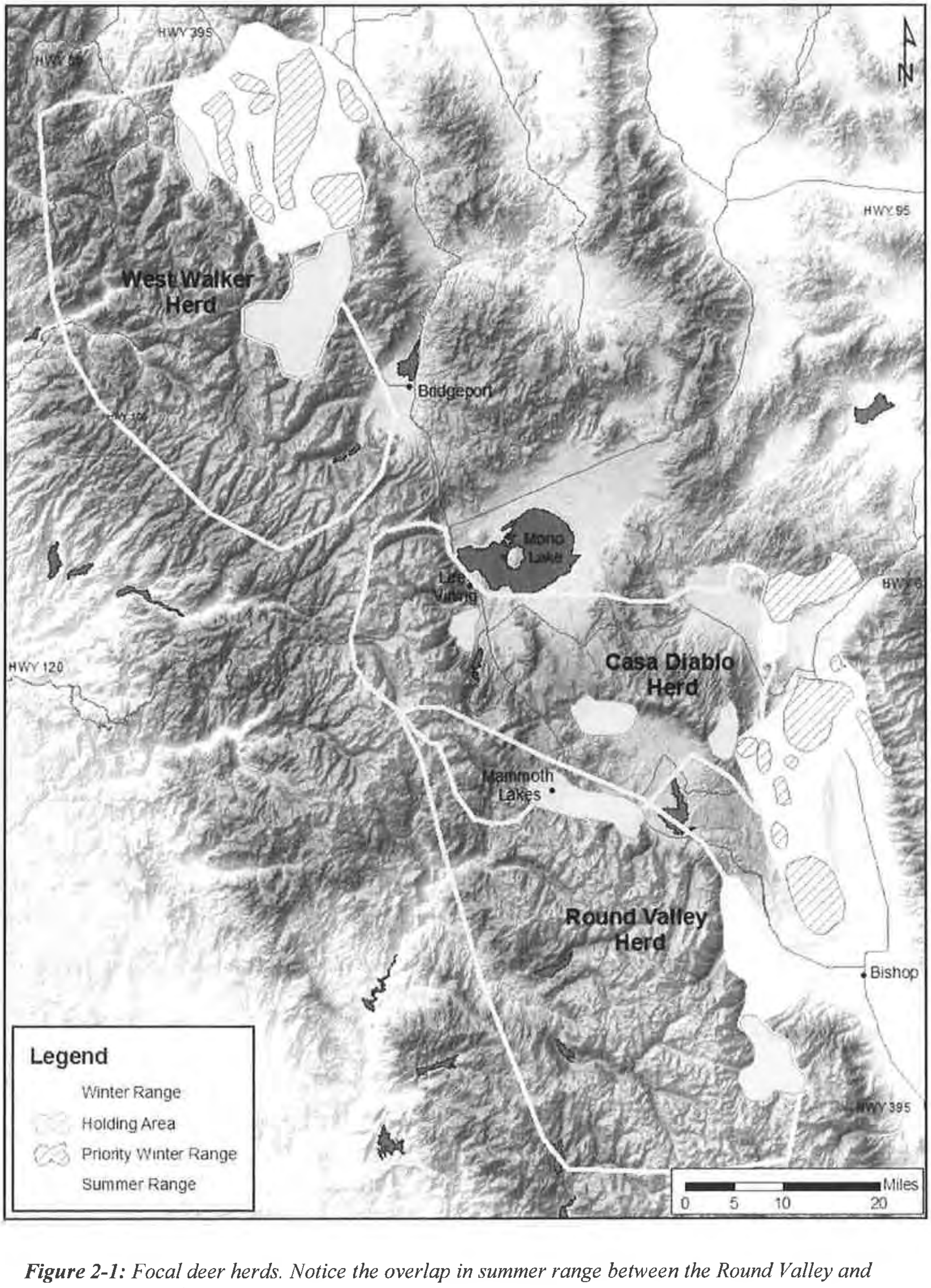


Figure 2-1: *Focal deer herds. Notice the overlap in summer range between the Round Valley and Casa Diablo Herds.*

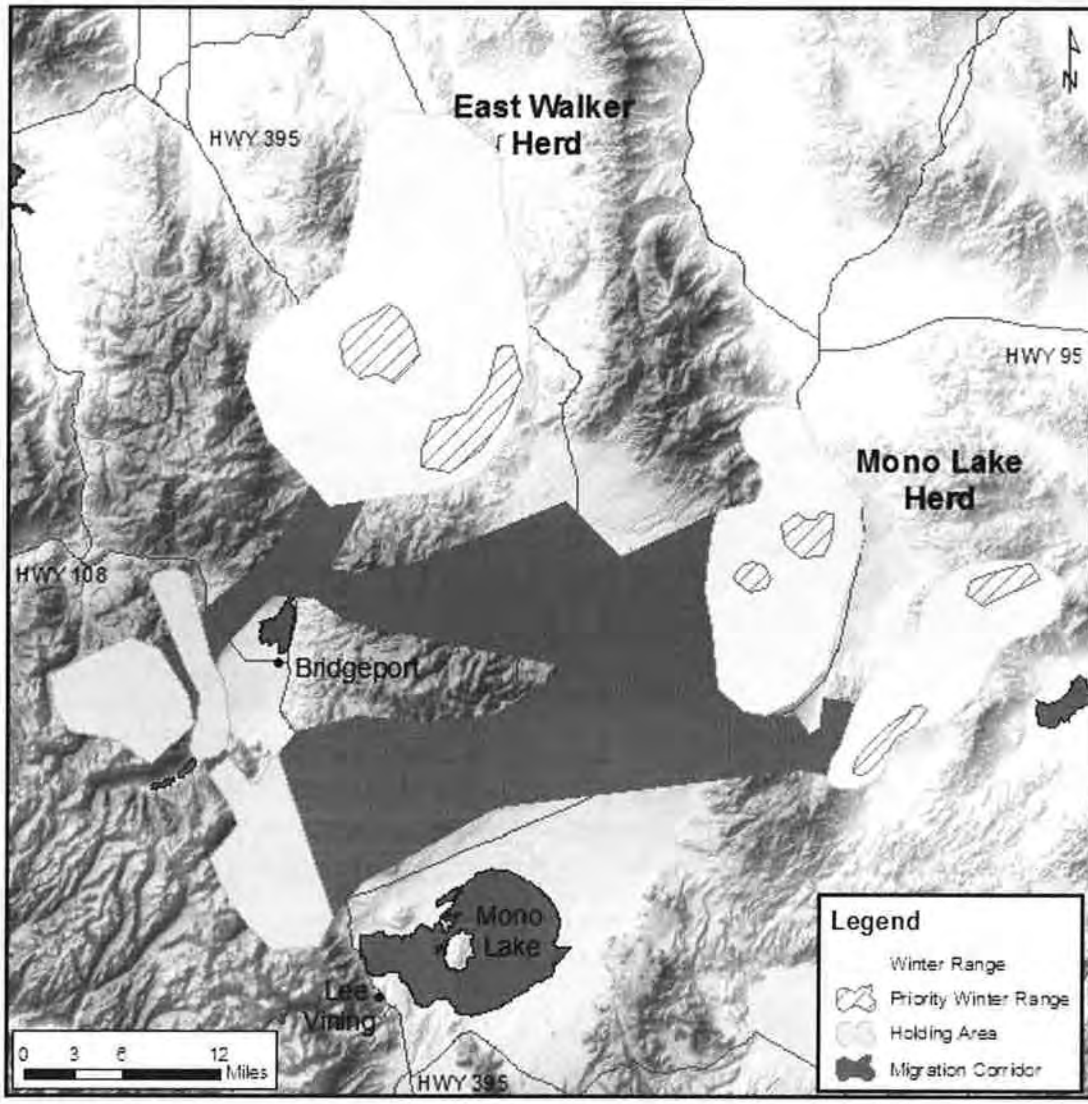


Figure 2-2: *East Walker and Mono Lake deer herds were excluded from the current study, but should be monitored for future threat or declines.*

The first step toward the conservation of the three focal herds is the delineation of seasonal ranges and migration routes. A review of published and non-published literature provides baseline data. The most recent information available for the West Walker herd is an almost decade-old management report produced by the California Department of Fish and Game (CDFG) (Taylor 1997). This report is based on radio-telemetry work done between May 1992 and June 1995 and includes topographical maps with seasonal ranges and migration routes hand drawn as polygon or line features. After scanning these maps, I geo-referenced the subsequent images in ArcMap 9.1 and created a shapefile showing seasonal ranges and migration routes based on the hand drawn polygons. In keeping with the format established in the CDFG management report, migration routes are drawn as linear features, rather than corridors or areas.

No current management report exists for the Casa Diablo herd; there is, however, an almost twenty-year old deer study report by CDFG (Taylor 1988). Between 1986 and 1988 CDFG biologist Tim Taylor monitored Casa Diablo deer using radio-telemetry techniques. Within the report, home ranges and migration routes are delineated on hand-drawn maps; however, there are no topographical base maps to give reference. Major points of reference, such as cities or lakes, are included, but since maps are not drawn to scale, they could not be easily geo-referenced in a GIS. Instead, I chose to digitize range boundaries by using heads-up-digitizing and a visual analysis of the maps. Reference points such as highways, lakes, cities, and mountains ensured as much accuracy as possible.

No current management report or herd study exists for the Round Valley herd. There is, however, a map showing range boundaries and migration routes available as a jpeg image. This map was created by CDFG and was clearly made using GIS technology. The map lacks metadata or information explaining how ranges were delineated, nor does it indicate the name of its creator, though a current CDFG employee suggests the creator may have been a previous intern. Current whereabouts of the original data used to create the map are unknown. After geo-referencing this map in ArcMap 9.1, I created a new shapefile showing the seasonal ranges and migration routes of the Round Valley herd. Since the origin of this information is unknown and the accuracy questionable, I considered this map a starting point only. In addition to the image, another source of information exists for the Round Valley Herd in a PhD dissertation; Dr. Tom Kucera monitored the Round Valley herd between January 1984 and May 1987 for his doctoral research (Kucera 1988). Dr. Kucera does not provide maps indicating range boundaries or migration routes in his printed dissertation. He does, however, describe broad range boundaries and migration routes within the text. Range boundary descriptions, although they coincide with the CDFG map, are at such a coarse scale that they can only loosely validate the CDFG map. Migration routes, however, are described in detail, particularly the locations where Round Valley deer cross the Sierra Nevada crest moving into summer range on the western slope of the Sierra. These locations are limited by the physical landscape and can be accurately pinpointed on a map by description alone. These descriptions were used to validate and update the Round Valley shapefiles.

After digitizing range boundaries and migration routes for all three herds, I printed a poster sized map (3' by 4') for each herd on 100k topographical base maps. I presented these maps during an interview with Tim Taylor, a CDFG wildlife biologist. Taylor is considered the local expert on both the West Walker and Casa Diablo herds and was author and lead researcher for the Casa Diablo and West Walker reports. In addition, Taylor still currently participates in annual helicopter counts for all three herds and is involved with on-going herd management and conservation. Taylor updated the poster-sized maps based on his personal knowledge by hand-drawing new and more accurate boundaries and migration routes and by delineating areas of known concentrations or critical importance. After using this information to update the original shapefiles in ArcMap, I repeated the process with Taylor a second time to ensure that no details were overlooked. Extensive interviews with Taylor provided additional information on the biology, conservation, and potential threats to each herd. I followed the same interview/map-updating process in a single meeting with Dr. Kucera. This ensured that any non-printed knowledge is reflected in all three herd maps.

Definition and delineation of Priority Areas

In the context of this research, priority areas are geographical spaces that if altered severely may cause significant declines in the overall population numbers of the herd. These areas provide some essential or integral component to the life history of the herd, and include important winter range, holding areas, bottlenecks in migration routes, and important summer range. The designation of priority areas is not meant to imply that areas within the herd range but not designated as *priority* are not important for the long-term persistence of the herd; only that priority areas are of a slightly higher importance and as such, should be protected first.

Heavy winter snowfall causes winter range in the eastern Sierra to be concentrated in lower-elevation valleys. During heavy snow winters, deer tend to congregate in areas where vegetation is still available and extends above the snow-pack. At the end of winter, some areas tend to "green up" first, providing forage earlier than other parts of winter range (Taylor 2005). Based on this information, I define priority winter range as areas of quality vegetative forage that either remain available through the heaviest months of winter or become available in the springtime when deer are in poor physical condition and in need of nutritious forage. These areas are recognized either by their known vegetative composition or as areas where deer congregate during winter periods.

Holding areas are sites along migration routes where deer linger several days or longer during migration (Bertrem and Rempel 1977, cited in Taylor 1988, p. 8) and typically occur at the base of a significant change in elevation (Taylor 2006a). In the eastern Sierra, deer leave winter range when weather is becoming excessively warm and forage is scarce; summer range, however, is still unavailable due to heavy snowpack (Taylor 2006a). Spring holding areas provide a temporary staging area where deer can find forage and wait until summer range becomes available. Fall holding areas are used at the other end of migration, when deer are moving back onto winter range. These areas provide additional forage before settling into winter range. For this research, major holding areas are considered priority habitat for the long term persistence of local mule deer herds.

To move between winter range, holding areas, and summer range, mule deer require functional migration corridors. Depending on the topography of the landscape, migration corridors can be wide and dispersed over a large area or small and constricted to a narrow passageway. Bottlenecks along migration corridors occur when the corridor becomes narrow and restricted on either side. These restrictions can be natural, such as mountains or lakes, or man-made such as dense development. In the context of this research, migration routes are drawn as linear features showing the general path of movement but ignoring boundary lines necessary to delineate a *migration corridor*. Corridors, and particularly bottlenecks in corridors, are identified in a visual examination of the physical and cultural landscape through which the migration route passes. Bottlenecks in major migration corridors stand out as priority habitat for this project because they have the potential to block migration and disconnect seasonal ranges.

The final type of priority habitat identified for this research is priority summer range, constituting fawning grounds or areas of quality vegetation where deer congregate during summer months. In general, summer range is much more dispersed and in this region more likely to occur on public lands than any other type of seasonal range. Certain key fawning areas, however, occur in at-risk locations and are important for mule deer conservation.

Delineation of priority habitat followed much the same process as delineation of range boundaries. Known priority areas were sketched on poster-sized maps by Taylor and Kucera during in-person interviews. A visual examination and discussion of physical and cultural landscapes then identified bottlenecks in migration routes.

Round Valley Density Analysis

After completion of range and migration delineations, an additional data source became available for the Round Valley Herd from Dr. Vern Bleich, a wildlife biologist for CDFG. Dr. Bleich's research focuses on ecological studies of mule deer from the Round Valley. From the years 2002–2004, GPS radio-collars were monitored non-continuously on 37 individual deer that winter-through in Round Valley. The subsequent database consists of over 45,000 point locations, which I brought into a GIS. Each point in this database represents a location of an individual deer at a given point in time. Questionable or outlier individuals were first removed from the database to eliminate the possibility that individuals not belonging to the herd could be included in the analysis. I then categorized points by date to create several distinct groups: 1) all points; 2) point locations during spring migration (April – June); 3) point locations during fall migration (Oct and November); 4) point locations during winter months (December – March); and 5) point locations during summer months (July – September). Using ArcMap 9.1, I performed a Point Density Analysis (Spatial Analyst) and a Fixed Kernel Density Estimator (Hawth's Tools) on each category to show locations of highest point densities. It is important to note that this analysis makes one major assumption – that each point is weighted equally toward determining overall herd density. The distribution of points, however, is not equal over time or between individuals, with some individuals monitored more frequently on given days or more frequently in general. This means that some individuals are weighted more heavily in the analysis as are some time periods. The large size of this database, however, makes it unlikely that such localized effects will have an impact on the broader results. The results of the density analysis were then compared to the herd maps created using expert opinion to see if these quantitative techniques provided a similar result as the qualitative methods used to delineate herd boundaries and priority areas. Although a similar result from these two distinct methods does not validate the accuracy of either method, it does improve our overall confidence in the accuracy of both methods.

Deer spend more time overall in seasonal ranges than in migration. During the three-month period when herd migration occurs, an individual deer spends only a small percentage of its time migrating, with most time spent on winter range or a spring holding area. Consequently, migration routes are not clearly identified by density analysis. To compensate for this, I created movement paths for each individual deer by connecting point locations in temporally sequential order using the "Convert Locations to Paths" function of the Hawth's Tools extension for ArcGIS. I then performed a visual examination of each movement path in comparison to the major migration corridor for the Round Valley herd previously delineated using expert opinion.

Data Acquisition

Ownership data are compiled from several sources including Mono County, Inyo County, and Alpine County (California), and Douglas County (Nevada). These data are considered the most accurate and up-to-date ownership information currently available for each county. Gaps in ownership data occur in small portions of ranges outside of the counties listed above. These gaps were filled, however, by layering California and Nevada GAP Analysis ownership files behind county ownership files.

Mono, Inyo, and Douglas counties all provided parcel GIS layers for their respective counties. Mono and Douglas counties additionally supplied land use designation (LUD) GIS layers. Inyo County provided LUD information for requested parcels, which I then attributed to the appropriate parcels. Alpine County supplied LUD maps as PDF images, but no parcel layer. I compiled all data into a GIS database to create fairly complete parcel and LUD data layers.

California wildfire history data came from the Inyo National Forest (U.S. Forest Service); Nevada wildfire data can be downloaded off the Nevada division of the U.S. Bureau of Land Management website. Additional cartographic or physical data came from the State of California website, Mono County, or the University of Nevada, Reno.

Planning and Threat Assessment

Threats evaluated in this research are chosen based on several sources including a literature review of known or suggested threats to mule deer, threats known to affect other species in the region, and expert opinion. Each threat is evaluated for its potential impact on mule deer conservation, past occurrences or effect, or the threat's potential for future occurrence within the herd ranges. Perceived threats include: urban development, catastrophic wildfire, deer-vehicle collisions, livestock grazing, and energy exploration. While it might perhaps be so used, this research is not intended to predict the future impact of these threats but rather to draw attention to the existence of potential threats and the need from a conservation perspective for these threats to be addressed.

Urban development is occurring on a widespread scale across the western United States. Important habitat for all focal herds occurs on some private land, and as a result faces some risk of development. Although all private land has a potential for development, the distribution and patterns of development will vary based on many factors including land value, land access, and land use planning. Conservation planning requires a clear understanding of the potential for development so that funds can be allocated effectively and efficiently. For this research, information on development came from three main sources: land use designations, general plans, and interviews with planners from

Douglas, Mono, and Inyo Counties. Questions posed to planners sought out information on current development proposals, potential for development in specified areas, and likelihood that given areas will be developed in the near future. The assessments based on this information are not predictive models of development; rather, this information is used to identify high-risk areas within priority deer habitat that should be considered a focal point for local conservation and land use planning.

Deer-vehicle collisions (DVCs) are a major problem in the western United States, causing a negative impact to both mule deer populations and motorists involved in the accidents (Sullivan and others 2004). Caltrans (region 5) maintains a database of DVCs dating back to 1965. Each collision is referenced by the date the deer carcass was found and highway postmile (recorded every 1/10 of each postmile). There are a few problems associated with this database; first, collisions are only recorded when deer carcasses are found on the highway. This means that collisions in which a deer did not die on impact and left the highway before dying, or did not die at all, are not included in the database. Until recently, most monitoring by Caltrans was done from a moving vehicle; consequently, any carcasses not easily seen from a moving vehicle are also excluded. In addition, several years of data (1996 – 2002) are currently unaccounted for and were correspondingly excluded from the database. Despite several shortcomings, this database is still an extremely useful asset for gaining an understanding of the magnitude of the problem and the spatial distribution of DVC occurrences.

To begin my analysis, I first brought the entire DVC database into Microsoft Excel. I then created a new worksheet that lists all postmile locations at which a DVC ever occurred. Locations are recorded at 1/10 mile accuracy. For each postmile location, the total number of DVCs occurring at that location were added and attributed to the postmile location. I exported the excel worksheet as a Dbase IV table and joined the new table to a postmile shapefile in ArcMap 9.1, at which point I selected and exported all attributed postmile point locations to create a new shapefile. Using spatial analyst, I calculated the Getis–Ord Gi* statistics for this dataset based on total number of collisions and used the values to identify DVC hotspots.

Threat from wildfire and energy exploration are identified spatially and discussed based on literature review, previous occurrences, and expert opinion. Information on proposed energy exploration on the Casa Diablo winter range came from the Bureau of Land Management. Discussion and recommendations on livestock grazing are based solely on literature review.

Chapter 3: The State of the Herd

Mule deer are enjoyed (thanks substantially to Disney's *Bambi*) by some of the population as charismatic and picturesque animals and valued by hunters as a desirable game species. Modern day wildlife biologists work in a field that had its origins in trying to maximize deer "yield," but now also includes the tricky world of threatened or endangered species and the dictates of the Endangered Species Act. Mule deer conservation, and in many ways wildlife biology in general, is inescapably linked to past and current deer management practices. Without a clear understanding of deer management, conservation efforts cannot be successful. A discussion of management, however, first requires a basic understanding of the history and ecology of this species. Mule deer occur throughout western North America. Although differences in deer behavior and ecology exist across regions, many similarities are consistent throughout the American West and provide insight into the species' unique characteristics and history.

Mule deer are primarily browsers, feeding on forbs and the leaves and twigs of shrubs. In contrast to other large ruminants, including cattle and elk, mule deer have a smaller rumen in relation to body size; instead of eating large quantities of low quality forage, deer must be more selective, feeding on only nutritious plants or parts of plants (Heffelfinger and Messmer 2003, 6). The breeding season for mule deer occurs in late fall (November-December). After a gestation period of about 7 months, single or twin fawns are born during summer (May-August). Deer fertility and fawn recruitment are directly linked to habitat conditions and nutritional level of females, particularly during late pregnancy and lactation (2003, 7). Range conditions, and specifically the availability of nutritious forage, thus have a significant impact on fawn recruitment. Factors such as livestock grazing, mule deer population density, invasive species, fire frequency, and climate all impact the quality and condition of rangelands.

In the past, mule deer management focused primarily on improving range condition to support higher densities of deer. This was accomplished through several techniques including low to moderate density livestock grazing to maintain early successional stages (Austin 2000, Heffelfinger and Messmer 2003, 7), increased water availability through artificial waterholes (Taylor 1988, Bleich and others 2005), prescribed burning (Taylor 1997), and food supplementation (Nelson 1997, 48). Although these methods successfully increase population densities, they raise concern over potential ecological consequences. Mule deer populations are well known for both their variability and their tendency to increase quickly under suitable conditions and crash when conditions are poor (Baron 2004). Dense deer populations can quickly decimate rangelands, clearly demonstrated in the well-known example of the Kaibab Plateau (Foster 1970). Although rangelands may not be destroyed when non-natural supplementation is occurring, techniques used to increase deer herd density artificially create dependency on human supplementation, which, if ever removed, could ultimately result in disasters such as the Kaibab case. It is not farfetched to predict that management techniques such as the ones described above could be changed or forgotten with normal employee turnover at agencies or when widespread political changes occur. For these reasons, techniques meant to improve deer habitat (not to be confused with restoration techniques meant to bring habitat back to a presumably "natural" state) should be approached with a degree of caution.

In a natural system, mule deer populations are kept in check through predation. This still occurs to some degree in the eastern Sierra Nevada through mountain lion predation. More often, however, natural predators have been regionally extirpated, allowing deer populations to quickly exceed carrying capacity (Baron 2004, 19-20). Despite the efforts of predator-reintroduction projects, which are themselves controversial, it seems unlikely that natural predators will ever occur at abundances equivalent to historic numbers. Overpopulation of mule deer herds can have negative impacts on range- or wildlands, leading to population crashes and severe habitat degradation. Mule deer management and conservation must ensure that populations remain within the carrying capacity of their habitat.

The easiest and most obvious way to achieve this goal is through regular monitoring and hunting. Although it may seem counter-intuitive, in the absence of sufficient natural predation or other environmental checks, hunting is necessary to keep populations at healthy levels and ensure that rangelands remain viable habitat. Most situations where deer populations exceed the carrying capacity of their environment occur when hunting is heavily or entirely restricted (Foster 1970, Baron 2004). Successful mule deer conservation is thus a balance between habitat protection and population management. If habitat is diminished in size or quality, deer populations will suffer and decline. If populations are allowed to over-flourish, they will ultimately destroy their own habitat, and again deer populations, in addition to other co-existing species, will suffer. Not all situations, of course, lead to over-population problems; many other factors, such as climate or competition, affect mule deer abundances. Management is an integral component to successful mule deer conservation.

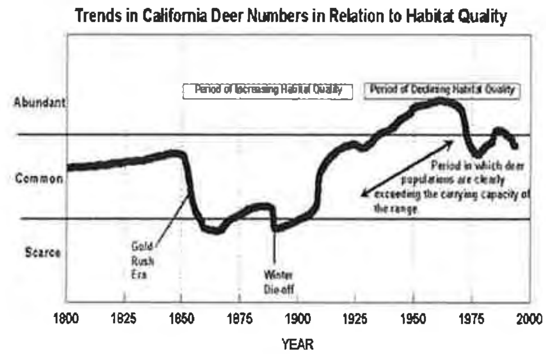


***Figure 3-1**: Long term trends in California deer abundance from the CDFG website (www.dfg.ca.gov). Abundant refers to populations of 700,000 to 1 million; common refers to populations between 400,000 and 700,000; scarce refers to populations lower than 400,000 individuals.*

Much of the debate surrounding mule deer conservation comes from the sparse amount known about mule deer populations or distributions before the arrival of early pioneers. In the introduction to *Mule Deer Conservation: Issues and Management Strategies* (2003), James Heffelfinger and Terry Messmer clearly explain the history of mule deer population fluctuations since the arrival of pioneers. It is widely accepted that mule deer abundance in the 1800s was below or equal to current numbers (figure 3-1). After settlement, most western states report major declines in populations due to unrestricted hunting, excessive livestock grazing, and unfavorable weather patterns. Mule deer abundances were scarce by the early 1900s. Through the 1920s populations increased due to new harvest regulations and the newly established wildlife conservation system. Anthropomorphic changes, such as cattle grazing, fire suppression, and logging created a landscape that could support higher mule deer population densities due to increased shrub quantities. Mule deer populations peaked in the late 1940s through the 1960s. A second widespread decline occurred in the 1960s and 1970s, but this time the reasons were less well understood and extremely varied. The 1980s brought general increases in deer abundance, but by the mid-1990s another widespread decline began that continues through the current day. Causes suggested for current declines include habitat loss to development, drought, harsh winters, competition, predation, disease, poaching, and increased hunting. Habitat loss, however, is generally accepted as the most significant cause of current declines (Heffelfinger and Messmer 2003, 8-9).

Such dramatic fluctuations over time, combined with a poor understanding of pre-settlement abundance and distributions, create challenges in setting conservation goals for mule deer. An emerging factor, however, distinguishes historic fluctuations from current declines – the effects of widespread habitat loss, especially the declining acreage of seasonally-crucial feed species that can't be substituted. Although historically deer populations eventually recovered from the previous impacts of over-hunting, over-population, or climatic fluctuations, the effects of continued habitat loss may not be so easily remedied, particularly when faced with the fact that habitat lost to development may never be converted back to habitat. It seems likely that declines caused by habitat loss will only continue as urban development continues to encroach on wild landscapes. Habitat conversion can be viewed as one of the most pressing threats to mule deer populations, and protection of habitat should be regarded as a main goal of mule deer conservation.

Mule Deer and the Eastern Sierra

Mule deer currently occur throughout the Great Basin. As in all western states, historic abundances and distributions are not well understood, although many biologists argue that mule deer were largely absent from the Great Basin 100 years ago (Berger and Wehausen 1991, Austin 2002). Joel Berger and John Wehausen propose that current mule deer distributions are an indirect consequence of cattle grazing in the Great Basin Desert. According to these biologists, the introduction of cattle grazing and wild horses caused a shift in vegetation composition toward shrubby vegetation types, consequently causing mule deer populations to irrupt. Mountain lions, a major predator of mule deer, increased in turn, creating what Berger and Wehausen refer to as a "Predator-Prey Disequilibrium" in the Great Basin. Other research provides additional support that grazing significantly altered Great Basin vegetation composition. Mack and Thompson (1982) give several convincing lines of evidence to support the theory that intermountain steppe communities evolved without selective grazing pressure and consequently are not adapted to deal with the impacts from livestock grazing, at least by cattle and horses, as "large-hooved herbivores." Dennis Austin (2000) presents results of numerous studies indicating that livestock grazing shifted plant succession toward seral shrub communities on mule deer winter range followed by dramatic increases in mule deer populations in the Great Basin. Although historic populations may never be completely understood, current research indicates that mule deer were probably scarce throughout the Great Basin in pre-settlement times.

The eastern Sierra Nevada, however, occurs on the edge of the Great Basin. Although many Great Basin characteristics shape the ecology of the eastern Sierra, unique forces at work in this region create a distinct environment. Mule deer are native to the eastern Sierra Nevada. Deer were part of the diet of Owens Valley Indians (Wilke and Lawton 1976, cited in Wehausen 1996, 477) indicating they existed in this region prior to euroamerican settlement. Many eastern Sierra mule deer migrate westward over the Sierra Nevada crest in summer months and intermingle with western slope herds (Loft and others 1989). Central Sierra herds from the western slope are well-documented during pre-settlement times in Native American diet and clothing (Powers 1875, cited in Berger and Wehausen 1991, 246). It seems likely that even if mule deer were not present in the eastern Sierra at some point in history, western herds would eventually drift down eastern slopes to find new winter habitat, especially with the presence of abundant summer range nearby. Despite clear indicators of mule deer presence in the eastern Sierra during pre-settlement times, historic abundance is unknown. This research assumes that population fluctuations in eastern Sierra herds follow patterns similar to elsewhere in California and the entire western U.S. and that significant future declines would cause populations to drop below common historic numbers (“common” area in figure 3-1).

This research focuses on three eastern Sierra mule deer herds: the West Walker herd, the Casa Diablo herd, and the Round Valley herd (figure 2-1).

West Walker Deer Herd

The West Walker (WW) herd is a bi-state mule deer herd, occupying winter range in both California (Mono County) and Nevada (Douglas County). Like most eastern Sierra herds, WW deer inhabit a relatively small, concentrated area of winter range (800 km^2) in comparison to a large, dispersed summer range (2,450 km^2) (Taylor 1997). Summer range is shared with Rocky Mountain mule deer from two other eastern Sierra herds (East Walker and Mono Lake herds) and California mule deer (*Odocoileus hemionus californicus)* from at least three western Sierra herds (Loft 1989, Taylor 1997). Most summer range occurs on public lands such as national forest and national park lands.

Winter range for the WW herd is concentrated into 800 km^2; in winter, females are typically pregnant, males are regaining strength from the fall rut, and winter storms

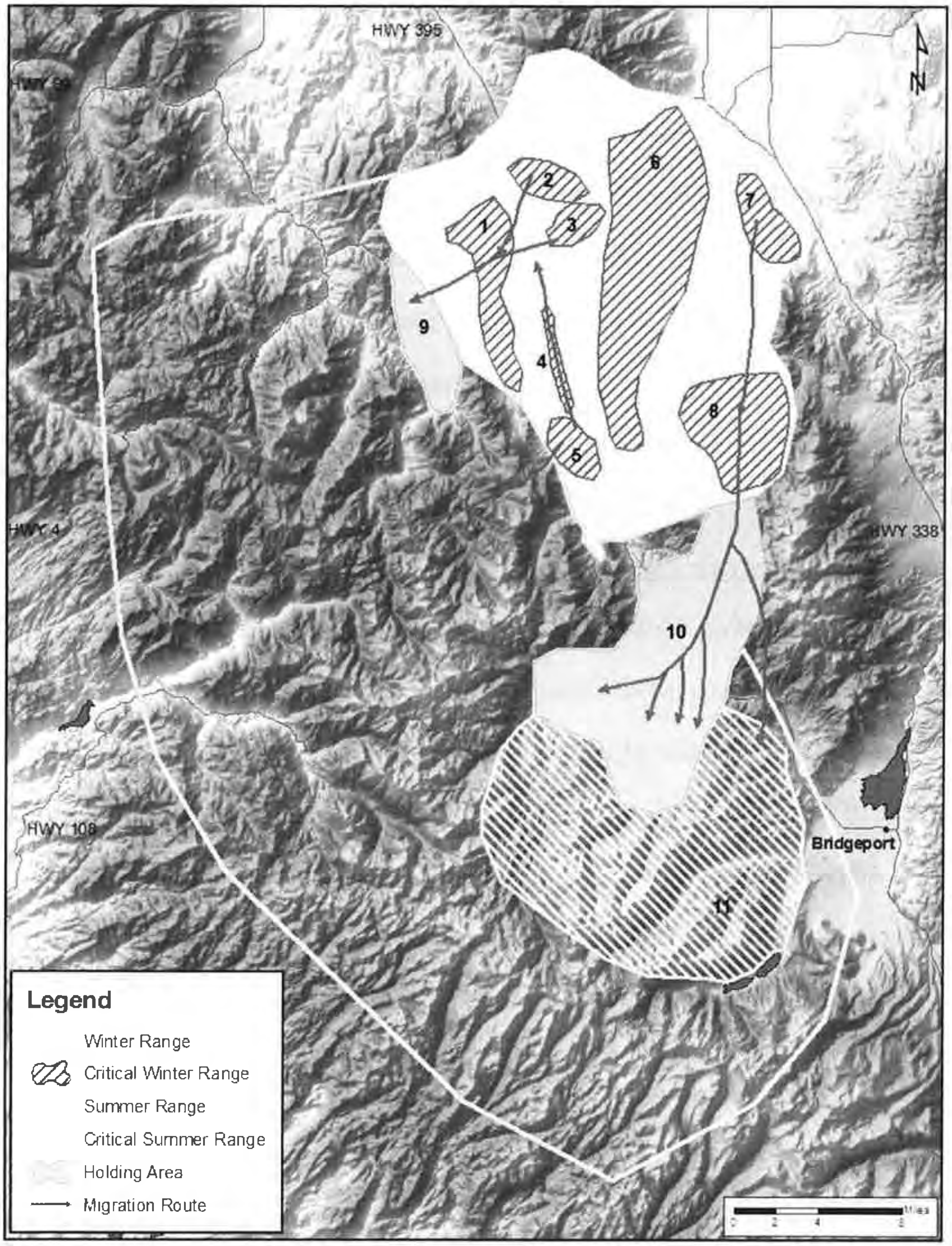


Figure 3-2: Seasonal ranges and migration routes of the West Walker herd. Numbered polygons show designated "critical areas."

increase energetic demands. Winter range must provide nutritious forage that remains available to deer until conditions allow for spring migration. Conservation of winter habitat requires a clear understanding of winter diet. In the Great Basin region, antelope bitterbrush (*Purshia tridentata)* and big sagebrush (*Artemisia tridentata*) are widely recognized as the most significant components of mule deer diets (Kucera 1988). Fecal pellet analysis on West Walker deer shows that antelope bitterbrush is the most common shrub in early winter diets, while sagebrush (*Artemisia* spp.) and saltbush (*Atriplex* spp.) are common during late winter when bitterbrush is no longer available because of snow cover in medium and upper elevations. Forb use increases in late winter to compensate for lower shrub availability. Common forbs include buckwheat (*Eriogonum spp.*), larkspur (*Delphinium spp.*), cinquefoil (*Potentilla spp.*), and Indian paintbrush (*Castilleja spp.*) (Taylor 1997). Although deer feed on both browse (shrubs) and forbs, browse is critical to winter survival because it is available in deep snow, when all other forage is buried. Browse is a better source of crude protein than grasses and forbs, offering more nutritional advantage (Taylor 1997). Bitterbrush is the most important browse species for WW deer in early winter; consequently, areas of abundant bitterbrush can be considered a high priority for conservation.

CDFG spring helicopter surveys in 2005 counted 1,730 individual deer in WW range; with 1,077 of these identified as adults, 394 as fawns, and 259 unclassified. Actual population size is probably much higher than helicopter counts. Although exact numbers are not available, CDFG biologist Tim Taylor indicates that this herd has seen significant declines in the last 10 to 20 years (Taylor 2006b) causing concern for the long-term persistence of the WW herd. In addition, this herd faces several current or anticipated future threats; these threats will be discussed in detail in chapter four of this thesis.

Priority Areas:

Winter range for the WW herd is already highly concentrated; consequently, the entire winter range can be considered of *high priority* for the long-term persistence of the herd. Certain subregions do provide more valuable forage than others and are utilized more heavily by deer than other winter range. For this research, these areas are called *"priority winter range;"* they are numbered and delineated in figure 3-2. Priority areas vary in importance depending on the timing and severity of winter. Some areas may be more important in late fall, others in the dead of winter, and still others in early spring. Certain areas may not be used during light winters but will become critically important during a severe winter. Deer move seasonally through these distinct areas and at any given time may be concentrated in one or more priority areas.

Priority range delineations also include holding areas and summer range. Definitions of holding areas and priority summer range are provided in chapter 2 of this thesis. Bottlenecks along migration routes are not a significant problem for the West Walker herd, and consequently are not included as priority areas.

Priority Winter Range:

1) ***Slinkard Valley*** – This area provides winter range, spring range, and a fall holding area for WW deer. A wildlife refuge, created and managed by CDFG, occurs within this area. The refuge protects winter habitat, but the Slinkard valley spring habitat is not currently protected.

2) ***Wild Oat Mountain*** – This area provides spring range. High concentrations of West Walker deer can be found in Wild Oat Mountain during early spring.

3) ***Gray Hills*** – This area also provides spring range. High concentrations of West Walker deer can be found in Gray Hills during early spring.

4) ***Topaz – Coleville Corridor*** – This corridor provides important winter range and functions as a movement corridor between priority winter ranges. The corridor stretches between highway 395 on the east and steep mountain faces on the west. Deer-vehicle collisions are a significant problem within the corridor.

5) ***Little Antelope Valley*** – This area provides both winter and spring range. Most of Little Antelope Valley is protected as a wildlife refuge, created and managed by CDFG.

6) ***Antelope Valley*** – Antelope Valley provides winter and spring range. It is larger in size than other priority areas and consequently provides an abundance of quality habitat.

7) ***Boulder Hills*** – Boulder Hills provides winter and spring range.

8) ***Jackass Flat*** – The west side of jackass flat provides early winter range. The east side provides late winter range.

<u>Holding Areas</u>:

9) ***Bagley Valley Holding Area*** –Although this spring holding area is used less than the Sonora holding area, it is important for deer that are migrating from northern winter range into northern summer range.

10) ***Sonora Holding Area*** – This is the most used spring holding area and migration route for WW deer. The majority of deer from this herd cross highway 395 near Sonora junction, within the Sonora holding area. Consequently, deer-vehicle collisions are a significant problem within this area.

Priority Summer Range:

11) This area is unnamed; it occurs north of twin lakes and includes three drainages: Buckeye Creek, Little Walker River, and West Walker River. This region provides important fawning habitat and is used primarily by female does during fawning periods.

Casa Diablo Deer Herd

The Casa Diablo (CD) herd is the smallest of all five mule deer herds occurring in Mono County with 662 individual deer counted in CDFG 2005 spring helicopter surveys (420 adults, 87 fawns, 155 unclassified). Population estimates project a total population size of approximately 1300 deer (Taylor 2006a). Unlike the West Walker or Round Valley herds, the Casa Diablo herd has not seen significant declines in recent times. Before 1993, widespread drought impacted herd numbers; the population has steadily increased since then, however, and currently remains stable (Taylor 2006a). Although this is encouraging for deer conservation, several potential and anticipated threats create concern for future herd prosperity. With deer population numbers already small, it is important to address these threats before they occur.

Like other eastern Sierra herds, the CD herd occupies a relatively small winter range (260 km^2) and large, dispersed summer range (1,940 km^2). Most deer summer along the east slope of the Sierra (~85%), but some move over the Sierra crest to spend summers on the western slope (Taylor 1988, Taylor 2005). Winter range may be especially important for this herd because deer are frequently in poor condition at the end of summer before moving onto winter range in the fall; this means that quality winter forage is critical for sustaining population numbers (Taylor 2005). Although no available studies document preferred forage for CD deer, feeding preferences probably follow similar patterns to that of West Walker deer with antelope bitterbrush as the most important browse species.

Priority Areas:

Priority areas for CD deer are defined by the same parameters as WW deer. Winter range is not as limited as for the WW herd, but because deer are leaving summer range in poor condition, quality winter range is crucial for population health. Priority areas are delineated and numbered in figure 3-3.

Migration corridors are fairly broad with no significant bottlenecks. The major migration route follows the base of the Glass Mountains. This route is restricted to the north by the Glass Mountains, but unrestricted to the south leaving ample space for a wide migration corridor.

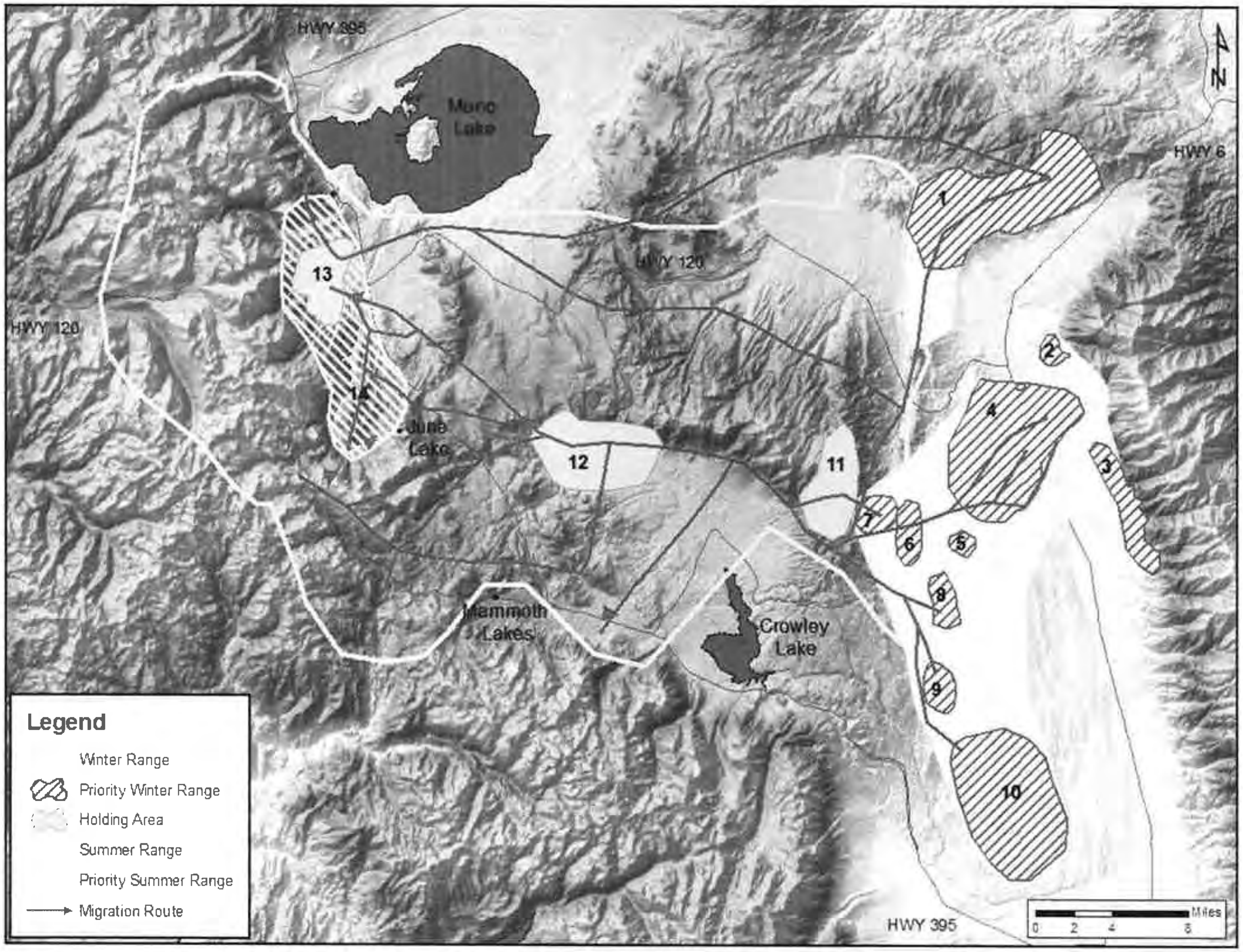


Figure 3-3: *Seasonal ranges and migration routes of Casa Diablo deer herd. Numbered polygons show designated "critical areas."*

<u>Priority Winter Range</u>:

1) ***Truman Meadows*** – This area includes the Truman meadows and surrounding areas. Deer use the meadows extensively during winter months then move to areas south of the meadows in the spring.

2) ***Montgomery Creek*** – The base of these canyons contain bitterbrush forage and are used extensively by deer.

3) ***Rock Creek to Cottonwood Canyon*** – This area includes the base of several canyons (Rock creek, Falls Canyon, Pellisier Creek, Middle Canyon, Birch Creek, Willow Creek, and Cottonwood Canyon) and contains bitterbrush forage.

4) ***Blind Springs / Marble Creek*** – Marble creek and Blind Springs have high deer concentrations in the springtime (February – April). The Marble Creek area is an alluvial fan and contains abundant bitterbrush. Blind Springs is arguably the most priority winter range for this herd. South- and east-facing slopes in Blind Springs are the most important; these areas contain bunch grasses and "green-up" early in the springtime, providing forage when it may not be available anywhere else. Deer also forage on cultivated alfalfa fields in this area.

5) ***Black Rock Mine*** – Black Rock Mine provides winter forage. It is used most heavily in the month of January.

6) ***Banner Ridge*** – Banner ridge provides winter forage. It is used most heavily in the month of January.

7) ***Wildrose Mine*** - Wildrose Mine provides winter forage. It is used most heavily in the month of January.

8) Chidago Flat – Chidago Flat provides winter forage. It is used most heavily in the month of January.

9) Casa Diablo Mountain – Casa Diablo Mountain has abundant bitterbrush. This is important habitat during winter months.

10) Volcanic Tablelands – The volcanic tablelands is mostly desert scrub and "greens-up" early. Deer that spent winter months on Casa Diablo Mountain move into the volcanic tablelands in the springtime.

Holding Areas:

11) Fall Holding Area – This area is unofficially called "Squawtit." It stays fairly open until December and is extremely important habitat in the fall, when more than a thousand deer can often be found here. It borders the eastern edge of the Glass Mountains and is high elevation sagebrush scrub.

12) Bald Mountain Holding Area (HA-1) – The Bald Mountain holding area is important during both spring and fall migrations. Irrigated meadows and abundant bitterbrush in the southwest region are used extensively by deer. The entire holding area has abundant water, making this an important area for several other species as well, including migratory waterfowl and raptors.

13) Bohler / Sawmill Canyons Holding Area (HA-2) – This holding area is not as heavily used by deer as other holding areas, although the majority of deer do go here. HA-2 overlaps summer range and is more important as fawning habitat than as a holding area. It contains both Aspen groves and bitterbrush which are used extensively by Casa Diablo deer.

Priority Summer Range:

14) June Lake Loop – This area encompasses the entire June Lake loop north to Mono Dome near highway 120 and contains valuable fawning habitat. During summer months, high concentration of female does with young can be found within this range.

Round Valley Deer Herd

The Round Valley (RV) herd is named for its winter range, which encompasses the entire Round Valley in southern Mono County and northern Inyo County. Previously, the RV herd was recognized as two distinct herds: the Buttermilk and the Sherwin Grade herds. This former separation distinguished deer from the Round Valley winter range migrating north up the Sherwin Grade from deer that migrate south through the Buttermilk region. Old management reports reflect this distinction. Current management, however, combines these deer into one group – the Round Valley deer herd.

Similar to the West Walker herd, the RV population has seen dramatic declines over the last 10 – 20 years (Taylor 2005, Bleich 2006); exact numbers are not available. Reasons for this decline include increased urban development, catastrophic wildfires, and deer-vehicle collisions. These problems are discussed in detail in chapter 4 of this thesis. Fecal pellet analysis indicates that RV deer have a similar diet to that of WW deer. Diet during winter months is > 93% shrubs, with antelope bitterbrush, sagebrush, blackbrush (*Coleogyne ramosissima*), and Gregg's ceanothus (*Ceanothus Gregii*) as the dominant shrub species. Bitterbrush is most frequent in the diet during the first few months and again in April (coinciding with spring growth). Sagebrush is most common during

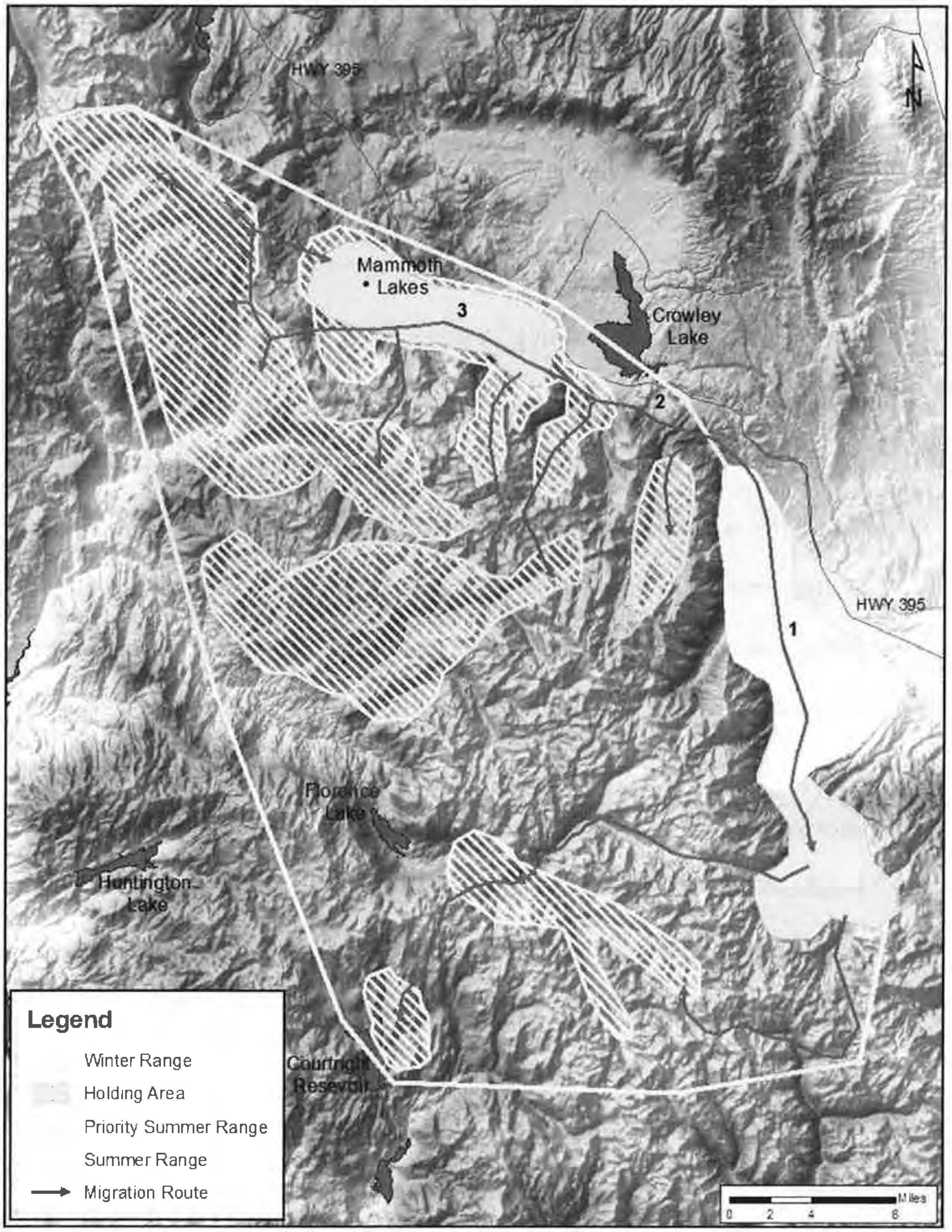


Figure 3-4: *Seasonal ranges and migration routes of the Round Valley deer herd. Numbered polygons or lines show designated "critical areas."*

mid-winter months. Blackbrush and ceanothus have lower and more variable levels in the diet. Spring diet is consistent with that of winter; bitterbrush, sagebrush, and ceanothus comprise >90% of RV deer spring diets (Kucera 1988).

Priority Areas:

Unlike the WW or CD herds, only three priority areas exist for RV herd (figure 3-4). These three areas, however, are more expansive than priority areas identified for other herds. Protection of these areas is crucial for the long-term persistence of RV population numbers; previous impacts within these areas contributed to current herd declines and serve to validate the overall need for protection of these areas.

1) ***Round Valley Winter Range*** – The entire winter range is considered of high priority for the RV herd. This range is concentrated and has lost habitat in the last 20 years through wildfires and development.

2) ***Round Valley Migration Corridor*** – Unlike the WW and CD herds, the RV migration corridor is narrow and restricted. This corridor extends from the southern Round Valley to Mammoth Lakes in the north and is bordered by steep mountains to the west, highway 395 to the east, and the city of Mammoth Lakes to the north. Migration routes extending off the major migration corridor and over the Sierra Crest are not considered part of this priority range. Three severe bottlenecks occur along the round valley corridor: (1) solitude canyon, (2) Mammoth Meadows, (3) and Crowley. Al-

though these bottlenecks are the most constricted portions, the entire corridor is narrow and considered of high priority.

3) ***Sherwin Holding Area*** – Round Valley deer use this holding area during spring migration, before crossing over the Sierra Crest. At a single time, over 2000 individual deer and 75% of the herd can be found within the Sherwin holding area, indicating it is heavily utilized (Taylor 2006a). Urban expansion from Mammoth Lakes has progressively reduced the size of the Sherwin holding area. Potential for future expansion creates concern for the future availability of the Sherwin holding area.

Round Valley Density Analysis

Between the years of 2002 and 2004, GPS radio-collars were monitored non-continuously on 37 individual deer that winter in the Round Valley. These data (figure 3-5) allow for an alternative quantitative method to delineate herd ranges – a point density analysis. If the results from this analysis match closely with the results from range delineation based solely on expert opinion, this increases confidence in the Round Valley range delineations. Ideally, a quantitative analysis would be used to cross-check boundaries for all three focal deer herds. GPS data, however, are not available for the West Walker or Casa Diablo herds. Since similar qualitative techniques were used to create all three herd maps, it seems safe to assume that accuracy levels should be similar for all three herds. A quantitative cross-check of Round Valley range delineations should serve as a suitable surrogate for the accuracy of the West Walker and Casa Diablo range delineations.

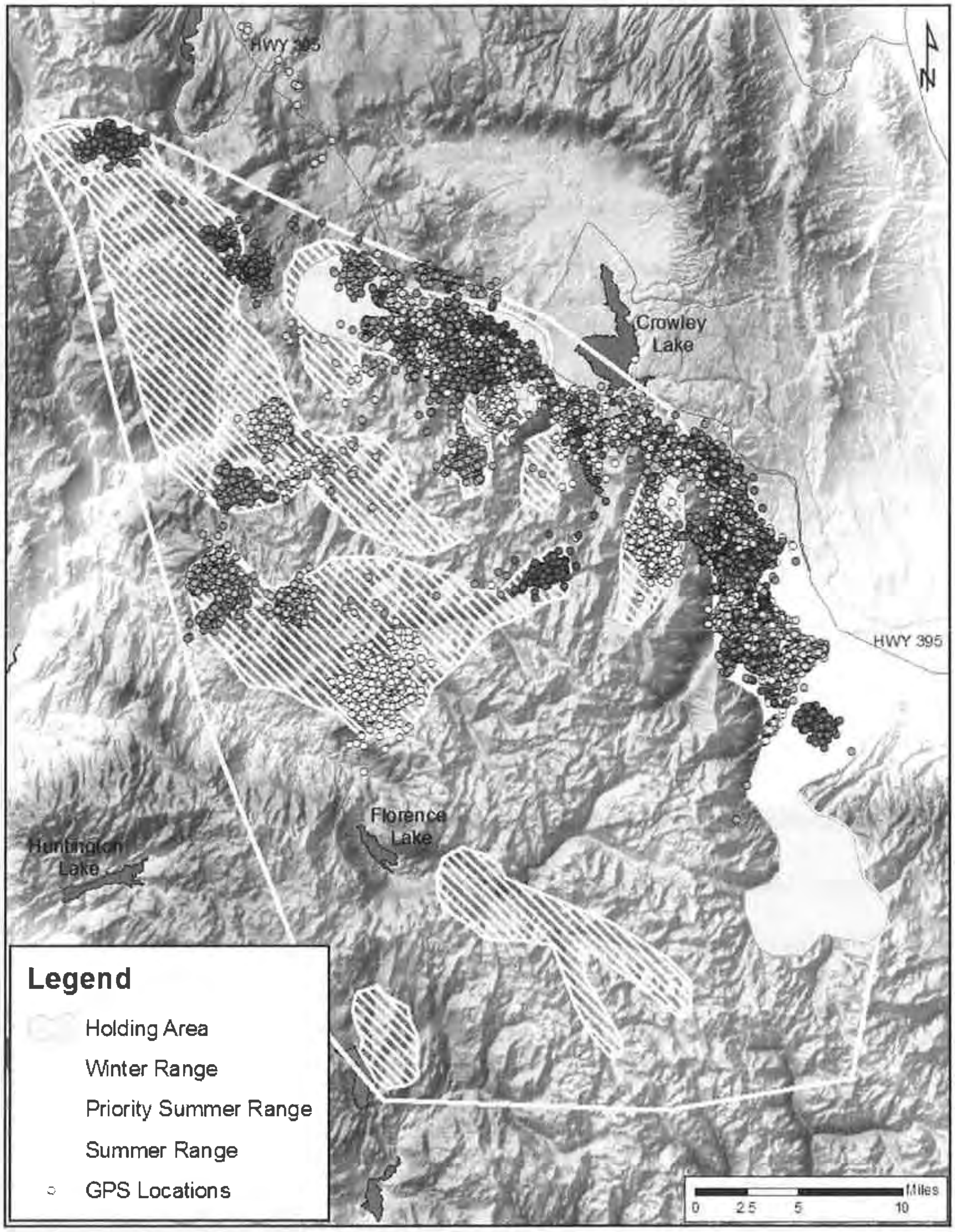


Figure 3-5: *GPS collar point locations of 37 Round Valley mule deer. Each individual deer is represented with a different color.*

Population density analysis shows where deer tend to congregate or where individual deer spend large amounts of time by identifying areas where point locations are concentrated. The fixed Kernel density estimator tool calculates a fixed kernel density estimate using the quartic approximation of a true Gaussian kernel function (Spatial Ecology 2006). Figure 3-6 shows the kernel density estimate for point locations during spring migration (April, May, and June). These results match expected distributions based on current range delineations. Point densities occur in the northern Round Valley winter range, along the major migration corridor, and in the Sherwin holding area. Kucera found that Round Valley deer leave winter range anytime between the beginning of April until the end of May. These deer rested in a holding area for several weeks, leaving to cross the Sierra crest between mid-may and the end of June. This same pattern was repeated for several years, regardless of the amount of snow on the ground (Kucera 1988). Based on Kucera's research, deer densities would be expected to be highest in the winter range, holding areas, and along major migration corridors, which is the exact result produced by the kernel density estimate. A few density clusters occur within summer range. These clusters probably represent individual deer that moved into summer range in late May or early June, thereby producing up to a month of point locations in a small area.

The Point Density tool "calculates the density of point features around each output raster cell. Conceptually, a neighborhood is defined around each raster cell center, and the number of points that fall within the neighborhood is totaled and divided by the area of the neighborhood" (ESRI 2005). Figure 3-7 shows point density analysis for point locations during spring migration (April, May, and June) displayed as a stretched value. Results are similar to kernel density estimates, with highest point densities occurring in winter range, holding areas, and along the major migration corridor (Figure 3-7). These results validate the accuracy of previous range boundary maps.

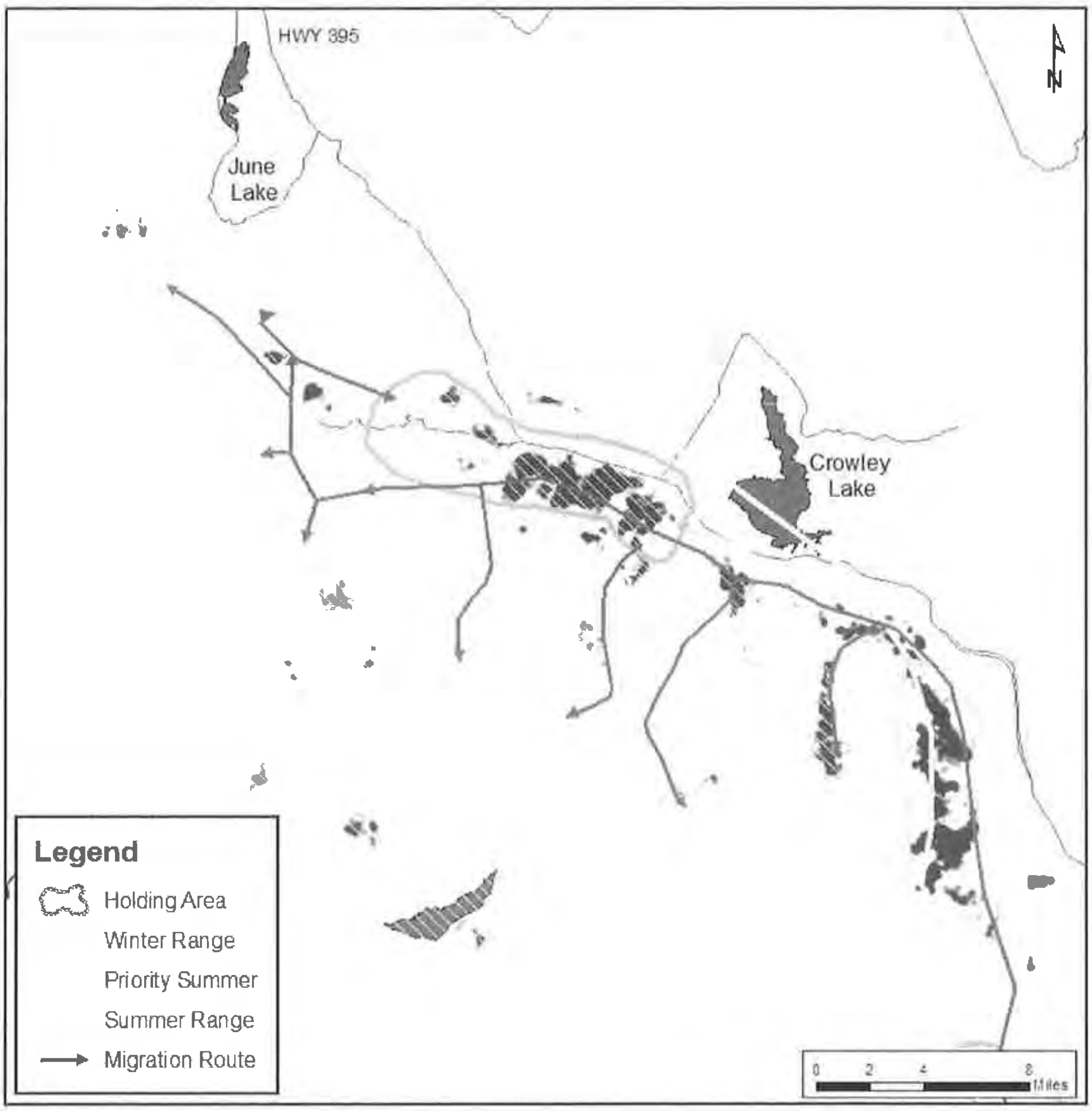


Figure 3-6: *Kernel density estimate for deer point locations during April, May, and June.*

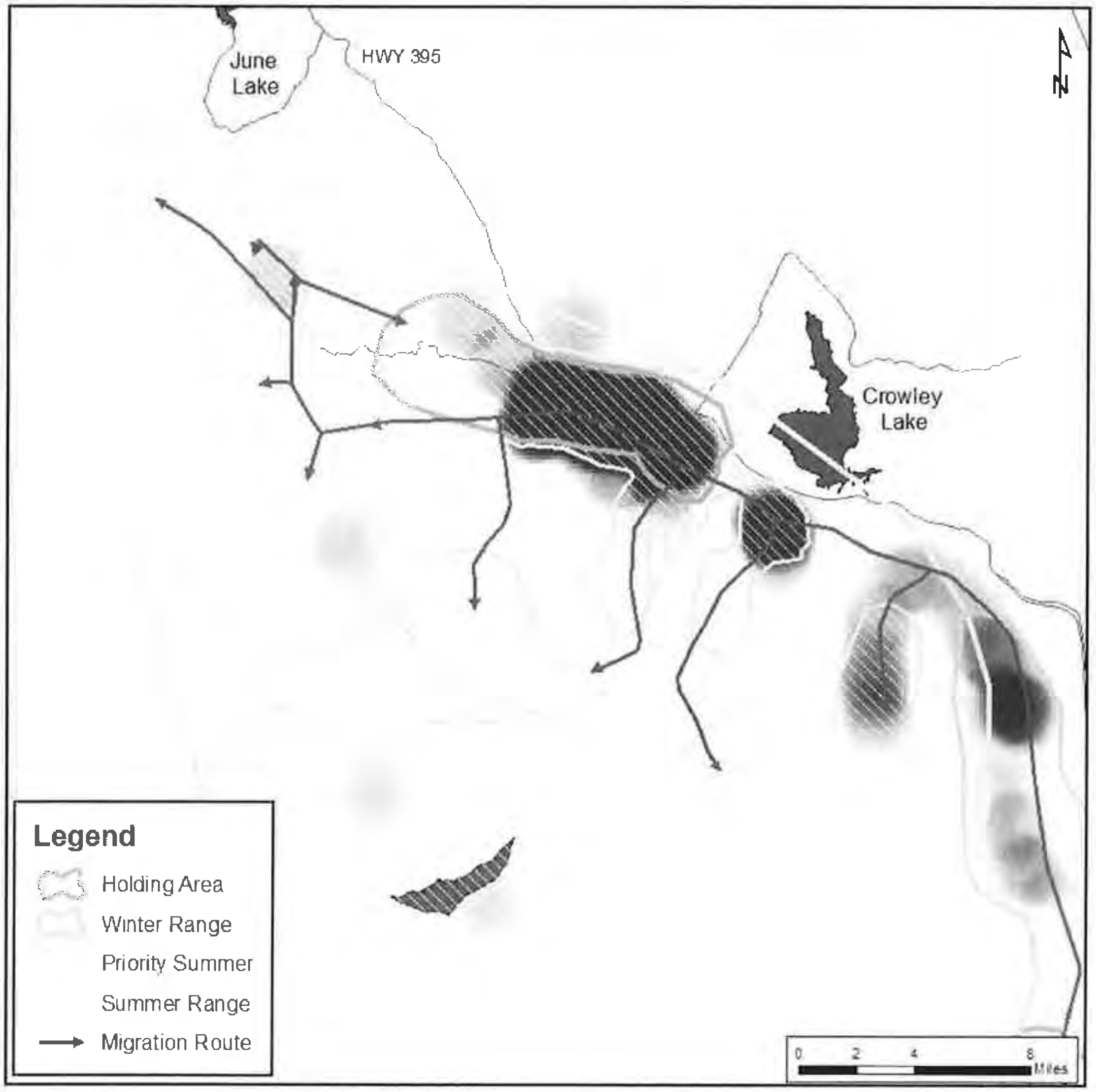


Figure 3-7: Point density analysis for deer point locations during April, May, and June.

Interestingly, point densities occur only in the northern range of the Round Valley herd. Figure 3-7 indicates that no individual deer from this study migrated south or utilized the southern holding area or summer range. Kucera found that 74% of deer in his study migrated north from winter range. He explains this noting that summer range to south is largely higher, rockier, and less vegetated than areas to the north, and it supports fewer deer (Kucera 1988). According to biologist Tim Taylor, approximately 70% of the Round Valley herd migrates north, but this number has dropped into the 60% range in recent times (Taylor 2006a). Since only 37 individual deer were fitted with GPS collars, it is possible that southern migrants were randomly excluded from the analysis. The sample could also be biased based on where deer were captured on the winter range. Regardless, enough sources (Kucera 1988, Kucera 1992, Taylor 2005, Bleich 2006) validate the presence of a small southern migration route to include it in the Round Valley herd range map.

Kernel density estimates and point density analysis performed on other seasonal categories (chapter 2 offers a complete list of categories) gave similar results to the spring migration analysis. In all situations deer densities occur in locations expected by current range maps, and provide support for the overall accuracy of the Round Valley deer distribution map.

Movement Paths

Although kernel density and point density analysis give some indication of major migration corridors, results are overpowered by the fact that individual deer spend most of the migration period on winter range and holding areas, and only a short amount of time in movement between the two. To determine what percentage of radio-collared deer made use of the major migration corridor, I converted point locations into movement paths for each individual animal then visually examined each movement path compared to the previously delineated migration route. Figure 3-8 shows movement paths for two individual deer as an example of this process. Overall, movement paths match closely with the main migration corridor between the Round Valley and Sherwin Holding area; 72% of monitored deer used the major migration corridor. Of the deer that did not demonstrate use of the major migration corridor, 90% were only monitored during winter months (Nov – Mar) and would not be expected to show migration patterns during this period. This means that 96% of deer monitored during spring migration moved through the major migration corridor. Movement off the holding area into summer range varied considerably between individual deer. These results support the suggested Round Valley migration corridor.

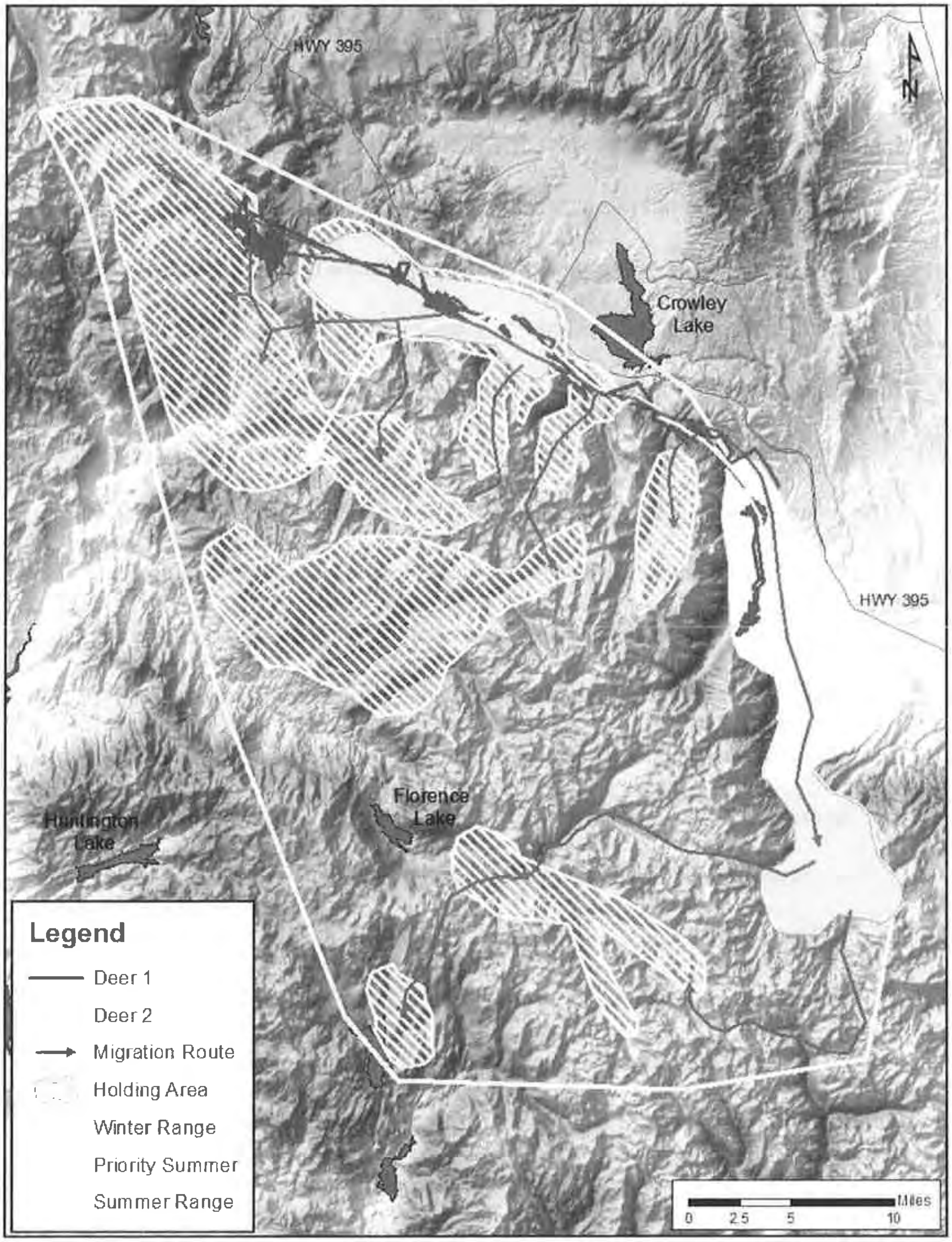


Figure 3-8: *Movement paths for 2 individual deer from the Round Valley herd shown in red and yellow. Green movement paths delineate the overall migration routes for the Round Valley herd.*

Chapter 4: Threats to Mule Deer Habitat

Habitat loss is widely recognized as the most important factor affecting current rates of species extinctions (Groves 2003). It is intuitively understood that all species require some amount of quality habitat to persist and flourish. Mule deer are no different. Ultimately, mule deer abundance and population health are determined by the quality and availability of habitat. As habitat is destroyed or degraded, mule deer populations either adapt to the new changes or diminish in size and ultimately disappear. Mule deer are known for widespread adaptability; they appear in a variety of habitat types throughout western North America and can often co-exist and even increase their numbers in the face of human-induced changes. Some habitat alterations, such as agricultural developments, even benefit deer populations. Compared to many species, deer are, in general, highly successful when faced with human presence – but there is undoubtedly a tipping point beyond which numbers decline. If habitat conversions exceed a certain threshold or occur in critical areas deer populations ultimately suffer. Although the effects of habitat loss are not always easily predicted, it is clear that mule deer conservation requires the protection of important habitat. In addition, if deer are to function as an umbrella species, as proposed in this thesis, habitat protection will benefit many co-existing species.

In this chapter, I explore several threats to mule deer persistence, all directly related to habitat loss or degradation, and their potential for occurrence in the eastern Sierra. The manifestation of these threats appears as urban development, catastrophic wildfire, deer-vehicle collisions, energy exploration, and livestock grazing. If mule deer and other species that share habitat are to remain a fixture in the eastern Sierra, each of these threats needs to be addressed and dealt with appropriately.

Urban Development

Urban development is occurring on a widespread scale in the western United States. Between 1992 and 1997, 5.4 million acres of farmland, forest, or other open spaces within the western U.S. were developed (Lutz and others 2003, 22). There is no reason to believe that this process has decreased in magnitude since then. Urbanization affects mule deer habitat in many ways, both negative and positive. Natural habitat is typically lost or altered as buildings, roads, and fences appear on the landscape. Migration routes can be blocked by development, and pets such as dogs can deter deer from coming near developed areas. And in some situations, urban development can increase the density of deer populations. Open spaces such as parks or backyards provide suitable deer habitat and ornamental shrubs and flowers provide plentiful forage (Lutz and others 2003, 22). In many places, as in the Front Range of Colorado, deer populations irrupted following the onset of urban development. With population increases came numerous new management problems. Heavy browsing on backyard plants makes homeowners angry; there are increases in deer-vehicle collisions and corresponding safety issues; and predators including mountain lions may be attracted to suburban neighborhoods where deer density is high (Lutz and others 2003, Baron 2004). Although deer populations may flourish in semi-urban habitat, these situations ultimately become the seeds of a disaster more than a successful act of conservation and ultimately fail to benefit either human communities or mule deer populations. Protecting natural habitat is a preferable method to maintain mule deer populations without associated societal problems.

Habitat protection in the eastern Sierra Nevada — as anyplace — is a complex process. Land ownership is a mélange of public and private land. The large proportion of land under public management reduces the potential for development. This is advantageous for the protection of habitat and is undoubtedly one of the primary reasons that such a rich diversity of wildlife and plants still exists. Despite an abundance of public lands, important wildlife habitat frequently occurs on privately owned land; mule deer habitat is no exception. As communities such as Bishop, Mammoth Lakes, or Walker expand, undeveloped private parcels are faced with increasing pressure for development. Limited availability of private land amplifies development pressure and skyrockets land values. Land uses such as ranching cannot compete economically with stratospheric income from land sold for subdivision and development. Although many ranches are not yet sold and converted, it appears to be only a matter of time before more profitable land uses win out and most remaining ranchlands are developed.

This bodes ill for mule deer conservation. If mule deer herds are to continue to flourish in this region important private parcels need protection as natural habitat. This can be done through many techniques: conservation easements, land use planning, or creation of wildlife refuges. These techniques are discussed in depth in chapter five. Regardless of the methods used to conserve habitat, it is first imperative that high priority areas be identified for each herd. These areas occur primarily on priority habitat that faces the possibility of future development.

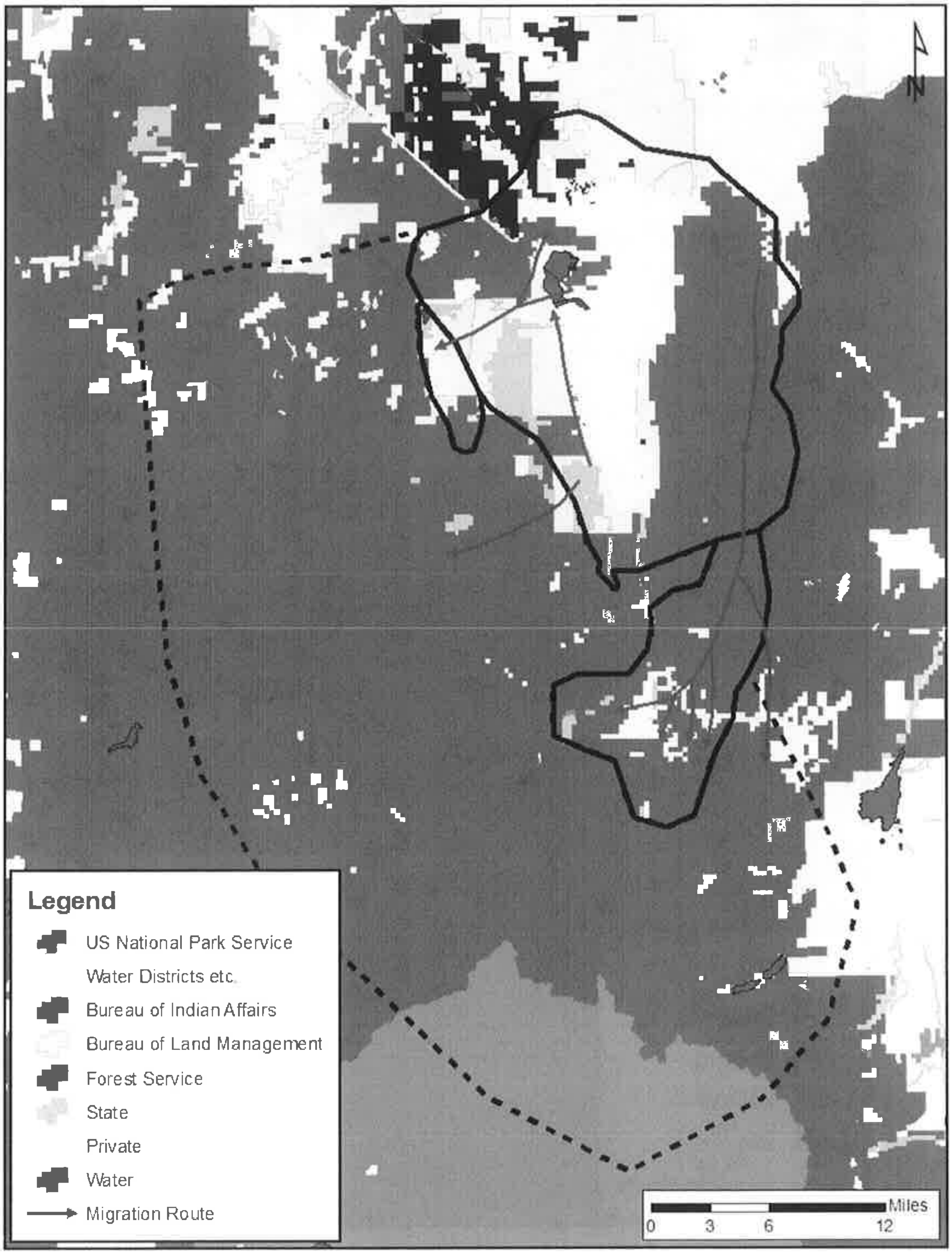


Figure 4-1: *Land ownership within the WW range. Seasonal range boundaries are outlined in black.*

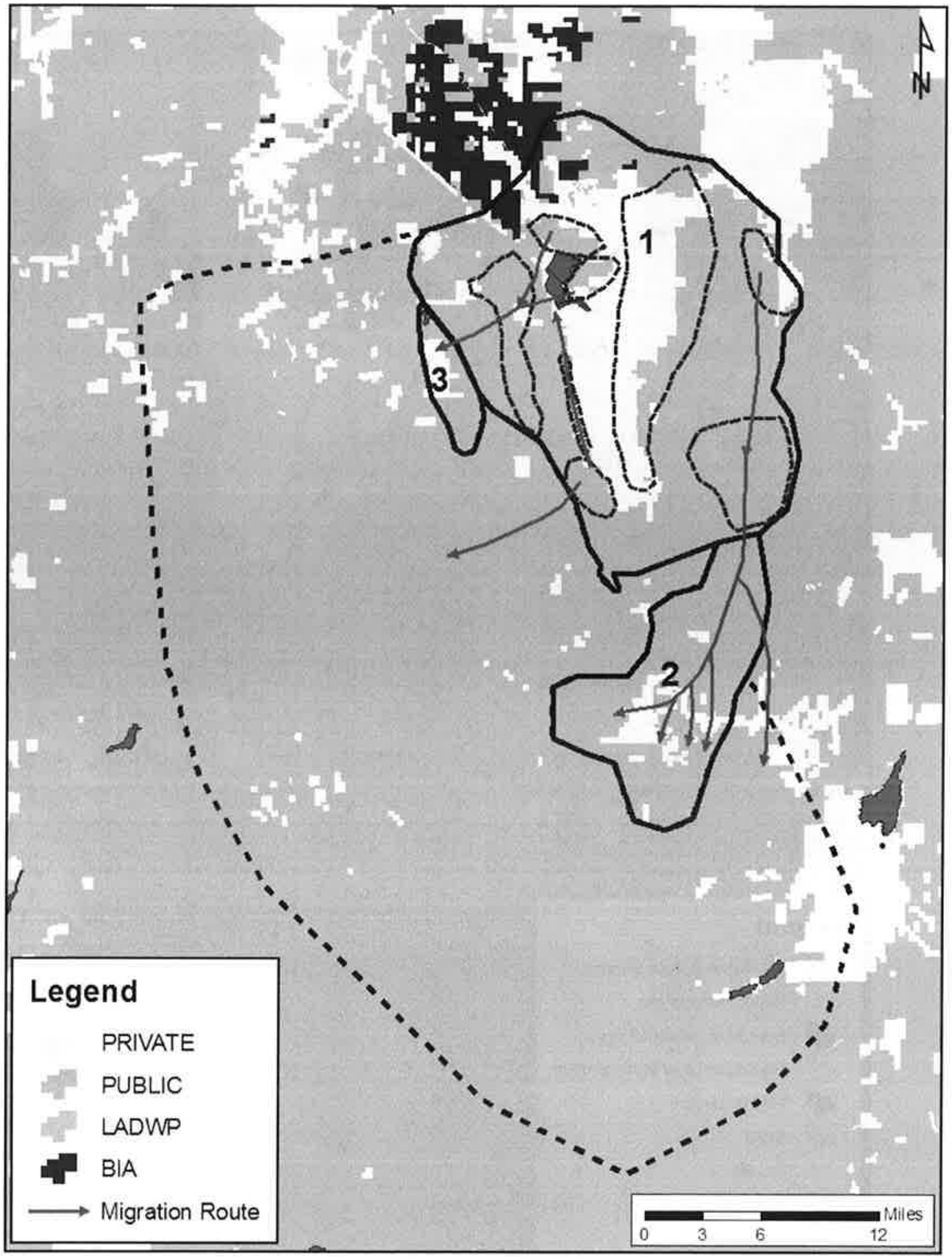


Figure 4-2: *Public vs. private land within WW range. Numbered areas represent high risk critical range.*

West Walker Herd

Private land in the WW range occurs primarily in winter habitat and holding areas. Summer range is dispersed and found almost entirely on national forest or national parklands. The few private in-holdings on summer range are not of major concern (figure 4-1).

Although different public lands offer varying levels of protection for wildlife species, in terms of urban development, they are generally considered at lower risk than private land. For extensive development to occur on public land, it generally first has to be sold or exchanged for private in-holdings. Within the WW range, there are no current proposals for either of these options, nor do they seem likely in the near future. The blue-yellow contrast in Figure 4-2 distinguishes between public and privately owned land. Two additional categories are included, the Los Angeles Department of Water and Power (LADWP) and Native American Lands (BIA). These two ownership types don't behave exactly the same as privately owned land, but still present an elevated possibility of development. Private areas that occur on priority habitat are numbered (1-3); these areas not only provide important habitat, but are at risk for future development.

1) **West Walker Winter Range:**

Winter range for the WW herd is concentrated in a relatively small area. Although some sites (designated as priority areas) provide particularly important habitat, the entire winter range is essential for this herd. Figure 4-3 shows private land on the WW winter range. A high percentage of this land is now in large (>40 acres), minimally developed parcels. As Minden and Gardnerville (Nevada) continue to develop in the north, it seems likely that pressure for development will slowly diffuse into this region (Newbry 2006). These effects are already being seen on a small scale. Last year alone, there were five (or six) subdivisions established in the town of Walker (Newbry 2006). The Topaz Ranch Estates continue to grow and currently has the potential for 650 additional units (in 2 acre minimum lots) without building additional infrastructure; there could be an additional 3000–4000 units if new infrastructure such as a sewer and water system is added. The Douglas County Planning Department anticipates an application for the 650 units within the next year (Moss 2006). Current zoning (figure 4-4) does not accommodate subdivision in most areas outside of existing communities. This coincides well with mule deer conservation and would be helpful if maintained. It is impractical to stop all development; ideally, future building should be nested around current communities such as Walker, Coleville, Topaz, or the Topaz Ranch Estates. Outside of these communities, subdivision should be restricted to parcel sizes larger than 10-15 acres with regulations on fences and free-roaming pets. Opinions vary among planners on whether the Antelope Valley and surrounding areas are likely to be developed. Some believe widespread subdivision is inevitable; others claim the combination of Master Plans and the local political environment make development unlikely. Despite this unpredictability, now is an ideal time to implement conservation efforts. Large tracts of undeveloped land still exist within the region, and urban growth has not yet become so intense to drastically inflate land values.

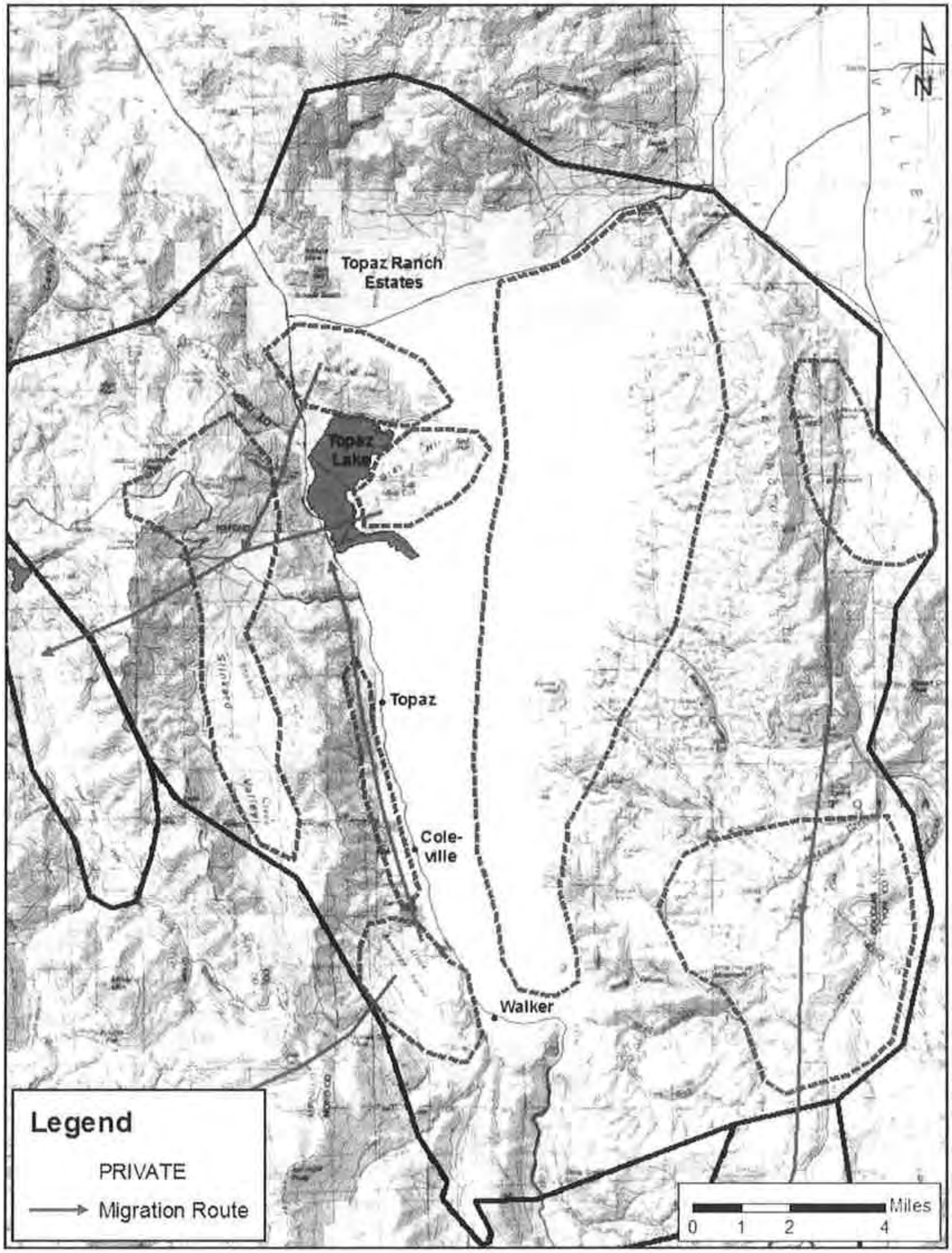


Figure 4-3: *Privately owned land in WW winter range. Dashed blue lines encompass critical winter habitat, although the entire winter range is important for this herd.*

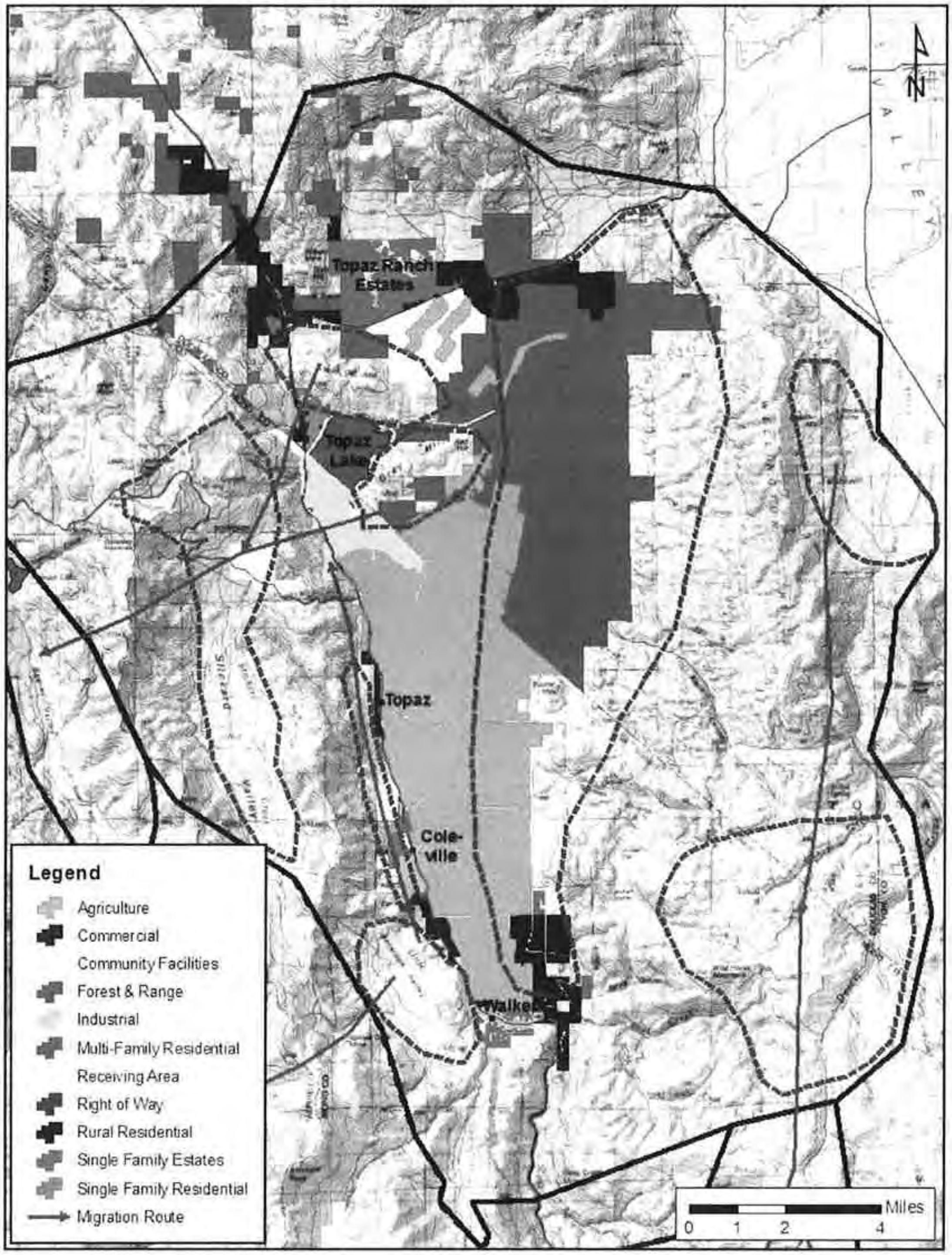


Figure 4-4: Land use designations on West Walker winter range.

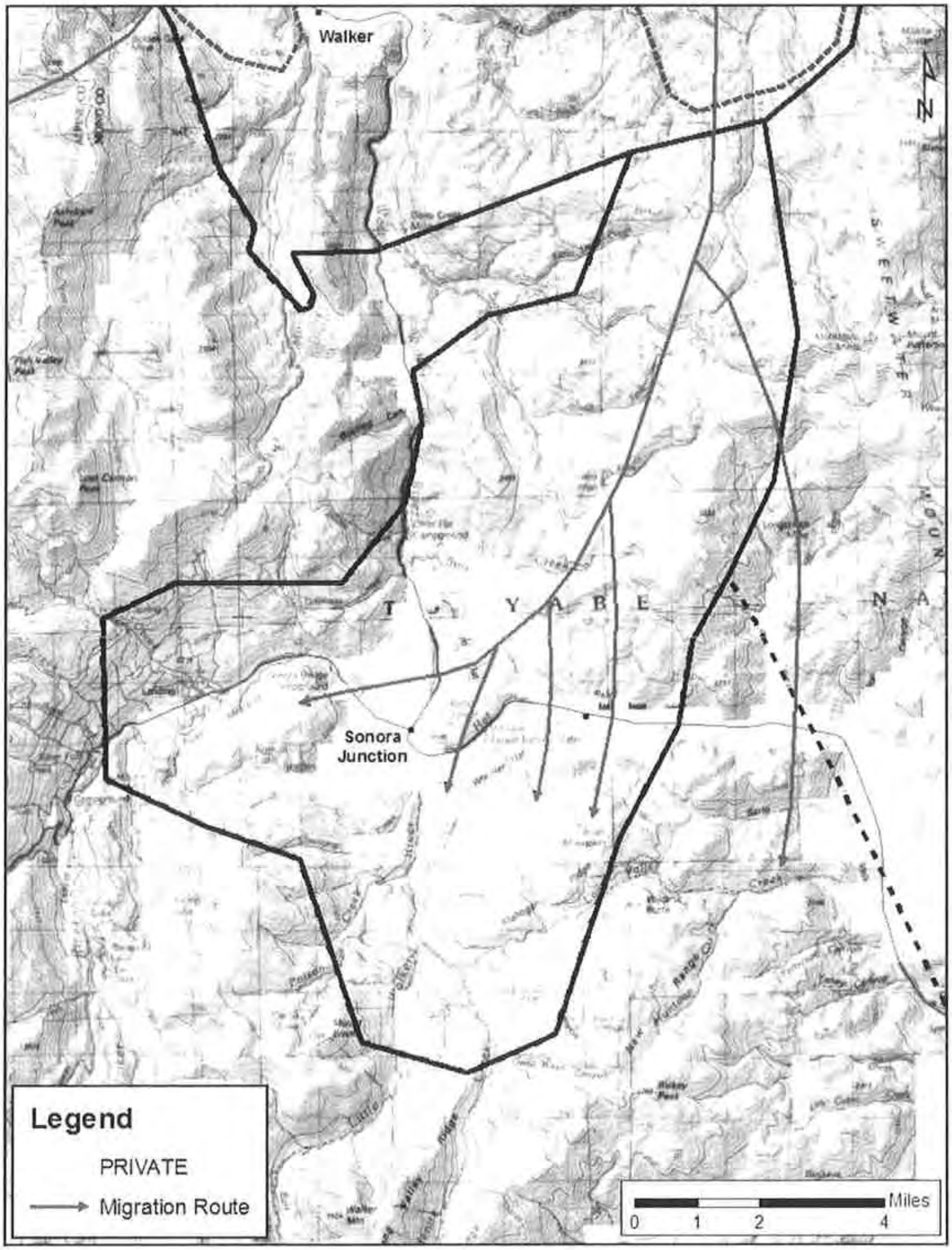


Figure 4-5: *Privately owned land near Sonora Junction could create a potential barrier to migration.*

2) Sonora Junction Migration Route

A corridor of private land runs along highway 395 and across the Sonora holding area. This corridor has the potential to block the major migration route into summer range for the WW herd. Already, Hwy 395 serves as a partial barrier to deer migration, clearly demonstrated by the high number of deer-vehicle collisions that occur within this region (figure 4-16 and 4-17). Intense subdivision creates many barriers to movement, including fences, buildings, and domestic dogs. Subdivision in this region would also increase traffic volume along hwy 395, contributing to already existing problems with deer-vehicle collisions. In addition to potential impacts on deer, an important sage grouse lek occurs on private land to the south of the Sonora Junction.

Currently, all parcels in this region are zoned as resource management.

3) Bagley Valley Holding Area:

A large in-holding of private land occurs in the Bagley Valley holding area. Development pressure is minimal and not a major cause for concern. This area should be monitored for future threat, but no current action is necessary.

Casa Diablo Herd

The vast majority of CD range occurs on public lands (figure 4-6). Overall, development is not a significant threat for the CD herd. Two priority areas exist that could potentially be cause for concern. These areas are identified in figure 4-7. The Bald Mountain holding area (#1 in figure 4-7) is particularly important because it provides habitat for several other wildlife species such as migratory waterfowl and raptors.

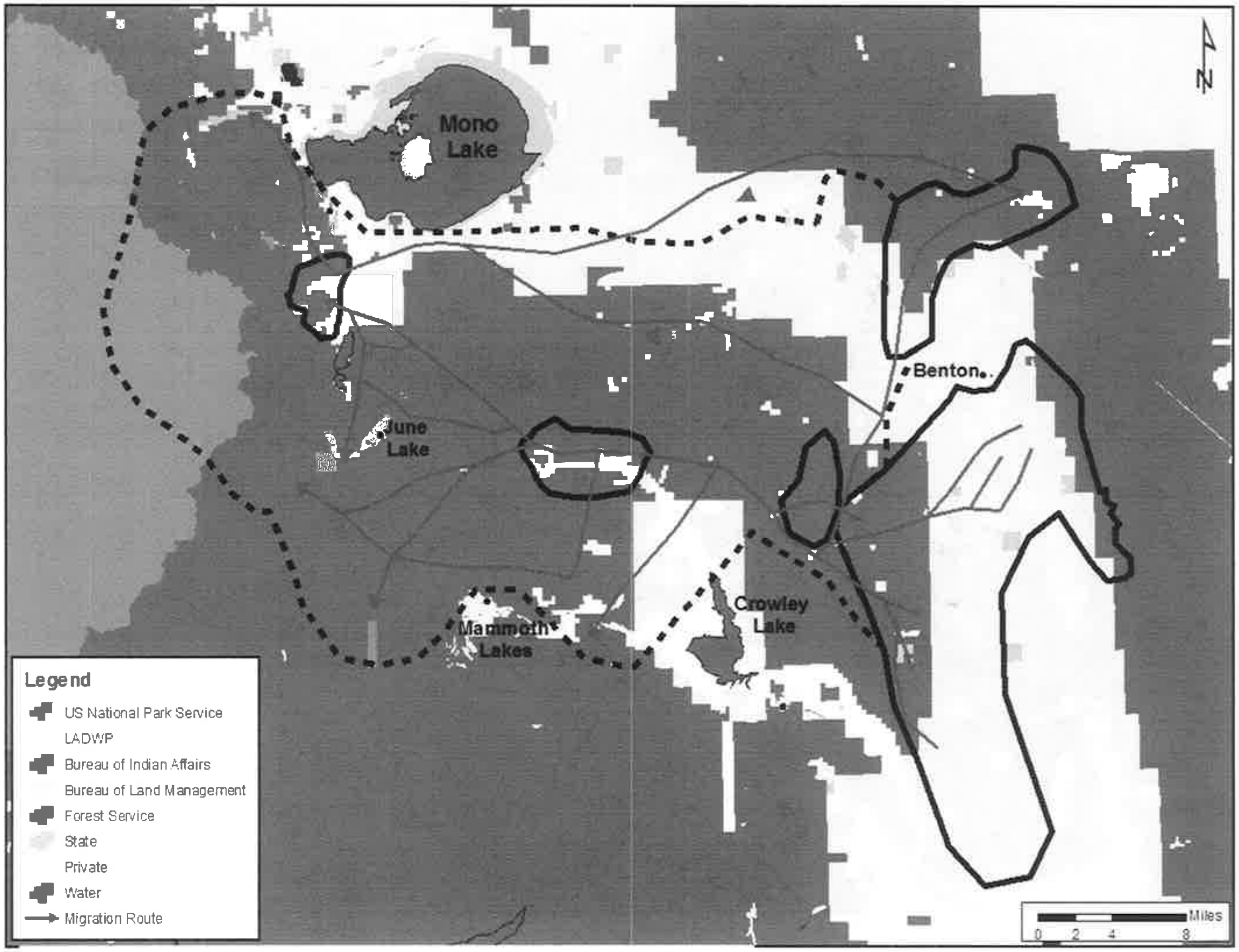


Figure 4-6: *Land ownership within Casa Diablo seasonal ranges.*

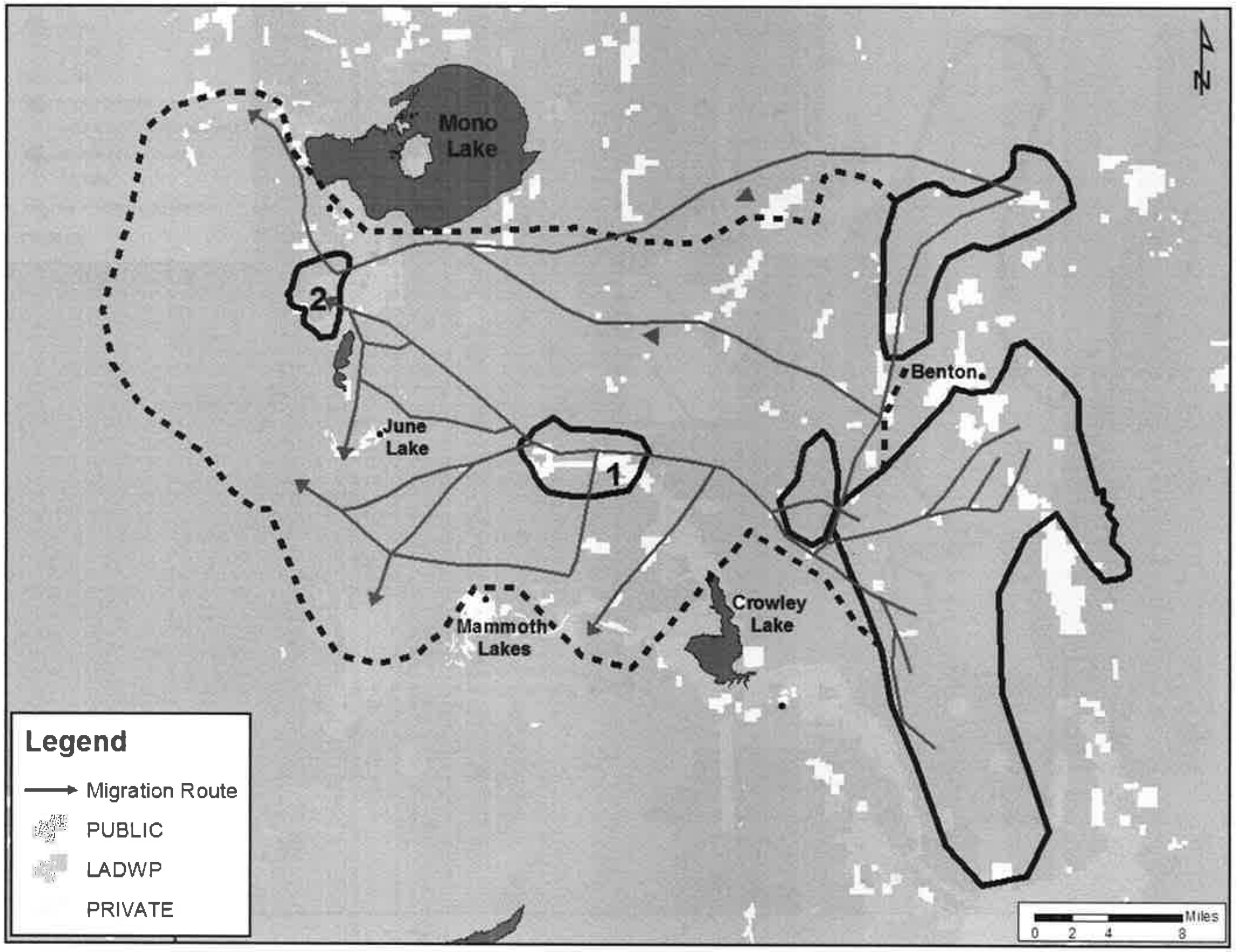


Figure 4-7: Public vs. Private land in the Casa Diablo Range.

1) Bald Mountain Holding Area:

Private land creates a corridor around the Owens River and its tributaries within the Bald Mountain holding area. These riparian zones are valuable locations for deer and other wildlife species, particularly in the dry climate and environment of the eastern Sierra. Currently, there is one development proposal along the base of the Owens River (Taylor 2005); the combination of close proximity to Mammoth Lakes and high scenic value makes future development likely. Currently, all parcels are zoned for "Agriculture" and exist as large ranches. Maintaining these ranchlands is a high priority for conservation of CD herd and wildlife habitat in general.

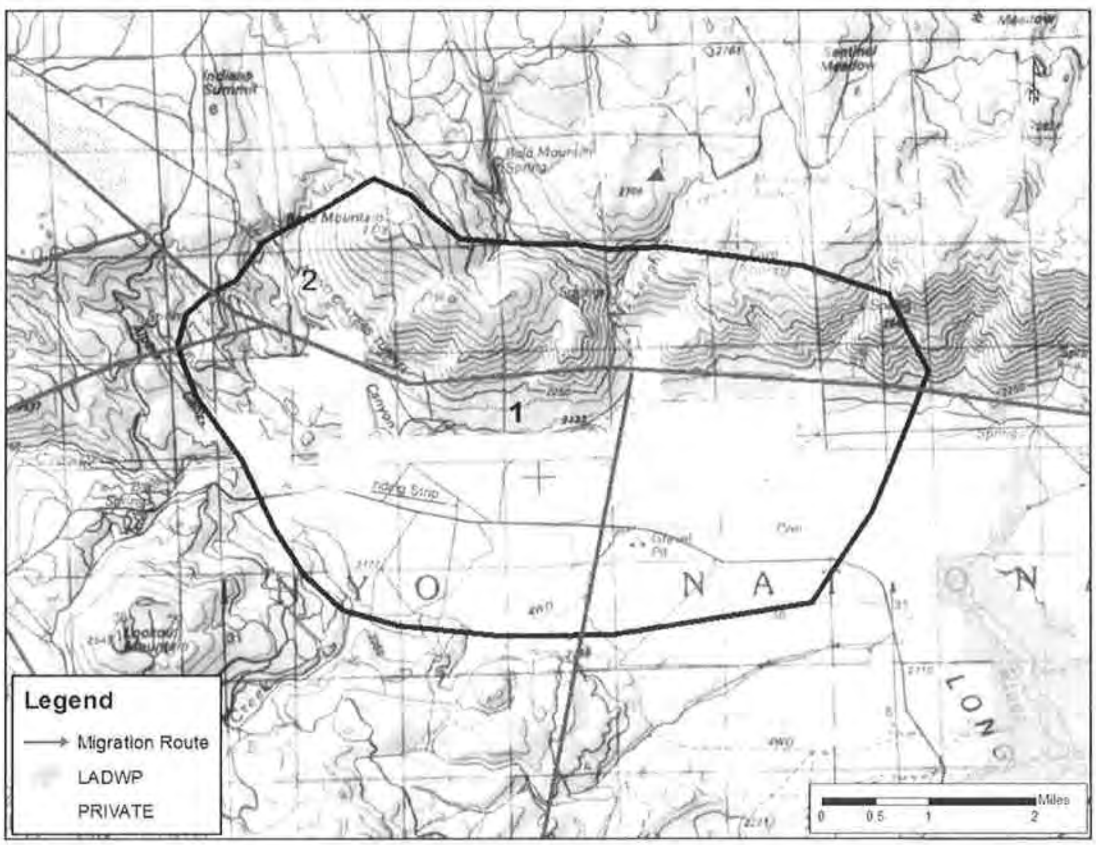


Figure 4-8: Bald Mountain Holding Area

2) **Bohler-Sawmill Canyons Holding Area (HA-2) and Priority Summer Range:**

The LADWP (Los Angeles Department of Water and Power) is a major landholder in Mono and Inyo counties (California). LADWP land currently exists as open space, but it is not reserved in any protective status. As land values increase, there is nothing to prevent the City of Los Angeles from deciding to develop portions of their property. If water use restrictions such as xeriscaping are included in development, the land potentially could be subdivided with minimal impact on the Los Angeles water supply (Newbry 2006). This particular area is in close proximity to the communities of Lee Vining and June Lake. Consequently, if LADWP ever decided to subdivide, this would be a prime spot. This land provides important fawning habitat and spring holding area for CD deer.

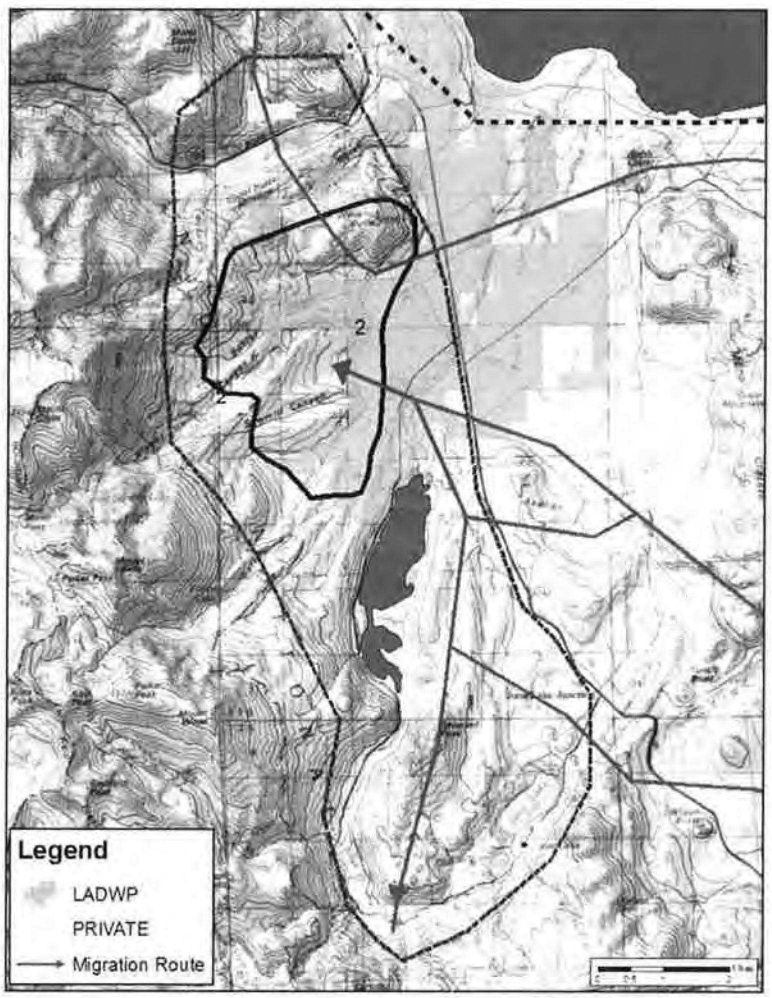


Figure 4-9: HA-2 and critical summer range.

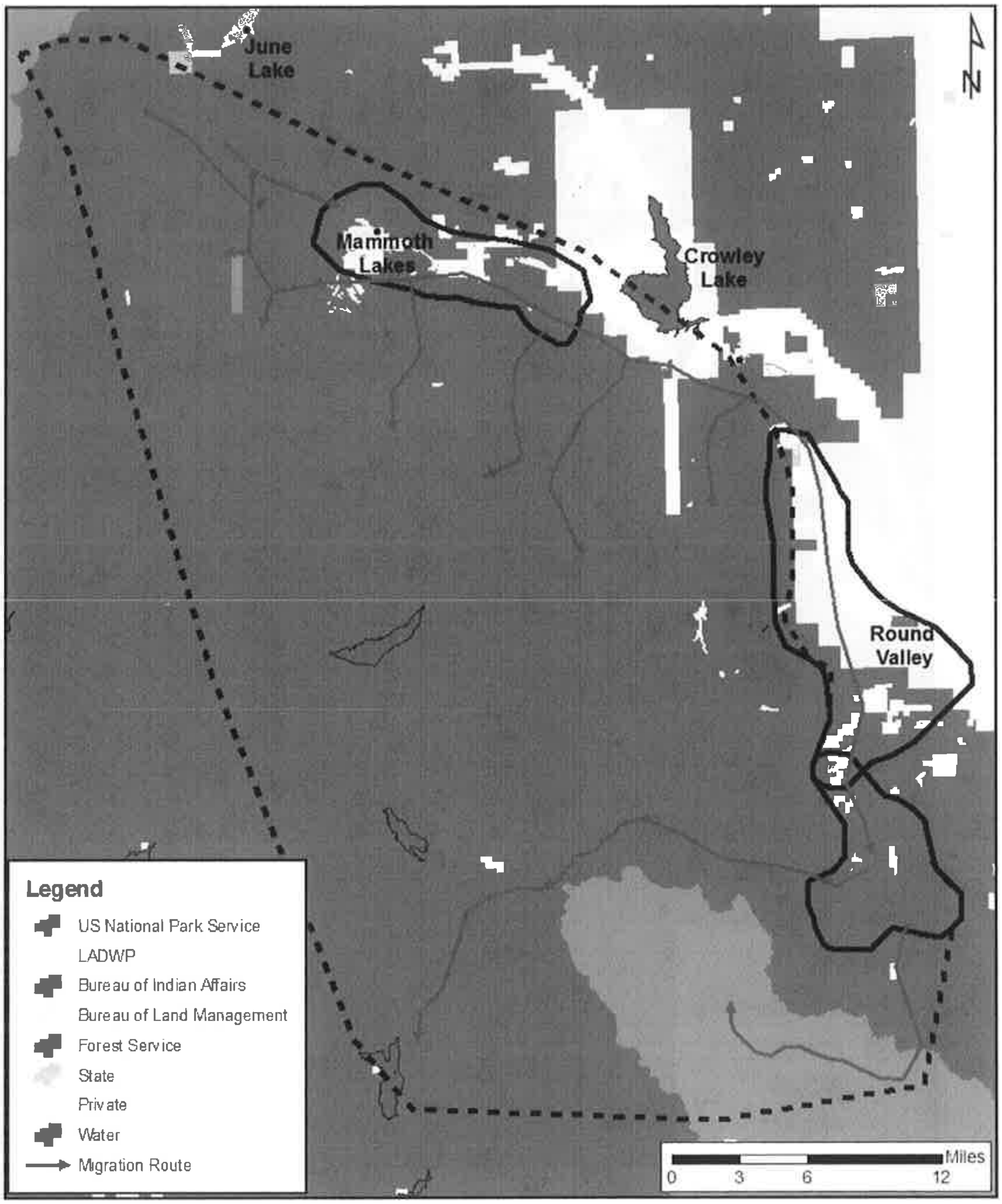


Figure 4-10: *Land ownership within Round Valley seasonal ranges.*

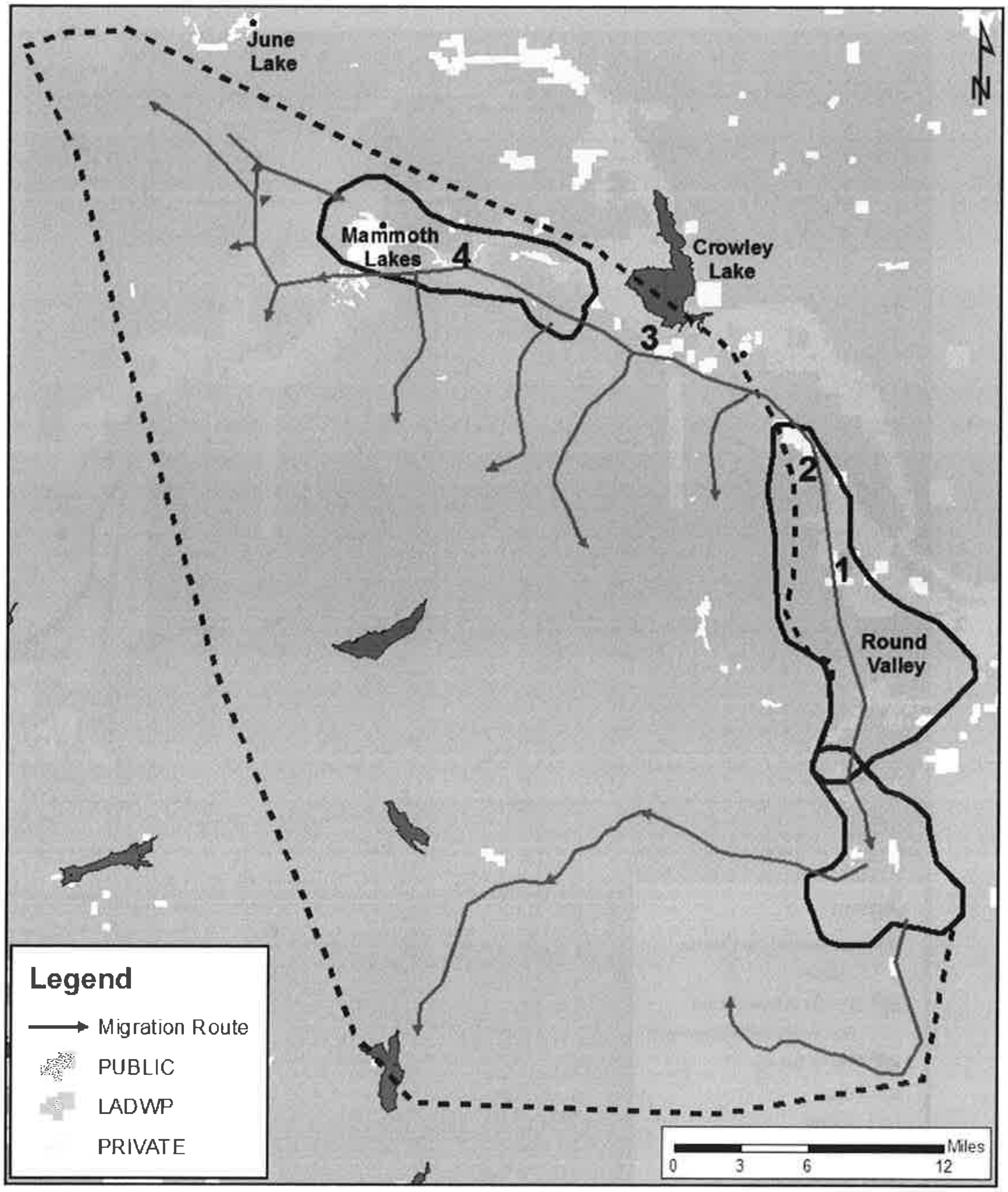


__Figure 4-11:__ Public vs. Private land in the Round Valley Range.

Round Valley Herd

In terms of urban development, three concerns exist for the RV herd: barriers to the Round Valley migration corridor, major habitat alterations in the Sherwin holding area, and major habitat alterations in low elevation winter range. Despite the fact that the majority of habitat for this herd occurs on public lands (figure 4-10), LADWP and private parcels occur in key positions along the migration corridor and winter range, giving only a small area of land the ability to dramatically impact the RV herd. Four locations in particular create concern over extensive development (figure 4-11):

1) Round Valley Winter Range:

Use of winter range varies depending on winter severity and timing. When snow accumulation is light, RV deer will move into steep canyons west of Rovana (figure 4-12). When snowpack becomes excessive, low-elevation range in the Round Valley is crucial. This land is primarily owned by LADWP or private landowners. Close proximity to Bishop and Mammoth Lakes and extraordinary scenic value place this area at a high likelihood of development. A subdivision proposal is currently in process in Rovana, in which an 80-acre parcel near Pine Creek will be subdivided into eight 10-acre parcels. According to the Inyo Planning department, restrictions on free-roaming dogs and wildlife-harmful fences will be implemented with this development (Larsen 2006). If these restrictions are enforced the only significant impact will be increased traffic in the Valley and a small amount of habitat conversion. Although this one subdivision will probably not have a strong negative impact, if this trend continues and lots are further subdivided, winter habitat could be severely affected, especially if a similar pattern follows on LADWP land.

2) Swall Meadows Migration Bottleneck:

As deer move north in springtime, the migration corridor passes through several bottlenecks, the first of which occurs at Swall Meadows (figure 4-12). This area is bordered by steep ridges and consists almost entirely of private land, zoned as residential. Three conservation easements protect several acres within this corridor, but many parcels that currently permit passage face the possibility of future subdivision. This could have a massive impact on northern migration for RV deer. Recent subdivisions and increasing land values make the potential for future development in Swall Meadows extremely high. Protection of the Swall Meadows bottleneck is of critical importance for the RV population.

3) Crowley Migration Bottleneck:

A second migration bottleneck occurs near Aspen Spring and the community of Crowley. Bordered by steep mountains to the west and water to the east, deer moving north are left with few options. The community of Crowley is already reasonably developed. Regulations restricting free-ranging pets and requiring wildlife-friendly fences should be implemented and enforced. Future subdivision should be limited to ensure continued passage.

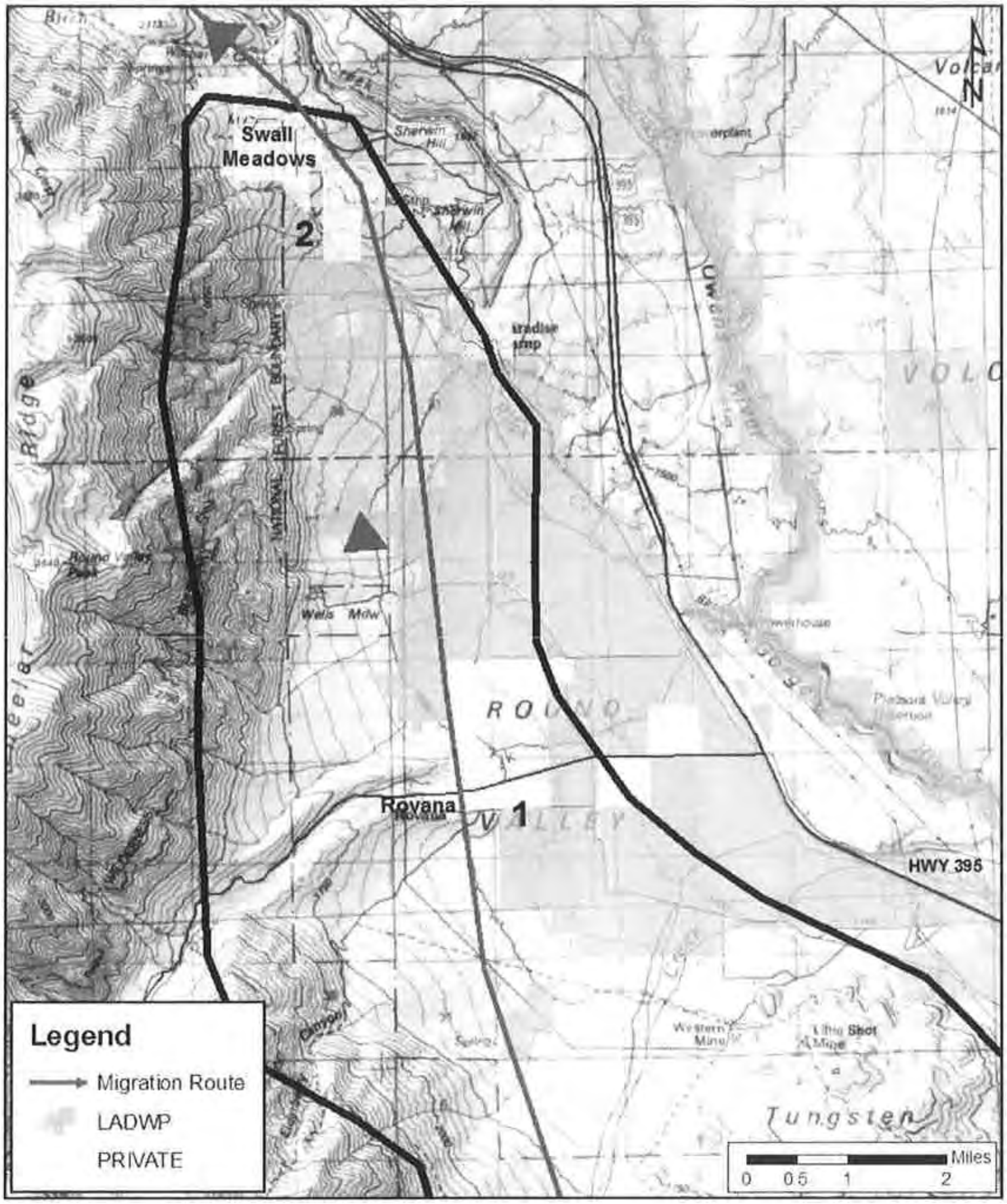


Figure 4-12: Northern Round Valley winter range and Swall Meadows migration bottleneck

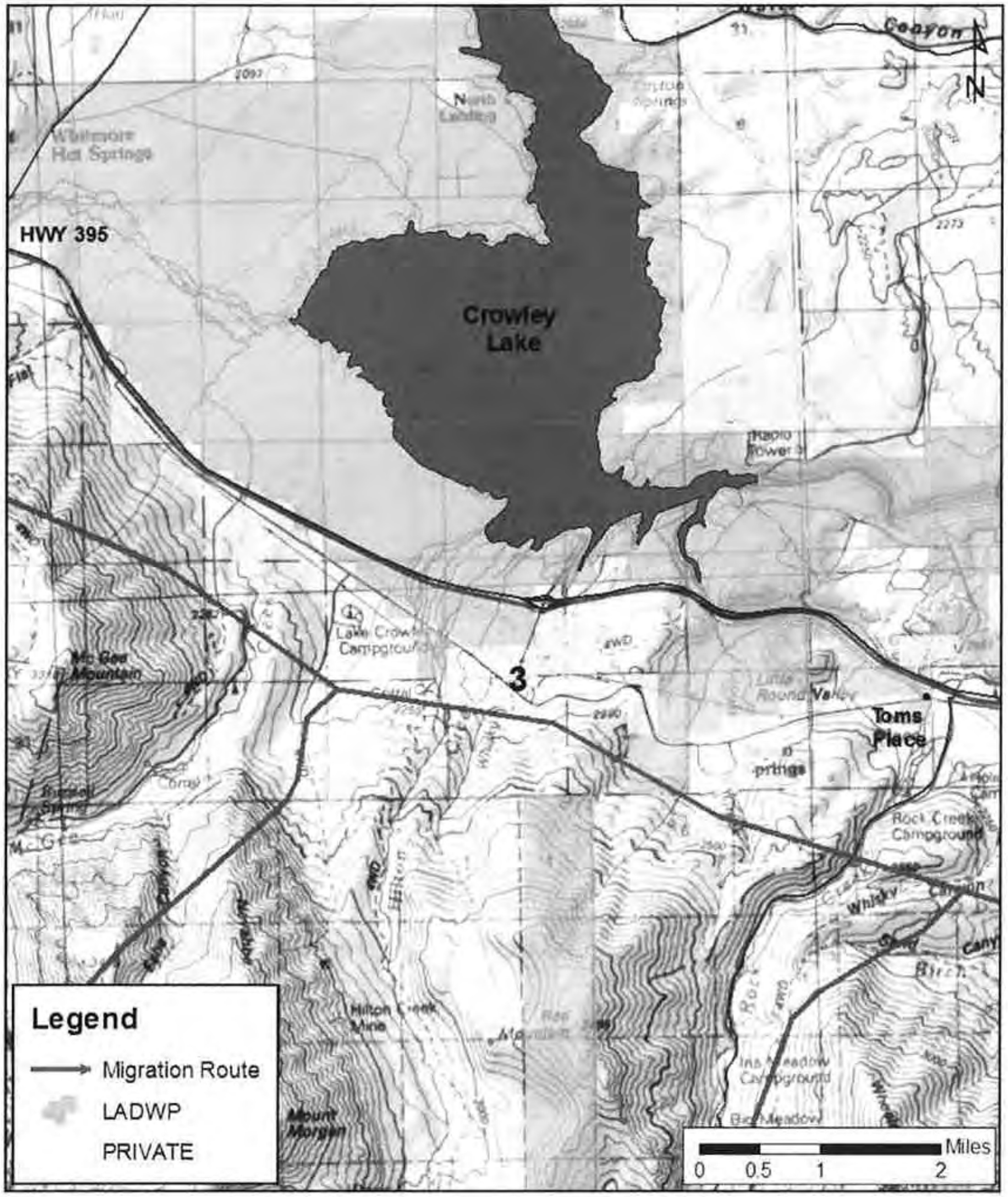


Figure 4-13: Crowley migration bottleneck

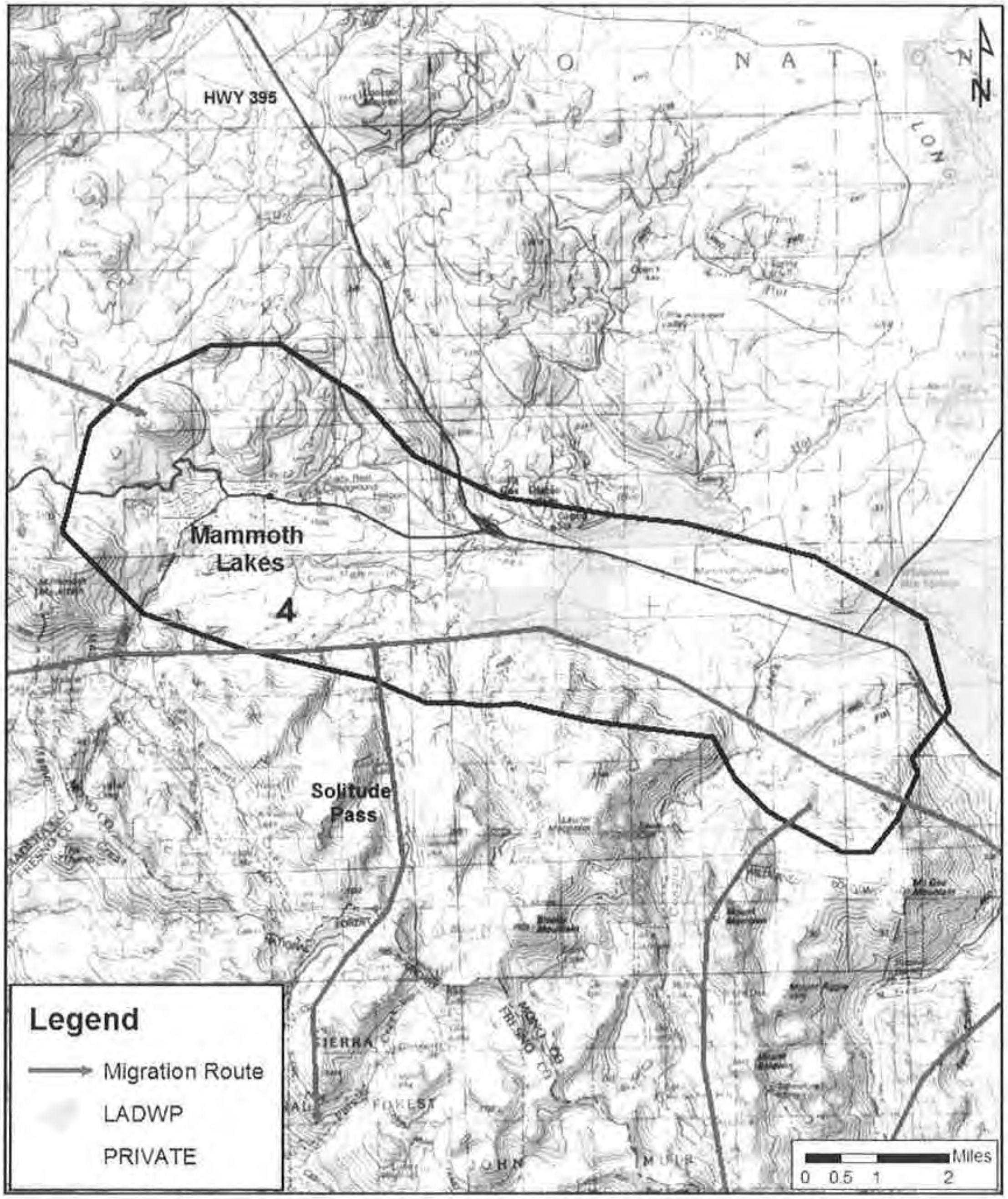


__Figure 4-14:__ Sherwin Holding Area

4) Sherwin Holding Area:

Current development within this important holding area is confined to the town of Mammoth Lakes. The area is already densely urbanized and no longer provides much deer habitat. The possibility exists for land exchanges between surrounding Forest Service owned land and private owners. Land trades are common near urban areas that are confined by public lands and growing rapidly. A land exchange in habitat as important as the Sherwin holding area would be extremely detrimental to the RV herd.

Approximately 25% of the RV herd crosses the Sierra Nevada crest at Solitude Pass – the top of a narrow canyon within the town limits of Mammoth Lakes (Kucera and McCarthy 1988). This canyon occurs on U.S.F.S. land, but the possibility exists of a new alpine ski resort that overlaps the Solitude Pass migration route (Kucera and McCarthy 1988, Taylor 2005). This land use change in such a severe migration bottleneck could reduce the ability of RV deer to move between seasonal ranges.

Wildfire

Disturbance regimes such as wildfires are a natural component of western environments. Historical accounts indicate that fire was the most important factor shaping earlier ecosystems in the West (Lutz and others 2003, 15). This created an environment widely adapted to, and even dependent on, regular, low-intensity wildfires. Many native species require low-intensity fires to germinate seeds or reduce understory vegetation. In turn, the characteristics of these species determine the frequency and intensity of regional wildfires, ultimately creating a fire regime cycle. Historic fire suppression affected natural fire regimes in two ways: first, it delayed fire frequency by suppressing small wildfires; second, elimination of regular small fires caused increased fuel loading, leading to catastrophic, high-intensity fires. By altering the return interval and intensity of wildfires, historic fire suppression resulted in dramatic changes in plant community composition. These include increases in tree and shrub densities, trends toward monotypic plant communities, reduction of herbaceous understories, and decreases in overall diversity (Lutz and other 2003, 15). These effects often have a negative impact on mule deer habitat, leading to problems such as loss of antelope bitterbrush (2003, 17), increased pinyon-juniper encroachment, or cheatgrass (*Bromus tectorum*) invasion. Regular controlled burning could help to improve some of these problems and restore mule deer habitat.

The situation is more complicated, however, than simply re-introducing wildfire to restore native habitat. Within the Great Basin, including the eastern Sierra, the invasion of cheatgrass has devastated natural environments and the potential to restore historic fire regimes. Cheatgrass was accidentally introduced into North America in the late 1800s as seeds carried on livestock (Lutz and others 2003, 24). This annual species typically invades a site after a disturbance event such as fire or heavy grazing. Characteristics such as early germination, high seed production, long seed dormancy, efficient uptake of soil moisture, and adaptability to a wide range of germination temperatures gives cheatgrass a competitive advantage over native species (2003, 25); cheatgrass often outcompetes both shrubs and grasses after a fire event. Although mule deer will feed on cheatgrass, this only occurs during early spring when the exotic annual is green. By early summer, individual plants dry out, leaving a monotypic landscape and poor habitat until the following spring. Dry cheatgrass provides a perfect fuel for wildfires; consequently, cheatgrass invasions also increase the frequency and intensity of wildfires (Brooks and others 2004).

Cheatgrass invasion thus affect mule deer habitat in two main ways: (1) by outcompeting more palatable and nutritious native plants; and (2) by altering the natural fire regime, ultimately destroying more native shrublands (Lutz and others 2003, 26).

Figure 4-15 shows recorded wildfires in the eastern Sierra. In the last 11 years, there have been seven large wildfires in mule deer habitat (figure 4-15, table 4-1). These fires removed many acres of quality forage, such as antelope bitterbrush, and facilitated multiple cheatgrass invasions. It comes as no surprise that the majority of acres burned on public lands. As shrublands are replaced by cheatgrass, the carrying capacity of previous habitat is reduced dramatically. This degradation of habitat on public lands only amplifies the need to protect important habitat on private land.

Until a widespread solution to cheatgrass invasion is found, alleviating problems associated with catastrophic wildfire will be a challenge. As more efficient methods known to reduce catastrophic fires and halt cheatgrass invasions become available, they should be implemented on wildlife habitat. In the mean time, protection of remaining stands of antelope bitterbrush, and other important forage should be given a high priority for mule deer conservation.

	Fire Name	Year	Acres
1	Iana	2004	3,161
2	Little Antelope Valley	2000	1,527
3	Cannon	2002	26,684
4	Mclaughlin	2001	2,714
5	Birch	2002	2,549
6	Pole	1995	4,746
7	Tom	1998	3,412

Table 4-1: *Recent wildfires in eastern Sierra mule deer habitat.*

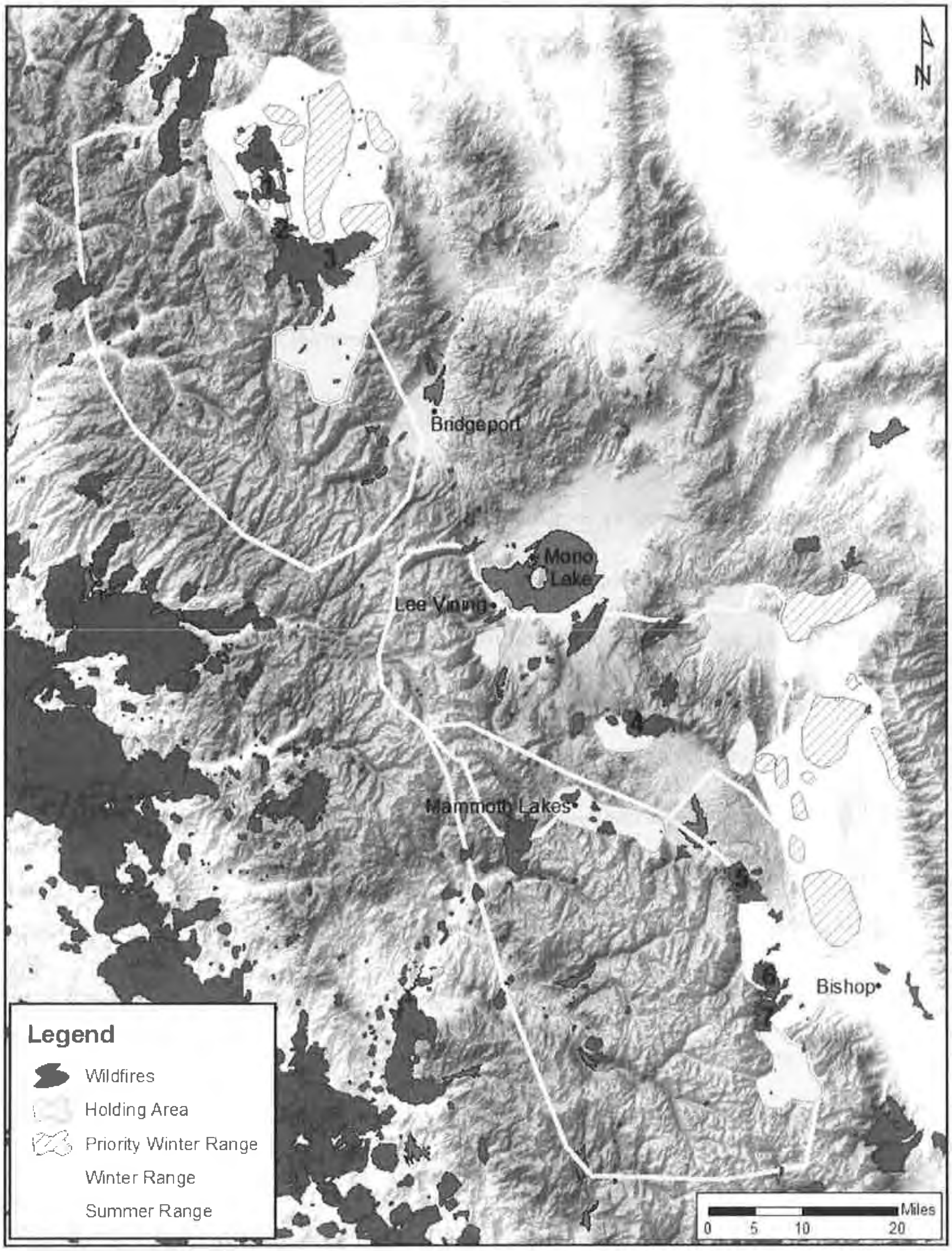


Figure 4-15: *California and Nevada wildfire history. California datasets include all recorded wildfires. Nevada datasets include wildfires from 1982 – 2000.*

Deer-Vehicle Collisions

Over 1.5 million deer-vehicle collisions (DVCs) occur annually in the United States causing significant injury, death, and damage to vehicles and heavily impacting many deer herds. Wildlife managers and transportation officials believe that these numbers are only increasing and attribute this growing problem to several factors including increased traffic volumes, higher traffic speeds, and abundant deer populations (Sullivan and others 2004, 907). Reducing these risks is essential to maintaining healthy mule deer populations and creating safer vehicle transportation routes.

Migratory mule deer are prone to habitat fragmentation from roads and highways because of their necessity to move between distinct seasonal ranges. Migratory routes frequently cross major highways, increasing the possibility of collisions during spring and fall migrations. Winter habitat routinely occurs in low-elevation valleys where humans prefer to live — or maintain second homes — which ultimately leads to fragmentation and increased traffic volume on winter range. Methods to reduce DVCs include highway fencing, warning signs, reduced speed limits, and over- or underpass tunnels for wildlife. But none of these solutions is perfect, and all have costs.

Highway fencing, if not combined with passageways, can block migration routes and effectively sever seasonal ranges. When combined with clear passageways, fencing can be extremely effective in reducing DVCs and still allow seasonal migration to occur. In a recent study, Ng and others (2003) documented many wildlife species, including deer, using highway undercrossings, including drainage culverts, tunnels, and freeway underpasses. A conservation project near Banff, Canada, combined highway fencing with a 50 yard wide overpass covered with soil, shrubs, trees, and grasses. Several wildlife species, including wolves, bears, cougars, elk, and deer, were observed using the crossing (Dean 2006). But these types of projects are expensive and difficult to implement on a widespread scale, and they require a high degree of cooperation between transportation agencies and wildlife custodians at the state or federal level.

Warning signs are a less expensive and commonly used method to reduce DVCs. Few studies, however, document any great effectiveness in the use of warning signs, despite their widespread implementation. Unlike fences that function to keep deer off of highways, warning signs attempt to increase driver awareness in high risk areas. These signs can only be effective if drivers heed the warning and travel more slowly and cautiously through potential DVC areas. In reality, drivers often become habituated to warning signs and after time no longer notice or adhere to them. One recent study looking at the effectiveness of temporary warning signs prominently displayed during spring and fall migration periods found that these signs reduced DVCs by approximately 50% (Sullivan and others 2004). After several years, habituation could still occur with temporary signs, but it is less likely than with permanent signs. Regardless of the method used, reduction of DVCs requires first identifying high-risk areas. There are two main ways to identify high-risk areas – either by finding locations where a significantly high percentage of DVCs occur (DVC hotspots) or by finding areas where a large proportion of deer are known to cross highways, such as migration route crossings or seasonal ranges that overlap highways. If done correctly, these two methods should provide similar results.

In the eastern Sierra Nevada, U.S. Highway 395 bisects the seasonal ranges of several mule deer herds. The WW and CD herds winter east of highway 395, but must cross to reach summer range on the western side. RV deer are not obliged to cross highway 395 during migration, but winter range occurs adjacent to 395, and the major migration corridor closely parallels the highway. Although highway 395 is not within the delineated boundaries of this herd, individual deer frequently cross in both directions. In addition, highway 203 cuts horizontally across the Sherwin holding area, where the majority of RV deer stage during spring migration.

The region 5 Caltrans DVC database indicates that DVCs occur consistently throughout the entire highway 395 stretch between Topaz Lake and Rovana. Certain areas appear to have higher densities of collisions; to identify these areas I calculated the Getis-Ord for each postmile location, based on the total number of DVCs that ever occurred at that location. The Getis-Ord statistic tells you whether high values or low values tend to cluster in a study area. A high Getis-Ord value indicates that values higher than the mean for the study area tend to be found near each other (ESRI 2005). Figure 4-16 shows the Getis-Ord value for each postmile location where a DVC occurred between 2002 and 2005. Values are graphed as horizontal bars, with longer bars indicating higher values, or clusters of DVCs. Based on these values I identified five obvious DVC hotspots: (1) highway 395 between Walker and Topaz Lake; (2) the Sonora junction; (3) the Bridgeport ranger station and surrounding highway; (4) highway 395 from Mono City north to Bodie road; (5) the June Lake loop; and (6) the Sherwin holding area. These six hotspots all occur along major migration routes and/or areas within seasonal ranges where deer tend to congregate. Although it is not shown on figures 4-16 or 4-17, hotspots #3 and #4 occur where the migration corridors for the East Walker and Mono Lake herds cross highway 395. This means that both methods of identifying high-risk areas support these results.

Figure 4-17 shows the Getis-Ord values calculated using the entire DVC dataset, from 1965 to 2005. This dataset clearly identifies the three northernmost hotspots; the fourth, fifth, and sixth hotspots near Mammoth Lakes, June Lake, and Mono City are barely present, however. This difference could be a consequence of increased growth in both Mammoth Lakes and June Lake in the last 10 to 20 years which would consequently produce more traffic on major highways. Alternatively, the absence of hotspots four through six could be a result of population fluctuations within the corresponding herds. If the herds were going through population declines during early years of data collection, fewer collisions would have occurred in these regions.

Currently, the California Department of Transportation (Caltrans) is in the process of planning a DVC reduction project near the Sonora Junction, which is clearly one of the most significant DVC hotspots identified in this study. This project will include a deer passageway, such as an overpass, combined with highway fencing to funnel deer toward the appropriate crossing. If done correctly, this project should bring about a vast reduction in DVCs near this region. A project similar to this would also be effective near Mono City (#4) and the June Lake loop (#5). In other hotspots such as the Sherwin holding area (#6), and the Topaz to Walker stretch (#1) fencing projects may be more challenging. These hotspots occur in seasonal range, where deer are not simply crossing but regularly moving back and forth to use habitat on both sides of the highway; fences may have more significant fragmentation effects in these regions than along migration routes. In these situations, temporary warning signs combined with heavily reduced speed limits would be the most effective way to reduce DVCs without adversely affecting deer herds.

State highway agencies, such as Caltrans, invest significant amounts of money into DVC reduction projects along major transportation routes. In order to maximize the effectiveness of these projects in reducing DVCs, it is important that they occur in known DVC hotspots. This will ensure the most cost-effective and successful use of state funds. My research provides two methods for identifying DVC hotspots: (1) hotspot analysis based on recorded deer vehicle collisions; and (2) use of expert opinion to identify locations where migration corridors or seasonal ranges cross major highways. The site location for the current DVC reduction project at the Sonora Junction was based solely on expert opinion. In the absence of a quantitative hotspot analysis, this is certainly an acceptable way to locate reduction projects. When available, the combination of these two methods will provide an even higher level of confidence in choosing sites for DVC reduction projects and ultimately improved chances for success.

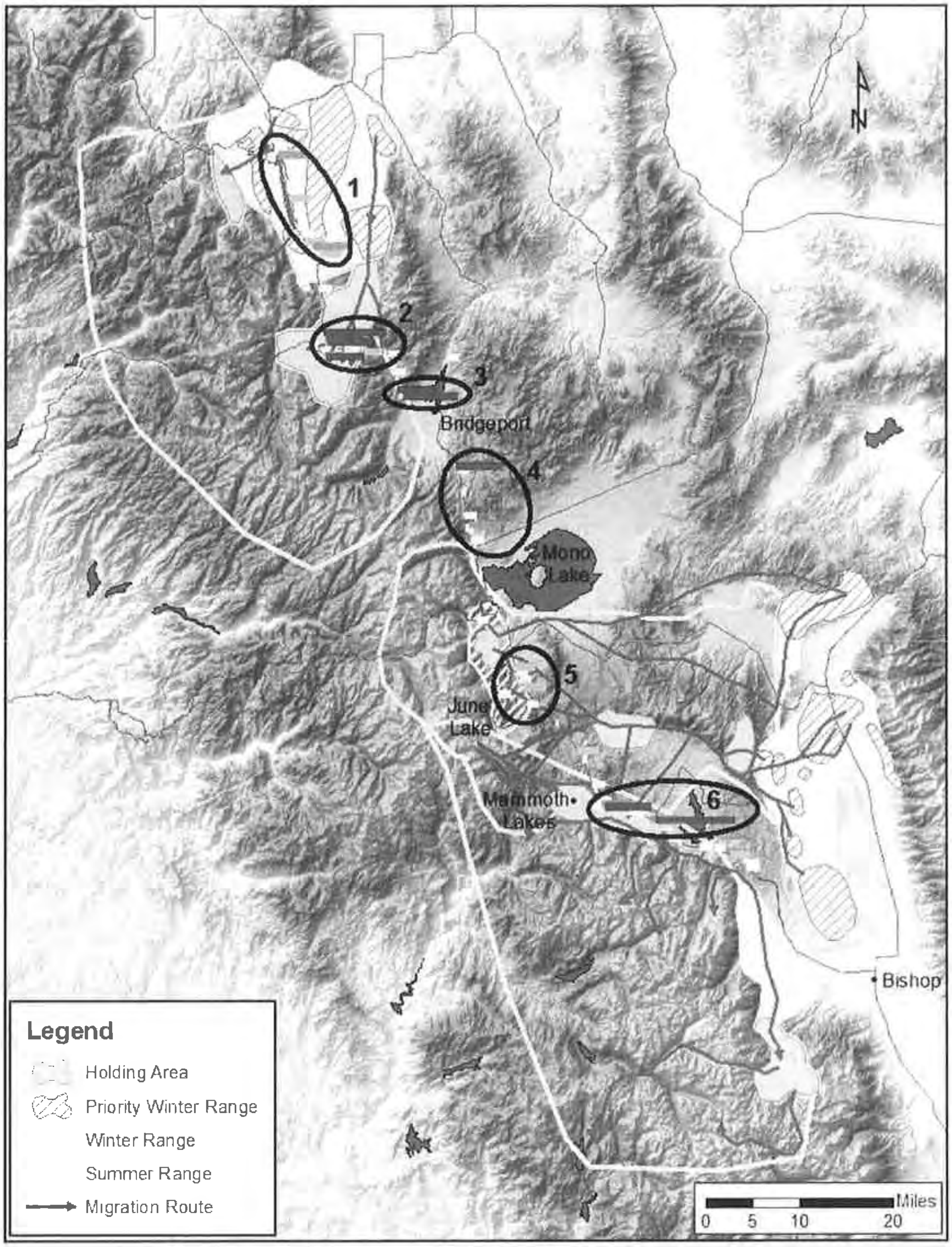


Figure 4-16: *DVC hotspots for 2002-2005. Horizontal bars indicate the Getis-Ord Value, based on total number of DVCs. Yellow bars show low values (0-1), orange bars show medium values (1-3), and red bars show high values (>3).*

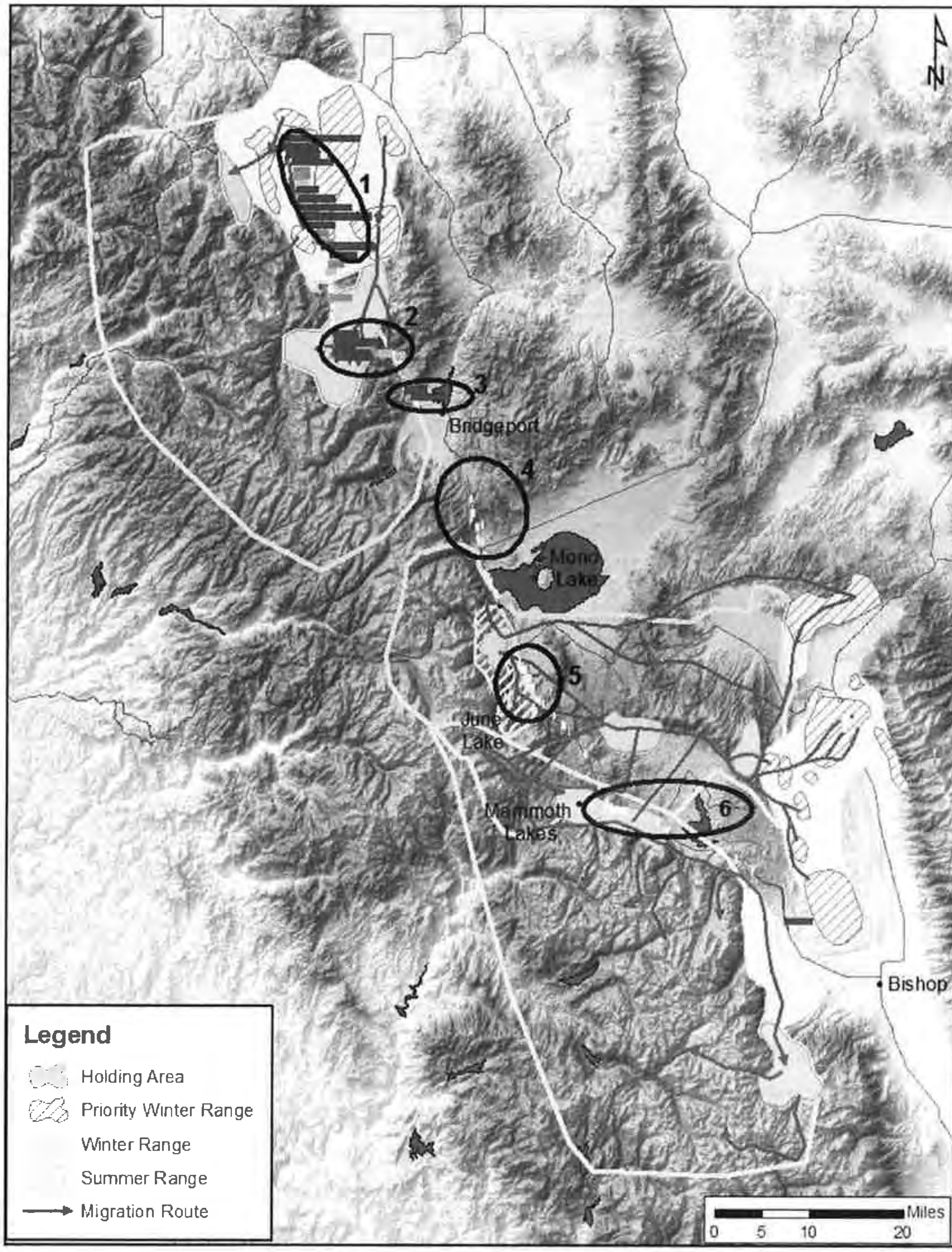


Figure 4-17: *DVC hotspots for 1965-2005. Horizontal bars indicate the Getis-Ord Value, based on total number of DVCs. Yellow bars show low values (0-1), orange bars show medium values (1-3), and red bars show high values (>3).*

Energy Exploration

On May 6, 2001, President Bush issued a national energy policy "designed to help the private sector, State and local governments, [and] promote dependable, affordable, and environmentally sound production and distribution of energy for the future" (BLM 2006). Over 20 of the recommendations within this policy affect the energy-related responsibilities of the Bureau of Land Management (BLM) such as the development of oil and gas resources, geothermal resources, renewable resources, and coal resources on public lands (BLM 2006). Other public agencies, such as the US Forest Service, are affected by this policy as well. Since a significant proportion of mule deer habitat in the eastern Sierra occurs on public lands, it is important to identify the potential impacts from this initiative.

Energy exploration and extraction can negatively impact mule deer populations in several ways depending on the extent and disturbance of the project. Direct impacts include mortality from a particular action or extensive habitat loss and fragmentation; indirect impacts are usually a consequence of increased human access and use of an area, such as increased road density or diminished use of habitat from noise or human presence (Lutz and others 2003). Even the most non-invasive forms of energy exploration can have a negative impact just by building roads and infrastructure in places where there previously were none. Increased road density can lead to introductions of invasive species, increased chances of wildfire, increased erosion, wildlife-vehicle collisions, and habitat conversions to forage less suitable for wildlife.

Habitat for the Casa Diablo herd occurs primarily on public lands. Winter habitat is especially important for this herd, because deer are often in poor condition when they leave summer range (Taylor 2006a). Currently, there is a proposed windmill project within important CD winter range. This project, if approved, will encompass approximately 2400 acres of land on Blind Springs Hill. The proposal is presently in the early stages of development; Clipper Wind Power Inc. has requested to build 3 instrument towers to monitor wind aspects and energy potential for three years (figure 4-18). The towers, which are each 50 meters high, will monitor wind speed, temperature, duration, peaks, and direction. After three years, Clipper Wind Power will either continue to monitor wind aspects or will submit a proposal with a build-out plan. If this plan is approved, a wind power generation facility will be built with a power line to Highway 6, and energy will be sold to the Southern California Edison (SCE) power company (Primosch 2006).

If successful, this project raises some interesting dilemmas regarding deer habitat. The Blind Springs area is among the most important winter range for the CD herd. Although I could not find any data indicating known effects of wind energy exploitation on mule deer populations, biologists from Cal. Fish and Game are extremely concerned with the potential impacts of this project on the CD deer population. If these biologists are correct, energy exploration on this range could potentially take a heavy toll on the CD deer population. Considering that this herd is already small in numbers, this impact could be devastating. This means that protection of Blind Springs is a high priority for mule deer conservation. But the BLM has a clearly mandated responsibility to provide for energy exploration on public lands. The nature of the agency itself dictates that it must provide for multiple land uses, including both energy extraction and habitat protection. Balancing land uses that do not easily coexist creates difficult management challenges. It is not within the realm of this research to decide which land use should take precedence in this

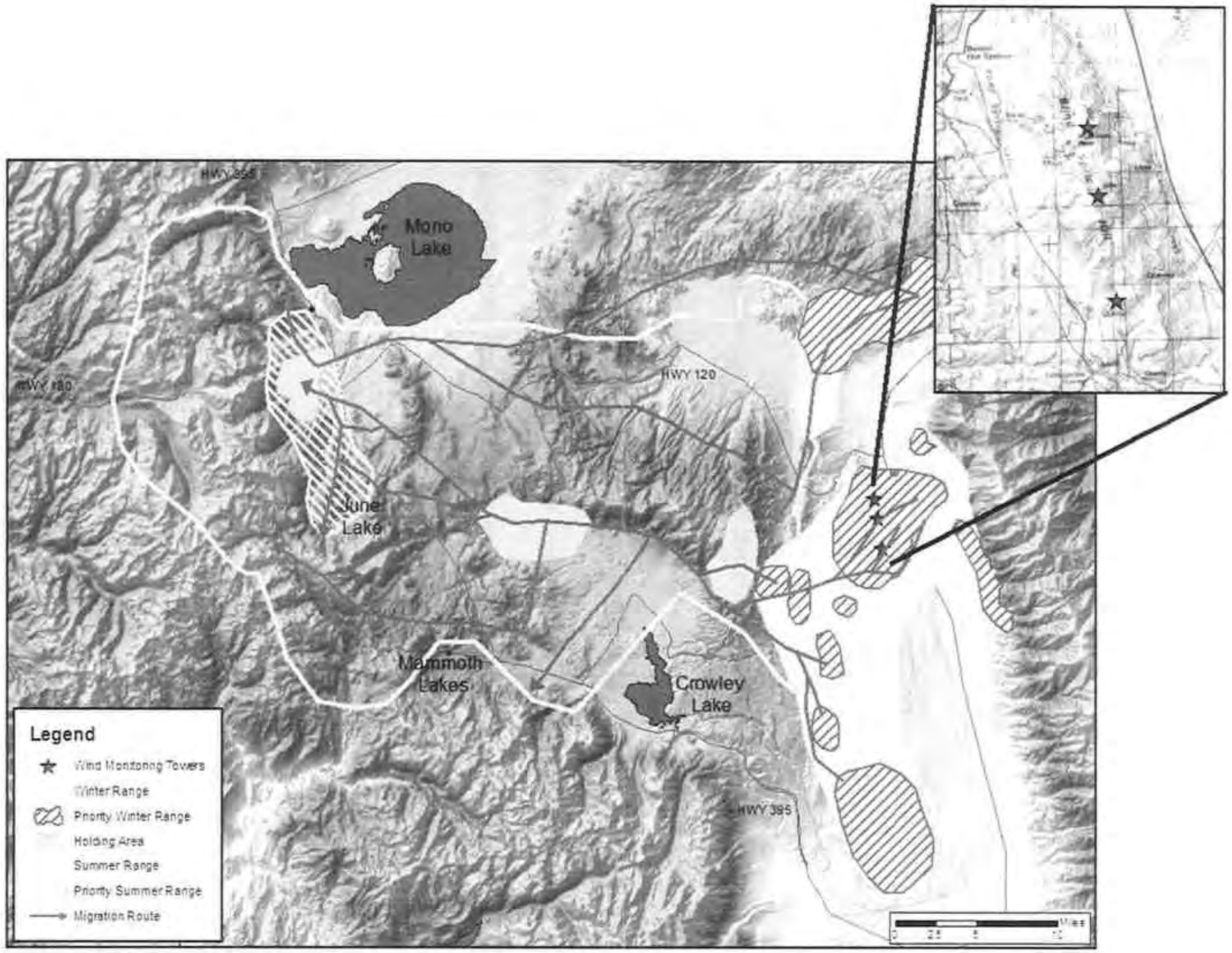


Figure 4-18: Potential sites for windmill monitoring towers occur on critical range for the Casa Diablo herd.

situation; however, if this windmill project is successfully approved, it is crucial that actions are taken to minimize its impact on mule deer habitat: keeping road and building infrastructure to a bare minimum; avoiding locations with healthy stands of Antelope Bitterbrush as building sites; and restricting human activity during winter months when deer are using this habitat extensively. Although there is no way of predicting the exact effects a windmill project would have on the CD deer population, these actions will help to minimize impact as much as possible.

Geothermal power is another potential source of energy in the eastern Sierra. At least one proposal for a geothermal power plant has occurred on seasonal range for the Round Valley herd (Kucera 1988). This research does not explore the extent or potential impacts of geothermal exploration within deer habitat. It is likely that geothermal energy extraction would have similar direct and indirect impacts as other types of energy exploration. Before any future geothermal exploration proceeds, the potential impacts to deer habitat should be thoroughly evaluated.

Livestock Grazing

Livestock and native ungulates, such as mule deer, frequently share rangelands in the western United States. Whether these species compete for resources is widely debated in the field of wildlife management (Kie and others 1991), raising concern over the potential impact of livestock grazing on wild ungulate populations. Competition theory suggests that if cattle and deer prefer similar habitats, then deer will use less preferred habitat as resources are depleted (Loft and others 1991). This could potentially affect the nutritional intake of individual deer and ultimately their overall fitness. Other research suggests that cattle grazing improves deer habitat by preferentially selecting for seral shrubs (Berger and Wehausen 1991, Austin 2000). These seemingly contradictory results can become confusing if not closely examined. Ultimately, the effects of livestock grazing appear to lie somewhere between these extremes, depending on grazing frequency, intensity, and timing.

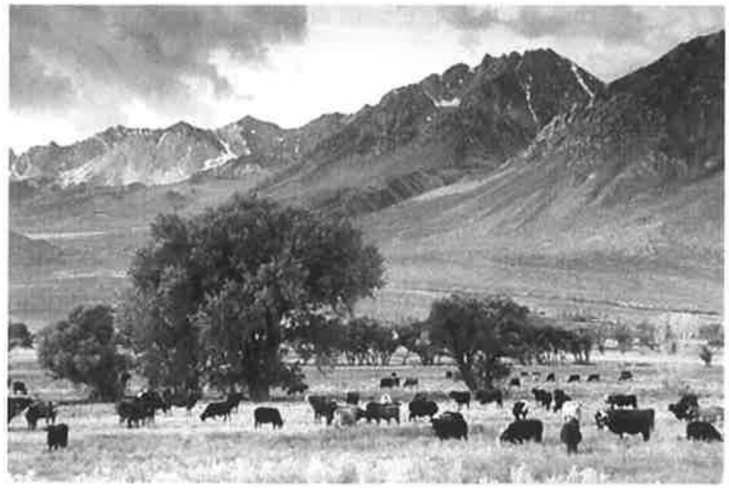


Figure 4-19: *Cattle Grazing in the Round Valley. Photograph by Gary Crabbe.*

Improper livestock grazing clearly results in habitat degradation and increased competition with native mule deer. In a manipulative field experiment in the McCormick basin of the central Sierra Nevada, Eric Loft, John Mink, and John Kie found that female deer became less selective for preferred habitat and less selective against avoided habitat as cattle grazing pressure increased. They attribute this change in selectivity to reduction of forage and cover abundances due to heavy grazing. Home range estimates increased with grazing pressure; estimates were 18% larger during moderate grazing and 41% larger during heavy grazing. In a side-study from this same experiment, these researchers found that deer spent more time feeding and less time resting with increased cattle stocking rates. Time spent feeding was negatively correlated with the availability of herbaceous forage in meadow-riparian habitats. A GIS analysis of these results indicates that deer and cattle are both attracted to meadow-riparian and aspen habitats where herbaceous forage is most available. However, in the presence of cattle, many deer avoid these areas (Kie and others 1991, Loft and others 1991, Loft and other 1993). These studies clearly indicate that cattle do in fact compete with native mule deer. The overall impact of this competition is correlated with the stocking rate, meaning that heavier grazing will have a more significant impact on deer vitality. Data on the effects of other types of livestock grazing, such as by domestic sheep, are not available; in any event, sheep grazing in the eastern Sierra is at a fairly steep decline from historic levels, and is markedly seasonal.

Despite obvious negative effects, livestock grazing can be a useful tool for enhancing wildlife habitat when managed correctly (Anderson et al. 1990, Austin 2000). If done at appropriate times and levels, livestock grazing can diversify habitat by opening up dense stands of vegetation and changing plant composition toward seral shrubs (Bennett 1999, cited in Lutz and others 2003, 17).

Dennis Austin (2000) and Lutz and co-authors (2003) make several recommendations to manage livestock in a way that minimizes impact on mule deer habitat, including:

1. Graze livestock in springtime on mule deer winter range, before livestock switch diet from grasses and forbs to shrub species.
2. Alternate between classes of livestock to maintain a better balance of grasses, forbs, and shrubs.
3. Use cattle breeds that impact native vegetation least.

4. Use a rest-rotation system so that each year 1/3 of the rangeland is rested from grazing
5. Graze livestock at an intensity that only removes 50% of the understory grasses and forbs or alternatively leaves an appropriate residual vegetation height (see Lutz and others 2003, 43 for recommended heights).
6. Make appropriate stocking adjustments during drought conditions, i.e. reduced intensity.
7. Improve riparian habitats by eliminating or reducing livestock grazing.
8. Monitor livestock use of rangelands by using permanent plots.

Implementing these techniques on eastern Sierra rangelands would benefit native mule deer and likely several other co-existing species. Unfortunately, recommendations that provide maximum wildlife benefit usually differ from those that provide maximum livestock production (Holechek and others 1982). Because grazing often occurs on public lands, it is important that agencies such as the forest service or BLM enforce regulations that maximize benefits to wildlife while still providing rangelands for livestock grazing. These recommendations will ultimately provide the most widespread advantage and effectively fulfill the multiple use mandate present in public agencies.

Chapter 5: Conservation Tools

Historian Patricia Limerick succinctly represented the history of the West in her statement, "If Hollywood wanted to capture the emotional center of Western History, its movies would be about real estate" (Limerick 1988, 55). Contrary to public sentiment, the west was not about cowboys and gunfights; it was based on land tenure and water acquisition, or as Limerick so eloquently phrases it – real estate. Although the landscape and people have changed, this core focus has not. Today, the central western conflict occurs between development and conservation; land is still the central focus.

Conservation planning embodies this conflict by determining what land should be protected and what land is acceptable to develop. As anyone involved in land conservation knows what *should* happen is not always what *does* happen; without implementation, conservation planning becomes nothing more than a practice in theory. Only planning recommendations combined with on-the-ground execution will result in effective and successful conservation. Until this point, I have focused on identifying important habitat and potential threats to that habitat – the planning component. This next chapter will move beyond these recommendations to explore the conservation tools available to protect real landscapes and the factors that need to be considered when choosing and implementing a conservation strategy. As Patricia Limerick reminds us, the factors shaping the western landscape today are not so different from those that affected it in the past. Understanding these factors and the many tools available to protect land will enable a conservation plan to effectively become written in the physical landscape for which it was made.

The Public Lands Paradigm

Most discussions on conservation begin with the public lands – a recitation of the history of American land conservation through the creation of the public domain. Although this conventional approach provides insight into American history, it is often incomplete and oversimplified; according to author Sally Fairfax and her co-authors: "histories of public land policy are presented as three-act plays: acquisition of the public domain by the federal government, disposition to private owners, and finally retention for federal management" (2005, 3). A more recent idea includes a "shift to privatization" during the final retention period, achieved through land trusts and other private organizations. Although these viewpoints are not entirely false, Fairfax and others believe they are misleading and unreliable, hiding the emergence of new ideas about government, property rights, and publicly owned lands.

If this paradigm is not correct, what is the *real* history behind land conservation, and how does this affect the current strategies used to protect land? According to Fairfax and others, the history of land acquisition is a complex issue, rather than a series of simple shifts. In many situations, a mosaic of public and private partnerships emerge, creating a mixture of conservation strategies and land ownership. The overly simplistic view of public agencies or private organizations acquiring land for conservation ignores these mosaics and hides the limitations of this conservation strategy. Fairfax and co-authors argue that it is critically important to understand the limits of land acquisition as a conservation strategy and the situations when other conservation techniques may be more appropriate.

One of the most significant limitations to mixed public and private land acquisitions is the lack of public accountability. This occurs on many different levels. All land trusts receive some form of federal funding, usually in the form of tax incentives or federal grant programs. Since land trusts all use federal funding, there should be some level of public accountability for their actions. Interactions and contracts between land trusts and private landowners are considered private records and are not available to public scrutiny. This means that the public has little say in what is being protected and how it is being protected, even though the government is ultimately funding these programs.

A lack of public accountability is taken to even another level when we consider the common strategy of land trusts acquiring private land and then passing ownership to a public agency such as the forest service or park service. Private industries (land trusts) are deciding what land will (and will not) be added to the public domain with no accountability for these decisions. Fairfax and others comment that many public land managers now begin by contacting private land trusts if they want to acquire land. This has implications on the social equity of land acquisition. A few elite conservationists choose which land will be protected; a kind of oligarchy is again created and validated, which is a cause of concern, at least for some (Dowie 2001). The benefits of conservation are consequently not shared by all citizens; rather, they focus on rural landscapes and often benefit wealthy landowners — a pattern that has existed since at least the early 1800s, when estates along the Hudson River spawned a movement for art and parks and improved urban sanitation and health but benefited the estate-owners most of all. According to the authors, conservation should include landscapes that are important to all citizens, such as urban parks, recreation areas, and landscapes that provide clean air and water.

A second limitation to land acquisition, according to Fairfax and others, is that sellers (not land trusts or government) drive the market and consequently the entire process. Key parcels are often sold at prices much higher than they are worth or traded for significantly more valuable parcels. This raises the question of whether that money was put to the best use. Fairfax and others suggest that in these situations alternative conservation strategies may be more effective. These could include condemnation, land use regulations, or implementation of legislation such as the Endangered Species Act. These techniques, however, are extremely controversial and in places where private autonomy is highly valued, these strategies may create a political nightmare.

Does this mean that land acquisition is a poor conservation strategy? To the contrary, private and public land acquisition has protected millions of acres of open space and wildlife habitat in the United States, including highly treasured locations such as the national parks, wilderness areas, and wildlife refuges. Land acquisition is an integral component of conservation and quite possibly the most effective strategy available to protect land. For one thing, the acquisition of land is at least in theory a permanent step; a move to set aside property in perpetuity for the betterment and protection of nature. Whether the management of such land is up to the task is another question, but the set-aside is genuine. Beginning this discussion with the *limitations* of the strategy instead of its *attributes* is not meant to minimize its value or potential but instead to provide perspective on the history and applicability of land acquisition before diving into the nuts and bolts of how and when it should be applied.

The Shift to Privatization

Limitations to private land acquisition clearly exist, yet privatization is quickly becoming a prevalent strategy in modern day conservation. According to the Land Trust Alliance, there are over 1200 land trusts in the United States today, with the total rising swiftly, each of which works to conserve land locally or regionally. The reasons for this expansive popularity are several-fold. First is the realization that important habitat is often found on private lands; habitat for 95% of threatened and endangered species occurs on private land, with 19% of these species found only on private parcels (Wilcove and others 1996, cited in Merenlender and others 2004, p. 66). In the Western United States, the most productive and well-watered lands are in private hands – a legacy of historic land disposition practices (Maestas and others 2001, Merenlender and others 2004). The same qualities that make these locations appealing to humans make them equally appealing to wildlife species. Short of Endangered Species Act enforcement, protecting these landscapes is inherently beyond the scope of public agencies.

The second underlying push for private conservation comes from its sensitivity toward private property rights and landowner autonomy. Participation with local land trusts is entirely voluntary. Not only are the landowners given the choice of protecting (or not protecting) their land, they are typically compensated for conservation at fair market value. Although this may create some complications, ultimately it minimizes conflict and animosity between conservationists, public agencies, and local landowners.

Land trusts and related organizations protect land through a complex collection of different techniques. These strategies can be divided into four different categories: (1) Status Quo – the continuation of historic land use and stewardship by private landowners;

(2) Negotiated term agreements for conservation and public access; (3) Conservation easements; and (4) Full acquisition of land parcels (Wright 1993, 22). Of all these methods, conservation easements are the most common. A conservation easement is a legal contract between a landowner and an outside party; it is based on a "bundle-of-rights" concept of land ownership – the idea that different property rights can be bought or sold separately (Merenlender and others 2004). Typically, the conservation easement transfers some development and management rights, such as the rights to subdivide, build homes, or cut trees to a non-profit organization that holds these rights in perpetuity. In exchange the land owner receives economic incentives such as tax breaks or a cash payment. The terms of the contract vary depending on each unique situation and the specific agreement between the land trust and the landowner. This contract is legally bound to the parcel of land, so that even if ownership changes hands, the easement remains (Merenlender and others 2004).

In many ways, the conservation easement is an ideal approach toward land conservation in the West. It enables the implementation of conservation while still maintaining local autonomy and positive relationships between conservationists and landowners. There are limitations to this strategy (Fairfax and others 2005), however, and with the emergence of so many land trusts and conservation easements come many unknowns (Merenlender and others 2004). For example, what are the long-term implications of a contract that lasts in perpetuity? What happens if the landscape changes? What happens if the political or social context changes? How can information that may become available in the future be written into a past contract? And most importantly, how will these contracts be enforced in perpetuity? Enforcement requires sufficient economic funding, but many of these land trusts are barely making ends meet financially at current times. What ensures that they will be able to come up with the necessary funds in the future? All of these questions provide unpredictable possibilities; conservation easements are indeed a powerful tool, but it is important that any participant in this contract be aware of the unknowns and that conservation practitioners continually work to understand and minimize the effects of future problems.

Alternative Strategies: Regulations, Land Use Planning, and Public Lands Management

Land acquisitions and conservation easements are techniques used to permanently protect land. These actions are not easily undone – a fact that undoubtedly puts the mind of many a conservationist at ease. In some situations, however, outright acquisition is not a possibility. Land may be too expensive or unavailable, or perhaps there is no local land trust to participate in the conservation contract. In these circumstances, other techniques can be substituted to reach conservation goals, such as the establishment and enforcement of regulations to protect wildlife habitat like the Endangered Species Act. Although most people believe this act is meant to protect individual plants or animals, the most important component of the Endangered Species Act (ESA) is actually habitat protection. By prohibiting activities on private and public land that negatively impact an endangered species, this legislation plays an extremely important role in conservation. There are limitations to the breadth and applicability of the ESA; for example, no protective status is offered to unlisted species or their habitats. In addition to national laws, regulatory enforcement can occur at local levels, such as the restriction of fences in mule deer habitat or reduced speed limits along migration corridors. Although some regulations are easily accepted by local communities (such as speed limit changes), most regulations are not well received by landowners who view them as a violation of their property rights and personal freedom. Consequently, enforcement of regulations can be expensive and met with local resentment.

Land use planning is another approach to land conservation in which planning agencies establish a vision of future land use and development through a general plan. By setting land use and zoning designations, planners can determine the specific land use practices allowed on a given parcel and the minimum size to which a parcel can be sub-divided. These tools are meant to ensure that development proceeds in an organized and appropriate fashion. Planning designations, however, are temporary and always subject to change during the next revision of the general plan or by petition. Although land use planning is certainly an important conservation tool, it is by no means a final solution. When used in conjunction with land acquisition and conservation easements, land use planning can have the most significant conservation impact.

The role of conservation on public lands is equally important to that on private lands. Public land management impacts species habitat in many ways – both positively and negatively. Practices such as overgrazing, mining, logging, or improper fire management adversely affect plants and wildlife by degrading habitat. If these practices are regulated at appropriate levels, or prohibited in areas of important habitat, they will have less impact or none at all. Protective designations, such as wilderness management, can be used to conserve areas of special value or concern.

Conservation and Geography

Time and experience reveal that not all conservation strategies are equivalent over time and space. The same action can bring about a different result in every unique location where it is presented. In the book *Rocky Mountain Divide,* author John Wright follows the history and cultural evolution of two neighboring states, Colorado and Utah, to offer an explanation of why the conservation ethic and land practices differ so dramatically between these regions. This case study provides insight into the many conservation successes and failures throughout the West.

Of all the western States, Colorado has been one of the most successful at conserving open space and biologically valuable landscapes. In 1993, some 27 land trusts existed in Colorado (as compared to only one in Utah) (in 2006, according to the Land Trust Alliance, Colorado had 32 and Utah 3). In addition to these land trusts, communities such as Boulder, Colorado, have set aside thousands of acres through county and city initiatives. Although development is still a major threat and many conservation battles have been lost in this state, public demand for open space is high and is comparable to the coastal states, not the other Great Plains and Rocky Mountain states. What has created the demand and consequent success of conservation practices in Colorado? According to Wright, Colorado is saturated with a history of commerce and mercantilism. The same mindset that motivated gold-rushers and land prospectors now drives the conservation sector. Land trusts and conservation easements are based on economic incentives. If you can't force conservation on private landowners then you purchase it. This mentality was quickly accepted by the entrepreneurial types of Colorado. Combine economic incentives with a growing environmental movement and an attachment to the land cultivated through decades of ranching, and the results give a fairly successful conservation movement.

Utah is a different story. As in Colorado, early white settlers were seeking land, but they were seeking something else, too – Zion. Lust for gold was replaced by the zeal of religion. Led by their proclaimed prophet Brigham Young, the Mormons moved west till they finally settled in the valleys below the Wasatch Front of Utah. Early Mormon writings presented ideas that would indicate a stewardship approach to the natural world and appeared in agreement with land conservation practices. This stewardship never came about. Mormon theology also emphasized economic and population growth. "Mormons had come to believe that all growth and all exploitation were the same as progress. Ethnocentrism gave them a clear sense that God approved of and guided their actions. There was little reason to make careful use of mountain lands when God would soon return and perfect the Earth as their paradisiacal home" (Wright 1993, 170). Forests, watersheds, and wetlands were quickly degraded. Growth, indicated by high birth rates and the exploding Mormon population, was encouraged by the church,. The Mormon people were building Zion but in the process destroying significant elements of the natural landscape. This mentality shaped the landscape and the conservation ethic (or absence thereof) present in Utah today. Conservation efforts have been highly unsuccessful (with a few exceptions, such as in and around the wealthy resort at Park City), and many organizations such as The Nature Conservancy won't even attempt to protect land in northern Utah. If land trusts are to find any success in Utah, they must first gain an understanding of Mormon spiritual and cultural attitudes about the best use of the land. Within this context, appropriate conservation goals may begin to emerge.

Through his explorations of both the modern day and historic Rocky Mountains, Wright revealed one of the integral components of land conservation – you must understand the biological, political, historical, and cultural context of a landscape before you can attempt to protect it. Although Colorado and Utah are similar in many respects, fundamental ideological differences have shaped diverging land conservation practices. A conservation strategy that is rooted in the local ideology will account for these differences and provide the most practical approach for that particular location.

Community-Based Conservation

Successful conservation must account for the human context where it is to be implemented. This much seems clear, yet, as always, the situation is much more complex. A controversial component to locally based conservation is the degree of local involvement in the planning process. Two main approaches appear at the polar ends of this debate. Comprehensive / rational planning consists of a centralized authority group that makes planning decisions for the good of the public. This approach is often criticized because it impedes communication between authorities and community members and often fosters resentment from the community. Community based conservation (or co-management) incorporates local citizens and encourages stakeholder participation in the planning process (Brown and Harris 2005). Incorporating local interests into the development of conservation plans is thought to carry multiple benefits including support within the local community, lower enforcement costs, higher compliance rates, and less conflict. In many aspects, community based conservation (CBC) appears to be a superior strategy; consequently, it has recently become something of a buzzword among the conservation community.

In practice this approach to conservation is not always as straightforward or successful as many people previously hoped. In a recent article, Nils Peterson and co-authors (2004) examine two situations where the CBC approach to management of endangered species (through the creation of habitat conservation plans) was unsuccessful: Key Deer in the Florida Keys and the Houston Toad in Bastrop County, Texas. In both situations, poor communication and unrealistic expectations created divisions between the habitat conservation plan committee members, ultimately resulting in abandonment of the CBC process and a failure to resolve land-use issues. The main reason for this failure is what the authors refer to as the "democratic paradox" – the intrinsic conflict, present in any democracy, between liberty (represented as property rights) and equality (popular sovereignty). In entering the CBC process, landowners set unrealistic expectations based on their perceived right to liberty. On the flip side, the USFWS and other environmental agents valued equality as the most important factor. Protecting species under the ESA was perceived to be of a higher priority than the rights of individual landowners. Peterson and others accurately identify that it is impossible to simultaneously optimize both liberty and equality because they interfere with each other's success. In creating a habitat conservation plan, if participants unknowingly place different levels of value on liberty and equality, the process could be doomed to failure from the beginning.

In another recent article, Brown and Harris (2005) discuss the results of a cultural study on co-management in the state of New York. Brown and Harris surveyed owners of properties in a proposed wildlife corridor in New York – the Algonquin to Adirondack corridor (A2A). Of the respondents, 83% had no previous knowledge of A2A. Most of the respondents thought protection of biological habitat and cultural/historical settings were important, and many respondents favored the concept of local participation in planning. Few, however, were willing to participate personally in that effort, and over half of the respondents were not willing to have their land become part of A2A. Brown and Harris interpret the results of this survey as support for the use of co-management in the A2A planning process. This is primarily based on the fact that private land is critical for the success of A2A and because 80% of the respondents felt that protecting wildlife habitat is important. The results of this study appear to be more complex than the authors let on. The majority of private landowners did not want to be personally involved with the planning process, even though they thought it was a good idea in principal. Co-management might be seen as more of a burden to them than an opportunity to participate. Over half of the landowners did not want their land to be part of A2A at all. For these particular landowners, it may be more effective for A2A planners to create incentives, such as tax breaks or payment, before approaching the owners to make involvement more appealing.

In both of these articles, it appears that community based conservation by itself is not an effective approach toward conservation. The extreme opposite approach of rational planning is well tested and creates equally as many problems as co-management. There is no straightforward answer to this conservation dilemma; no single solution will satisfy everyone all of the time. Ultimately, all conservation requires a degree of compromise. The optimal approach toward conservation planning is likely also a compromise between rational planning and community based conservation. For example, an alternative to co-management in the A2A proposal could be a central planning committee that submits regular surveys to landowners. These surveys would allow landowners to voice their opinions and demonstrate their desires without forcing them to sacrifice their time or allow them to drastically alter the planning process. It would also enable planners to monitor changing perceptions in the community and tailor planning to the local social context. In each conservation scenario, practitioners will need to tailor a compromise suitable for that particular situation.

Conservation in the eastern Sierra Nevada

As in so many other places, conservation in the eastern Sierra Nevada requires a combination of supplementing strategies. Management on public lands is undoubtedly a key factor in this region, because such a large area of land is encompassed within the public domain. Through the designations of wilderness/protected areas and enforcement of appropriate rangeland practices such as light to moderate livestock grazing, proper fuel control to minimize catastrophic wildfires, and control of invasive species such as cheatgrass, public lands will provide the highest quality mule deer habitat possible (and likely the highest quality wildlife habitat in general).

Habitat conservation on private land is, of course, a different situation. The entrepreneurial history that made incentive based conservation successful on the front range of Colorado appears to also exist in the eastern Sierra Nevada. Many of the families that settled this region came to mine, ranch, or farm the land. The passing of several generations has cultivated an attachment to and stewardship for the land that appears as common sentiment. More recent immigrants moved to the eastern Sierra for several reasons including high scenic value, the abundance of wildlands, or to take part in the economic boom occurring in communities such as Mammoth Lakes. Most residents of the eastern Sierra remain there for these same reasons – economic advantage, attachment to the land and history, or the scenic value and outdoor lifestyle. All of these motivating factors fit well with an incentive-based approach to conservation. Based on the historical and social context of the eastern Sierra, it seems likely that this type of conservation, including private land acquisition and conservation easements, could be highly successful.

A significant problem exists, however, to base conservation on economic incentives in the eastern Sierra – the rising real estate market is quickly exceeding the available funding of non-profit organizations such as land trusts. A broader real estate boom that has made property in urban California the most expensive, on average, in the United States is spreading to formerly rural parts of the state, and land costs have risen accordingly. It is becoming increasingly challenging for land trusts to provide the economic incentives dictated by the local market. This means that to succeed land trusts and other non-profit organizations will need to devise a degree of innovation and find solutions that satisfy local landowners.

The most powerful incentive that the land trust can offer is a tax incentive. After placing an easement on their land, the owners can deduct the value of the easement over six consecutive years (Ingram and Ingram 2005). The value of the easement is determined by subtracting the appraised value of the land after the easement from its original value. For landowners that earn a high income the tax deduction can be reason alone to put an easement on their land. If the owner chooses to take the entire deduction, the land trust does not spend a dime on purchasing the easement, and can consequently produce the easement with a limited budget. In situations where the landowner does not earn a substantial income, however, the tax deduction is of little economic value. For example, one landowner reported that before conserving her land, she was receiving offers to sell for up to $1.8 million. After the easement was completed, the landowner was only able to sell her land for $700,000; this means that the conservation easement was worth ~$1.1 million. Because this owner earns a comparatively moderate income she will never be able to take the full value of the tax write-off. Overall, she took a huge monetary loss in putting an easement on the land. In this particular situation, ensuring that this land remained undeveloped was sufficient motivation for the owner to choose a conservation easement. Many landowners, however, would not take such a substantial economic loss, regardless of their views on conservation. Some owners need the full value of the land to purchase a new piece of property, or perhaps the land is their only retirement. In these situations, additional incentives are necessary.

There are two alternative methods of creating conservation easements: the easement can be purchased outright, or a combination of tax incentives and outright purchase can be used. If the easement is fully purchased the landowner is not eligible for tax deductions. In the previous example, the land trust would have to purchase the easement at its market value - $1.1 million – a hefty sum of money for a non-profit to secure. Many landowners prefer a combination between a purchase and tax deduction; for example, the owner will get paid for half the value of the easement and deduct the other half. This works well because the owner pays fewer taxes on the income they receive for the half-purchase and the land trust only has to come up with half the value of the easement.

An alternative to outright purchase or tax deduction is *Conservation Development* – an approach that uses land protection and limited development to add value, rather than reduce it. With this technique, development is clustered in one or more carefully chosen sites; the remainder of the land is protected under a conservation easement. The land-owner can profit from subdividing a small portion of the land then subsequently use the tax deduction on the income received from subdividing. In many ways this is seen as a win-win situation – the landowner achieves financial goals while still minimizing impact on the land.

Although conservation is typically thought to decrease land value, Anthony Anella and John Wright (2004) identify several ways in which conservation development actually increases land value:

1) Conservation development increases long-term value by preserving the integrity, stability, and beauty of the land, in contrast to conventional development that degrades the same resources that made the land suitable for development in the first place.
2) Conservation development adds value by maintaining open space. Future buyers prefer lots that are located adjacent to protected land and will pay more to have close access to protected land.
3) Conservation development enables buyers to purchase a smaller lot and still enjoy all of the protected land, thereby giving the buyer more for their money.
4) Conservation development provides income for the original landowners to take full advantage of tax deductions.
5) Conservation development attracts buyers who are looking to preserve the western landscape, rather than despoil it. This creates value by allowing the buyer to feel good about his or her purchase and the legacy that it leaves.

Conservation development, although not a *purist* approach toward conservation, can be a pragmatic solution to challenging conservation situations. Ultimately, a small amount of development occurs, but the majority of the natural landscape is protected. Clustering minimizes the overall impact of the development on the environment and remaining protected areas. In areas such as the eastern Sierra where land values are high and private property is scarce, conservation development creates a method to generate funds for large conservation projects that otherwise would be economically impossible. It also allows a small amount of urban growth, which can financially benefit local communities. Overall, this strategy is an effective conservation tool and well-suited for conservation in the eastern Sierra Nevada.

A final method that has seen widespread success in the conservation of private land is acquisition through the use of local taxes. In this situation, local citizens vote in favor of a tax to procure parks and open space. Funds generated from this tax are used to purchase lands that will benefit local communities and become public parks. These can be small parcels within neighborhoods or expansive areas of lands on the outskirts of towns that provide recreation trails for hiking. These taxes can be well received by local communities because all community members will directly benefit from the tax; consequently they view this as money well spent. This type of strategy has been successful in many areas in California and the front range of Colorado. It is likely to have the most success in communities such as Mammoth Lakes, where local citizens are beginning to feel the intense pressure for development.

The Eastern Sierra Land Trust (ESLT)

Currently, there is one local organization implementing private land conservation in the eastern Sierra – the ESLT. This relatively new organization was founded in 2001 and initially operated entirely under volunteer support. In 2003, the ESLT hired its first professional staff person and later in the same year completed its first two conservation easements. Since that time, several more have been successfully completed. From the start, the ESLT has taken a planning approach toward conservation, meant to ensure that high priority areas get protected first. This is done through focus on three areas of emphasis: (1) the Mono Basin program – to protect the Mono Lake region; (2) working landscapes – to protect local ranches and farms; and (3) wildlife and plant communities – to maintain the viability of native species. According to executive director Julie Bear, planning is going to become even more important to the ESLT in the near future because it is beginning to receive more proposals for easements than it has resources to undertake; this means that it will need to prioritize.

Although this organization is relatively new, there appears to be great potential for success, especially if it makes use of innovative techniques such as conservation development and continues to garner community support. A recent collaboration of the many environmental and conservation groups in the eastern Sierra through regular working group meetings provides optimism for the direction of future conservation in this region.

Conclusions

The implementation of a conservation plan is no simple matter; nor is there is no cookie cutter approach suitable for all conservation situations. Implementing conservation is a complex procedure that requires a thorough examination of the many tools available and the situational factors that either will enforce the effectiveness of a strategy or render it useless and counter-productive. Strategies recommended in this thesis are rooted in the unique attributes of the eastern Sierra Nevada at the time of writing. These tools and methods may or may not be optimal or even effective in another location. It is my recommendation, and that of many conservationists more experienced than myself, that before creating and implementing a conservation plan, researchers become intimately familiar with the cultural, historical, and physical landscape. Conservation can then be given the best chances for success against the many challenges it may face.

Chapter 6: Recommendations

The ultimate goal of conservation planning is to make informed and scientifically sound conservation recommendations, followed up with work to implement recommendations on a regional or local scale. At times, academic research may be able to procure funds that would never be feasible in an applied conservation situation. Although this may serve to benefit the single task at hand, it contributes little to the widespread field of conservation by using a method that cannot be replicated in other situations. My personal objective in this research was not only to provide recommendations applicable to my region of study, but also to use a method that could be repeated either by conservationists in the eastern Sierra at a later point in time, by researchers in an entirely different location, or even by interested and motivated groups within the public: bioregional organizations, watershed alliances, or even resource- or game-advocacy groups. The following recommendations are not only based on sound science, but also are testament to the existence of both cost-effective and simultaneously credible conservation planning.

These recommendations, as in any conservation plan, represent a snapshot in time. As the landscape of the eastern Sierra continues to evolve and future studies reveal new understandings, recommendations must be updated to reflect the new changes. At time of writing, this information represents the most up-to-date knowledge available, obtained from the many biologists, land managers, scientists, and planners that contributed to this research. Implementation of these recommendations will provide a significant contribution to mule deer conservation and wildlife habitat in general.

From this research, nine distinct conservation recommendations emerge:

1) Focus the protection of private land on priority-at-risk areas identified in chapter 4. This will most effectively be done through the use of conservation easements and land acquisition. Five areas in particular should be given highest priority:
   a) ***West Walker Winter Range****: including the Antelope Valley and surrounding habitat*
   b) ***Sherwin Holding Area****: this primarily involves the prevention of public – private land exchanges within this priority range.*
   c) ***Sonora Holding Area****: maintaining open space within this area is necessary to protect the major migration corridor for the WW deer herd.*
   d) ***Bald Mountain Holding Area****: this area is not only important for deer, but also for many other native wildlife species. Protecting this holding area will provide an umbrella effect for all of these species.*
   e) ***Swall Meadows and Crowley migration Bottleneck****: maintaining open space within these two bottlenecks will protect the major migration corridor for the RV deer herd.*

2) Use innovative solutions such as conservation development for parcels that are otherwise impossible to protect. Whenever possible, cluster development to minimize impacts on the natural landscape.

3) Avoid public-private land exchanges on priority habitat, as in the Sherwin holding area.

4) Maintain minimum parcel subdivision sizes on parcels >10 acres in high-risk areas and enforce regulations on fencing and roaming pet restrictions on private land.

5) Research and implement strategies to minimize risk of catastrophic wildfire on deer habitat and minimize invasions of cheatgrass following wildfire, particularly in priority areas.

6) Implement strategies to reduce deer vehicle collisions at all major hotspots (identified in chapter four). At locations where major migration corridors cross highways combine highway fencing with an overpass or underpass crossing for deer; in areas where seasonal range overlaps highways or roads, use temporary warning signs and enforce reduced speed limits.

7) Avoid energy exploration on priority deer habitat. If exploration must proceed, minimize impacts by avoiding healthy stands of antelope bitterbrush, building the minimum number of roads possible, and limiting access during deer high use periods.

8) Monitor impacts of livestock grazing on public lands. If applicable, implement expert recommended grazing strategies given in chapter 4.

Chapter 7: Final Comments

Faced with the impending chaos of a holiday weekend, I recently chose to spend the fourth of July in one of the few places I know where you can truly escape from everything and everyone – backpacking in rural Nevada. After a three-hour car drive through sagebrush desert and a full day hike up a steep Toiyabe Canyon, my partner and I chose an aspen grove to set up camp, then quickly climbed a nearby hill to watch the sunset. As we neared the top, I realized quickly that we were not alone. A young doe perked her ears then bounded several leaps until turning to stare at us. The wildness in her eyes was shadowed by a deep curiosity – clearly she did not see many humans in this area. After holding gaze at each other for several passing moments, she turned and bounded effortlessly across the slope and out of sight. The countless hours I had spent studying and researching deer were quickly erased from my head, leaving only the excitement of the experience to resonate through my mind. According to Richard Nelson, "research on attitudes toward nature affirms that Americans and Canadians value deer more highly than any other wild creature" (1997, 19). In this brief moment, I understood the magnitude of this statement. My interaction with this doe forged an experience with wildness that is difficult to find otherwise and reaffirmed my belief that deer are incontrovertibly linked to our western culture and our underlying views on wildlife. To most Americans, deer ARE wildlife.

There will always be debate within conservation – the approaches used, the sites protected and consequently those left unprotected, the ultimate goals, and the conservation targets chosen to reach those goals. In reality there is no single correct answer, but as

I have tried diligently to argue in this thesis, each answer must emerge from the context of the local setting. My research focuses on the conservation of Rocky Mountain mule deer with the hope that not only will the protection of these species provide for many biological conservation goals, but that it will simultaneously achieve cultural goals within the eastern Sierra Nevada. It is my belief that experiences such as my recent one in rural Nevada, or the many other positive interactions that humans have with deer on a daily basis, will continue to cultivate the environmental ethic that Rachel Carson first inspired decades ago.

Literature Cited

Abele, L.G., and E. F. Connor. 1979. Application of island biogeography theory to refuge design: making the right decision for the wrong reasons. Paper read at *Proceedings of the First Conference on Scientific Research in the National Parks*, at New Orleans, LA.

Anderson, W. E., D. L. Franzen, and J. E. Melland. 1990. Rx grazing to benefit watershed-wildlife-livestock. *Rangelands* 12 (2): 105 - 111.

Anella, A., and J.B. Wright. 2004. *Saving the ranch: conservation easement design in the American West*. Washington D.C.: Island Press.

Austin, D. 2000. Managing livestock grazing for mule deer (Odocoileus hemionus) on winter range in the Great Basin. *Western North American Naturalist* 60 (2):198 - 203.

Baron, D. 2004. *The beast in the garden: the true story of a predator's deadly return to suburban america*. New York: W.W. Norton & Company, Inc.

Beier, P., and R.F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1451 - 1454.

Benett, L. E. 1999. Current Shrub management issues in Wyoming – a white paper preared for the Wyoming Game and Fish Department. Contract number 06SC0403104. Cheyenne.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18 (2):320 - 331.

Berger, J., and J. Wehausen. 1991. Consequences of a mammalian predator-prey disequilibrium in the Great Basin desert. *Conservation Biology* 5 (2):243 - 248.

Bertrem, R.C.and R.D. Rempel. 1977. Migration of the North Kings deer herd. Calif. Department of Fish and Game. 203 pp.

Bleich, V. C., J. G. Kie, E. R. Loft, T. R. Stephenson, M. W. Oehler, and A. L. Medina. 2005. Managing Rangelands for Wildlife. In *Techniques for wildlife investigations and management*, ed. C. E. Braun. Baltimore, MD: Port City Press.

Bleich, V. C. 2006. Personal Interview. Bishop, Ca, 30 January.

BLM. 2006. http://www.blm.gov/energy/policy.htm (Consulted 11 June).

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Ditomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54 (7):677 - 688

Brooks, R., G. A. B. Da Fonseca, and A. S. L. Rodrigues. 2004. Species data and conservation planning. *Conservation Biology* 18 (6):1682 - 1688.

Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. *Journal of Wildlife Management* 56:246 - 253.

Brown, R., and G. Harris. 2005. Comanagement of wildife corridors: the case for citizen participation in the Algonquin to Adirondack proposal. *Journal of Environmental Management* 74 (2):97- 106.

Carson, R. 1962. *Silent Spring*. New York: Houghton Mifflin Company.

Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. *BioScience* 50 (7):593 - 601

Dean, C. 2006. Home on the range: a corridor for wildlife. *New York Times*, 5/23/2006, F1 - F4.

Dowie, M. 2001. *American foundations: an ivestigative history*. Cambridge, Mass.: MIT.

ESRI. 2005. ArcGIS Desktop Help, Redlands, CA.

Fairfax, S. K., L. Gwin, M. A. King, L. Raymond, and L. A. Watt. 2005. *Buying nature: the limits of land acquisition as a conservation strategy, 1780 – 2004*. Boston, MA: MIT Press.

Fleishman, E., D. D. Murphy, and P. F. Brussard. 2000. A new nethod for the selection of umbrella species for conservation planning. *Ecological Applications* 10:569 - 579.

Foster, J. C. 1970. The deer of Kaibab: federal - state conflict in Arizona. *Arizona and the West* 12:255 - 268.

Gilpin, M. E., and J. M. Diamond. 1980. Subdivisions of nature reserves and the maintenance of species diversity. *Nature* 285:567 - 568.

Groves, C. R. 2003. *Drafting a conservation blueprint: a practitioners guide to planning for biodiversity*. Washington, D.C.: Island Press.

Heffelfinger, J.R, and T.A. Messmer. 2003. Introduction. In *Mule deer conservation issues and management strategies*, edited by DeVos, J. C., M. R. Conover, and N. E. Headrick, 1 - 12. Logan, UT: Berryman Institute Press, Utah State University.

Hess, G. R., and R. A. Fischer. 2001. Communicating clearly about conservation corridors. *Landscape and Urban Planning* 55 (3):195 - 208.

Holechek, J. L., R. Valdez, R. Pieper, S. D. Schemnitz, and C. Davis. 1982. Manipulation of grazing to improve or maintain wildlife habitat. *Wildlife Society Bulletin* 10: 204 – 210.

Ingram, K., and S. Ingram. 2005. Personal Interview. Swall Meadows, Ca, 29 October.

Kie, J. G., C. J. Evans, E. R. Loft, and J. W. Menke. 1991. Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55 (4):665 - 674.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Ph.D. Dissertation, University of California, Berkeley.

Kucera, T.E., and C. McCarthy. 1988. Habitat fragmentation and mule deer migration corridors: a need for evaluation. *Transactions of the Western Section of the Wildlife Society* 24: 61 – 67.

Kucera, T.E. 1992. Influences of sex and weather on Migration of mule deer in California. *Great Basin Naturalist* 52 (2): 122 - 130.

Larsen, J. 2006. Personal Interview. Bishop, Ca, 20 March.

Lawton, J. H., and R. M. May. 1995. *Extinction Rates*. Oxford, UK: Oxford University Press.

Limerick, P.N. 1988. *The legacy of conquest: the unbroken past of the American West*. New York: W.W. Norton.

Loft, E. R., R. C. Bertram, and D. L. Bowman. 1989. Migration patterns of mule deer in the central Sierra Nevada. *Calif. Fish and Game* 75 (1):11 - 19.

Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 551 (1):16 - 26.

Loft, E. R., J. G. Kie, J. W. Menke. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. *Calif. Fish and Game* 79 (4): 145 - 166.

Lutts, R.H. 1992. The trouble with Bambi: Walt Disney's Bambi and the American vision of nature. *Forest and Conservation History* 36 (4): 160 - 171.

Lutz, D. W., M. Cox, B. F. Wakeling, D. McWhirter, L. H. Carpenter, S. Rosenstock, D. Stroud, and L. C. Bender. 2003. Impacts and changes to mule deer habitat. In *Mule deer conservation issues and management strategies*, edited by DeVos, J. C., M. R. Conover, and N. E. Headrick, 13 - 61. Logan, UT: Berryman Institute Press, Utah State University.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *The American Naturalist* 119 (6):757 - 773.

Maestas, J. D., R. L. Knight, and W. C. Gilgert. 2001. Biodiversity and land-use change in the American mountain west. *The Geographical Review* 91 (3): 509 – 524.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405 (6783):243 - 253.

Merenlender, A. M., L. Huntsinger, G. Guthey, and S. K. Fairfax. 2004. Land trusts and conservation easements: who is conserving what for whom? *Conservation Biology* 18 (1):65 - 75.

Nelson, R. 1997. *Heart and blood: Living with deer in America*. New York: Vintage Books - Random House Inc.

Newbry, G. 2006. Personal Interview. Mammoth Lakes, Ca, 24 April.

Ng, S. J., J. W. Dole, R. M. Sauvajot, S. P. D. Riley, and T. J. Valone. 2004. Use of highway undercrossings by wildlife in southern California. *Biological Conservation* 115 (3):499 - 507.

Nicholson, M.C., R.T. Bowyer, and J.G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. *Journal of Mammology* 78 (2): 483 - 504.

O'Neil, T. A., P. Bettinger, B. G. Marcot, B. W. Luscumbe, G. T. Koeln, H. J. Bruner, C. Barrett, J. A. Pollock, and S. Bernatas. 2005. Application of spatial technologies in wildlife biology. In *Techniques for wildlife investigations and management*, ed. C. E. Braun, 418 - 447. Baltimore: Port City Press.

Peterson, M. N., S. A. Allison, M. J. Peterson, T. R. Peterson, and R. R. Lopez. 2004. A tale of two species: habitat conservation plans as bounded conflict. *Journal of Wildlife Management* 68 (8):743 - 761.

Powers, S. 1875. *Tribes of California*. Berkeley, Ca: University of California Press. (1976 reprint).

Prendergast, J. R., R. M. Quinn, and J. H. Lawton. 1999. The gaps between theory and practice in selecting nature reserves. *Conservation Biology* 13 (3):484 - 492.

Primosch, L. 2006. Personal Interview. Bishop, Ca, 25 January.

Rosenberg, D., and B. Noon. 1997. Biological corridors: form, function, and efficacy. *BioScience* 47 (10):677 - 688.

Simberloff, D. S., J. Farr, J. Cox, and D. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6 (4):493 - 504.

Simberloff, D. S., and L. G. Abele. 1982. Refuge design and island biogeographic theory: effects of fragmentation. *American Naturalist* 120:41 - 50.

Smith, G. 2000. Introduction. In *Sierra east*, ed. G. Smith. Berkeley, CA: University of California Press.

Soulé, M. E., and D. S. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation* 35:19 - 40

SpatialEcology. 2006. http://www.spatialecology.com/htools/kde.php.

Storer, T.I. and R.L. Usinger. 1968. *Sierra Nevada natural history*. Berkeley, CA: University of California Press.

Sullivan, T. L., A.E. Williams, T. A. Messmer, L. A. Helling, and S. Y. Kyrychenko. 2004. Effectiveness of temporary warning signs in reducing deer-vehicle collisions during mule deer migrations. *Wildlife Society Bulletin* 32 (3):907 - 915.

Taylor, T. 1988. Migration and seasonal habitats of the Casa Diablo deer herd: Casa Diablo deer study. Calif. Department of Fish and Game, 48 pp.

———. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker and Mono Lake Deer Herd Study. Calif. Department of Fish and Game, 155 pp.

———. 1997. West Walker deer herd study. Calif. Department of Fish and Game, 85 pp.

———. 2005. Personal Interview. Bridgeport, Ca, 27 October.

———. 2006a. Personal Interview. Bridgeport, Ca, 2 February.

———. 2006b. Personal Interview. Bridgeport, Ca, 21 February.

Wehausen, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. *Wildlife Society Bulletin* 24 (3).

Wilcove, D., M. Bean, R. Bonnie, and M. McMillan. 1996. Rebuilding the ark: toward a more effective Endangered Species Act for private land. *Environmental Defense Fund*, Washington, D.C.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to impleriled species in the United States. *BioScience* 48 (8):607 - 615.

Wilke, P.J., and H.W. Lawton, eds. 1976. *The expedition of captain J.W. Davidson from Fort Tejon to Owens Valley in 1859*. Secorro, NM: Ballena Press.

Williams, P. H. 1998. Key sites for conservation: area-selection methods for biodiversity. In *Conservation in a changing world*, eds. G. M. Mace, A. Balmford and J. R. Ginsberg. Cambridge, UK: Cambridge University Press.

Wright, J. B. 1993. *Rocky mountain divide: selling and saving the west*. Austin: University of Texas Press.

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Top-down versus bottom-up forcing: evidence from mountain lions and mule deer

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We studied mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) inhabiting a Great Basin ecosystem in Round Valley, California, to make inferences concerning predator–prey dynamics. Our purpose was to evaluate the relative role of top-down and bottom-up forcing on mule deer in this multiple-predator, multiple-prey system. We identified a period of decline (by 83%) of mule deer (1984–1990), and then a period of slow but steady increase (1991–1998). For mule deer, bitterbrush (*Purshia tridentata*) in diets, per capita availability of bitterbrush, kidney fat indexes, fetal rates (young per adult female), fetal weights, and survivorship of adults and young indicated that the period of decline was typical of a deer population near or above the carrying capacity (K) of its environment. Numbers of mountain lions also declined, but with a long time lag. The period of increase was typified by deer displaying life-history characteristics of a population below K, yet the finite rate of growth ($\lambda = 1.10$) remained below what would be expected for a population rebounding rapidly toward K ($\lambda = 1.15$–1.21) in the absence of limiting factors. Life-history characteristics were consistent with the mule deer population being regulated by bottom-up forcing through environmental effects on forage availability relative to population density; however, predation, mostly by mountain lions, was likely additive during the period of increase and thus, top-down forcing slowed but did not prevent population growth of mule deer. These outcomes indicate that resource availability (bottom-up processes) has an ever-present effect on dynamics of herbivore populations, but that the relationship can be altered by top-down effects. Indeed, top-down and bottom-up forces can act on populations simultaneously and, thus, should not be viewed as a stark dichotomy.

Key words: density dependence, limitation, mountain lion, mule deer, nutrition, *Odocoileus hemionus*, predation, *Puma concolor*, regulation, Sierra Nevada

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The concepts of top-down and bottom-up forcing are central to the development of modern ecological theory (Hunter and Price 1992; Power 1992; Strong 1992). These processes influence trophic cascades (Berger et al. 2001; Terborgh et al. 2001, 2006), ecosystem structure and function (McNaughton 1977; Molvar et al. 1993), biodiversity (Jacobs and Naiman 2008; Ripple and Beschta 2008; Stewart et al. 2009), and the conservation of rare or endangered species (Aaltonen et al. 2009). Large mammalian herbivores and their predators are important for studying top-down and bottom-up relationships because theory developed from small animals may not apply to large ones (Caughley and Krebs 1983; Sinclair and Krebs 2002).

Density-dependent mechanisms play an important role in population dynamics of large herbivores (Boyce 1989; Kie et al. 2003; McCullough 1979; Stewart et al. 2005). Diet quality and niche dimensions vary with population density (Kie and Bowyer 1999; Mobæk et al. 2009; Nicholson et al. 2006; Stewart et al. 2011), and life-history characteristics of large herbivores are influenced strongly by density dependence (Fowler 1981; McCullough 1999). The degree of resource limitation (proximity to carrying capacity [K]) determines the relative importance of top-down and bottom-up influences on population dynamics (Bowyer et al. 2005; Kie et al. 2003). The classic definition of *K* is when a population is at equilibrium with its environment (Caughley 1977; McCullough 1979). We extend that definition to include the long-term ability of a particular environment to support viable populations of large herbivores, wherein the population fluctuates around some mean point of equilibrium. There may be, however, directional changes in *K* as a result of long-term environmental change (Kie et al. 2003).

There is considerable debate over the terms limitation and regulation (Berryman 2004; White 2007); we argue that all mortality factors are limiting, but only those resulting in a density-dependent feedback are regulating. Herbivore populations near *K* are characterized by females attempting to produce more young than can be recruited successfully into the population (Bartmann et al. 1992; McCullough 1979), resulting in mortality from predators that is primarily compensatory (i.e., the prey population remains near *K*)—the population is limited by predation, but regulated by density-dependent factors associated with *K*. Conversely, in populations backed far away from *K*, attempts to recruit young can be more successful if predation was reduced because resources are not limiting; in such situations mortality from predation tends to be additive—the population is not limited by resources, but is regulated by predation. We contend that information on kill rates or predation rates (Vucetich et al. 2011) are less meaningful than data concerning the life-history characteristics of ungulates in understanding predator–prey dynamics, because of the differences in the consequences of mortality as a function of the proximity of the prey population to *K*.

The long-term investigations necessary to understand these complex predator–prey relationships for large mammals are uncommon, although several examples do exist (Jędrzejewska and Jędrzejewski 2005; Vucetich et al. 2002). Nonetheless, factors underpinning dynamics of large herbivores continue to be debated, especially the role that large predators play in affecting vital rates and demographics (Frank 2008; Terborgh and Estes 2010; Terborgh et al. 2006). A lack of understanding of the role of top-down forcing in ecological systems as a result of the loss of large apex predators (Estes et al. 2011) and the predator-centric focus of numerous predator–prey models (Bowyer et al. 2005; Person et al. 2001) likely has hampered our understanding of top-down and bottom-up processes for these large mammals.

The theoretical development and debate over effects of top-down and bottom-up forcing on large herbivores largely began with the "world is green" or Hairston, Smith, and Slobodkin hypothesis (Hairston et al. 1960), which predicted that herbivores were seldom limited by food and were, thus, regulated by predation. In support of that hypothesis, cascading effects of the absence of large predators are well documented (Estes et al. 2011; Ripple and Beschta 2006, 2008; Terborgh and Estes 2010; Terborgh et al. 2006), and in multiple-predator, multiple-prey systems, predation can regulate prey at low densities relative to *K* (Bowyer et al. 1998; Dale et al. 1994; Gasaway et al. 1992; Van Ballenberghe and Ballard 1994). Nonetheless, the occurrence of predation does not necessarily equate to top-down regulation; the degree of predation and the interaction between the herbivore population and its food supply determine the potential for top-down regulation (Bartmann et al. 1992; Bowyer et al. 2005). Assessing the relative strengths of top-down and bottom-up forcing on regulation of populations, however, is of greater theoretical value than debating which force is operating, because both processes can occur simultaneously (Bowyer et al. 2005; Boyce and Anderson 1999; Hunter and Price 1992).

We used a long-term data set on mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*) that inhabited a Great Basin ecosystem to evaluate the relative influences of top-down and bottom-up forcing, because shifting dynamics of this predator–prey system allowed for unique insights into the role of large carnivores in regulating their ungulate prey. We cast our predictions based on a conceptual model of life-history characteristics for large herbivores proposed by Bowyer et al. (2005; Table 1). In populations of mule deer regulated by top-down forcing, the population would be held far away from *K*, mortality would be mostly additive, intraspecific competition would be reduced, and individuals would have a more-nutritious diet, resulting in better physical condition and, thus, greater reproductive rates and higher survival. Conversely, in populations regulated by bottom-up forcing, animals would be at or near *K*, mortality would be largely compensatory, intraspecific competition would be intensified, and a less-nutritious diet would lead to poor physical condition and, thereby, lower reproductive rates and decreased survival (Table 1). In the absence of the aforementioned dichotomy, some degree of nutritional limitation and effects of predation may co-occur, especially at intermediate densities in relation to *K*.

Materials and Methods

Study area.—Round Valley (37°24′N, 118°34′W), located east of the Sierra Nevada in California, is the winter range for a migratory population of mule deer, and the mountain lions that prey upon them (Kucera 1992; Monteith et al. 2011; Pierce et al. 1999). Mule deer inhabiting this Great Basin ecosystem are the primary prey for mountain lions (Bleich et al. 2006; Pierce et al. 2000b, 2004; Villepique et al. 2011). Annual precipitation in the region was highly variable, and ranged from 5.3 to 25.2 cm. Precipitation was strongly seasonal, with about 72% occurring during November–March, and mean monthly temperatures ranged from 0°C to 16°C.

The predominant vegetation type in Round Valley is sagebrush steppe (Pierce et al. 2004), and includes stands of sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus nauseosus*); patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) also were common. Forbs, which were generally unavailable to deer in winter, included *Eriogonum kennedyi* and *Lomatium* sp. Common grasses were *Stipa speciosa*, *Oryzopsis hymenoides*, *Sitanion jubatum*, *Sitanion*

Table 1.—Life-history characteristics, measures of physical condition, and vital rates of large herbivores, including predictions tested in this study based on populations characterized by top-down forcing by large carnivores or bottom-up forcing through nutritional limitation (adapted from Bowyer et al. [2005]).

Life-history characteristic	Top-down forcing	Bottom-up forcing	Predictions tested in this study
Physical condition of adult females	Better	Poorer	Yes
Pregnancy rate of adult females	Higher	Lower	Yes
Fetal rate	Higher	Lower	Yes
Weight of neonates	Heavier	Lighter	Yes
Mortality of young	Additive	Compensatory	Yes
Diet quality	Higher	Lower	Yes
Pause in annual production by adult females	Less likely	More likely	No
Yearlings pregnant	Usually	Seldom	No
Corpora lutea counts of adult females	Higher	Lower	No
Age at 1st reproduction for females	Younger	Older	No
Age at extensive tooth wear	Older	Younger	No

hystrix, and *Bromus tectorum*. *Salix* spp., *Rosa* spp., and *Betula occidentalis* occurred in riparian areas (Kucera 1988).

Most mule deer inhabiting Round Valley during winter migrated to high elevations (>2,500 m) on the west side of the Sierra Nevada (Kucera 1992; Monteith et al. 2011; Pierce et al. 1999), where they used high-quality forage during summer (Kucera 1997). Summer ranges were typified by high mountain meadows associated with a variety of coniferous species including Jeffrey (*Pinus jeffreyi*) and lodgepole (*P. contorta*) pine. Deer remained on summer range until autumn, when winter storms pushed them eastward over the Sierra crest and downward to the valley floor (Monteith et al. 2011).

The population of mule deer overwintering in Round Valley declined steadily from about 6,000 animals (66 deer/km^2) in 1985 (Kucera 1988) to 939 (10 deer/km^2) in 1991. Subsequently, the deer population rose to 2,165 (24 deer/km^2) by January 1999 (Fig. 1). The deer decline was associated with a severe drought during 1987–1990, when water content of winter snowpack was 27% of the long-term mean.

Fig. 1.—Phases of population trajectory for mule deer (*Odocoileus hemionus*) defined by piecewise regression, 1985–1999, and population trajectory for mountain lions (*Puma concolor*), 1993–1999, during winter in Round Valley, California. Error bars for the deer population from 1994 to 1999 are 95% confidence intervals. Adapted from Bowyer et al. (2005).

In winter 1984, hunters killed 200 female mule deer (~3.3% of the population) on the northern one-half of the study area (Kucera 1988). Limited sport hunting for male mule deer occurred during autumn in all years of our study. Hunting opportunity on winter range in Round Valley resulted in the harvest of approximately 15 males per year, but harvest of male mule deer on summer range was difficult to estimate because deer from Round Valley mingled with deer from other populations. Nevertheless, limited harvest of males would have had a negligible influence on population dynamics of deer (Kie et al. 2003; McCullough 1979, 2001). No sport hunting of mountain lions occurred during our study, and mountain lions were killed only if they preyed on pets or livestock (depredation), endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), or posed a threat to human safety (Torres et al. 1996), a policy that had been in place for >1 decade prior to the onset of our investigation.

Data collection.—In many instances, we used results from earlier investigations (Kucera 1988, 1991, 1997) combined with our data to evaluate characteristics of this mule deer population during a declining phase and the subsequent increasing phase. We tested for differences in diets of deer (percent of bitterbrush), per capita availability of bitterbrush, physical condition (kidney fat index [KFI]), fetal rate (young per adult female), fetal weight, survival of young, and survival of adults during the periods of decline and increase of the deer population. We also determined sources of mortality, and estimated population sizes of mule deer and mountain lions.

We used microhistological analyses of fecal pellets (Sparks and Malechek 1968) and digestibility of forages (Pierce et al. 2004) obtained monthly during winter to index percentage of bitterbrush occurring in diets of mule deer from the northern (n = 10 groups) and southern (n = 10 groups) parts of the study area. We collected only fresh (≤1-day-old) pellets, and composited samples, by area, each month. Microhistological identification of plant fragments was completed at the Composition Analysis Laboratory, Fort Collins, Colorado.

Current annual growth (leader lengths) for bitterbrush was sampled annually along 5 or 6 transects in autumn during most years by personnel from the United States Bureau of Land Management. Leader lengths were measured from ≥6 whorls

Comment Letter I9

$\leq$1.5 m above ground on 5 randomly selected plants along each transect. All leaders of current year growth from each whorl were measured until a minimum of 20 leaders on each plant was measured.

We collected 20 female mule deer annually in March 1991–1995, following methods described by Kucera (1997). We attempted to shoot only adult female deer, which were selected at random throughout the study area and age, weight, body condition, and fetal rate were recorded. Although we attempted to collect only adult ($\geq$2 years old) females, a few yearling females were collected but differences in pregnancy and fetal rates between adults and yearlings were accounted for in subsequent analyses. We used 1 kidney from each deer to determine physical condition with the KFI (Riney 1955). We recorded weight of fetuses ($\pm$ 1 g), but only of the heaviest if $>$1 were present (Kucera 1988).

We used a helicopter and net gun (Krausman et al. 1985) to capture mule deer (217 females and 93 males) in Round Valley and fitted them with very-high-frequency radiocollars each winter ($\sim$7% of the population) from 1993 to 1997. We distributed collars among adult males and adult females in proportion to their occurrence in the population (1:3). In addition, we captured young ($<$1 year old; $n = 113$) at random and fitted them with expandable collars (Bleich and Pierce 1999). We intentionally avoided capturing deer from groups that contained animals collared during previous years. We monitored telemetered deer 6 or 7 times per week during winter to determine survival and cause-specific mortality, and monthly during summer to determine survival.

We conducted helicopter surveys each January to estimate the proportion of adult male, adult female, and young ($<$1 year old) mule deer on winter range, and obtain information on population size. Aerial transects were flown with 3 observers, and transects extended across the entire winter range to an elevation at which deer tracks in snow were no longer evident. In the early years (1984–1993), a total count of deer was conducted (Kucera 1988) and no measures of variance could be developed; nonetheless, the general trend of declining and subsequently increasing deer numbers was unequivocal (Bowyer et al. 2005). During 1994–1999, we used collared animals to estimate the deer population and associated variances (Chapman 1951); we used aerial telemetry 1 day before each of these surveys to determine the number of marked adult females within the survey area.

From 1994 to 1997, mule deer were evaluated for evidence of diseases capable of causing a marked decline: brucellosis ($n = 538$), infectious bovine rhinotracheitis ($n = 416$), parainfluenza-3 ($n = 397$), bluetongue ($n = 538$), epizootic hemorrhagic disease ($n = 538$), leptospirosis ($n = 532$), and anaplasmosis ($n = 535$). Those data yielded no evidence of pathogens that could have affected the population. Moreover, necropsy results ($n = 194$ deer) during 1984–1996, yielded no evidence of any ongoing disease.

During November 1991–April 1999, we used hounds and techniques described by Davis et al. (1996) to capture 21 adult mountain lions (12 females and 9 males) in Round Valley and fitted them with very-high-frequency radiocollars. We conducted regular and intensive searches for mountain lions throughout the study area during 1991–1997, because these large felids are capable of dispersing long distances (Thompson and Jenks 2010). These intensive searches provided strong evidence that all mountain lions that regularly used winter range in Round Valley (i.e., resided for $>$30 days) were fitted with radiocollars by 1993, and that immigrants were detected and collared within 1 month of their arrival on winter range. Detailed descriptions of searches for mountain lions and mule deer killed by predators were provided previously (Pierce et al. 1998, 2000b, 2004).

We determined the mean number of collared mountain lions on the study area during telemetry flights at weekly intervals during November–March, and used that value to index the number of adult mountain lions on winter range each year. We excluded winter 1991–1992, because we captured the 1st mountain lion during November 1991 and continued to capture new, unmarked lions in Round Valley until November 1992, by which time we had captured 12 adults. From then on our ability to detect and capture new, unmarked lions was constant from year to year (Pierce et al. 2000a, 2000b).

We also evaluated the number of depredation permits issued for mountain lions to provide information on the annual abundance of lions prior to 1992; number of permits issued, however, does not represent the number of lions killed. We assumed that depredation permits would be positively associated with lion abundance, because additional conflicts are expected as lion density increases (Torres et al. 1996). All research methods were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks, and complied with guidelines published by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

Analyses.—We estimated number of deer born on summer range by multiplying fetal rates in March by the estimated number of adult females in the population. Survivorship of young to 6 months-of-age was calculated from the number of young estimated to have been born on summer range, and the number of those young that arrived on the winter range, based on composition counts conducted in early winter (Bleich et al. 2006). Survivorship of adult deer with radiocollars was calculated with the Kaplan–Meier estimator (Pollock et al. 1989) and proportions of cause-specific mortality during winter were determined according to Heisey and Fuller (1985).

We used piecewise regression (Neter et al. 1990) to define periods of population change, although an estimate for the population was not available for 1990; thus, we used regression analysis to estimate the value for 1990 for use in subsequent analyses. We calculated the finite rate of population growth (λ) as the inverse log of the slope of the regression on the natural log of population size through time (Caughley 1977). We used analysis of covariance (Neter et al. 1990), with Julian date of collections as a covariate to adjust weight of fetuses among years for dates of collection. We developed a density-dependent index to the availability of bitterbrush as an indication of forage available to deer (mean leader-length per deer in the population during winter × 100); this index is influenced by changes in the number of bitterbrush leaders over time in relation to the density of the deer population.

We tested for effects of weather on forage availability and condition of mule deer, as well as the relationships between deer diet, body condition, reproduction, and λ using the Spearman rank correlation (r_s—Conover 1980). We also used r_s to test for the relationship between survivorship of young on summer range and λ for all years pooled, and for the same comparisons during periods of decline and increase in the deer population. Spearman rank correlations make no assumptions about the shape of relationships between variables (Conover 1980); thus, figures include lines of best fit only as an aid to interpret those relationships.

We used the Mann–Whitney *U*-test (Conover 1980) to examine differences in mean temperatures during December–February, leader length of bitterbrush, the index to the availability of bitterbrush, percent bitterbrush in diets, KFI, fetal rates, fetal weights, and survivorship of young and adult mule deer between periods of decline and increase of the deer population. We maintained an $\alpha = 0.05$ for those comparisons, except analyses where KFI, fetal rate, and fetal weight were obtained from the same individual; for those tests, we corrected experiment-wide error with a sequential Bonferroni procedure (Rice 1989). We also used this correction for correlations between weather variables and life-history characteristics of deer. We used r_s to compare the number of depredation permits issued with our index to lion abundance from 1993 to 1999, and subsequently to evaluate the relationship between deer abundance and number of depredation permits issued during both phases of population change.

We used a life table with 3 age classes (0, 1, and 2–12 years of age) and sexes combined to estimate adult survivorship each year. We did not calculate survivorship of deer directly because those data were available for only 4 years; for consistency, we used the life-table analysis to calculate survivorship for the entire study period. We used fetal rates corrected for the entire population, survivorship of young on summer range, and the λ estimated for each year in the life-table analyses. We assumed survivorship for yearlings and adults to be similar, and survivorship was adjusted until a λ matching the observed value for a particular year was obtained. Violation of this assumption would have had negligible effects on resulting survival rates for adults because yearlings comprised a small component of the population relative to adults. For yearlings, fetal rates during the period of decline were set at 0; we used fetal rates of 0 during 1991–1993, and of 1 during 1994–1996, based on data from deer collections.

Life tables assume a stable age distribution, and can overestimate the importance of adult survivorship when λ is fixed (Bowyer et al. 1999; Caughley 1977; Eberhardt 1985); however, calculating parameters repeatedly on an annual basis minimized that potential bias. Moreover, we did not use that analysis to determine the relative role of adult survivorship on population growth, but only to compare survivorship between 2 periods for which it was estimated in the same manner. Thus, any upward bias in the importance of adult survivorship should not have affected our results markedly.

Testing predictions for whether top-down or bottom-up forcing occurred in this population of mule deer involved a variety of statistical procedures, all of which were directed at a similar hypothesis (Table 1). Consequently, we combined probabilities from those statistical tests using the method of Sokal and Rohlf (1981):

$$\chi^2 = -2\sum \ln P,$$

with $2k$ degrees of freedom, where k is the number of separate tests. We recognize that our tests were not completely independent; accordingly, we reduced alpha for this analysis to 0.02 (Bowyer et al. 2007). Meta-analyses using this approach have been increasingly recognized as valuable tools in ecology when probabilities used in the analyses are focused on single hypotheses (Arnqvist and Wooster 1995; Osenberg et al. 1999).

Results

Predation and population trajectory.—Piecewise regression identified 2 trajectories of population size for mule deer: a declining phase (1984–1990) and an increasing phase (1991–1998; Fig. 1). The λ of the deer herd in Round Valley during the drought of the late 1980s reflected a marked decline ($r^2 = 0.98$, $P < 0.001$) followed by a phase of slow population growth ($r^2 = 0.82$, $P < 0.001$) in the 1990s (Fig. 1).

Mean number of adult mountain lions inhabiting Round Valley during winter declined from 6.1 in winter 1992–1993 to 0.6 in winter 1998–1999 ($r^2 = 0.95$, $P < 0.001$; Fig. 1). During that period, we documented 20 mortalities of radiocollared lions: 10 males and 10 females. Sources of mortality included malnutrition ($n = 3$), killed because of depredation on domestic sheep or Sierra Nevada bighorn sheep ($n = 6$), intraspecific strife ($n = 2$), illegal killing ($n = 3$), vehicle collision ($n = 1$), and causes that could not be determined ($n = 5$). Of the 6 mountain lions killed on depredation permits, 3 were in poor physical condition. The population of mountain lions tracked mule deer numbers downward, but with a time lag of about 8 years (based on data from 1992 to 1999; Fig. 1). In addition, the number of depredation permits was strongly correlated with lion abundance from 1993 to 1999 ($r_s = 0.81$, $P = 0.027$); this outcome substantiated the annual number of depredation permits as an index to the abundance of mountain lions.

Despite the directional change in the trajectory of the deer population in 1991 (Fig. 1), and with the exception of an outlier in 1985, depredation permits issued for mountain lions declined from 1986 to 1999 (Fig. 2). Prior to 1985, when the deer population was probably high or increasing, few annual permits for lion depredation from 1972 to 1984 were issued ($\bar{X} = 1.3$, $SE = 0.44$). During the declining phase of the deer population, lion abundance was not related to deer numbers ($r_s = 0.29$, $P = 0.27$), even though substantially more permits for lion depredation were issued annually ($\bar{X} = 11.6$, $SE = 1.03$).

The increased killing of mountain lions had no discernible effect on the continued decline of mule deer through 1990 (Fig. 2), a pattern contrary to expectations if top-down forcing occurred. Following the crash of the deer population, number of depredation permits issued continued to decline ($\bar{X} = 7.6$, $SE = 1.44$), with the exception of 1996 when an abnormally high number of permits was issued (Fig. 2). Nevertheless, number of depredation permits issued was negatively related to deer abundance ($r_s = -0.63$, $P = 0.069$). Predation by mountain lions was the most significant cause of mortality for mule deer in all years (Fig. 3) except 1998, when predation by coyotes (*Canis latrans*) surpassed that of mountain lions.

Diet, animal condition, reproduction, and survival.—Per capita availability of bitterbrush and the percent of bitterbrush in diets of mule deer were significantly greater during the period of population increase than during the period of decline (Table 2). We identified a strong relationship between leader length of bitterbrush and total water content of snowpack measured in April (Fig. 4). That relationship was positive during the period of decline ($r_s = 0.83$, $P = 0.010$), and waned during the period of increase ($r_s = 0.43$, $P = 0.29$). A strong positive relationship also existed between per capita availability of bitterbrush and body condition of deer (as indexed by KFI) during the declining phase ($r_s = 1.0$, $P < 0.001$); this relationship weakened during the increasing phase ($r_s = 0.2$, $P = 0.74$). As percent bitterbrush in the diet in March increased from 2% to 10%, physical condition (as indexed by KFI) of mule deer rose exponentially and became asymptotic when bitterbrush in diet was >30% (Fig. 5). Mean winter temperature also was positively related to KFI, but not significantly so following a Bonferroni correction ($r_s = 0.62$, $P = 0.05$), and did not differ between periods of population decline and increase ($U_{11} = 33.0$, $P = 0.9$).

FIG. 2.—Phases of population trajectory for mule deer (*Odocoileus hemionus*) and the number of mountain lion (*Puma concolor*) depredation permits issued in Inyo and Mono counties, 1985–1999, Round Valley, California. Error bars for the deer population from 1994 to 1999 are 95% confidence intervals. Depredation permits were positively correlated with number of lions present in Round Valley and, hence, provided a viable index to mountain lion abundance.

FIG. 3.—Cause-specific mortality ($n = 115$) of mule deer (*Odocoileus hemionus*) during winter in Round Valley, California, during the increasing phase, 1993–1998 (error bars are 95% confidence intervals).

Fetal rates were 13% lower during the period of population decline than when the population was increasing (Table 2). Following a Bonferroni correction, fetal rates were related positively to KFI of female mule deer, which was significant during the increasing phase ($r_s = 0.94$, $P = 0.005$) but not during the decline ($r_s = 0.83$, $P = 0.05$). Mean weight of fetuses adjusted for age also was 14% less during the period of decline than during the period of increase (Table 2). The relationship between KFI and fetal weight was not significant during the decline ($r_s = 0.20$, $P = 0.8$), but was strongly negative during the period of increase ($r_s = -0.89$, $P < 0.001$). That negative relationship, however, more likely was driven by the higher fetal rate during the period of population increase ($r_s = -0.94$, $P < 0.001$) than during the decline ($r_s = 0.52$, $P = 0.2$; Table 2).

Mean annual survivorship of adults differed significantly and was 24% lower during the period of decline than the period of increase (Table 2). Reduced survivorship among adult females was likely the underlying demographic cause of the population crash from 1985 to 1990. In contrast, survivorship of young on summer range was statistically similar between periods of decline and increase (Table 2). Following Bonferroni corrections, meta-analysis indicated that characteristics of mule deer differed during periods of population increase and decline ($\chi^2_{14} = 38.8$, $P < 0.001$).

Finite rate of increase (λ).—When population trajectories of mule deer were considered separately, in all instances, λ was <1.0 when the mean percent of bitterbrush in diets of mule deer in March was ≤10%. Although KFI of mule deer was positively correlated with λ, that relationship was not significant ($r_s = 0.31$, $P = 0.36$). No significant relationship ($r_s = 0.32$, $P = 0.38$) existed between winter temperature and λ for the deer population across years. A significant relationship

TABLE 2.—Population characteristics of a wintering population of mule deer (*Odocoileus hemionus*) in Round Valley, California, during decreasing and increasing trajectories of population size. *P*-values are results of Mann–Whitney *U*-tests for differences in characteristics of the population between decreasing and increasing phases. Results from the declining phase are from Kucera (1988). All *P*-values $\leq$ 0.02 are significant following a Bonferroni correction.

	Declining phase (1984–1990)			Increasing phase (1991–1998)			
Population characteristic	$\bar{X}$	*SE*	Range	$\bar{X}$	*SE*	Range	*P*-value
Bitterbrush in deer diets (%)	5.40	1.10	2.5–10.0	43.40	13.20	7.3–78.9	0.006
Per capita availability of bitterbrush (cm/deer × 100)	0.13	0.05	0.01–0.34	0.56	0.12	0.12–1.24	0.007
Kidney fat index	28.00	8.70	12.0–68.0	33.30	7.70	10.4–56.0	0.750
Fetal rate (young/adult)	1.40	0.08	1.2–1.72	1.60	0.08	1.4–1.8	0.100
Fetal weight (g)[a]	156.70	13.10	116.3–202.2	182.10	18.60	126.1–258.8	0.260
Survivorship of young	0.22	0.01	0.16–0.25	0.26	0.03	0.16–0.38	0.390
Survivorship of adults	0.65	0.03	0.59–0.73	0.86	0.04	0.69–1.0	0.012

[a] Weight was adjusted by Julian day of collection.

between λ and survival of young during the period of decrease ($r_s = 0.90$, $P = 0.04$) did exist, but not when the population was increasing ($r_s = -0.21$, $P = 0.65$).

Discussion

Our approach was to evaluate the relative role of top-down and bottom-up forcing in a mule deer population using a conceptual model (Bowyer et al. 2005; Table 1) based on the life-history characteristics of ungulates (Eberhardt 1985; Gaillard et al. 2000) linked with their nutritional condition (Parker et al. 2009) to parameterize deer population characteristics in relation to *K*. The conceptual model was developed in reference to directional changes in important life-history characteristics that are expected under top-down or bottom-up regulation, but does not necessarily make assumptions about the magnitude of change for a particular variable. The significance of a single variable in this interpretation is less important than the overall pattern and direction of an influential set of life-history characteristics. Therefore, we used a weight-of-evidence approach (sensu Bowyer et al. 2003), wherein information from a single variable is insufficient to draw conclusions, but when multiple variables are considered in concert, a strong and clear pattern may emerge.

Although some of the individual population characteristics in Table 2 did not differ between periods of decline and increase, all differences were in the predicted direction based on the physical condition of deer. Characteristics were consistent with bottom-up forcing regulating the population of mule deer through environmental effects on forage availability relative to population density; however, top-down forcing (i.e., predation) had a modest, but negative effect (a reduction of 5–11% per annum) on population growth while the population was recovering from the crash (Fig. 1; Table 2). These outcomes align with the premise that variation in

FIG. 4.—Length of annual growth of bitterbrush leaders (important winter forage for mule deer [*Odocoileus hemionus*]) in relation to water content of snowpack measured in April during the declining phase (1985–1990) and increasing phase (1991–1998) of the population of mule deer in Round Valley, California.

FIG. 5.—Percent bitterbrush in diet of mule deer (*Odocoileus hemionus*) during March in relation to mean kidney fat index of female mule deer collected in March during the declining phase (1985–1990) and increasing phase (1991–1998) of the population of mule deer in Round Valley, California. Results from the decreasing phase are from Kucera (1988).

resource availability (bottom-up) permeates through the system and has an ever-present effect, which may be altered by top-down effects (Hunter and Price 1992). Indeed, top-down and bottom-up forces can act on populations simultaneously and, thus, should not be viewed as a stark dichotomy (Bowyer et al. 2005; Boyce and Anderson 1999), an outcome that is inconsistent with expectations of the Hairston, Smith, and Slobodkin hypothesis.

Our results illustrate the importance of obtaining long-term information on the physical condition and vital rates of the prey population, which also has been emphasized by others (Barboza et al. 2009; Bishop et al. 2009; Parker et al. 2009). Considering only the size or density of the population of mule deer (and in later years the number of mountain lions) would have supported a conclusion that mountain lions regulated mule deer in the declining phase and failed to do so during the increasing phase (Figs. 1 and 2)—a supposition contradictory to our conclusions. Studies assessing the degree of top-down and bottom-up forcing typically have not included data on physical condition of prey, an omission that may cloud interpretation of results. Furthermore, a less lengthy investigation might have concluded that forcing was either from below or above, depending on the phase of the population trajectory sampled (Fig. 1).

The population decline of mule deer probably was not the result of severe winter weather in this Great Basin ecosystem; we documented only positive effects of snowpack on mule deer via increased forage growth (Fig. 4) that, in turn, resulted in improved physical condition. During the period of increase, we observed limited effects of snowpack on forage consumption or λ, likely because deer were released from severe nutritional limitation (Table 2). Bitterbrush in diets of deer was positively correlated with the KFI during the decline, but not when the deer population was increasing. Consequently, density-independent factors (e.g., severe weather) likely were not responsible for the population decline via effects on the energy budget of deer, and were unrelated to population characteristics during the period of increase. Moreover, no evidence existed that diseases were responsible for the decline in numbers of mule deer, or for slowing their rate of recovery.

If predation was an additive source of mortality during the decline, the condition of deer should not have been strongly correlated with their food supply (Bowyer et al. 2005; Kie et al. 2003; McCullough 1979). Indeed, we would not have expected mortality to be additive (i.e., top-down forcing) when levels of bitterbrush in diets of deer were low ($<10\%$), deer were in comparatively poor physical condition, and reproductive rates were low—all characteristic of a declining and nutritionally regulated population. Primarily top-down forcing should have resulted in deer being in good physical condition, because they would have been better buffered against, and less influenced by, slight fluctuations in their food supply, particularly during the period of decline. Bitterbrush in diets of deer, per capita availability of bitterbrush, KFIs, fetal rates, fetal weights, survivorship of young, and survivorship of adult females all were lower during the period of decline than the period of increase for mule deer (Table 2). These results clearly indicate that mule deer in Round Valley were at or near K of the winter range—conditions that precipitated the population decline—and that mortality during that time, regardless of the proximal cause, was largely compensatory.

The prolonged drought during the period of decline likely lowered K for mule deer. This deer population, however, was in decline before the start of the drought, which commenced in 1987 (Fig. 1). Similarly, McCullough (2001) demonstrated that strong density-dependent processes continued to operate for a population of deer during the course of a 6-year drought. Although we cannot determine conclusively what caused the initial crash in mule deer numbers, an overshoot of K followed by a severe drought is a plausible explanation. Populations of large herbivores exhibit strong density dependence (Kie et al. 2003; McCullough 1999; Stewart et al. 2005), and population irruptions with overshoots of K are well documented (Forsyth and Caley 2006; Klein 1968; McCullough 1979).

Several lines of reasoning indicate that top-down forcing was operating during the period when mule deer numbers were increasing. Although a proximal cause of mortality is insufficient evidence to interpret the consequences of mortality (Bartmann et al. 1992; Bleich et al. 2006), mountain lions were the primary source of winter mortality for mule deer during the increase (Fig. 3). We obtained little evidence that food was limiting during the period of increasing numbers of mule deer (Table 2). Indirect effects of predation risk (Berger 2010) were likely minimal because deer selected habitat that simultaneously reduced predation risk and enhanced forage benefits (Pierce et al. 2004). Christianson and Creel (2010) reported a similar situation for North American elk (*Cervus elaphus*) preyed upon by gray wolves (*Canis lupus*). Moreover, the stress and associated physiological responses to predation risk should have been strongest after the population crash when mountain lion abundance lagged behind the deer population (Creel et al. 2007). In contrast to that presumption, fetal rates and nutritional status were greater during the period of increase than during the declining phase (Table 1).

In June 1995, a fire burned 22 km^2 (24%) of the winter range dominated by sagebrush and bitterbrush. The loss of winter habitat associated with the fire in 1995 did not markedly affect variables associated with the physical condition or life-history characteristics of mule deer, because the deer population was relatively low (Fig. 1) and forage availability remained high (Table 2). Therefore, predation by mountain lions likely was an additive source of mortality during the period of increase. Moreover, λ for mule deer was only 1.10 during the increase, whereas mule deer can attain $\lambda = 1.15$–1.21 when not limited by food or predation (Kie and Czech 2000). Top-down forcing by mountain lions and other carnivores likely slowed, but did not prevent, recovery of mule deer in this Great Basin ecosystem. Whether the deer population ultimately will return to the 6,000 animals present on the winter range in the 1980s, and how changes in available resources will alter K, is a topic for future research.

We encountered several challenges while conducting our research. We combined our results with those reported by Kucera (1988, 1991, 1997) to obtain a sufficient number of years to encompass the trajectories of this population of mule deer. As a result, we often had access to only mean values with no associated measures of variance, which necessitated the use of nonparametric statistics for most analyses. Our approach also required that we duplicate the methods of Kucera (1988) as closely as possible to allow meaningful comparisons. These methodologies led to some inconsistencies in our results. For example, KFI is less sensitive to changes in physical condition when cervids have high fat reserves (Cook et al. 2007), which explains why KFI exhibited a curvilinear pattern with increasing bitterbrush in diets (Fig. 5) and did not differ markedly between periods of differing population trajectories (Table 2).

Sampling only the largest fetus may have caused us to underestimate the total weight of fetuses from females with twins. Fetal rates were higher during the period of increase than decline and, consequently, twins were more plentiful (Table 2). Singletons often weigh more than individuals from a set of twins (Kucera 1991), which likely introduced a bias into our data; total fetal weight might have produced a greater difference between phases of population decline and increase. Another factor reducing the difference in fetal weights and associated survivorship of young between periods of population decline and increase could be a residual maternal effect (Monteith et al. 2009). Indeed, survivorship of young increased only slightly during the increasing phase (Table 2). Intergenerational maternal effects caused by severe nutritional limitation during the decline may have resulted in lags in population response, and thereby have the potential to mask expected patterns related to top-down or bottom-up forcing from the body size of animals (Monteith et al. 2009).

Grange and Duncan (2006) reported that populations of plains zebras (*Equus quagga*) were more resistant to drought than were populations of other grazing ruminants such as blue wildebeest (*Connochaetes taurinus*) and buffalo (*Syncerus caffer*). Those authors concluded that zebras were more likely to be influenced by top-down forcing by African lions (*Panthera leo*), whereas populations of wildebeest and buffalo were limited principally by their food supply. Moreover, Wilmers et al. (2007) concluded that stalking predators, such as mountain lions, were more effective at suppressing fluctuations in their prey than were cursorial hunters, such as wolves and coyotes. Even an effective stalking predator such as the mountain lion (Knopff et al. 2010; Pierce et al. 2000a, 2000b), however, only slowed the recovery of the mule deer population in Round Valley. The resistance of the prey population to food shortages, and the type of predator and its hunting style, hold potential to influence the magnitude of bottom-up and top-down forcing.

Our results demonstrate that top-down forcing from multiple predators may limit population growth but does not always regulate prey populations. Mountain lions and other large carnivores in our study area slowed, but did not regulate, the growth of a mule deer population. More attention needs to be given to the specific conditions that lead to equilibria or disequilibria between populations of large mammalian predators and their prey (Hunter and Price 1992), and whether those factors lead to population irruptions and overshoots of *K* with subsequent effects on ecosystem structure and function. This approach is likely to be critically important for the conservation of large mammals in a changing climate, where directional changes or dramatic variation in *K* may become the norm.

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Literature Cited

Aaltonen, K., A. A. Bryant, J. A. Hostetler, and M. K. Oli. 2009. Reintroducing endangered Vancouver Island marmots: survival and cause-specific mortality rates of captive-born versus wild-born individuals. Biological Conservation 142:2181–2190.

Arnqvist, G., and D. Wooster. 1995. Metaanalysis: synthesizing research findings in ecology and evolution. Trends in Ecology & Evolution 10:236–240.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer-Verlag, Berlin, Germany.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:1–39.

Berger, J. 2010. Fear-mediated food webs. Pp. 241–253 in Trophic cascades: predators, prey, and the changing dynamics of nature (J. Terborgh and J. A. Estes, eds.). Island Press, Washington, D.C.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator–prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. Ecological Applications 11:947–960.

Berryman, A. A. 2004. Limiting factors and population regulation. Oikos 105:667–670.

Bishop, C. J., G. C. White, D. J. Freddy, B. E. Walking, and T. R. Stephenson. 2009. Effects of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172:1–28.

Bleich, V. C., and B. M. Pierce. 1999. Expandable and economical radio collars for juvenile mule deer. California Fish and Game 85:56–62.

Bleich, V. C., B. M. Pierce, J. Jones, and R. T. Bowyer. 2006. Survival and cause-specific mortality among young mule deer. California Fish and Game 92:24–38.

Comment Letter I9

Bowyer, R. T., V. C. Bleich, X. Manteca, J. C. Whiting, and K. M. Stewart. 2007. Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. Ethology 113:1048–1060.

Bowyer, R. T., G. M. Blundell, M. Ben-David, S. C. Jewett, T. A. Dean, and L. K. Duffy. 2003. Effects of the *Exxon Valdez* oil spill on river otters: injury and recovery of a sentinel species. Wildlife Monographs 153:1–53.

Bowyer, R. T., M. C. Nicholson, E. M. Molvar, and J. B. Faro. 1999. Moose on Kalgin Island: are density-dependent processes related to harvest? Alces 35:73–89.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pp. 342–361 in Large carnivores and the conservation of biodiversity (J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, eds.). Island Press, Washington, D.C.

Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79:1332–1334.

Boyce, M. S. 1989. The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, New York.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. Pp. 265–284 in Carnivores in ecosystems: the Yellowstone experience (T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, eds.). Yale University Press, New Haven, Connecticut.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York.

Caughley, G., and C. J. Krebs. 1983. Are big mammals simply little mammals writ large? Oecologia 59:7–17.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.

Christianson, D., and S. Creel. 2010. A nutritionally mediated risk effect of wolves on elk. Ecology 91:1184–1191.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd ed. John & Wiley Sons, Inc., New York.

Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934–1943.

Creel, S., D. Christianson, S. Liley, and J. A. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644–652.

Davis, J. L., et al. 1996. A device to safely remove immobilized mountain lions from trees and cliffs. Wildlife Society Bulletin 24:537–539.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Forsyth, D. M., and P. Caley. 2006. Testing the irruptive paradigm of large-herbivore dynamics. Ecology 87:297–303.

Fowler, C. W. 1981. Density dependence as related to life-history strategy. Ecology 62:602–610.

Frank, D. A. 2008. Evidence for top predator control of a grazing ecosystem. Oikos 117:1718–1724.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:1–59.

Grange, S., and P. Duncan. 2006. Bottom-up and top-down processes in African ungulate communities: resources and predation acting on the relative abundance of zebra and grazing bovids. Ecography 29:899–907.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Jacobs, S. M., and R. J. Naiman. 2008. Large African herbivores decrease herbaceous plant biomass while increasing plant species richness in a semi-arid savanna toposequence. Journal of Arid Environments 72:889–901.

Jędrzejewska, B., and W. Jędrzejewski. 2005. Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. Pp. 230–246 in Large carnivores and the conservation of biodiversity (J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, eds.). Island Press, Washington, D.C.

Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004–1020.

Kie, J. G., R. T. Bowyer, and K. M. Stewart. 2003. Ungulates in western forests: habitat relationships, population dynamics, and ecosystem processes. Pp. 296–340 in Mammal community dynamics: management and conservation in the coniferous forests of western North America (C. Zabel and R. G. Anthony, eds.). Cambridge University Press, New York.

Kie, J. G., and B. Czech. 2000. Mule and black-tailed deer. Pp. 629–657 in Ecology and management of large mammals in North America (S. Demarais and P. R. Krausman, eds.). Prentice Hall, Upper Saddle River, New Jersey.

Klein, D. R. 1968. The introduction, increase and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32:350–367.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management 74:1435–1447.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada California. Ph.D. dissertation, University of California, Berkeley.

Kucera, T. E. 1991. Adaptive variation in sex ratios of offspring in nutritionally stressed mule deer. Journal of Mammalogy 72:745–749.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122–130.

Comment Letter I9

KUCERA, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. Journal of Wildlife Management 61:550–560.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University Michigan Press, Ann Arbor.

MCCULLOUGH, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130–1146.

MCCULLOUGH, D. R. 2001. Male harvest in relation to female removals in a black-tailed deer population. Journal of Wildlife Management 65:46–58.

MCNAUGHTON, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. American Naturalist 111:515–525.

MOBÆK, R., A. MYSTERUD, L. E. LOE, Ø. HOLAND, AND G. AUSTRHEIM. 2009. Density dependent and temporal variability in habitat selection by a large herbivore: an experimental approach. Oikos 118:209–218.

MOLVAR, E. M., R. T. BOWYER, AND V. VAN BALLENBERGHE. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479.

MONTEITH, K. L., ET AL. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art 47.

MONTEITH, K. L., L. E. SCHMITZ, J. A. JENKS, J. A. DELGER, AND R. T. BOWYER. 2009. Growth of male white-tailed deer: consequences of maternal effects. Journal of Mammalogy 90:651–660.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models. R. D. Irwin, Homewood, Illinois.

NICHOLSON, M. C., R. T. BOWYER, AND J. G. KIE. 2006. Forage selection by mule deer: does niche breadth increase with population density? Journal of Zoology (London) 269:39–49.

OSENBERG, C. W., O. SARNELLE, S. D. COOPER, AND R. D. HOLT. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80:1105–1117.

PARKER, K. L., P. S. BARBOZA, AND M. P. GILLINGHAM. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

PERSON, D. K., R. T. BOWYER, AND V. VAN BALLENBERGHE. 2001. Density dependence of ungulates and functional responses of wolves: effects on predator–prey ratios. Alces 37:253–273.

PIERCE, B. M., V. C. BLEICH, AND R. T. BOWYER. 2000a. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462–472.

PIERCE, B. M., V. C. BLEICH, AND R. T. BOWYER. 2000b. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543.

PIERCE, B. M., V. C. BLEICH, C.-L. B. CHETKIEWICZ, AND J. D. WEHAUSEN. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.

PIERCE, B. M., V. C. BLEICH, J. D. WEHAUSEN, AND R. T. BOWYER. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986–992.

PIERCE, B. M., R. T. BOWYER, AND V. C. BLEICH. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533–541.

POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

POWER, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. Ecology 73:733–746.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

RINEY, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. New Zealand Journal of Science and Technology, B. General Research 36:429–463.

RIPPLE, W. J., AND R. L. BESCHTA. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation 133:397–408.

RIPPLE, W. J., AND R. L. BESCHTA. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biological Conservation 141:1249–1256.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SINCLAIR, A. R. E., AND C. J. KREBS. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 357:1221–1231.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry 2nd ed. W. H. Freeman, New York.

SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a microscope technique. Journal of Range Management 21:264–265.

STEWART, K. M., R. T. BOWYER, B. L. DICK, B. K. JOHNSON, AND J. G. KIE. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

STEWART, K. M., R. T. BOWYER, B. L. DICK, AND J. G. KIE. 2011. Effects of density-dependence on diet composition of North American elk *Cervus elpahus* and mule deer *Odocoileus hemionus*: an experimental manipulation. Wildlife Biology 17:417–430.

STEWART, K. M., R. T. BOWYER, J. G. KIE, B. L. DICK, AND R. W. RUESS. 2009. Population density of North American elk: effects on plant diversity. Oecologia 161:303–312.

STRONG, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754.

TERBORGH, J., AND J. A. ESTES (eds.). 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C.

TERBORGH, J., ET AL. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

TERBORGH, J., K. FEELEY, M. SILMAN, P. NUNEZ, AND B. BALUKJIAN. 2006. Vegetation dynamics of predator-free land-bridge islands. Journal of Ecology 94:253–263.

THOMPSON, D. J., AND J. A. JENKS. 2010. Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. Ecosphere 1(4):art 8.

TORRES, G. S., T. M. MANSFIELD, J. E. FOLEY, T. LUPO, AND A. BRINKHAUS. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin 24:451–460.

VAN BALLENBERGHE, V., AND W. B. BALLARD. 1994. Limitations and regulation of moose populations: the role of predation. Canadian Journal of Zoology 72:2071–2077.

VILLEPIQUE, J. T., B. M. PIERCE, V. C. BLEICH, AND R. T. BOWYER. 2011. Diets of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey. Southwestern Naturalist 56:187–192.

VUCETICH, J. A., M. HEBBLEWHITE, D. W. SMITH, AND R. O. PETERSON. 2011. Predicting prey population dynamics from kill rate, predation

Comment Letter I9

rate and predator–prey ratios in three wolf–ungulate systems. Journal of Animal Ecology 80:1236–1245.

Vucetich, J. A., R. O. Peterson, and C. L. Schaefer. 2002. The effect of prey and predator densities on wolf predation. Ecology 83:3003–3013.

White, T. C. R. 2007. Resolving the limitation–regulation debate. Ecology Research 22:354–357.

Wilmers, C. C., E. Post, and A. Hastings. 2007. The anatomy of predator–prey dynamics in a changing climate. Journal of Animal Ecology 76:1037–1044.

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SELECTION OF MULE DEER BY MOUNTAIN LIONS AND COYOTES: EFFECTS OF HUNTING STYLE, BODY SIZE, AND REPRODUCTIVE STATUS

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Predation on mule deer (*Odocoileus hemionus*) by mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) was examined to test effects of hunting style and body size, and for mountain lions reproductive status, on selection of prey. Mountain lions, which hunt by stalking, selected ≤1-year-old mule deer as prey. Body condition of mule deer did not affect prey selection by coyotes or mountain lions, and both predators preyed upon females and older adult deer more often than expected based on the percentage of these groups in the population. Female mountain lions selected female deer, but male mountain lions did not. Female mountain lions without offspring, however, did not differ from male mountain lions in prey selection. Coyotes did not select for young deer. Female mountain lions with kittens were selective for young deer in late summer.

Key words: California, *Canis latrans*, coyote, mountain lion, mule deer, *Odocoileus hemionus*, predation, prey, *Puma concolor*

Differences in age, sex, and physical condition may predispose parts of an ungulate population to predation and cause important changes in the demography and dynamics of prey (Curio 1976; Taylor 1984). For example, selection by wolves (*Canis lupus*) for older age classes of moose (*Alces alces*) on Isle Royale led to a younger population of moose but also contributed to population fluctuations of both species (Mclaren and Peterson 1994). Susceptibility to predation may vary with size of predator (Bekoff et al. 1984; Huggard 1993; Ross and Jalkotzy 1996) or method of hunting (stalking versus coursing—Kruuk 1972; Kunkel et al. 1999). Ungulate populations are subject to predation by both canids and felids, and these predators often vary in body size and style of hunting (Mech 1970; Packer et al. 1990; Schaller 1972). Physical condition of prey can affect their ability to escape predation (Huggard 1993; Peterson 1977), and predators may kill animals in poor condition preferentially (Ackerman et al. 1984; Mech 1970) because selection for more vulnerable prey requires less energy and poses less risk to the predator. Further, antipredator strategies of prey may vary with group size, age, sex, and habitat use by prey (Bleich 1999; Bowyer 1987; Karanth and Sunquist 1995).

Large mammalian carnivores exhibit different styles of hunting. Some species use coursing tactics; others use stealth to stalk and ambush prey (Kleiman and Eisenberg 1973). Coursing predators, such as wolves, may pursue moose for long distances (Mech 1970), apparently assessing moose condition and the likelihood of a successful kill (Peterson 1977). Wild dogs (*Lycaon pictus*) also pursue prey over great distances (Estes and Goddard 1967), and Kruuk (1972) noted that spotted hyenas (*Crocuta*

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crocuta) were more successful at killing prey if the chase was >300 m. Coyotes (*Canis latrans*) exhibit variability in their social behavior (Bowen 1981; Harrison 1992; Messier and Barrette 1982) and have been reported to stalk or lie in wait when hunting small mammals (Bowyer 1987; Wells and Bekoff 1982). Hunting of ungulates by coyotes, however, typically involves coursing tactics in which prey are approached, tested, and sometimes pursued over long distances (Bleich 1999; Bowyer 1987; Gese and Grothe 1995).

Most felids are stalking predators (Ewer 1973; Leyhausen 1979) that rely on cover and stealth (Seidensticker 1976; Sunquist 1981) to approach prey closely and then rush and pursue an individual over a relatively short distance (Bank and Franklin 1998; Elliott et al. 1977; Van Orsdol 1984). This form of ambush hunting has been reported for mountain lions (*Puma concolor*—Bank and Franklin 1998; Beier et al. 1995). When prey occur in groups (e.g., mule deer, *Odocoileus hemionus*—Bowyer 1984), the stalking technique of felids could limit their ability to select for young, old, or weakened animals (Schaller 1972).

Body size of prey also may influence selection by carnivores (Bekoff et al. 1984; Kunkel et al. 1999). Most ungulates are sexually dimorphic, with males substantially larger than females (Ralls 1977; Weckerly 1998). Additionally, males often possess horns or antlers that can increase the risk of injury to a predator (Hornocker 1970). Most felids are solitary hunters and tend to kill species weighing more than half their own body weight (Gittleman 1985; Packer 1986). Because male mountain lions can be >50% larger in body size than females (Dixon 1982), sexual dimorphism may lead to differences between males and females in ability to kill prey and risk associated with doing so. Furthermore, mountain lions are substantially larger than coyotes; in California, these canids weigh about 9.8–11.2 kg (Hawthorne 1971). Although coyotes can hunt in packs (Bowen 1981; Bowyer 1987), thereby increasing size of prey they kill, body size still may play a role in selection of prey.

Prey selection also may vary among social categories within a predator species as a result of differences in behavior or energetic needs. Male and female mountain lions may encounter different sex and age classes of deer at varying frequencies because of differences in habitat selection, timing and amount of movement, or home-range size of these large predators. Energetic needs of male and female mountain lions likely vary because of differences in body size or demands of rearing young, but data on this topic are few.

We compared mortality caused by mountain lions and coyotes versus that caused by automobiles for a single population of mule deer to examine selection of ungulate prey by predators that differ substantially in body size, hunting style, and reproductive status. We predicted that coyotes, a small coursing predator, would be more likely than mountain lions, a large stalking hunter, to select mule deer that were younger or in poor physical condition. We also predicted that male and female mountain lions would not differ in their selection of prey unless other factors besides hunting style (e.g., body size or reproductive state) were important determinants of prey selection. We predicted that female mountain lions would kill a greater proportion of young deer than would males and that female mountain lions also would kill a greater proportion of adult female deer than would male mountain lions. If body size affected prey selection by coyotes and mountain lions, we also predicted that such marked differences in body size would lead to a preponderance of small prey items in the diet of coyotes, even though these canids often hunt in packs. We also predicted that mountain lions with different reproductive demands would kill mule deer differentially with respect to sex and age classes of deer.

Materials and Methods

Study area.—Round Valley is located on the east side of the Sierra Nevada in eastern California (37°24′N, 118°34′W). Deer inhabit about 90 km^2 during November–April, but the area of use varies with snow depth (Kucera 1988). Most mule deer that overwinter in Round Valley migrate in spring to high-elevation ranges in summer (Kucera 1992; Pierce et al. 1999). A small proportion of the herd, however, remains on the eastern side of the mountains and is prey for resident mountain lions and coyotes throughout the year.

Dominant vegetation is characteristic of the Great Basin (Storer and Usinger 1968) and includes a mosaic of bitterbrush (*Purshia tridentata*), sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus nauseosum*). Patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) also are interspersed. *Salix, Rosa,* and *Betula occidentalis* occur in riparian areas. Detailed descriptions of the study area were provided by Kucera (1992) and Pierce et al. (1999).

Our study began in November 1991 at the end of a prolonged drought. Annual precipitation during the study was highly variable: the coefficient of variation of annual precipitation was 51% during 1983–1998, and annual precipitation ranged from 5.3 to 25.2 cm, with 72% occurring between November and March. Mean monthly temperatures on the winter range (November–March) varied from 0°C to 16°C. Estimated numbers of deer on the winter range increased gradually over the period of the study from 939 (10 deer/km^2) in 1991 to 1,913 (21 deer/km^2) in 1997, whereas mean number of mountain lions decreased from 6.1 in winter 1992–1993 to 3.0 in 1996–1997 (Pierce et al., in press).

Sampling prey and predators.—Three hundred ten mule deer (217 females, 93 males) were captured and fitted with radiocollars during winter or spring 1993–1997. Deer were captured using Clover traps (n = 9—Clover 1956), drop nets (n = 2—Conner et al. 1987), and a net gun fired from a helicopter (n = 299—Krausman et al. 1985). Deer were captured on their winter range, and individuals from groups that already included an animal with a collar were intentionally avoided. Collars were distributed among adult males and females in the approximate proportion of their occurrence in the population (1:3). Deer <1 year old (n = 113) were fitted with expandable collars (Bleich and Pierce 1999); their sex ratio was close to 1:1. Twenty-one adult mountain lions (12 females, 9 males) and 21 offspring (<1 year old; 14 male, 7 female) were captured with the aid of hounds (adults and kittens; n = 38—Davis et al. 1996) or foot snares (n = 4) during November 1991–May 1996. We weighed mountain lions to the nearest 2.5 kg using a spring scale, and mean weight of adult mountain lions was determined using the 1st recorded weight for each individual. All adults were fitted with radiocollars. Nine kittens (≤6 months old) from 3 litters were captured in natal dens (Bleich et al. 1996). Age of young mountain lions was estimated with weight, pelage characteristics, and patterns of tooth eruption (Anderson 1983; D. Ashman et al., in litt.). All methods used in this research were approved by an Institutional Animal Care and Use Committee at the University of Alaska–Fairbanks.

Helicopter surveys were conducted annually in January to determine number of deer in the study area and proportions of adult males, adult females, and young. Transects were flown with 3 observers and extended across the entire study area at an elevation where deer tracks in snow could no longer be seen.

Deer mortality and predation.—We located mule deer killed by mountain lions and coyotes during 1991–1998 by back-tracking lions from daytime positions, investigating mortality signals from transmitter-equipped deer, locating mountain lions at night via telemetry, and investigating locations of scavenging birds. All marked deer were monitored daily for mortality signals, and causes of mortality were determined by examining wounds, tracks, and feces in the vicinity of carcasses. Additionally, remote photography (Pierce et al. 1998) facilitated determination of the predator responsible for a kill. Lower incisors and femurs were collected from all carcasses of mule deer for age analysis with cementum annuli (Low and Cowan 1963) and for analysis of fat with ether extraction of marrow in long bones (Neiland 1970).

We collected feces of carnivores opportunistically for analysis of diets. Although many feces for both predators were gathered near locations of kills, coyote feces were located throughout the study area, especially along roads. Feces of mountain lions were numerous at latrines (locations used repeatedly for scent marking) and near resting areas. Feces of mountain lions also were located by hounds while trailing mountain lions. Identification of food in fecal samples was determined from remains of bone, teeth, and claws and from hair samples examined for color, length, thickness, and medullary characteristics (Big Sky Laboratory, Florence, Montana). Remains identified from carnivore feces were categorized as mule deer, small animals (<15 kg), or other and were summarized as percentage occurrence in feces.

We used data from deer killed by automobiles during 1991–1998 to estimate sex, age class, and physical condition of prey available to predators. Use of such animals as a random sample of a population has been questioned (O'Gara and Harris 1988) because deer in poor condition may be more likely to use roadways for paths of travel through deep snow. This potential problem, however, was not a consideration for our study area. Most deer (55% of 191 deer) killed by automobiles were collected from Highway 395, and snow depth rarely was greater than a few centimeters in the vicinity of that roadway; deer killed along the roadway were not there to avoid deep snow. To ensure our sample of deer killed by automobiles was not biased, we tested for differences in age composition of those deer killed during winter (October–April) against data obtained from aerial surveys conducted in January of each year.

In addition to using deer killed by automobiles as a sample of the deer population, we estimated proportion of postnatal deer (<4 months old) in the population during late summer (July–September) by fetal rates. Adult females were shot at random annually in March following the methods of Kucera (1997). The mean number of fetuses per adult female (n = 86) in 1992–1996 was used to estimate the proportion of postnatal deer in the population in late summer. Use of fetal rates to estimate the available proportion of postnatal deer during late summer did not account for mortality and therefore was an overestimate. Thus, our estimate of selection for postnatal deer by predators was conservative.

Data analysis.—We used chi-square analysis (Zar 1984) to compare the proportion of <1-year-old deer killed by automobiles in late summer (July–September) with the proportion of postnatal deer (<4 months old) expected, based on fetal rates of adult females collected in March. Consequently, we used only data from October–June to test for prey selection by mountain lions and coyotes. For comparisons made within the adult age category (e.g., sex and age of adults), data from throughout the year were used because they were not biased by the birthing season of mule deer.

Analysis of variance (Neter et al. 1990) was used to test for differences in age of adult deer killed by automobiles, mountain lions, and coyotes. Differences in the percentage of fat in the marrow of adult females killed by vehicles in March 1993 and 1994 and adult females collected in March of the same years also were evaluated with analyses of variance. We used multidimensional chi-square analysis (Zar 1984) to determine if there were differences in categories of age and condition and in sex of mule deer killed by automobiles, mountain lions, and coyotes in October–June. Mule deer were categorized as young (<1 year) or adult and good condition (>50% fat in bone marrow) or poor condition to meet assumptions of chi-square analysis (Zar 1984). Use of bone-marrow fat to index condition may be problematic because these fat deposits are the last to be used by ungulates (Mech and DelGiudice 1985); therefore, an animal that has used most of its body-fat reserves and is in poor condition may still have some fat in the marrow of their long bones. Measures of body condition based on kidney fat and heart fat rarely were available for deer killed by mountain lions and coyotes because those organs often were consumed. When bone-marrow fat in red deer (*Cervus elaphus*) reached about 50%, kidney fat approached about 25% (Riney 1955). Low kidney fat coincides with other indices of malnutrition; therefore, our results assumed that deer with ≤50% bone-marrow fat were in poorer condition than those deer with >50% bone-marrow fat. We used multidimensional chi-square analysis to test for differences in age, condition, and sex of mule deer (from all months) killed by automobiles and in social categories of mountain lions. Social categories of mountain lions included solitary adult males, solitary adult females, adult females with juveniles (>6 months old but not independent), and adult females with kittens (≤6 months old—Pierce et al. 1998).

Because female mountain lions gave birth to litters in late summer (Bleich et al. 1996), females with young consistently had a higher proportion of young deer available as prey relative to other social categories. Therefore, we parti-

TABLE 1.—Proportion of adult (≥1 year old) and young (<1 year old) mule deer in poor (≤50% bone-marrow fat) and good (>50% bone-marrow fat) condition killed by automobiles and predators in the eastern Sierra Nevada, California (1991–1998). Proportions were not different among sources of mortality for young deer or adults ($P > 0.05$).

	Deer age and physical condition					
	Adult			Young		
Source of mortality	Good (%)	Poor (%)	*n*	Good (%)	Poor (%)	*n*
Automobiles	80	20	106	50	50	24
Mountain lions	80	20	99	69	31	74
Coyotes	74	26	27	62	38	13

tioned our data to test for prey selection by female mountain lions with kittens. Using a chi-square test, we compared the proportion of postnatal deer killed by female mountain lions with kittens with the proportion of postnatal deer in the population during late summer as estimated from fetal rates.

RESULTS

Analysis of prey remains in carnivore feces indicated that mule deer were the primary food of mountain lions, occurring in 73% of feces, whereas remains of mule deer occurred in 17% of coyote feces ($\chi^2 = 65.21$, $d.f. = 1$, $P < 0.001$). Desert cottontails (*Sylvilagus audubonii*) and black-tailed jack rabbits (*Lepus californicus*) were the primary species of small animals in the diet of mountain lions and coyotes.

The proportion of young in the population as determined by aerial surveys (26% ± 4.4 *SD*) did not differ from that estimated from deer killed by automobiles (25% ± 8.4%) during all years pooled ($\chi^2 = 0.16$, $d.f. = 1$, $P = 0.69$) or during any year ($P \geq 0.19$). Additionally, percentage of fat in the bone marrow of mule deer collected in March (78% ± 20%, $n = 31$) did not differ from the percentage observed for adult females killed by vehicles in March (64% ± 19%, $n = 6$; $F = 2.70$, $d.f. = 1, 36$, $P = 0.10$). For deer killed during all months, more young deer than adults in the population were in poor condition ($\chi^2 = 5.6$, $d.f. = 1$, $P < 0.05$; Table 1); however, no selection occurred with respect to physical condition for deer killed by predators or by automobiles among young deer or adults (Table 1). Additionally, mule deer in poor condition comprised a small proportion of the deer killed by all sources (Table 1).

Analysis of age, sex, and condition of mule deer killed by automobiles, mountain lions, and coyotes from October to June indicated no difference in the sex or condition of mule deer for all ages combined (Table 2). Mountain lions, however, killed a greater proportion of young deer than did automobiles ($P < 0.01$; Fig. 1). Coyotes did not select more young (26%) than expected based on the proportion killed by automobiles (21%; $P = 0.42$; Fig. 1). When comparing sex and age of adult mule deer among sources of mortality, mountain lions and coyotes killed more females than did automobiles ($P < 0.05$; Fig. 1), and the mean age of adult deer killed by predators was greater than that of adult deer killed by automobiles ($P < 0.001$; Fig. 2).

Mean weight of 8 adult male mountain lions (55 kg ± 7.7 *SD*) was >25% the mean weight of 11 adult females (40 ± 5.1 kg). Social categories of mountain lions did not differ when contrasted with sex or condition of deer preyed upon by these animals and of deer killed by automobiles, when age categories of deer were combined (Table 3). When only adult deer were considered, however, a higher percentage of female deer were killed by female mountain lions (79%) than were killed by automobiles (63%; $\chi^2 = 6.02$, $d.f.= 1$, $P < 0.05$), but female and male (81%; $\chi^2 = 2.70$, $d.f.$

TABLE 2.—Proportion of male and female mule deer in poor (≤50% bone-marrow fat) or good (>50% bone-marrow fat) condition killed by automobiles or predators in the eastern Sierra Nevada, California, October–June (1991–1998). Data collected from July through September were excluded because of a high proportion of postnatal deer (<4 months old) in the populations that were under-represented in mortality data. Proportions were not different among sources of mortality for condition or sex ($P > 0.05$).

	Deer physical condition and sex					
	Condition			Sex		
Source of mortality	Good (%)	Poor (%)	*n*	Male (%)	Female (%)	*n*
Automobiles	81	19	101	38	62	144
Mountain lions	78	22	157	36	64	152
Coyotes	72	28	43	24	76	46

= 1; $P = 0.10$) mountain lions killed the same percentage of female deer. Female mountain lions killed a greater proportion of young deer than did males ($\chi^2 = 4.81$, $d.f. = 1$, $P < 0.05$) or automobiles ($\chi^2 = 31.01$, $d.f. = 1$, $P < 0.001$; Fig. 3). Considered separately, solitary females still selected proportionally more young deer than were killed by automobiles ($\chi^2 = 11.12$, $d.f. = 1$, $P < 0.001$); however, solitary females did not differ from male mountain lions in selection of age categories of deer ($\chi^2 = 1.18$, $d.f. = 1$, $P = 0.18$; Fig. 3).

Despite the concordance between proportions of young deer killed by automobiles during October–April and proportions observed in annual surveys, comparison of

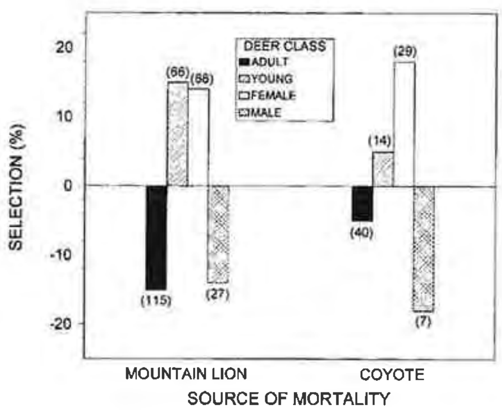

FIG. 1.—Proportion of <1-year-old and adult mule deer killed from October to June and proportion of adult male and female deer killed annually by mountain lions and coyotes in the eastern Sierra Nevada, California, 1991–1998. Proportion of deer in different sex and age categories killed by predators was compared with the proportion available in the population as indexed by deer killed by automobiles (0 on y-axis; % selection = % use − % available). Sample sizes are given in parentheses.

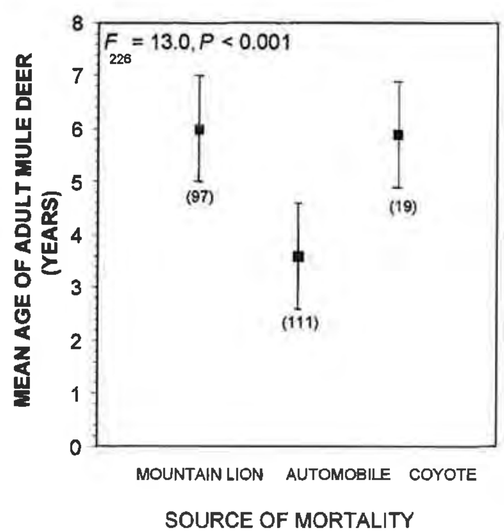

FIG. 2.—Mean (± SE) age of adult mule deer killed by mountain lions, coyotes, and automobiles in the eastern Sierra Nevada, California, 1991–1998. Ages of deer were determined by analysis of cementum annuli. Adult deer killed by mountain lions and coyotes were older than those killed by automobiles. Sample sizes are shown in parentheses.

TABLE 3.—Proportion of male and female mule deer killed in poor (≤50% bone-marrow fat) or good (>50% bone-marrow fat) condition that were killed by automobiles or various social categories of mountain lions in the eastern Sierra Nevada, California (1991–1998). There was no difference ($P > 0.05$) in the condition or the sex of mule deer killed by mountain lions and those killed by automobiles when all age categories and all months were combined.

	Deer physical condition and sex					
	Condition			Sex		
Source of mortality	Good (%)	Poor (%)	*n*	Male (%)	Female (%)	*n*
Automobiles	78	22	132	40	60	111
Mountain lions						
Solitary males	77	23	22	34	76	25
Solitary females	68	32	47	38	72	57
Females with juveniles	86	14	28	41	59	22
Females with kittens (≤6 months old)	73	27	37	47	53	32

the proportion of young deer killed by automobiles (15%) and the estimated proportion of young deer based on fetal rates (51%) in late summer indicated that postnatal deer were underrepresented in our sample of deer killed by automobiles ($\chi^2 = 21.70$, $d.f. = 1$, $P < 0.001$). Mountain lions with kittens still selected postnatal deer

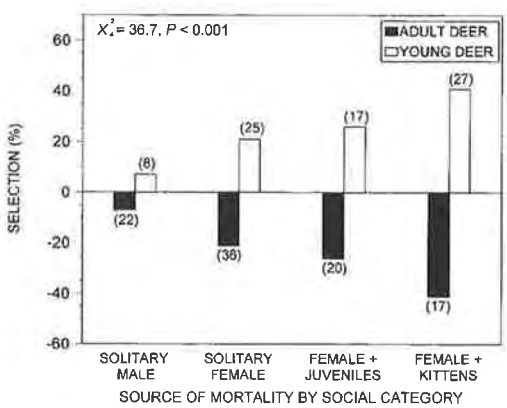

FIG. 3.—Proportion of <1-year-old and adult mule deer killed by mountain lions of different social categories: solitary males, solitary females, females with juveniles (>6 months old but not independent), and females with kittens (≤6 months). Proportion of young and adult deer killed by each social category of mountain lion was compared with the proportion available as indexed by deer killed by automobiles (0 on *y*-axis; % selection = % use − % available).

(92%) during late summer compared with the proportion of postnatal deer estimated by fetal rates ($\chi^2 = 7.94$, $d.f. = 1$, $P < 0.01$).

DISCUSSION

Hunting style was not an important factor in prey selection of mule deer; only mountain lions selected young deer (Fig. 1), but both mountain lions and coyotes selected older deer among adults (Fig. 2). Previous researchers (Hornocker 1970; Spalding and Lesowski 1971) also reported similar results with mountain lions selecting young prey. Predation on older age classes has been reported for wolves preying on white-tailed deer (*O. virginianus*—Pimlott et al. 1969), moose (Mech 1970; Peterson et al. 1998), caribou (*Rangifer tarandus*—Kuyt 1972), and Dall's sheep (*Ovis dalli*—Murie 1944). Neither mountain lions nor coyotes selected individuals with low percentages of bone-marrow fat. That outcome indicated that predation on younger and older deer was not associated with especially poor body condition. The hypothesis that a stalking predator would not be as selective as a coursing predator was rejected because mountain lions were as selective, relative to availability of different age and condition categories of prey, as were coyotes.

The hypothesis that body size of the

predator affects prey selection was supported for predation by mountain lions and coyotes on prey species of different sizes and for predation by mountain lions on adult mule deer. Coyotes had a higher proportion of small prey in their diets than did mountain lions, despite the ability of coyotes to hunt in packs and kill large prey (Bowen 1981; Bowyer 1987). Collection of feces throughout the 6 years of our study helped prevent biases associated with population fluctuations and prey switching in coyotes (O'Donoghue et al. 1998; Patterson et al. 1998) and biases associated with changes in density and distribution of mountain lions and their primary prey (Pierce et al. in press). Coyotes also were more omnivorous than mountain lions, which were strict carnivores, a pattern that has been observed previously for canids and felids (Bowyer et al. 1983; Litvaitis and Harrison 1989). Further, female mountain lions selected female deer, whereas male mountain lions did not. Selection of female deer by mountain lions in our study was contrary to the findings of Hornocker (1970) but was consistent with those of Bleich and Taylor (1998), who reported that female deer from populations directly north of Round Valley were killed by mountain lions in greater proportion than expected based on their frequency in the population. Hornocker (1970) reported selection for male prey and proposed that male deer and elk (*Cervus elaphus*) were weakened during the mating season and therefore more prone to predation by mountain lions. Male ungulates also spatially segregate from females seasonally (Bleich et al. 1997; Bowyer 1984; Bowyer et al. 1996) and may select habitats that place them at more risk for predation than do females (Bleich et al. 1997; Hornocker 1970). The proportion of adult male deer on the winter range in Round Valley, as indexed by aerial surveys, increased during 1992–1997 from 12% to 45% of the adult population compared with 19% for the population of ungulates in Idaho (Hornocker 1970). Such an increase in the proportion of males in the deer population suggests a probable increase in the proportion of young animals in that segment of the population; therefore, a large proportion of the male deer available to mountain lions and coyotes in Round Valley may have been younger and not in weakened physical condition from mating activities.

Predation on both young and adult deer by both coyotes and mountain lions caused us to reject the hypothesis that body size differences between these 2 predators underlie differences in prey selection because coyotes did not select for young deer (Fig. 1). Because our results were for October–June, postnatal deer may have been underrepresented in predator kills because fewer remains of young are left and their carcasses are more difficult to locate (Johnsingh 1993; Schaller 1967). No deer killed by coyotes were located during late summer, possibly because coyotes completely consumed postnatal deer before we could locate carcasses. During other studies, coyotes have preyed heavily on young deer in late summer (Andelt 1985; Bowyer 1987; Litvaitis and Shaw 1980). Coyotes also often hunted in packs in Round Valley (B. M. Pierce, in litt.) and elsewhere (Bowen 1981; Bowyer 1987; Messier and Barrette 1982) and may benefit energetically by killing larger prey (Kruuk 1975; Peterson 1977).

Female mountain lions rearing offspring selected young deer as prey. This outcome may be the result of physiological constraints of lactation. During lactation, female mountain lions may need a more consistant intake of protein than do males. Because protein is stored as muscle, drawing upon protein reserves for too long can affect locomotion (Wannemacher and Cooper 1970). Young deer may be easier than adults to catch because young animals lack experience in escaping predators and may lack stamina (Curio 1976; Schaller 1972); therefore, young deer may provide a smaller but more consistant source of food. We hypothesize that for lactating females the risk of an unsuccessful hunt and the accom-

Comment Letter I9

panying drain on protein reserves may overshadow the benefit of killing larger prey. Male mountain lions may have lower killing rates, killing larger prey less often and gorging themselves to store fat. Such a strategy would allow males to make long-range movements in search of females and in defense of their relatively large territories (Anderson et al. 1992).

Sexual segregation in both predator and prey also may have led to differences in prey selection with respect to age categories of deer. Female mountain lions with kittens were located at relatively low elevations during the late summer compared with other mountain lions (Pierce et al. 1999). Male deer segregate from females with young during spring and summer (Bowyer 1984; Bowyer et al. 1996; Main and Coblentz 1996) and consequently may have been encountered at lower frequencies by mountain lions at lower elevations.

Our study demonstrated that presence of dependent young was a critical factor affecting prey selection by mountain lions. Contrary to our prediction, differences in hunting style between mountain lions and coyotes was not important in prey selection; the stalking predator was as selective as the coursing predator. Differences in body size between coyotes and mountain lions may be important for the selection of prey species but not for the selection of deer from October to June. Body size was not an important factor for selection of deer by mountain lions because solitary male and female mountain lions both killed young and adult deer in proportion to their availability.

Other investigators (Hornocker 1970; Mech 1970; Mech and Frenzel 1971) have reported similar results for prey selection among multiple species of prey or by a single species of predator. Our results, however, emphasize the importance of considering reproductive status of the predator when attempting to predict how that species of predator may affect a prey population. Further study of the effects of the energy demands of reproduction on prey selection by carnivores is needed to understand predator–prey relationships more completely.

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Literature Cited

Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in southern Utah. The Journal of Wildlife Management 48:147–155.

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:1–45.

Anderson, A. E. 1983. A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife, Special Report 54:1–91.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife, Technical Publication 40:1–116.

Bank, M. S., and W. L. Franklin. 1998. Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). Mammalia 62: 599–605.

Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during differ-

Comment Letter I9

ent behaviors. Journal of Mammalogy 76:1056–1070.

BEKOFF, M., T. J. DANIELS, AND J. L. GITTLEMAN. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191–232.

BLEICH, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy 80:283–289.

BLEICH, V. C., R. T. BOWYER, AND J. D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

BLEICH, V. C., AND B. M. PIERCE. 1999. Expandable and economical radio collars for juvenile mule deer. California Fish and Game 85:56–62.

BLEICH, V. C., B. M. PIERCE, J. L. DAVIS, AND V. L. DAVIS. 1996. Thermal characteristics of mountain lion dens. The Great Basin Naturalist 56:276–278.

BLEICH, V. C., AND T. J. TAYLOR. 1998. Survivorship and cause-specific mortality in five populations of mule deer. The Great Basin Naturalist 58:265–272.

BOWEN, D. W. 1981. Variation in coyote social organization: the influence of prey size. Canadian Journal of Zoology 59:639–652.

BOWYER, R. T. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410–417.

BOWYER, R. T. 1987. Coyote group size relative to predation on mule deer. Mammalia 51:515–526.

BOWYER, R. T., J. G. KIE, AND V. VAN BALLENBERGHE. 1996. Sexual segregation in black-tailed deer: effects of scale. The Journal of Wildlife Management 60:10–17.

BOWYER, R. T., S. A. MCKENNA, AND M. E. SHEA. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. The American Midland Naturalist 109:266–273.

CLOVER, M. R. 1956. Single-gate deer trap. California Fish and Game 42:199–201.

CONNER, M. C., E. C. SOUTIERE, AND R. A. LANCIA. 1987. Drop-netting deer: costs and incidence of capture myopathy. Wildlife Society Bulletin 15:434–438.

CURIO, E. 1976. Ethology of predation. Springer-Verlag, Berlin, Germany.

DAVIS, J. L., ET AL. 1996. A device to safely remove immobilized mountain lions from trees and cliffs. Wildlife Society Bulletin 24:537–539.

DIXON, K. R. 1982. Mountain lion. Pp. 711–727 in Wild mammals of North America (J. A. Chapman and G. A. Feldhamer, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

ELLIOT, J. P., I. MCT. COWAN, AND C. S. HOLLING. 1977. Prey capture by the African lion. Canadian Journal of Zoology 55:1811–1828.

ESTES, R. D., AND J. GODDARD. 1967. Prey selection and hunting behavior of the African wild dog. The Journal of Wildlife Management 31:52–70.

EWER, R. F. 1973. The carnivores. Cornell University Press, Ithaca, New York.

GESE, E. M., AND S. GROTHE. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. The American Midland Naturalist 133:36–43.

GITTLEMAN, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. Oecologia 67:540–554.

HARRISON, D. J. 1992. Social ecology of coyotes in northeastern North America: relationships to dispersal, food resources, and human exploitation. Pp. 53–72 in Ecology and management of the eastern coyote (A. N. Boer, ed.). Wildlife Research Unit, University of New Brunswick, Fredricton, New Brunswick, Canada.

HAWTHORNE, V. M. 1971. Coyote movements in Sagehen Creek Basin, northeastern California. California Fish and Game 57:154–161.

HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.

HUGGARD, D. J. 1993. Prey selectivity by wolves in Banff National Park. I. Prey species. Canadian Journal of Zoology 71:130–139.

JOHNSINGH, A. J. T. 1993. Prey selection in three large sympatric carnivores in Bandipur. Mammalia 56:517–526.

KARANTH, K. U., AND M. E. SUNQUIST. 1995. Prey selection by tiger, leopard and dhole in tropical forests. The Journal of Animal Ecology 64:439–450.

KLEIMAN, D. G., AND J. F. EISENBERG. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Animal Behaviour 21:637–659.

KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

KRUUK, H. 1972. The spotted hyena. The University of Chicago Press, Chicago, Illinois.

KRUUK, H. 1975. Functional aspects of social hunting in carnivores. Pp. 119–141 in Function and evolution in behaviour (G. Baerends, C. Beer, and A. Manning, eds.). Oxford University Press, Oxford, United Kingdom.

KUCERA, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Ph.D. dissertation, University of California, Berkeley.

KUCERA, T. E. 1992. Influences of sex and weather on migration of mule deer in California. The Great Basin Naturalist 52:122–130.

KUCERA, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. The Journal of Wildlife Management 61:550–560.

KUNKEL, K. E., T. K. RUTH, D. H. PLETSCHER, AND M. G. HORNOCKER. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park. The Journal of Wildlife Management 63:901–910.

KUYT, E. 1972. Food habits of wolves on barren-ground caribou range. Canadian Wildlife Service Report 21:1–35.

LEYHAUSEN, P. 1979. Cat behavior: the predatory and social behavior of domestic and wild cats. Garland STPM Press, New York.

LITVAITIS, J. A., AND D. J. HARRISON. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180–1188.

LITVAITIS, J. A., AND J. H. SHAW. 1980. Coyote movements, habitat use, and food habits in southwestern

Comment Letter I9

Oklahoma. The Journal of Wildlife Management 44: 62–68.

LOW, W. A., AND I. M. COWAN. 1963. Age determination of deer by annular structure of dental cementum. The Journal Wildlife Management 27:466–471.

MAIN, M. B., AND B. E. COBLENTZ. 1996. Sexual segregation in Rocky Mountain mule deer. The Journal Wildlife Management 60:497–507.

MCLAREN, B. E., AND R. O. PETERSON. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555–1558.

MECH, L. D. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, New York.

MECH, L. D., AND G. D. DELGIUDICE. 1985. Limitations of the marrow-fat technique as an indicator of body condition. Wildlife Society Bulletin 13:204–206.

MECH, L. D., AND L. D. FRENZEL. 1971. Ecological studies of the timber wolf in north-eastern Minnesota. United States Forest Service Research Paper NC 52:1–62.

MESSIER, F., AND C. BARRETTE. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60:1743–1753.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States, Fauna Series 5:1–238.

NEILAND, K. A. 1970. Weight of dried marrow as an indicator of fat in caribou femurs. The Journal of Wildlife Management 34:904–907.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models. Richard D. Irwin, Homewood, Illinois.

O'DONOGHUE, M., S. BOUTIN, C. J. KREBS, G. ZULETA, D. L. MURRAY, AND E. J. HOFER. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79:1193–1208.

O'GARA, B. W., AND R. B. HARRIS. 1988. Age and condition of deer killed by predators and automobiles. The Journal of Wildlife Management 52:316–320.

PACKER, C. 1986. The ecology of sociality in felids. Pp. 429–451 in Ecological aspects of social evolution: birds and mammals (D. I Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey.

PACKER, C., D. SCHEEL, AND A. E. PUSEY. 1990. Why lions form groups: food is not enough. The American Naturalist 136:1–19.

PATTERSON, B. R., L. K. BENJAMIN, AND F. MESSIER. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. Canadian Journal of Zoology 76:1885–1897.

PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. United States National Park Service Scientific Monograph 11:1–210.

PETERSON, R. O., N. J. THOMAS, J. M. THURBER, J. A. VUCETICH, AND T. A. WAITE. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy 79:828–841.

PIERCE, B. M., V. C. BLEICH, AND R. T. BOWYER. In press. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology.

PIERCE, B. M., V. C. BLEICH, C.-L. B. CHETKIEWICZ, AND J. D. WEHAUSEN. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222–226.

PIERCE, B. M., V. C. BLEICH, J. D. WEHAUSEN, AND R. T. BOWYER. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986–992.

PIMLOTT, D. H., J. A SHANNON, AND G. B. KOLENSKY. 1969. The ecology of the timber wolf in Algonquin Park. Ontario Department of Lands and Forests, Wildlife Research Report 87:1–92.

RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. The American Naturalist 111:917–938.

RINEY, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. New Zealand Journal of Science and Technology Section B 36:429–463.

ROSS, P. I., AND M. G. JALKOTZY. 1996. Cougar predation on moose in south-western Alberta. Alces 32: 1–8.

SCHALLER, G. B. 1967. The deer and the tiger: a study of wildlife in India. The University of Chicago Press, Chicago, Illinois.

SCHALLER, G. B. 1972. The Serengeti lion. The University of Chicago Press, Chicago, Illinois.

SEIDENSTICKER, J. 1976. On the ecological separation between tigers and leopards. Biotropica 8:225–234.

SPALDING, D. J., AND J. LESOWSKI. 1971. Winter food of the cougar in south-central British Columbia. The Journal of Wildlife Management 35:378–381.

STORER, T. I., AND R. L. USINGER. 1968. Sierra Nevada natural history. University of California Press, Berkeley.

SUNQUIST, M. E. 1981. The social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. Smithsonian Contributions in Zoology 336:1–98.

TAYLOR, R. J. 1984. Predation. Chapman and Hall, New York.

VAN ORSDOL, K. G. 1984. Foraging behavior and hunting success of lions in Queen Elizabeth National Park, Uganda. African Journal of Ecology 22:79–99.

WANNEMACHER, R. W., JR., AND W. K. COOPER. 1970. Relationship between protein metabolism in muscle tissue and the concept of "protein reserves." Pp. 121–138 in Protein metabolism and biological function (C. P. Bianchi and R. Hilf, eds.). Rutgers University Press, New Brunswick, New Jersey.

WECKERLY, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79:33–52.

WELLS, M. C., AND M. BEKOFF. 1982. Predation by wild coyotes: behavioral and ecological analyses. Journal of Mammalogy 63:118–127.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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SURVIVORSHIP AND CAUSE-SPECIFIC MORTALITY IN FIVE POPULATIONS OF MULE DEER

Vernon C. Bleich[1,2] and Timothy J. Taylor[3]

ABSTRACT.—We used retrospective analyses to investigate cause-specific mortality and survivorship among 5 populations of mule deer (N = 168 telemetered animals) wintering in the western Great Basin during 1986–1994. These populations existed under similar environmental conditions, but survivorship functions differed among them. Monthly survival ranged from 0.964 to 0.990, and annual survival ranged from 0.643 to 0.884. The proportion of deaths attributed to predation and malnutrition or anthropogenic causes did not differ among the 5 populations. Predation was the leading cause of mortality; mountain lions were responsible for approximately 90% of the deer killed by predators. No difference existed among these populations in the proportion of telemetered deer that were killed by mountain lions, but proportionally more females than males were killed by these large felids. Predation by mountain lions is the primary source of mortality and a widespread phenomenon among the populations of mule deer we investigated.

Key words: California, Felis concolor, Odocoileus hemionus, *mule deer, mortality, mountain lion, predation, survivorship.*

Populations of mule deer (*Odocoileus hemionus*) have been declining in western North America for many years (Workman and Low 1976), and effects of nutrients, competition, predation, and climate on these populations have been debated among numerous investigators. Mule deer are thought to be density dependent in their response to resource availability (McCullough 1990). In unpredictable environments (typical of much of the Great Basin), however, it may be difficult to base management recommendations on density-dependent responses anticipated to follow population declines (Mackie et al. 1990). Whatever factors, singularly or in combination, regulate mule deer populations remain open to discussion. Indeed, there is general agreement that no single cause can be invoked. Detailed and specific investigations are necessary to evaluate factors that may regulate populations of these important game animals (Hornocker 1976, Knowlton 1976, Connolly 1981).

Recently, Wertz (1996) expressed concern about the dynamics of several mule deer populations wintering in the western Great Basin. Highway mortality has been a basis for this concern, as have the effects of predation and disease. Persistent drought has lowered the carrying capacity of deer winter ranges in this general area, with resultant negative influences on the physical condition of these large herbivores (Kucera 1988, Taylor 1996). Moreover, the harsh winter of 1992–93 killed many deer, particularly in northeastern California and northwestern Nevada (Wertz 1996).

To better understand factors affecting deer populations in the western Great Basin, we investigated seasonal distribution, habitat selection, cause-specific mortality, and survivorship in 5 populations of mule deer wintering in eastern California and western Nevada. In this paper we use retrospective analyses based on telemetered animals (White and Garrot 1990) to compare cause-specific mortality among 5 mule deer populations that winter in the western Great Basin. Additionally, we describe and compare survivorship functions for female deer in these populations.

DESCRIPTION OF THE STUDY AREA

Our study area is located in Mono and Inyo counties, California, and Douglas County, Nevada (Fig. 1). Deer from the West Walker, East Walker, Mono Lake, and Casa Diablo winter ranges are migratory and display annual patterns of movement and range use. In spring they make long-distance movements, sometimes >60 km, and spend summers on both the east and west slopes of the Sierra Nevada

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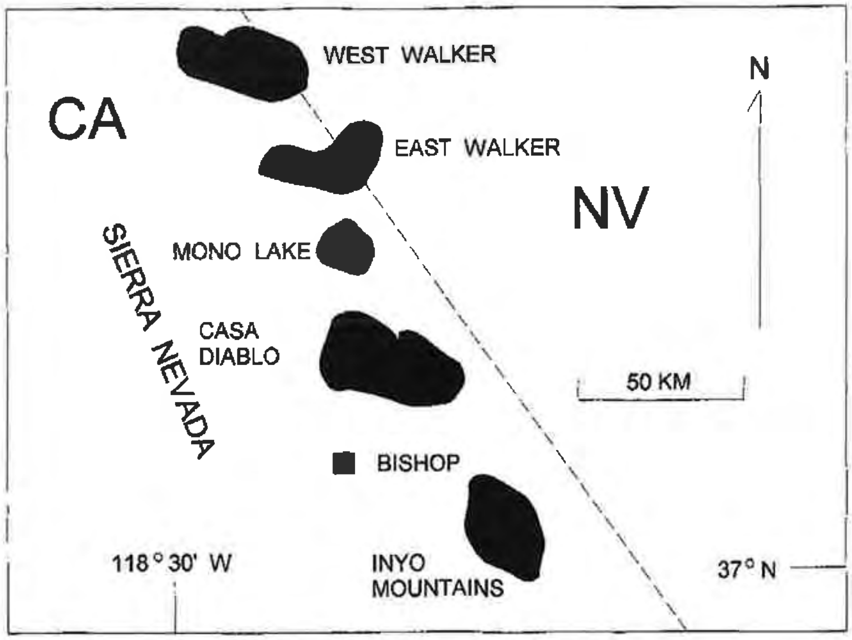

Fig. 1. Location of 5 winter ranges in northeastern California and western Nevada. Mule deer concentrate on these areas from approximately 1 November to 15 May each year.

(Taylor 1988, 1991). During autumn deer from these populations return to discrete winter ranges on the western edge of the Great Basin, where they remain from about 1 November to 15 May (Taylor 1988, 1991). Deer inhabiting the Inyo Mountains undergo altitudinal migrations similar to those described by Nicholson et al. (1997), but generally do not exhibit the extensive movements made by deer from the other 4 populations. Currently, 4 of the populations (West Walker, East Walker, Mono Lake, Casa Diablo) are classified as Rocky Mountain mule deer (*O. h. hemionus*); deer occupying the Inyo Mountains are classified as Inyo mule deer (*O. h. inyoensis*), a taxon of questionable validity (Wallmo 1981, Cronin and Bleich 1995).

During winter all 5 populations of deer occur largely in sagebrush (*Artemisia tridentata*) steppe or pinyon pine (*Pinus monophylla*) habitat, ranging in elevation from 1500 m to 2300 m (Taylor 1988, 1991, V.C. Bleich and D. Racine unpublished data). The primary winter forage for the 4 northern populations is bitterbrush (*Purshia* spp.; Taylor 1988, 1991). Although bitterbrush occurs in the Inyo Mountains (DeDecker 1991), specific data on deer diets in that range are lacking.

The Sierra Nevada creates a formidable rain shadow, and during winter these deer occupy an arid region with low and unpredictable precipitation (Fig. 2), similar to that described by Kucera (1988). Since 1986, the Great Basin immediately east of the Sierra Nevada has experienced repeated annual droughts; as a result, ecological carrying capacity of many winter ranges has declined (Taylor 1991). Migratory populations of mule deer can be substantially affected by drought conditions on winter ranges despite adequate forage during summer (Kucera 1988). During years of low precipitation, bitterbrush production is poor and deer subsist on suboptimal diets consisting largely of conifers, sagebrush, and blackbrush (*Coleogyne ramosissima;* Kucera 1988, Taylor 1991).

METHODS

During 1986–1991, we used Clover (1956) traps, a helicopter and linear drive nets (Thomas and Novak 1991), and a hand-held net gun fired from a helicopter (Krausman et al. 1985) to capture mule deer. We fitted adult (≥1-yr-old) animals with color-coded ear tags and telemetry collars (Model 500, Telonics, Inc., Mesa, AZ) that incorporated a mortality sensor with a 6-h delay. We collared each animal at its capture site and released it when processing was completed. By distributing our

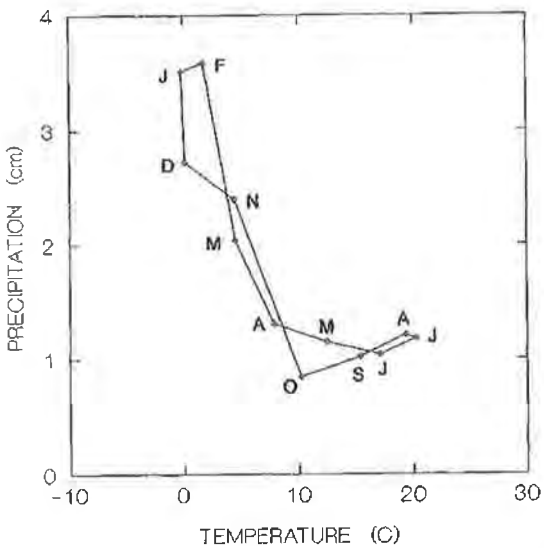

Fig. 2. Climate throughout the study area typically is cold during winter and hot during summer. Precipitation occurs primarily as snowfall during winter, but variance in annual precipitation is high. The climograph was developed from data obtained 1961–1990 from the Western Regional Climate Center using the mean of monthly mean values of minimum and maximum temperatures for Bishop, Bridgeport, Bodie, and Independence, California

capture efforts throughout all winter ranges, we minimized potential biases associated with heterogeneous use of those areas by deer. We collared male and female deer in the approximate proportion of their occurrence in each population. Each winter, we used ground-based chemical immobilization or a helicopter and net gun to capture and radio-collar additional deer in each population.

In the 4 northern populations, we used aerial and ground telemetry to monitor the status of deer at intervals ≤1 wk; thus, date of death could be closely estimated. Using only aerial telemetry in the Inyo Mountains, we monitored those deer at approximately 2-wk intervals. For animals for which we could not ascertain the date of death, we assumed death occurred midway between the last known live observation and the date on which a mortality signal was first received.

We attempted to determine the cause of mortality for every deer that died. For animals killed by predators, we used the criteria of Shaw (1983) and Woolsey (1985) to identify the species of predator in all but one instance. Nutritional status was indexed by condition of marrow in long bones (Cheatum 1949). When we could not ascertain the source of mortality, we listed the cause of death as undetermined. G-tests were used for categorical analyses, and a binomial test compared the proportion of deer killed by mountain lions during different years (Zar 1984).

We used the Kaplan-Meier (1958) estimator, as modified by Pollock et al. (1989), for staggered entry of telemetered females into each population, and determined survivorship on a monthly basis. To compare survivorship functions, we used the log-rank test (Cox and Oakes 1984) as modified by Pollock et al. (1989). We calculated the most conservative chi-square statistic presented by Pollock et al. (1989) to enhance the probability that any differences detected between survivorship functions were real.

Survivorship was not evaluated on all winter ranges concurrently, and deer were not initially collared at the same time of year. To minimize seasonal effects on mortality in this retrospective analysis, we compared survivorship of females from paired populations from the beginning of the 1st April during which collared deer from each population pair were available to the end of the period for which paired monthly data were available for those particular populations. For example, we studied cause-specific mortality in the West Walker population during April 1992–January 1995, and in the Inyo Mountains population during October 1991–December 1994; for this pair, comparisons of survivorship curves spanned a period of 2 yr and 9 mon, from 1 April in year 1 to 31 December in year 3. Using this method, we compared survivorship over periods of 21 mon for 4 pairs of populations, and over 27 mon for 5 other pairs. To facilitate comparisons, we also calculated finite, annual, and monthly survivorship for females in each population. We restricted our analyses to females because the genders of sexually dimorphic ungulates may occupy different habitats, experience different risks of natural mortality (Bleich et al. 1997), and respond differently to the threat of predation (Bleich in press).

We collected data for a minimum of 24 mon in the Casa Diablo population and a maximum of 39 mon in the Inyo Mountains. Although the investigations did not all run concurrently, these 5 populations occupy similar habitats in close proximity to each other, they were exposed to similar climatic regimes (Table 1),

TABLE 1. Correlation matrices for climatological data obtained 1961–1990 from the Western Regional Climate Center for Bishop, Bridgeport, Bodie, and Independence, California. These stations are all located on or near the winter ranges investigated herein.

	Average monthly maximum temperature			
	Bishop	Bodie	Bridgeport	Independence
Bishop	1.000	0.988	0.995	1.000
Bodie	0.996	1.000	0.995	0.987
Bridgeport	0.996	0.997	1.000	0.995
Independence	0.999	0.997	0.995	1.000
	Bishop	Bodie	Bridgeport	Independence
	Average monthly minimum temperature			

	Average monthly precipitation			
	Bishop	Bodie	Bridgeport	Independence
Bishop	1.000	0.936	0.972	0.996
Bodie		1.000	0.934	0.935
Bridgeport			1.000	0.979
Independence				1.000

and several of the investigations were ongoing simultaneously. Thus, we assumed that qualitative differences among these winter ranges were minimal.

RESULTS

We radio-collared 168 adult mule deer (27 males, 141 females) and monitored them for 21–39 mon (2829 telemetry-months; Table 2). We determined the proximate source of mortality for 76% of the females (41 of 54) and 85% of males (11 of 13) that died. Among females, confirmed causes of death ranged from 57% in the Inyo Mountains to 100% in the East Walker population. Among the 41 mortalities of females for which the cause of death is known, 83% were attributed to predation, 4.8% were human-induced, and 12.2% were due to malnutrition. In the northernmost population (West Walker), 3 of 10 mortalities resulting from predation occurred during or immediately after the severe winter of 1992–93, and 7 of 10 occurred during or following the mild winter of 1993–94 ($P > 0.10$). Among males that died, predation by mountain lions accounted for 36% and hunting for 64% of the 11 mortalities for which the cause of death was determined; the source of mortality for 2 males could not be ascertained. We detected no evidence of malnutrition among animals killed by predators or among those dying of anthropogenic causes.

Predation accounted for >70% of the known causes of death for females on each winter range (Fig. 3). The proportion of deaths attributed to predation did not differ among these populations ($G = 5.987$, $df = 4$, $P = 0.200$) when human-induced mortality and malnutrition were pooled. For males, sample sizes were too small to allow a comparison among populations.

Of 34 female mule deer killed by predators, mountain lions accounted for 91% of the deaths (Fig. 4). No difference existed among the 5 populations in the proportion of females killed by mountain lions ($G = 2.979$, $df = 4$, $P = 0.561$). Overall, the proportion of female deer whose deaths were attributable to predation by mountain lions (31 of 41) was significantly greater than the proportion of males killed by these large felids (4 of 11; $G = 5.751$, $df = 1$, $P = 0.016$).

Survivorship functions of female deer differed significantly for 3 of 10 pairwise comparisons (Table 3). Survivorship for the West Walker population differed from the Mono Lake, Inyo Mountains, and East Walker populations, and was marginally nonsignificant for the Casa Diablo population. The finite survival

TABLE 2. Sample sizes and estimates of monthly and annual survivorship for West Walker (WW), Casa Diablo (CD), East Walker (EW), Mono Lake (ML), and Inyo Mountains (IM) mule deer populations, Inyo and Mono counties, California, and Douglas County, Nevada, 1986–1994.

Winter range[a]	Deer (*N*)	Telemetry-months (*N*)	Monthly survivorship	$s_{\bar{x}}$	Annual survivorship	$s_{\bar{x}}$
WW	48	823	0.964	0.004	0.643	0.010
CD	27	469	0.985	0.004	0.837	0.014
EW	23	428	0.990	0.004	0.884	0.014
ML	23	512	0.979	0.006	0.777	0.018
IM	20	597	0.973	0.008	0.717	0.022

[a]Inclusive dates of each investigation were WW, April 1992–January 1995; CD, January 1986–December 1987; EW, March 1988–June 1990; ML, March 1988–June 1990; IM, October 1991–December 1994.

rate among these populations ranged from about 0.75 in the East Walker population to about 0.30 in the West Walker population, which had the highest proportion of mortality caused by malnutrition. Among these populations monthly survival estimates ranged from 0.964 to 0.990, and annual survival estimates ranged from 0.643 to 0.884 (Table 2). Too few males were marked to allow a meaningful estimate of survivorship for males occurring in these populations.

DISCUSSION

Predation was the most common cause of mortality among 5 mule deer populations that winter east of the Sierra Nevada (Fig. 3). Human-induced mortality and malnutrition varied among these populations. Based on our analyses, we conclude that sources of mortality were similar among these winter ranges for the periods we studied. Deaths of female deer resulting from human activities were recorded only in the West Walker and Casa Diablo populations. Death resulting from malnutrition was restricted to the West Walker and Mono Lake populations and accounted for 25% and 21% of the mortality in those populations, respectively. Malnutrition overall (9.8%) was, however, not an important cause of death.

Among deer killed by carnivores, mountain lions were the most common predator, and no differences existed in the proportion of female deer killed by mountain lions among the 5 populations we investigated (Fig. 4). Our findings are consistent with previous ones that mule deer are important prey of mountain lions throughout western North America (Hornocker 1976, Russell 1978). Proportionally more telemetered females than males were killed, suggesting that females may be more vulnerable to predation by mountain lions.

There was a difference in survivorship functions between 3 of 10 pairs of populations that we compared (Table 3), and the results were but marginally nonsignificant for a 4th pair. Small samples possibly influenced our ability to detect differences (Pollock et al. 1989) between other population pairs, but the magnitude of differences between 6 pairs, when compared to the remaining 4, suggests sample size was not problematic (Table 3). These findings were somewhat unexpected given the physical, climatological, vegetational, and faunal similarities among the winter ranges we examined, and may be attributable to the high proportion of mortality from malnutrition in the West Walker population during the winter of 1992–93; that winter was especially severe in northeastern California (Wertz 1996).

In none of our study populations are historical demography and habitat quality adequately known to begin to factor out the relative roles of nutrition, predation, and climate as factors influencing the dynamics of these populations. Additionally, the effects of these factors on survival of young <1 yr old were not investigated. With the exception of the Mono Lake and West Walker populations, the absence of animals dying of malnutrition suggests that mortality from predation generally was not compensatory. Many female deer collected from the West Walker winter range were in poor physical condition following the winter of 1992–93 (Taylor 1996), and some animals in that population may have been predisposed to death by predation during our investigation. Nevertheless, only 3 of 10 animals killed by predators in the West Walker population died that winter, but 7 of 10 were killed during the mild winter of 1993–94. Despite the deaths of 2 females from malnutrition in the Mono Lake population, individuals there were in much better condition than were West Walker females

Comment Letter I9

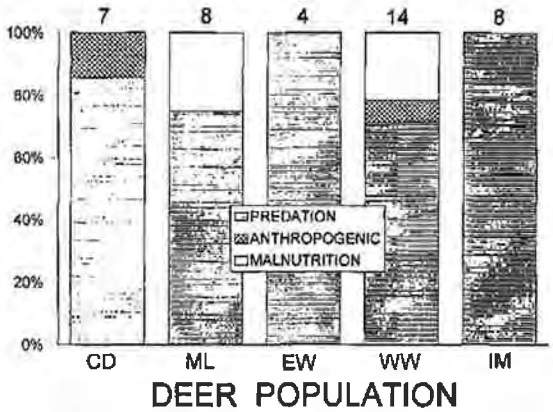

Fig. 3. Proportion of mortalities (N = 41) of female deer that can be attributed to predation, anthropogenic causes, and malnutrition in each of 5 deer populations inhabiting eastern California and western Nevada, 1986–1994. Numbers above each bar are total mortalities from known causes for each population; CD = Casa Diablo, EW = East Walker, ML = Mono Lake, WW = West Walker, and IM = Inyo Mountains.

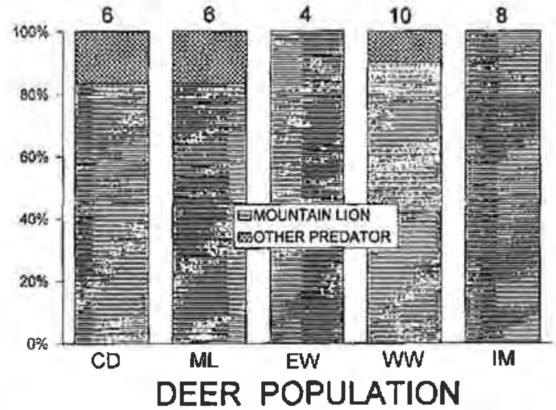

Fig. 4. Proportion of predation on female deer attributed to mountain lions and other predators in each of 5 deer populations studied in eastern California and western Nevada, 1986–1994. Numbers above each bar represent total mortality attributed to predators for each population; CD = Casa Diablo, EW = East Walker, ML = Mono Lake, WW = West Walker, and IM = Inyo Mountains.

during 1992–93 (Taylor 1991). Body condition of Mono Lake females during the period they were under study approached that of the West Walker population during 1994, a year when no animals died of malnutrition. None of the animals killed by predators exhibited evidence of depleted fat reserves upon examination of femur marrow. If malnutrition was an important factor predisposing individuals to death by other causes, we would have expected to find evidence of such among victims of predation or human-induced mortality; this was not the case.

The role of predation in regulating populations of large mammals remains open to debate (Skogland 1991), and predation as a factor potentially regulating deer populations has not been widely accepted (Connolly 1981). For example, the effects of mountain lion predation have been described as unimportant (Janz and Hatter 1986) and conversely as having strong local effects (McNay and Voller 1995) on deer occurring in the same geographic area. These large felids were responsible for most mortality of adult female deer in each of the populations we investigated. Although we noted few adults killed by coyotes (*Canis latrans*), these canids can have important effects on deer population dynamics, especially through their influence on fawn survival (Knowlton 1976, Bowyer 1987).

Predation may warrant special consideration as a factor in the dynamics of mule deer occupying unpredictable environments. Indeed, investigations in boreal systems have suggested that predation by wolves (*Canis lupus*) and bears (*Ursus* spp.) can preclude recovery of large mammal populations that have become depressed by a single source, or a combination of several sources, of mortality (Gasaway et al. 1983, 1992, Van Ballenberghe 1987). Based on observations in the Sierra Nevada, Wehausen (1996) suggested that predation by mountain lions has substantially influenced the population dynamics of mountain sheep in part of the western Great Basin. Removal of several mountain lions was necessary to preclude the extirpation of one population of these specialized ungulates (Bleich et al. 1991), and that population of mountain sheep is sympatric with the Casa Diablo deer population for part of the year (Taylor 1991).

Given the similarities in cause-specific mortality and the importance of predation as a cause of death among the populations we studied, the potential for predation to regulate deer populations might be reconsidered and further investigated, particularly for migratory deer inhabiting the arid, unpredictable ecosystems typical of the western Great Basin. In such systems predation clearly is an important source of mortality and may assume greater importance

TABLE 3. Pairwise comparisons of survivorship functions for West Walker (WW), Casa Diablo (CD), East Walker (EW), Mono Lake (ML), and Inyo Mountains (IM) mule deer populations, Inyo and Mono counties, California, and Douglas County, Nevada, 1986–1994. Chi-square statistics are shown above the diagonal; probabilities that survivorship functions did not differ are shown below the diagonal. For all comparisons, degrees of freedom = 1.

Population	Chi-square values				
	WW	EW	ML	CD	IM
WW	——	7.611	4.235	2.458	4.977
EW	<0.01	——	0.388	0.326	0.231
ML	<0.05	>0.50	——	0.248	0.130
CD	>0.10	>0.50	>0.50	——	0.012
IM	<0.05	>0.50	>0.50	>0.90	——
	Probability that survivorship did not differ				

in population limitation than in more mesic environments where the effects of climate are more tempered and more predictable.

In highly variable systems, density-independent events (i.e., droughts and harsh winters) occur unpredictably (Mackie et al. 1990) and can result in unanticipated population declines that confound conservation strategies. Nonetheless, density dependence would continue to operate (McCullough 1990) in such systems and could indirectly affect predation rates (McCullough 1979). Only through carefully designed, long-term investigations, however, will it be possible to reach meaningful conclusions regarding effects of predation and other sources of mortality on populations of migratory deer occupying Great Basin ecosystems.

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LITERATURE CITED

BLEICH, V.C. In press. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. Journal of Mammalogy.

BLEICH, V.C., R.T. BOWYER, AND J.D. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

BLEICH, V.C., C.D. HARCIS, J.A. KEAY, AND J.D. WEHAUSEN. 1991. Interagency coordination and the restoration of wildlife populations. Pages 277–284 *in* J. Edelbrock and S. Carpenter, editors, Natural areas and Yosemite: prospects for the future. U.S. National Park Service, Denver Service Center, Denver, CO.

BOWYER, R.T. 1987. Coyote group size relative to predation on mule deer. Mammalia 51:515–526.

CHEATUM, E.L. 1949. Bone marrow as an index of malnutrition. New York State Conservationist 3:19–22.

CLOVER, M. 1956. Single-gate deer trap. California Fish and Game 42:199–201.

CONNOLLY, G.E. 1981. Limiting factors and population regulation. Pages 245–285 *in* O.C. Wallmo, editor, Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

COX, D.R., AND D. OAKES. 1984. Analysis of survival data. Chapman and Hall, Inc., New York.

CRONIN, M.C., AND V.C. BLEICH. 1995. Mitochondrial DNA variation among populations and subspecies of mule deer in California. California Fish and Game 81:45–54.

DEDECKER, M. 1991. Shrubs and flowering plants. Pages 108–241 *in* C.A. Hall, Jr., editor, Natural history of the White-Inyo Range, eastern California. University of California Press, Berkeley.

GASAWAY, W.C., R.D. BOERTJE, D.V. GRANGAARD, D.G. KELLEYHOUSE, R.O. STEPHENSON, AND D.G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120:1–59.

GASAWAY, W.C., R.O. STEPHENSON, J.L. DAVIS, P.K. SHEPHERD, AND O.E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84:1–50.

HORNOCKER, M.G. 1976. The possible influences of the mountain lion on mule deer populations. Pages 107–109 *in* G.W. Workman and J.B. Low, editors, Mule deer decline in the west: a symposium. College of Natural Resources, Utah State University, Logan.

JANZ, D.W., AND I.W. HATTER. 1986. A rationale for wolf control in the management of the Vancouver Island predator-ungulate system. British Columbia Ministry of the Environment, Wildlife Bulletin B-45:1–35.

KAPLAN, E.L., AND P. MEIER. 1958. Nonparametric survivorship estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

KNOWLTON, F.F. 1976. Potential influence of coyotes on mule deer populations. Pages 111–118 *in* G.W. Workman and J.B. Low, editors, Mule deer decline in the West: a symposium. College of Natural Resources, Utah State University, Logan.

KRAUSMAN, P.R., J.J. HERVERT, AND L.L. ORDWAY. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71–73.

KUCERA, T.E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Unpublished doctoral dissertation, University of California, Berkeley.

MACKIE, R.J., K.L. HAMLIN, D.F. PAC, G.L. DUSEK, AND A.K. WOOD. 1990. Compensation in free-ranging deer populations. Transactions of the North American Wildlife and Natural Resources Conference 55:518–526.

MCCULLOUGH, D.R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor.

______. 1990. Detecting density dependence: filtering the baby from the bathwater. Transactions of the North American Wildlife and Natural Resources Conference 55:534–543.

MCNAY, R.S., AND J.M. VOLLER. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. Journal of Wildlife Management 59:138–146.

NICHOLSON, M.C., R.T. BOWYER, AND J.G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

POLLOCK, K.H., S.R. WINTERSTEIN, C.M. BUNCK, AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

RUSSELL, K.R. 1978. Mountain lion. Pages 207–225 *in* J.L. Schmidt and D.L. Gilbert, editors, Big game of North America, ecology and management. Stackpole Books, Harrisburg, PA.

SHAW, H.G. 1983. Mountain lion field guide. Arizona Game and Fish Department Special Report 9:1–27.

SKOGLAND, T. 1991. What are the effects of predators on large ungulate populations? Oikos 61:401–411.

TAYLOR, T.J. 1988. Migration and seasonal habitats of the Casa Diablo deer herd. California Department of Fish and Game, Bishop.

______. 1991. Ecology and productivity of two interstate deer herds in the eastern Sierra Nevada: East Walker and Mono Lake deer herd study. California Department of Fish and Game, Bishop.

______. 1996. Condition and reproductive performance of female mule deer in the central Sierra Nevada. California Fish and Game 82:122–132.

THOMAS, R.D., AND B.K. NOVAK. 1991. Helicopter drive-netting techniques for mule deer capture on Great Basin ranges. California Fish and Game 77:194–200.

VAN BALLENBERGHE, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. Swedish Wildlife Research Supplement 1:431–460.

WALLMO, O.C. 1981. Mule deer and black-tailed deer distribution and habitats. Pages 1–25 *in* O.C. Wallmo, editor, Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

WEHAUSEN, J.D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471–479.

WERTZ, P. 1996. Deer hunt forecast: a mixed bag for '96. Tracks [California Department of Fish and Game] 13:3–5.

WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, CA.

WOOLSEY, N.G. 1985. Coyote field guide. Arizona Game and Fish Department Special Report 15:1–39.

WORKMAN, G.W., AND J.B. LOW, EDITORS. 1976. Mule deer decline in the West: a symposium. College of Natural Resources, Utah State University, Logan.

ZAR, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

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POPULATION DYNAMICS OF MULE DEER IN THE EASTERN SIERRA NEVADA: IMPLICATIONS OF NUTRITIONAL CONDITION

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Abstract: Mule deer populations routinely fluctuate in size and managers are rarely afforded the opportunity to understand factors that determine such changes. Our goal was to understand the factors that limit population growth of mule deer in the Sierra Nevada, with an emphasis on developing our understanding of the nutritional constraints associated with reproduction and survival, and the application of those nutritional relationships to management of mule deer. We conducted research on a population of mule deer that spends winters in Round Valley, on the east slope of the Sierra Nevada, and spends summers on high elevation ranges on both sides of the Sierra crest. We monitored annual survival, reproduction, and nutritional condition of adult females during 1997-2009 and monitored survival of neonatal mule deer during 2006-2008. The population size of mule deer residing in Round Valley has been highly variable since 1985, largely in response to the highly variable climate in the Sierra Nevada. Post-winter nutritional condition of adult females was influenced by both intraspecific competition for forage (density dependence) and its association with forage production in response to winter precipitation. In addition to intrinsic habitat value, autumn body fat was influenced by reproductive status of each female and her summer residency. Females that spent summers west of the crest experienced lower reproductive success, but also lower somatic cost of reproduction compared with females that spent summers east of the Sierra crest. The major proximate cause of mortality for young mule deer was predation and most young west of the Sierra crest were lost to bear predation. Body fat of adult females following winter provided an encompassing measure of population health and predicted adult female survival, reproduction, recruitment of young, an index to abundance of males, and overall population trajectory during the following year. Nutritional limits on survival and recruitment of deer in Round Valley clearly indicate bottom-up limitation on deer dynamics and the importance of data on nutritional condition when interpreting dynamics of deer populations. Estimation of nutritional condition provided the greatest insight into multiple population parameters and predicted population rate of change (λ). Recent nutritional (March mean body fat = 2.6%) and demographic data suggests that Round Valley is experiencing a new, reduced carrying capacity (K). Less somatic cost of reproduction, but also lower recruitment for west-side females suggests that some predation experienced by west-side young is additive. Although a reduction in bear numbers might result in increased recruitment by west-side females, the increased number of animals on winter range would simply exacerbate the effects of an already forage

limited winter range. Implementation of a female harvest on winter range in Round Valley would lower the population density with respect to *K*, which should result in improved nutritional condition of adult females and a population less susceptible to minor perturbations. Lack of fires on west side summer range and recent fires on winter range also may have altered the forage base and reduced *K*.

INTRODUCTION

Mule deer populations have experienced periodic declines over much of the last century and causes of the declines remain speculative and controversial (Connolly 1981; deVos et al. 2003). Cited causes of the declines include loss of habitat due to development, deterioration of nutritional forages, competition with other ungulates, predation, disease, increased hunting mortality, poaching, severe winter weather, and droughts (deVos et al. 2003). Similar widespread declines across regions suggest that large-scale environmental conditions may trigger those declines (Unsworth et al. 1999). Failure to identify factors that regulate populations, however, has precluded the detection of the underlying causes. Detailed and long-term investigations are necessary to identify the factors regulating populations of mule deer to improve their conservation and management (Caughley 1977, Connelly 1981, deVos et al. 2003, Mackie et al. 2003). Indeed, the scarcity of long-term investigations of large herbivores has limited the use of scientific approaches to manage and conserve those large mammals (Bleich et al. 2006, Lindstrom 1999).

Population parameters such as age-specific survival and reproduction are determinants of the dynamics of large mammal populations (Coulson et al. 2001, Gaillard et al. 2000, Lande et al. 2002) and those parameters are influenced by a combination of stochastic environmental variation and density dependence (Albon et al. 2000, Sæther 1997). Research has traditionally focused on the role of predation in limiting populations of ungulates with less focus given to resource availability (Sæther 1997). That predator-centric focus likely has hampered the understanding of predator-prey dynamics (Bowyer et al. 2005). Bottom-up versus top-down limitation of populations has remained a central theme of ecological studies and holds implications for both theoretical and applied ecology (Bowyer et al. 2005, Hairston et al. 1960, Sinclair and Krebs 2002). Controversy over whether populations of large mammals are top-down or bottom-up regulated, however, continues. Although often considered a dichotomy, top-down and bottom-up influences are rather a continuum and act simultaneously on populations (Bowyer et al. 2005). Bowyer et al. (2005) suggested that assessment of top-down versus bottom-up limitation may be most accurately and efficiently determined by understanding prey population dynamics.

Demographic (vital) rates of large herbivores are believed to respond to resource limitation in a predictable sequence from increased age of first reproduction, decreased survival of young, decreased reproduction by adults, and lastly, decreased survival of adults (Gaillard et al. 1998; 2000, Eberhardt

2002). That variability in reproduction and survival is largely determined by animal condition (Cameron and Ver Hoef 1994, Testa and Adams 1998, Keech et al. 2000, Stewart et al. 2005, Bender et al. 2007). Moreover, the use of population vital rates and mortality factors to make inferences for top-down and bottom-up forces without knowledge of seasonal deficiencies in nutrition may be of limited value (Bowyer et al. 2005, Brown et al. 2007). Understanding patterns of nutritional condition and its relative impact on population dynamics will enhance our knowledge of life-history strategies and population regulation of ungulates (Stephenson et al. 2002, Cook et al. 2004, Parker et al. 2009); nutrition likely provides the basis for most life-history strategies (Parker et al. 2009). Measures of nutritional condition may ultimately function as the mechanism through which intraspecific competition for resources are mediated, and could provide the most direct and sensitive measure of resource limitation because effects of resource limitation on animal condition are realized before expression in reproduction and survival parameters (Bender et al. 2008).

Nutritional ecology is defined as the science relating an animal to its environment through nutritional interactions (Parker et al. 2009). Animal body condition is the integration of both nutrient intake and energetic costs. Knowledge of animal condition is critical to evaluate habitat conditions and predict population productivity because condition is related to nearly every parameter of productivity and survival (Short 1981). Animal condition reflects previous conditions encountered including precipitation and forage growth, deer population density, and energetic costs of reproduction (Cook et al. 2004, Stewart et al. 2005). Moreover, animal condition forms a predictable link between future survival and reproduction (Keech et al. 2000, Lomas and Bender 2006, Bender et al. 2007; 2008). Our overarching goal was to understand the factors that limit population growth of mule deer in the western Great Basin, with an emphasis on developing an understanding of the nutritional constraints associated with reproduction and survival, and the application of those nutritional relationships to management of mule deer. Indeed, knowledge of life-history characteristics and the inherent influence of nutritional constraints will provide insight into factors that regulate mule deer populations and allow for sound management decisions based on empirical data (Bowyer et al. 2005, Parker et al. 2009). Furthermore, understanding resource limitation will aid in developing harvest criteria for deer populations.

Additional objectives of this research included: (1) calculate annual population size using mark-resight estimates, (2) monitor annual patterns of survival and factors that influence survival of adult female mule deer, (3) determine survival and cause-specific mortality of neonatal mule deer born on either side of the Sierra crest, (4) determine the somatic costs of reproduction with respect to migratory patterns of female mule deer, (5) identify factors that underpin dynamics of mule deer in the western Great Basin and develop techniques to quantify carrying capacity for mule deer populations, and (6) apply those relationships to management of mule deer in Round Valley and the eastern Sierra Nevada. (7) Understanding deer population performance and trends is a critically important factor to be considered in the protection and, ultimately, the recovery of Sierra Nevada bighorn sheep. Further, deciphering and clarifying the "ecosystem link" between deer, lion, and sheep populations will result from this effort and ultimately will serve to solidify ecosystem conservation objectives in the eastern Sierra Nevada. Lastly, (8) preparation of manuscripts is currently underway and formal publication of the results obtained from the work in Round Valley will occur in the appropriate professional journals.

We conducted research on a population of mule deer that winters on the east side of the Sierra Nevada in Round Valley (37°24′, 118°34′W), Inyo and Mono Counties, California (Kucera 1998). Mule deer inhabited approximately 90 km^2 of Round Valley during November-April, but the size of the area of use was dependent on snow depth (Kucera 1998). Most of those mule deer migrate northward and westward to high-elevation ranges in summer (Kucera 1992, Pierce et al. 1999); many migrate over passes to the west side of the Sierra Crest while others remain on the east side (Figure 1). As recently as 1981, 87% of the mule deer wintering in Round Valley migrated to occupy summer ranges west of the Sierra Crest (Kucera 1998). The habitats on either side of the Sierra crest contrast substantially, which afforded a unique opportunity to evaluate influences of summer range quality on patterns of recruitment, energetic cost of reproduction, and life-history tradeoffs associated with reproduction.

STUDY AREA

The Sierra Nevada is a massive granite block that tilts to the western side with a gradual slope of only 2-6% encompassing 75 to 100 km before reaching a crest. Conversely, the spectacular eastern slope of the Sierra Nevada is characterized by steep slopes rising abruptly from the bordering valleys that merge with the western edge of the Great Basin. The Owens Valley area extending from the Sherwin Grade occurring north of the town of Bishop, south about 120km, is demarcated by elevation from 4200m at the mountain summits to 1220m at the valley floor which occur over horizontal distances of <10 km (Kucera 1988).

Within the Sierra, 95% of the precipitation including rain or snow accumulates between October and May (Storer et al. 2004). Winter storms from the Pacific Ocean deposit moisture as they move up the western slope, with a rain shadow effect leaving a more arid landscape on the eastern slope where the Great Basin Desert begins. At 1,676m in elevation, precipitation on the western slope severely contrasts the lack of moisture on the eastern slope creating a dramatically different flora and fauna on either side of the crest (Storer et al. 2004). The dense pine-fir stands and rivers commonly found on the west side contrast the sparse forests changing to sagebrush scrub below 2130m and few small streams found on the east side. The formidable Sierra Crest sharply delineates the western slope from the eastern slope of the Sierra Nevada and is traversable by a series of passes that increase in elevation from north to south (Kucera 1988).

Winter range

Round Valley is bounded to the west by the Sierra Nevada, particularly Mount Tom (4,161 m) and Wheeler Ridge (3,640 m), to the south by large boulders and granite ridges of the Tungsten Hills and Buttermilk's, and to the east by Highway 395 connecting Reno, Nevada to the Los Angeles Basin, California (Figure 2). The northern end of Round Valley gradually rises from the valley floor at 1,375 m to the top of the Sherwin Grade at 2,135 m. Open pasture land comprised about 18.3 km^2 of the eastern portion of the valley and 3.2 km^2 of Round Valley was developed residential housing. Deer only used pasture when heavy snows forced them from higher elevation areas dominated by bitterbrush (Pierce et al. 2004).

Vegetation of Round Valley was characteristic of that portraying the western Great Basin and the sagebrush belt (Storer et al. 2004). Typical vegetation composing habitats used by mule deer in Round Valley included bitter brush (*Purshia glandulosa*), sage brush (*Artemesia tridentata*), blackbrush (*Coleogyne ramosissima*), desert peach (*Prunus andersonii*), rabbitbrush (*Chrysothamnus nauseosus*),and Mormon tea (*Ephedra nevadensis*). Riparian areas consisted of willow (*Salix* sp.), Rose (*Rosa* sp.), and water birch (*Betula occidentalis*), although forbs and graminoids were uncommon in Round Valley during winter (Kucera 1988, Kucera 1992, Kucera 1997, Pierce et al. 2000; 2004).

Summer range

Summer range for mule deer that overwinter in Round Valley occurs on both sides of the Sierra crest at elevations ranging from 2,200 to >3,600m (Kucera 1988; Figure 2). Summer ranges west of the Sierra crest are substantially more mesic and forested than that east of the crest (Bleich et al. 2006). The western slope of the summer range is dominated by the upper montane and mixed conifer vegetation zones (Storer et al. 2004) consisting of conifer stands with little understory including red fir (*Abies magnifica*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), Jeffery pine (*Pinus jeffreyi*), and quaking aspen (*Populus tremuloides*). Nevertheless, montane chaparral consisting of dense stands of manzanitas (*Arctostaphylos* sp.), Ceanothus (*Ceanothus* sp.), and bush chinquapin (*Chrysolepis sempervirens*) often exists at lower elevations within drainages on the western slope (Storer et al. 2004). Mountain springs and streams, including large rivers, are common within the western Sierra.

The eastern slope of the Sierra Nevada up to approximately 2,130 m is dominated by the sagebrush vegetation zone (Storer et al. 2004). This zone is dominated by sagebrush, but also includes other shrub species such as bitterbrush, ceanothus, manzanitas, rabbitbrush, mountain mahogany (*Cercocarpus betuloides*), and contains pure stands of Jeffrey pine in some areas (Storer et al. 2004).

Grizzly bears (*Ursos arctos*) formerly existed west of the Sierra crest, but have since been extirpated (Storer and Tevis 1955). Nonetheless, areas occupied by migratory mule deer include a full complement of predators of both winter and summer ranges consisting of mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*; Pierce et al. 2000). Black bears (*Ursus americanus*) are frequently encountered on summer ranges west of the Sierra crest, but are uncommon in the eastern Sierra Nevada (Wildlife Programs Branch 2006).

METHODS

Adult Capture and Handling

During March 1997-2009 and November 2002-2008, we captured adult female mule deer on winter range in Round Valley using a hand-held net gun fired from a helicopter (Barrett et al. 1982, Krausman et al. 1985). We hobbled and blindfolded each animal prior to being ferried by helicopter to a central processing station with shelter and processing crews. During processing, we frequently monitored temperature, pulse, and respiration of each animal. When necessary, we placed cold water on the animals head, chest, and abdomen to facilitate cooling. In addition, if animals with elevated body temperatures were reluctant to return to a safe level, we administered Banamine. Captured animals were administered prophylactics including antibiotics, vitamin E/selenium, and vitamin E. We measured chest circumference, length of the metataurus, body mass, and collected blood and a fecal sample from each individual. To allow aging by cementum annuli technique (Matson's Laboratory), we removed one incisiform canine using techniques previously described by Swift et al. (2002), which have been verified to have no effect on body mass, percent body fat, pregnancy rate, or fetal rate (Bleich et al. 2003). We fitted each animal with a radiocollar equipped with mortality sensor and finished with orange tape or plastic to ensure visibility during mark/resight population surveys.

During captures, we employed ultrasonography using an Aloka 210 portable ultrasound device (Aloka, Wallinford, CT) with a 5-MHz transducer to determine body fat as a measure of nutritional condition in mule deer. We used ultrasound to measure maximum thickness of subcutaneous fat deposition at the thickest point cranial to the cranial process of the tuber ischium to the nearest 0.1 cm (Stephenson et al. 2002). We also measured the thickness of the bicep femoralis and longissimus dorsi to provide a measure of protein catabolism for animals in poor condition (Cook et al. 2001, Stephenson et al. 2002). We complemented ultrasonography with palpation to achieve a body condition score validated for mule deer (Cook et al. 2007) to aid in evaluating nutritional condition of animals that have mobilized subcutaneous fat reserves (<5.6% ingesta-free body fat). We calculated rLIVINDEX as subcutaneous rump fat thickness plus rump body condition score (Cook et al. 2001). We used rLIVINDEX to calculate ingesta-free body fat where, ingesta-free body fat = 2.920*rLIVINDEX-0.496 (Cook et al. 2007). We incorporated data on nutritional condition with that reported by Kucera (1988) and Pierce (1999). We calculated ingesta-free body fat from kidney fat indices collected 1984-1996 (Kucera 1988, Pierce 1999) following equations provided by (Stephenson et al. 2002).

During March captures, we used ultrasonography with an Aloka 210 portable ultrasound unit (Aloka, Inc., Wallinford, Connecticut USA) with a 3-MHz linear transducer to determine pregnancy and fetal rates of captured females during the second trimester of pregnancy (Stephenson et al. 1995). We shaved the left caudal abdomen behind the last rib and applied lubricant to facilitate transabdominal scanning. Presence and number of fetuses were determined, as well as fetal-eye diameter when fetus orientation was suitable for measurement. Upon completion of ultrasonography, numerous pregnant females were fitted with vaginal implant transmitters (VITs) during 2006-2008. Chemical immobilization was not necessary to fit females with vaginal implants (Bishop et al. 2006), thus all animals were physically restrained during processing. In pregnant females, we inserted VITs using a technique similar to that described in detail by Bishop et al. (2006). We placed VITs approximately 20 cm into the vaginal canal or until the silicone wings were pressed firmly against the cervix. We used VITs (M3930, Advanced Telemetry Systems, Isanti, Minnesota), which have been sufficiently described in detail elsewhere (Bowman and Jacobson 1998, Carstensen et al. 2003, Johnstone-Yellin et al. 2006) to identify and characterize birthing habitat and facilitate locating and capturing neonatal mule deer. Antennas of the VITs were approximately 9.5 cm in length and the tips were encapsulated in a resin bead to avoid fraying of the antenna. We used a temperature-sensitive switch (Carstenson et al. 2003, Johnstone-Yellin et al. 2006, Bishop et al. 2006) that increased pulse rate from 40 pulses to 80 pulses per minute when the temperature decreased below 32° C representative of the VIT being expelled by the deer. Vaginal implant transmitters have been employed without any reproductive problems or effects on female survival (Bowman and Jacobson 1998, Carstensen et al. 2003, Bishop et al. 2006) and are likely a practical technique for locating birth sites and subsequently, the capture of neonates (Carstensen 2003, Johnstone-Yellin 2006, Bishop et al. 2007).

Neonate capture and handling

During 3 years, 2006-2008, we located and captured neonatal mule deer from 15 June-20 July by searching for and observing females that exhibited postpartum behavior and by the use of VITs (White et al. 1972, Bishop et al. 2006). We located radiocollared females and monitored VITs for evidence of parturition at first daylight on a daily basis during the typical parturition period (i.e., 15 June – 31 July) using a Cessna 180 fitted with 2 2-element Yagi antennas. When a VIT exhibited a fast pulse (i.e., postpartum), the fixed-wing pilot acquired the approximate location of the implant and ground telemetry was employed to immediately locate the VIT. We used the location of the VIT and the location and behavior of the female to identify the search area. When searches failed to produce neonates, we evaluated whether the location of VIT was an actual birthsite and confirmed that supposition by observing pregnancy status and behavior of female. If the female appeared to have undergone parturition and if personnel were available, we attempted to observe the female from a safe distance to avoid disturbing the female and utilized her postpartum behavior to locate neonates. We also opportunistically observed random females at first light with binoculars or spotting scopes and focused on those that exhibited maternal behavior to locate neonatal mule deer (Carstenson Powell et al. 2003). When a neonate was located, we hiked to the area the neonate had bedded and conducted ground searches to locate and capture the neonate.

When we located neonatal mule deer, we captured them by hand and placed them in a cloth bag containing sage brush to minimize scent transfer, although that likely would have had little influence on potential abandonment (Carstensen Powell et al. 2005). We determined sex of each neonate and approximate age by appearance of hooves, umbilicus, and passiveness (Haugen and Speake 1958). We also acquired a measurement of new hoof growth using a dial calipers to calculate age of neonates >2 days old (Brinkman et al. 2004, Robinette et al. 1973). We determined the weight of each fawn to the nearest 0.10 kg within the cloth bag using a hand-held spring scale. We characterized and recorded the global positioning system (GPS) location of each capture site and processed all fawns as quickly as possible to minimize the potential for abandonment or attraction of predators (Livezey 1990). We fit all fawns with an expandable radiocollar (Advanced Telemetry Systems, Inc., Isanti, MN; Telemetry Solutions, Walnut Creek, CA) with a 4-hour mortality delay.

Survival and cause-specific mortality

We monitored all radiocollared animals with ground telemetry on winter range approximately 3 days per week from October through April. We monitored radiocollared neonates from a fixed-wing aircraft and ground-based radiotelemetry daily from capture until 31 August, when risk of mortality is relatively high, and approximately 3 days per week thereafter. Frequent monitoring of all animals on winter range and of neonates during summer allowed us to determine cause of most deaths. When mortality was detected, ground telemetry was used to locate the carcass as quickly as possible. When located, we examined carcass to estimate time of death and condition of the animal. We evaluated and recorded the location and arrangement of the carcass, presence and position of tooth marks, ante- and postmortem bleeding or bruising, fractures and remaining organs. We identified other physical evidence of predation including tracks and scat (Elbroch 2003) and collected hair for further confirmation (Moore et al. 1997). When the cause of death could not be ascertained, the carcass was either taken from the field to the laboratory to be necropsied or field necropsies were performed when animal location precluded removal from field.

We classified proximate causes of death as: 1) predation, if an animal died due to predation regardless of whether exact predator was identified; 2) malnutrition, included small and weak neonates and adults with <12% femur marrow fat; 3) disease, if carcass was intact, did not show signs of predation, starvation, or trauma, and postmortem examination indicated infection or disease; 4) accident, if a carcass was located mainly intact with broken bones or other premortem physical trauma and included deer-vehicle collisions and drowning; 5) other natural, if cause of death could not be ascertained, but carcass was primarily intact with no signs of predation; and 6) undetermined, if cause of death could not be categorized in the aforementioned categories or lack of evidence precluded determination of cause of death. For predation related mortalities, we attempted to identify the predator responsible for the death. For neonates we also included abandonment and stillborns as a proximate cause of mortality. We considered a neonate as abandoned if it was apparently healthy with postmortem necropsy revealing an empty omasum, indicative of an absence of nursing (Church 1988). We considered the proximate cause of mortality as the ultimate cause except for those adult animals that had femur marrow fat <12% (Neiland 1970). Femur marrow fat <12% is indicative of acute starvation, thus we considered the cause of mortality as malnutrition, regardless of proximate indicators (Depperschmidt et al. 1987, Ratcliffe 1980).

During summer, we only opportunistically monitored adult females for survival on summer range because of logistical constraints and the vast expanse of summer range. Infrequent monitoring often precluded determination of cause of death, but provided an estimate of survival. We attempted to locate each animal at least once during 15 June – 30 September to determine summer occupancy and migratory status. We grouped animals by their migratory status as an "east" or "west" side animal by its use of summer range on the east or west side of the Sierra crest.

During each autumn, we determined recruitment status of each marked female as they arrived to winter range in late-Oct through Nov. We located each radiocollared female using ground-based telemetry and stalked within visible range. We observed each female using binoculars and/or spotting scopes until we could confidently determine the number of young-at-heel. We identified the number of young-at-heel by observing nursing and other maternal behavior (Geist 1981). We defined recruitment status of radiocollared females as the number of young-at-heel identified each autumn.

Population Survey

We conducted 2 helicopter surveys during each January to (1) estimate the number of deer wintering in Round Valley and (2) the proportion of adult males, adult females, and young. We completed surveys in a Bell Jet Ranger 206 BIII with 3 observers and the doors removed to improve visibility (Clancy 1999). Two observers in the rear of the helicopter determined the number of deer in each group on either side of the helicopter and a third member of the crew seated alongside the pilot recorded deer on the centerline that were not noted by the other observers. We noted the number of marked deer in each group, but did not classify deer with respect to age class or gender, thereby alleviating the need for the pilot to deviate from and then attempt to return to the transect line. The pilot made every effort to maintain an elevation of 25 m AGL and a ground speed of approximately 40 knots. For mark-resight surveys, we flew a series of parellel transects that were perpendicular to a baseline that bisected the study area (Norton-Griffiths 1978). Location of the initial transect was established randomly, but subsequent transects were parallel to the initial transect and spaced at intervals of approximately 0.5 km. Sampling was considered systematic without replacement. Observers recorded the group size and number of marked animals in each group observed within 200m of centerline along transects.

For population composition surveys, we flew aerial transects and classified deer as encountered with 3 observers and thus, sampling was systematic without replacement. For each group observed, we carefully identified the size and composition of each group, which included adult males, adult females, and young.

Analyses

For some analyses, we combined our results with those collected by Kucera (1988) and Pierce (1999) to expand our available data to approximately 1985 for many population characteristics including, population size, body fat, and fetal and pregnancy rates. We used Chapman's (1951) modification of the Lincoln-Peterson estimator to calculate an unbiased estimate of population size from the mark-resight data collected during the annual helicopter surveys. We used one- and two- way analysis of covariance (ANCOVA) to compare levels of ingesta-free body fat between years, fetal rates, recruitment status, and summer residency of adult females (Zar 1999). Age was included as the covariate in all ANCOVA's to control for the effect of age on various reproductive variables. To determine the influence of summer residency and year on autumn recruitment status of adult females we used multi-way, log-linear models (Zar 1999). We also used log-linear models to determine the influence of year, sex, and summer residency on the frequency of causes of mortality of neonatal mule deer that were radiomarked during 2006-2008.

We calculated monthly survival up to 5 months for neonates and annual and seasonal (i.e., winter and summer) survival for adult female mule deer using the Kaplan-Meyer procedure modified to allow staggered entry and exit of marked animals (Pollock et al. 1989). We censored all mortalities of adult females that occurred within 14 days of capture by helicopter, regardless of proximate cause. We evaluated differences in survival rates among years and specific animal groups using a generalized Chi-square test in program CONTRAST (Sauer and Williams 1989) and maintained experiment-wise error rate for multiple comparisons using Bonferroni corrections (Neter et al. 1996). We used simple linear regression to evaluate the relationship between estimated population parameters, λ, and environmental variation (Neter et al. 1996).

RESULTS AND DISCUSSION

Mule deer inhabiting winter range in Round Valley have been subjected to the vagaries of climate during the last 20 years with further influences of density dependence (Kucera 1988) and thus have exhibited great variation in population size. Kucera (1988) observed a marked decline in the population of deer wintering in Round Valley during a severe drought. Total numbers declined from 5,978 animals (66/km^2) in 1985 to a low of 939 (10/km^2) in 1991 (Kucera 1988, Pierce et al. 2000). During the population decline, pregnancy rates, fetal rates, fetal sizes, adult weights and kidney fat varied with precipitation and forage growth on winter range (Kucera 1988). Kucera (1988) also concluded that influences of climate conditions and density dependence contributed to poor animal condition and population decline. Following the prolonged drought and population low in 1991, numbers increased to 1,931 (21/km^2) in 1997 (Pierce et al. 2000) when we began to estimate body fat of live animals. Since then, we have continued to acquire population estimates using mark-resight techniques. The population of mule deer in Round Valley has slowly recovered and increased to near 3,000 animals (33/km^2), but has leveled off and initiated a decline during recent years (Figure 3). Those patterns in population growth were associated with a concomitant decline in nutritional condition of females that spent winters in Round Valley (Figure 4). Following the population crash in 1991, nutritional condition of females improved and the population increased to about 2,000 animals. As the population size reached an asymptote near 2,000 animals in 1997-1998, nutritional condition began to decline and continued to exhibit a declining trend through 2009. Body fat (mean = 2.6%) of females in Round Valley during March 2009 was the lowest observed during the past 15 years and substantially less than peak values (mean = 9.9%) observed during March 1996.

Annual survival (Jan-Dec) of adult females has been variable from 1998 to 2008 (Figure 5), has ranged from 80% to 100%, and differed among years (χ^2=175.7, *df*=10, *P*<0.001). Seasonal survival also exhibited similar variability (Figure 6,7). Winter survival (16 Oct – 15 Apr) was typically >90% (Figure 8), whereas summer survival (16 Apr – 15 Oct) of adult females was <90% during 2005-2008 (Figure 7). Furthermore, winter (χ^2=73.0, *df*=9, *P*<0.001) and summer (χ^2=69.5, *df*=10, *P*<0.001) survival differed among years. During 1998-2009, mean summer and winter survival, however, was not different (93.6%; (χ^2=0.0009, *df*=1, *P*=1.0). Annual survival of adult female mule deer in 3 western states was similar among states and among years, despite annual variation in climatic conditions within the Intermountain West (Unsworth et al. 1999). The increased variability in adult survival that we observed was partially related to the substantial changes in population size of mule deer in Round Valley as they recovered from the population crash after 1991. Survival was high in 1998, declined until 2001, and has been variable until 2009 as the population has likely approached *K* because nutritional condition of adult females has continued to decline, predisposing them to mortality (Bender et al. 2007).

We also considered annual and seasonal survival of adult females separately based on their migratory designation, whether they resided east or west of the Sierra crest during the summer (Figure 8). Overall annual survival for east-side females (87.8%) was lower compared with west-side females (89.0%), but was statistically similar (χ^2=0.44, *df*=1, *P*=0.51). Likewise, both summer and winter survival for east-side females (93.6% and 93.8%; respectively) was lower than west-side females (94.3% and 96.1%; respectively), but summer and winter survival between side of crest did not differ (χ^2=0.17, *df*=1, *P*=0.69; χ^2=2.5, *df*=1, *P*=0.22).

Recruitment rate (i.e., number of young-at-heel in autumn) of radio-marked females ranged from 0.35–0.66 young-at-heel during 1998-2008 (Figure 9) and varied significantly by year (χ^2=54.6, *df*=36, *P*=0.024). Nevertheless, number of young recruited per adult female was dependent on both year and side-of-crest (χ^2=112.0, *df*=87, *P*=0.037). During most years, number of recruited young was greater for females that summered east of the Sierra crest than those that resided west of the crest (Figure 10). Indeed, east-side females recruited significantly more young than west-side females (χ^2=17.72, *df*=3, *P*<0.001).

Body fat in November from 2002-2008 was highly variable (Figure 11) and differed among years ($F_{6,335}$=5.1, P<0.001). Depending upon recruitment status, mean body fat in November varied from 1 – 13%; biological maxima for mule deer exceeds 20% (Cook et al. 2007). Moreover, females that resided on the west side of the Sierra crest during the summer on average had 67% more body fat (Figure 12) and differed from east-side females ($F_{6,335}$=74.6, P<0.001). Nevertheless, body fat of females in November was dependent on the number of young recruited to winter range in Round Valley. Females that were unsuccessful in recruiting young were consistently in the best nutritional condition in November, followed by those that recruited 1 or more young (Figure 13). Indeed, body fat differed by recruitment status ($F_{6,269}$=23.8, P<0.001), but also by side of crest ($F_{6,269}$=34.1, P<0.001). Females that summered west of the Sierra crest had more body fat with respect to recruitment status compared with east-side females (Figure 14). Moreover, recruitment status of each female in November held residual influence through the winter, with increasing levels of recruitment resulting in decreased body fat the following March ($F_{3,437}$=4.04, P=0.007). Accordingly, west-side females were in marginally better nutritional condition with respect to recruitment status (Figure 15; $F_{1,437}$=3.3, P=0.070). Considering body condition of large herbivores has an influence on probability of survival (Bender et al. 2007, 2008), somatic costs associated with reproduction inherently holds a trade-off associated with survival of the female. That tradeoff may explain the slightly lower survival exhibited by east-side females because they typically experienced higher costs of reproduction compared with west-side females. Forage quality and quantity are greatest during the growing season and thus, fat and protein deposition during summer are typically greatest and prepare animals for the food limited winter months. Nonetheless, nutritional requirements for late gestation, lactation, and growth of young are taxing for large herbivores (Moen 1978, Sadlier 1982); consequently, reproductive status during summer had a direct influence on body condition of females prior to winter (Figure 14). When forage resources are sufficient, however, reproductive females may be capable of attaining similar fat reserves by mid-autumn compared with non-lactating females (Cook et al. 2004, Piasecke and Bender 2009). Generally, females are thought to be in best condition with the onset of winter (Mautz 1978, Parker et al. 2009). The influence of the effects of summer range and reproductive status on body condition of females prior to the onset of winter underscores the importance of summer range in providing adequate forage for reproduction and accumulation of fat reserves for winter (Mautz 1978, Cook et al. 2004, Parker et al. 2009).

Seasonal patterns of nutritional condition followed consistent changes from autumn to late-winter. Adult females were had consistently less body fat following winter compared with autumn body fat; on average, they lost from 20 – 80% of their fat reserves. (Figure 16). Body condition of adult females in March varied by year ($F_{12,836}$=23.7, P<0.001) and on average, body fat of west-side females differed and was 11.7% greater than east-side females ($F_{3,438}$=29.5, P=0.002). Both temperate and northern herbivores track seasonal cycles in nutrient intake following seasonal changes in quality and quantity of food resources, with marked declines during the dormant season. Seasonal changes in food availability and energetic costs lead to concurrent cycles in deposition and catabolism of fat (Mautz 1978), the primary energy reserve of the body. Conditions on winter range are typically characterized by a decline in quantity and quality of forage; consequently, ungulates have adapted physiologically and behaviorally to decrease metabolic rate, nutrient demand, and activity (Moen 1978, Parker et al. 1993, Taillon et al. 2006). Nevertheless, catabolism of body fat for maintenance normally occurs during winter and may be exacerbated when foraging conditions are poor (Short et al. 1966, Torbit et al. 1985).

Fetal rate of adult females wintering in Round Valley was dependent upon year and residency status of female (χ^2=112.0, *df*=87, *P*=0.037). Overall, fetal rate was greater for females that resided west of the Sierra crest during the summer (Figure 17; χ^2=17.7, *df*=3, *P*<0.001). West-side females were consistently in better nutritional condition in autumn compared with east-side females because west-side females incurred lower somatic costs of reproduction (Figure 14). Nutritional status plays a considerable role in litter size of adult female cervids (Swihart et al. 1998, Testa and Adams 1998). Nutritional condition of adult females in November affected fetal rate the following March ($F_{3,260}$=4.8, *P*=0.003), but pairwise comparisons indicated that differences only occurred between females pregnant with singletons compared with twins (*P*=0.053). Females pregnant with twins had greater body fat compared with females pregnant with only singletons (Figure 18). Although, nutritional condition for females that were not pregnant and those pregnant with triplets was on average greater than females with singetons or twins, sample size in those 2 groups was insufficient to interpret those results (not pregnant: *n*=4, triplets: *n*=5).

We measured neonatal survival during 2006-2008 on both sides of the Sierra crest, but sample size was greater for east-side neonates (Table 1). Prior to 150 days-of-age, we censored 1 animal in 2006 and 4 animals in 2007 because they prematurely shed their collars. We assumed the fate of those animals was independent of the shedding of the collars. Monthly survival of neonates varied by year (χ^2=24.0, *df*=2, *P*<0.001), and ranged from 31 – 47% with survival to 5 months being greatest in 2006 (Figure 19). Average monthly survival to 5 months was 40.4% (±0.05). Male and female neonates exhibited similar patterns of monthly survival (Figure 20; χ2=1.12, *df*=1, *P*=0.28). Monthly survival of young born on the west side of the Sierra crest, however, was approximately 40% lower and differed from young born east of the Sierra crest (Figure 21; χ^2=79.0, *df*=1, *P*<0.001).

Causes of mortality were similar among the 3 years of study (χ^2=17.5, *df*=14, *P*=0.231), with predation comprising the greatest amount of neonatal loss in all years (60% of mortality; Table 2). Within 5 months of age, predators had taken 30% or more of young mule deer during the 3 years of this study (Table 2). Although cause-specific mortality was similar between neonates on either side of the Sierra crest (χ^2=7.9, *df*=7, *P*=0.34), 77% of the deaths of neonates born on the west side of the Sierra crest were caused by predation, whereas, predation was responsible for 48% of neonatal deaths east of the Sierra crest. Of the predation caused mortality, black bears were responsible for 87% west of the

Sierra crest and only 16% on the east-side. Coyotes were responsible for 53% of predation caused mortality east of the Sierra crest compared with only 4% west of the Sierra crest (Table 3).

The ratio of young:adult females and males: adult females has varied considerably since the 1950's. The young:adult female ratio reached low's of near 20 young per 100 females in the early 1990's during the population crash, but then increased to near 60 following the population crash and has declined more recently until 2009 (Figure 22). The male:female ratio has followed a similar pattern with a low of approximately 10 males per 100 females in the early 1990's, which then increased to 30-40 following the population crash (Figure 23). More recently however, the male:female ratio has decreased to under 20 males per 100 females (Figure 23).

Climate in the Sierra Nevada is highly variable, with April snowpack varying from 0.5 cm to 122.7 cm during 1950-2008 (CV = 77%). In other variable and arid environments, forage abundance and its nutritional quality is inextricably linked to patterns of precipitation (Marshal et al. 2005a, 2005b). Furthermore, timing of seasonal precipitation is important for forage growth, particularly in the Sierra Nevada where the majority of the annual precipitation falls as snow between October and April (Storer et al. 2004, Concilio et al. 2009). We acquired data on leader growth of bitterbrush in Round Valley from the Bureau of Land Management (BLM) for most years. Bureau of Land Management measured new leader growth of bitterbrush during most autumns in Round Valley. Annual growth of bitterbrush, the primary winter forage for mule deer in Round Valley (Kucera 1988), was predicted by water content of April snowpack (r^2=0.65, P=0.001; Figure 24). Accordingly, extreme variation in winter precipitation had significant effects on nutritional condition of adult females during winter. April snowpack had a strong positive influence on nutritional condition of adult females in Round Valley the following March (r^2=0.53, P<0.001; Figure 25). Similarly, a coarse index to body condition in the Sonoran Desert yielded significant relationships with the accumulated rainfall 6-12 months prior to sampling (Marshal et al. 2008). Subcutaneous fat reserves are mobilized to support metabolic need during periods of forage scarcity (Stephenson et al. 1998, Cook et al. 2001). Forage availability however, is influenced by both forage growth, which is clearly influenced by winter precipitation in the Sierra Nevada, and by intraspecific competition for forage (density dependence).

Prior to the crash in 1991, there was no relationship between population size and nutritional condition (P=0.21) of adult females post-winter; however, following the crash, nutritional condition of mule deer in Round Valley tended towards a density dependent effect (r^2=0.17, P=0.088; Figure 26). Within that analysis however, 1993 was a severe outlier. That year was characterized by a wintering deer population at relatively low density, but low winter snowfall the previous year resulted in little new growth of forage in Round Valley, thereby driving the relationship between forage growth and deer condition. With 1993 removed, nutritional condition of mule deer in Round Valley exhibited strong density dependence, with population size having a significant negative effect on nutritional condition (r^2=0.38, P=0.009; Figure 26). As a population progresses towards *K*, intraspecific competition for forage causes a decline in per capita availability of forage resources, that may include both quality and quantity. Consequently, lower per capita availability of forage resources is reflected in declining body condition as the population nears *K* (Kie et al. 2003). Nevertheless, this arid system in the western Great Basin is clearly influenced by annual precipitation, which may cause annual deviations from long-term trends in *K*. Range conditions in the Sierra Nevada are largely influenced by winter snowfall and the corresponding forage growth that results in annual fluctuations in *K*, a pattern identified in other arid systems (Marshal et al. 2002, 2005a).

Nutritional condition of adult females in March explained much of the variation in both young:adult female and male:adult female ratios the following January. Following the crash in 1991, the male:adult female ratio lagged behind the population response to improved conditions and low density, which resulted in 2 outliers in the relationship between ingesta-free body fat of adult females in March and the male:adult female ratio the following January. With those outliers removed, ingesta-free body fat of adult females in March explained >70% of the variation in the male:adult female ratio the following January (Figure 27). We do not imply cause and effect in this relationship. Clearly, there is no biological mechanism where a declining nutritional condition of females would cause a decrease in the number of adult males. We believe, however, that this relationship suggests the importance of understanding nutritional condition as a collective measure of population health. Nutritional condition of adult females in March represents the physical condition of females following winter, when animals typically experience a negative energy balance and poor foraging conditions (Mautz 1978, Barboza et al. 2009). Adult males follow a slightly different fat cycle compared with females. Females presumably will have the opportunity to replenish some fat reserves that were utilized to support reproduction during the summer before poor foraging conditions prevail on winter range (Cook et al. 2004, Parker et al. 2009). In contrast, adult males expend nutritional reserves to support breeding activities during late-November and early-December. Therefore, it follows that males enter the winter season in poorer physical condition than females and males would, therefore, be most susceptible to factors of mortality on winter range. We believe that nutritional condition of adult females in March serves as a reliable predictor of the number of males relative to females because nutritional condition of females post-winter is a reliable indicator of herd health. As nutritional condition of adult females decline in response to increasing population density or decreasing winter precipitation, we expect that the number of males relative to females will accordingly decline. Although this prediction remains largely untested, the small amount of research on over-winter survival of adult males is suggestive of their higher level of susceptibility to natural mortality factors following the breeding season compared with females (Ditchkoff et al. 2001, Webb et al. 2006). In polygynous mating systems, males are probably more likely than females to succumb to resource limitation (Clutton-Brock et al. 1985). Lower survival of males in ungulate populations is common (Loison et al. 1999) and studies that failed to document intersexual differences in survival were probably expanding populations that were not food limited (Fancy et al. 1994, Toïgo et al. 1997). Although often considered negligible, the presence and proportion of adult males in ungulate populations can have cascading effects on population demographics (Mysterud et al. 2002). Presence of mature males can stimulate estrus in females and therefore, influences length of breeding season and subsequently, timing of parturition (Mysterud et al. 2002). In turn, timing of parturition can influence forage quality (Bowyer 1991, Côté and Festa-Bianchet 2001), neonatal survival (Bowyer 1991, Feder et al. 2008), and over-winter survival by affecting the time available for mass gain of young prior to the onset of winter (Loison et al. 1999, Holand et al. 2003).

Physical condition of adult females in March was positively associated with the number of young per female recruited to winter range the following January (Figure 28). Maternal condition during the last trimester of gestation affects birth mass and subsequent investment in young (Sams et al. 1996, Pekins et al. 1998, Testa and Adams 1998), which directly influence probability of survival and susceptibility of young to mortality (Julander et al. 1961, Pederson and Harper 1987, Lomas and Bender 2006, Bender et al. 2007). Growth and subsequent production from entire cohorts of animals may be impacted by maternal condition during gestation (Albon et al. 1987, Anderson and Linnell 1997, Rose et al. 1998, Forchhammer et al. 2001). Poor conditions during gestation can result in the transmission of negative maternal effects on offspring that can persist through adulthood and into subsequent generations resulting in time lags in population response to improved conditions (Monteith et al. 2009). Physical condition of maternal females during gestation provides insight into expected reproductive performance the following year, despite confounding influences of summer range conditions (Julander et al. 1961).

Physical condition of adult females in March also explained 50% of the variation in annual survival of those females (Figure 29). Poor nutritional condition of adult females in March provided inference into annual survival due to the influence of nutritional condition on an animals susceptibility to mortality. Previously, poor physical condition was thought to only influence the probability of death of an animal near starvation (<12% bone marrow fat). Nevertheless, recent evidence suggests that animals may be susceptible to mortality factors across a range of physical condition (Bender et al. 2008), which corroborates the relationship between nutritional condition and annual survival.

Adult survival is consistently identified as the vital rate with the greatest elasticity on population growth with λ being relatively insensitive to changes in survival of young (Gaillard et al. 2000, Eberhardt 2002, Garrott et al. 2003). The impact of a demographic rate on population growth is a function of both its influence (elasticity) and its variability (Gaillard et al. 1998, Raithel et al. 2007). Nevertheless, the variability in demographic rates actually determine the temporal variation in λ, not its elasticity (Raithel et al. 2007). We regressed population vital rates, winter precipitation, and physical condition of females to determine their relative influence on λ. Although the relationship between winter precipitation and λ was significant ($P = 0.04$), winter precipitation explained only a small amount of the variation in λ the following year ($r^2 = 0.18$). Annual survival of adult females exhibited no relationship with λ (Figure 30). Indeed, mean annual survival of adult females was 89% with a CV of only 8.7%. Small temporal variation of adult survival likely plays a minimal role in influencing annual changes in λ (Raithel et al. 2007). Conversely, with the exception of 1991, recruitment of young (young:female) had a CV of 29%, was positively associated with λ, and explained 45% of the annual variation in λ (Figure 31). Following the population crash in 1991, ingesta-free body fat of adult females in March also was positively associated with λ during the same year (Figure 32). Body fat of adult females in March explained 44% of the variation in lambda during the same year, probably because of the influence of nutritional condition on survival of the female (Figure 29) and their subsequent reproductive investment and probability of survival of young (Figure 28). Body fat integrates energetic conditions experienced by an individual including nutrition as determined by intrinsic habitat value and density dependent competition for forage resources. Consequently, understanding the nutritional status of individuals within a population isolates the role of bottom-up vs. top-down influences on population limitation.

MANAGEMENT IMPLICATIONS

Nutritional condition of adult females in autumn was influenced strongly by reproductive effort expended by females during the summer. Their nutritional condition in autumn then influenced fetal rates as measured the following March. Lactation is the most energetically demanding time of year for female cervids (Moen 1985); therefore, we expected reproductive status in autumn to influence physical condition of females. Increasing recruitment of young resulted in decreasing nutritional condition in November. Nevertheless, the cost of reproduction was greater for females that resided on the east-side of the Sierra crest compared with those on the west side. Habitats and annual moisture regimes differ considerably between either side of the Sierra crest (Storer et al. 2004). The more mesic environment and lower deer densities on the west-side of the Sierra crest probably resulted in better foraging conditions for deer, thereby, lessening the somatic costs of reproduction. Less costly reproduction might suggest improved recruitment for those west-side females. Nonetheless, recruitment of young was consistently higher for east-side females since 1997. Higher recruitment by east-side females despite concomitantly higher somatic costs to reproduction suggests that a portion of the mortality of young on the west-side of the Sierra crest had an additive effect on the population. Disparity in recruitment in the absence of a difference in survival between east- and west-side females, was likely responsible for the shift in migratory components of the population. In 1987, Kucera (1988) determined that >80% of the population migrated to the west-side of the Sierra crest during summers. Currently, only about 55% of the marked segment of adult females migrates to west-side summer ranges. Apparently selective pressures in Round Valley mule deer have shifted during the most recent decade in favor of animals that spend summers on the east-side of the Sierra crest. Predation pressures on young born on the west-side were nearly double that experienced by east-side animals (Table 2) and 87% of that predation was caused by black bears (Table 3), whereas, only 16% of predation was caused by black bears on the east-side of the Sierra crest. The increasing abundance of black bears on the west-side of the Sierra crest has likely played a significant role in influencing the shift in demographics between the east and west-side segments of the Round Valley deer population.

Although removal of predators, namely bears, likely would result in an immediate response in recruitment of young by west-side females, it also would exacerbate the impact of an already limited winter range. Nutritional condition of females during March 2009 indicated that the deer population was at or beyond nutritional *K* and to expect poor recruitment, poor adult survival, and a population decline during 2009. Increased recruitment by west-side females would simply result in an increase in the density-dependent constraints of winter range. Nevertheless, if managers are concerned of the shifting demographics within the deer population, bear control and habitat manipulations on the west-side of the Sierra crest should be accompanied by either habitat improvements or density reductions on winter range in Round Valley. Considering that habitat manipulations in sage-brush steppe are often very costly and ineffective, however, we suggest that density reduction be employed to lessen competition for limited forage on winter range and lessen the magnitude of another decline (Berryman and Lima 2006, Simard et al. 2008). Intersexual differences in body size, metabolic demand, and digestive function commonly results in partitioning of resources between sexes of dimorphic ruminants (Kie et al. 1999, McCullough 1999, Barboza and Bowyer 2000). Therefore, density reductions should be focused on females to minimize density-dependent effects on nutritional condition and productivity (McCullough 1979, 1999).

Release from major density-dependent influences should result in a more stable and predictable system. With density-dependent effects interacting with environmental variation, minor perturbations in the system can have profound effects on overwinter survival and subsequent reproduction (Kie et al. 2003; Figure 33). Resource limitation has already constrained nutritional condition of mule deer and minor deviations from normal precipitation regimes will cause extreme fluctuations in population growth. Lower population size with respect to *K* would result in a deer population less susceptible to annual variation in environmental conditions. Nevertheless, severe drought conditions will continue to influence population parameters even when the population is at lower density (1993 for example), but patterns of nutritional condition, survival, and reproduction should be less susceptible to minor deviations in environmental conditions. In populations held below *K*, harvest may be maintained if managed for maximum sustained yield, but this assumes that predation does not unduly limit recruitment required to support such harvest.

In June 1995, a fire burned 22 km^2 of the winter range in an area dominated by bitterbrush and sagebrush. Due to the intensity of the fire, little regrowth of bitterbrush occurred in subsequent years and has become dominated by desert peach and cheat grass (Bromus tectorum), both of which offer little forage value to deer (Pierce et al. 2004). Coincident with the fire was the closure of an alfalfa ranch that was frequented by hundred's of deer on a daily basis. The devastating fire and closure of the alfalfa ranch clearly resulted in a decline in *K* of winter range because of the loss in quantity of critical winter forage, which likely prevented recovery of the population to the 6000 animals present in 1985 (Figure 3). Furthermore, acute overbrowsing of forage species on winter range may have influenced subsequent growth and recovery of habitat in subsequent years (Kie et al. 2003, Simard et al. 2008). The marked changes in density that the mule deer population in Round Valley has experienced may result in continued transient dynamics caused by the effects of severe resource limitation on growth and development of young, age at first reproduction, entire cohorts, and causing negative maternal effects (Eberhardt 2002, Coulson et al. 2004, Monteith et al. 2009). Lagged effects from severe nutritional limitation caused by the increased deer density in Round Valley and the corresponding changes in habitat condition may continue to persist for decades (Coulson et al. 2004, Monteith et al. 2009). Current body condition of adult females following winter in Round Valley clearly indicates continued resource limitation through density dependent feedbacks and variation in winter precipitation.

Nutritional condition has an influence on nearly every component of survival and reproduction of large herbivores (Cameron and Ver Hoef 1994, Testa and Adams 1998, Keech et al. 2000, Stewart et al. 2005, Bender et al. 2007). Furthermore, others have identified animal condition as a valuable tool to collate population health (Parker et al. 2009, Barboza et al. 2009). Nutritional condition of adult female mule deer in Round Valley following winter was sensitive to conditions of winter habitat because it was influenced by intraspecific competition for forage (Figure 26) and the availability of new growth of the bitterbrush as influenced by water content of winter snowpack the previous April (Figure 25). Moreover, nutritional condition in March was related to male:female and young:female ratios the following autumn (Figure 27,28), annual survival of adult females (Figure 29), and itself, held predictive value for population growth during the same year (Figure 30). Physical condition of adult females following winter provided an encompassing measure of population health and expected measures of adult female survival, recruitment of young, an index to abundance of males, and overall population trajectory during the following year. Nutritional limitations on survival and recruitment of deer in Round Valley clearly indicate bottom-up limitation on deer dynamics and the importance of data on nutritional condition when interpreting dynamics of deer populations. Consequently, levels of nutritional condition within a population may be used to determine carrying capacity (Piasecke and Bender 2009).

The patterns of population demographics collected from research on mule deer in Round Valley also should be applicable to other deer populations in California, particularly those with winter ranges that reside in the western Great Basin, which includes the Gooddale, White Mountains, Walker, Mono Lake, Casa Diablo, and other mule deer populations. Climatic variation has an influence on mule deer in arid regions (Marshal et al. 2005, 2005a; this study). Patterns of precipitation have an indirect influence on body condition through its direct influence on forage quality and quantity. Nutritional condition then influences nearly all population parameters. Region-wide variability in climatic conditions should be similar in the western Great Basin, therefore, dynamics of deer populations in that area are likely correlated. For example, across Idaho, Colorado, and Montana, Unsworth et al. (1999) determined that general patterns in dynamics of mule deer populations were similar despite some difference in climate and geography. Mule deer populations likely respond to large-scale climatic variation across wide geographical areas.

Overall, the research that has been conducted on the population of mule deer in Round Valley has provided new and valuable insight into research methodology, reproductive ecology, population dynamics, and management of mule deer in a highly variable environment (Table 4). The data collected from this population will continue to advance wildlife science during the next few years as the current dataset is more rigorously analyzed and interpreted for peer-reviewed publication, and to provide the Department with practical management recommendations. Numerous peer-reviewed publications are in progress and are forthcoming in the next few years (Table 5).

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LITERATURE CITED

Albon, S. D., T. H. Clutton-Brock, F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69-81.
Andersen, R., and J. D. C. Linnell. 1997. Variation in maternal investment in a small cervid; the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. Oecologia 109:74-79.
Anderson, R., and J. D. C. Linnell. 1997. Variation in maternal investment in a small cervid; the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. Oecologia 109:74-79.
Barboza, P. S., and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. Journal of Mammalogy 81(2):473-489.
Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer, Verlag Berlin Heidelberg, Germany.
Barrett, M. W., J. W. Nolan, and L. D. Roy. 1982. Evaluation of a hand-held net-gun to capture large mammals. Wildlife Society Bulletin 10:108-114.
Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk *Cervus elaphus*. Wildlife Biology 14:70-80.
Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118-1124.
Berryman, A., and L. Mauricio. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis provided new interpretation of soay sheep dynamics. The American Naturalist 168:784-795.
Bishop, C. J., D. J. Freddy, G. C. White, B. E. Watkins, T. R. Stephenson, and L. L. Wolfe. 2007. Using vaginal implant transmitters to aid in capture of mule deer neonates. Journal of Wildlife Management 71:945-954.
Bleich, V. C., T. R. Stephenson, B. M. Pierce, and M. J. Warner. 2007. Body condition of radio-collared mule deer while injured and following recovery. Southwestern Naturalist 52:164-167.
Bleich, V. C., T. R. Stephenson, N. J. Holste, I. C. Snyder, J. P. Marshal, P. W. McGrath, and B. M. Pierce. 2003. Effects of tooth extraction on body condition and reproduction of mule deer. Wildlife Society Bulletin 31:233-236.
Bowden, D. C., G. C. White, and R. M. Bartmann. 2000. Optimal allocation of sampling effort for monitoring a harvested mule deer population. Journal of Wildlife Management 64:1013-1024.
Bowman, J. L., and H. A. Jacobson. 1998. An improved vaginal-implant transmitter for locating white-tailed deer birth sites and fawns. Wildlife Society Bulletin 26:295-298.
Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy 72:138-145.
Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for

biodiversity. Pages 342-361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington DC, USA.

Bowyer, R. T., D. M. Leslie, Jr., and R. L. Rachlow. 2000. Dall's and Stone's sheep. Pages 491–516 *in* S. Demarais, and P.R. Krausman, editors. Ecology and Management of Large Mammals in North America. PrenticeHall, Upper Saddle River, New Jersey, USA.

Brinkman, T. J., K. L. Monteith, J. A. Jenks, and C. S. DePerno. 2004. Predicting neonatal age of white-tailed deer in the Northern Great Plains. The Prairie Naturalist 36: 75-81.

Brown, G. S., L. Landriault, D. J. H. Sleep, and F. F. Mallory. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. Oecologia 154:485-492.

Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58:674-679.

Carstensen Powell, M., G. D. DelGiudice, and B. A. Sampson. 2003. Using doe behavior and vaginal-implant transmitters to capture neonate white-tailed deer in north-central Minnesota. Wildlife Society Bulletin 31:634–641.

Carstensen Powell, M., G. D. DelGiudice, and B. A. Sampson. 2005. Low risk of marking-induced abandonment in free-ranging white-tailed deer neonates. Wildlife Society Bulletin 33:643–655.

Caughley, G. 1977. Analysis of vertebrate populations. The Blackburn Press, Caldwell, New Jersey, USA.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with application to zoological sample censuses. University of California Publications in Statistics 1:131-160.

Church, D. C. 1988. The ruminant animal. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

Clancy, T. F. 1999. Choice of survey platforms and technique for broad-scale monitoring of kangaroo populations. Australian Zoologist 31:267-274.

Clutton-Brock, T. H., M. Major, and F. E. Guinness. 1985. Population regulation in male and female red deer. Journal of Animal Ecology 54:831-846.

Compton, B. B., P. Zager, and G. Servheen. 1995. Survival and mortality of translocated woodland caribou. Wildlife Society Bulletin 23:490-496.

Connolly, G. E., 1981. Assessing populations. Pages 287-245 *in* O. C. Wallmo, editor. Mule deer and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebreaska, USA.

Cook, J. C., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs No. 155.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for rocky mountain elk. Journal of Wildlife Management 65:973-987.

Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934-1943.

Côté, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230-238.

Côté, S.D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230-238.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528-1531.

Coulson, T., F. Giunness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. Ecology 85:411-422.

Cransac, N., A. J. M. Hewison, J.-M. Gaillard, J.-M. Cugnasse, and M. L. Maublanc. 1997. Patterns of mouflon (*Ovis gmelini*) survival under moderate environmental conditions: effects of sex, age and epizootics. Canadian Journal of Zoology 75:1867-1875.

de Vos, Jr. J. C., M. R. Conover, and N. E. Headrick. 2003. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, Utah, USA.

Depperschmidt, J. D., S. C. Torbit, A. W. Alldredge, and R. D. Deblinger. 1987. Body condition indices for starved pronghorn. Journal of Wildlife Management 51:675-678.

Ditchkoff, S. S., E. R. Welch, Jr., R. L. Lochmiller, R. E. Masters, and W. R. Starry. 2001. Age-specific causes of mortality among male white-tailed deer support mate-competition theory. Journal of Wildlife Management 63:552-559.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841-2854.

Elbroch, M. 2003. Mammal tracks and sign. Stackpole Books, Mechanicsburg, Pennsylvania.

Fancy, S. G., K. R. Whitten, and D. E. Russell. 1994. Demography of the Porcupine caribou herd 1983-1992. Canadian Journal of Zoology 72:840-846.

Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, and J. Jorgenson. 2008. Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. Oecologia 156:773-781.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721-729.

Gaillard, J. -M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.
Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33-45.
Giest, V. 1981. Behavior: adaptive strategies in mule deer. Pages 157-224 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. Univeristy of Nebraska Press, Lincoln, Nebraska, USA.
Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421-425.
Haugen, A. O., and D. W. Speake. 1958. Determining age of young fawn white-tailed deer. The Journal of Wildlife Management 22:319-321.
Holand, Ø, K. H. Røed, A. Mysterud, J. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. The Journal of Wildlife Management 67:25-33.
Holand, Ø., K. H. Røed, A. Mysterud, J. M. Kumpula, M. Nieminen, and M. E. Smith. 2003. The effect of sex ratio and male age structure on reindeer calving. Journal of Wildlife Management 67:25-33.
Johnstone-Yellin, T. L., L. A. Shipley, and W. L. Myers. 2006. Effectiveness of vaginal implant transmitters for locating neonatal mule deer fawns. Wildlife Society Bulletin 34:338-344.
Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife Management 25:54-60.
Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.
Kie, J. G., and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004-1020.
Kie, J. G., R. T. Bowyer, and K. M. Stewart. 2003. Ungulates in western forests: habitat relationships, population dynamics, and ecosystem processes. Pages 296-340 *in* C. Zabel and R. Anthony, editors. Mammal community dynamics in western coniferous forests: management and conservation. The Johns Hopkins University Press, Baltimore, Maryland.
Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. Wildlife Society Bulletin 13:71-73.
Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the Eastern Sierra Nevada, California. Ph.D. Dissertation. University of California, Berkely, California, USA.
Kucera, T. E. 1991. Adaptive variation in sex ratios of offspring in nutritionally stressed mule deer. Journal of Mammalogy 72:745-749.
Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122-130.

Kucera, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. Journal of Wildlife Management 61:550-560.

Lande, R., S. Engen, B.-E. Sæther, R. Filli, E. Matthysen, and H. Weimerskirch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. American Naturalist 159:321-337.

Livezey, K. B. 1990. Toward the reduction of marking-induced abandonment of newborn ungulates. Wildlife Society Bulletin 19:193-203.

Loison, A., R. Langvatn, and E. J. Solberg. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. Ecography 22:20-30.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884-894.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005a. Dynamics of mule deer forage in the Sonoran Desert. Journal of Arid Environments 60:593-609.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2005b. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360-365.

Marshal, J. P., P. R. Krausman, and V. C. Bleich. 2008. Body condition of mule deer in the Sonoran Desert is related to rainfall. The Southwestern Naturalist 53:311-318.

Marshal, J. P., P. R. Krausman, V. C. Bleich, W. B. Ballard, and J. S. McKeever. 2002. Rainfal, El Niño, and dynamics of mule deer in the Sonoran Desert, California. Journal of Wildlife Management 66:1283-1289.

Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88-90.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130-1146.

Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. Journal of Wildlife Management 42:715-738.

Monteith, K. L., L. E. Schmitz, J. A. Jenks, J. A. Delger, and R. T. Bowyer. 2009. Growth of male white-tailed deer: consequences of maternal effects. Journal of Mammalogy 90:651-660.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1997. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Cheyenne, WY, USA.

Neiland, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. Journal of Wildlife Management 34:904-907.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models. Fourth Edition. McGraw-Hill. Boston, Massachusetts.

Norton-Griffiths, M. 1978. Counting animals. 2nd edition. Serengeti Ecological Monitoring Programme, African Wildlife Leadership Foundation, Nairobi, Kenya.
Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57-69.
Pederson, J. C., and K. T. Harper. 1978. Factors influencing productivity of two mule deer herds in Utah. Journal of Range Management 31:105-110.
Pederson, J. C., and K. T. Harper. 1984. Does summer range quality influence sex ratios among mule deer fawns in Utah. Journal of Range Management 37:64-66.
Pekins, P. J., K. S. Smith, and W. W. Mautz. 1998. The energy cost of gestation in white-tailed deer. Canadian Journal of Zoology 76:1091-1097.
Piasecke, J. R., and L. C. Bender. 2009. Relationships between condition of adult females and relative carrying capacity for Rocky Mountain Elk. Rangeland Ecology and Management 62:145-152.
Pierce, B. M. 1999. Predator-prey dynamics between mountain lions and mule deer: effects on distribution, population regulation, habitat selection and prey selection. PhD Dissertation, University of Alaska Fairbanks, Fairbanks, Alaska.
Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.
Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533-1543.
Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. Terry Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986-992.
Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.
Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795-803.
Ratcliffe, P. R. 1980. Bone marrow fat as an indicator of condition in Roe Deer. Acta Theriologica 25:333-340.
Robbinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:312-326.
Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. Journal of Animal Ecology 67:979-986.
Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. The Journal of Animal Ecology 67:979-986.

Sadlier, R. M. F. S. 1980. Milk yield of black-tailed deer. Journal of Wildlife Management 44:472-478.

Sadlier, R. M. F. S. 1982. Energy consumption and subsequent partitioning in lactating black-tailed deer. Canadian Journal of Zoology 60:382-386.

Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143-149.

Sams, M. G., R. L. Lochmiller, C. W. Qualls, Jr., D. M. Leslie, Jr., and M. E. Payton. 1996. Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. Journal of Mammalogy 77:179-190.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137-142.

Short, H. L. 1981. Nutrition and metabolism. Pages 99-127 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. Univeristy of Nebraska Press, Lincoln, Nebraska, USA.

Short, H. L., D. E. Medin, and A. E. Anderson. 1966. Seasonal variations in volatile fatty acids in the rumen of mule deer. Journal of Wildlife Management 30:466-470.

Simard, M. A., S. D. Côté, R. B. Weladji, and Jean Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. Journal of Animal Ecology 77:678-686.

Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society of London Series B 357:1221-1231.

Stephenson, T. R., B. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557-564.

Stephenson, T. R., J. W. Testa, G. P. Adams, R. G. Sasser, C. C. Schwartz, and K. J. Hundertmark. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167-172.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85-93.

Storer, T. I., and L. P. Tevis, Jr. 1955. The California grizzly. University of California Press, Berkeley, California, USA.

Storer, T. I., R. L. Usinger, and D. Lukas. 2004. Sierra Nevada Natural History. University of California Press, Berkeley, California, USA.

Swift, P. K., V. C. Bleich, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal. 2002. Tooth extraction from live-captured mule deer in the absence of chemical immobilization. Wildlife Society Bulletin 30:253-255.

Swihart, R. K., H. P. Weeks, Jr., A. L. Easter-Pilcher, and A. J. DeNicola. 1998. Nutritional condition and fertility of white-tailed deer (*Odocoileus* *virginianus*) from areas with contrasting histories of hunting. Canadian Journal of Zoology 76:1932-1941.

Taillon, J., D. G. Sauvé, and S. D. Côté. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. Journal of Wildlife Management 70:1445-1454.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345-1354.

Toïgo, C., J.-M. Gaillard, and J. Michallet. 1997. Adult survival of the sexually dimorphic Alpine ibex (*Capra ibex ibex*). Canadian Journal of Zoology 75:75-79.

Torbit, S. C., L. H. Carpenter, D. M. Swift, and A. W. Alldredge. 1985. Differential loss of fat and protein by mule deer during winter. Journal of Wildlife Management 49:80-85.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315-326.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555-558.

Zar, J. H. 1999. Biostatistical Analysis. 4th Edition. Prentice Hall. Upper Saddle River NewJersey.

Table 1. Number of neonatal mule deer captured and monitored on summer range each year in the Sierra Nevada.

Year	East	West	Censored	Total
2006	32	10	1	41
2007	20	14	4	30
2008	29	14	0	43

Table 2. Survival rate (5 months) and percent of cause-specific mortality of neonatal mule deer captured and monitored on summer range each year and for 2006-2007 combined with respect to their natal range occurring on either side of the Sierra crest.

Year & side crest	% Survival	% Abandon-ment	% Accident	% Malnutrition	% Other natural	% Predation	% Starvation	% Stillborn	% Unknown
2006	47.8	0.0	2.4	7.3	7.3	29.3	0.0	0.0	7.3
2007	30.7	3.0	6.1	0.0	0.0	45.5	0.0	6.1	9.1
2008	41.8	0.0	4.7	7.0	2.3	34.9	4.7	0.0	4.7
East	49.7	1.3	5.1	3.8	3.8	24.4	2.6	1.3	9.0
West	21.3	0.0	2.7	8.1	2.7	62.2	0.0	2.7	2.7

Table 3. Percent of total mortality caused by predation and the percent of that predation contributed to each predator of neonatal mule deer captured and monitored on summer range during 2006-2007 in the Sierra Nevada with respect to their natal range occurring on either side of the Sierra crest. Percents are total percent predation and of that, the predators responsible.

Side of crest	% Predation	% Bear	% Bobcat	% Coyote	% Eagle	% Lion
East	48	16	10	53	5	16
West	77	87	9	4	0	0

Table 4. Citations from peer-reviewed literature published involving research on mule deer in Round Valley, Bishop, California.

Bleich, V. C., and B. M. Pierce. 1999. Expandable and economical long-term collars for juvenile mule deer. California Fish and Game 85:56-62.

Bleich, V. C., and B. M. Pierce. 2001. Accidental mass mortality of migrating mule deer. Western North American Naturalist 61:124-125.

Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265-272.

Bleich, V. C., B. M. Pierce, J. L. Jones, and R. T. Bowyer. 2006. Variance in survival of young mule deer in the Sierra Nevada, California. California Fish and Game 92:24-38.

Bleich, V. C., J. T. Villepique, T. R. Stephenson, B. M. Pierce, and G. M. Kutiyev. 2005. From the field: efficacy of aerial telemetry as an aid to capturing specific individuals – a comparison of 2 techniques. Wildlife Society Bulletin 33:332-336.

Bleich, V. C., T. R. Stephenson, B. M. Pierce, and M. J. Warner. 2007. Body condition of radio-collared mule deer while injured and following recovery. Southwestern Naturalist 52:164-167.

Bleich, V. C., T. R. Stephenson, N. J. Holste, I. C. Snyder, J. P. Marshal, P. W. McGrath, and B. M. Pierce. 2003. Effects of tooth extraction on body condition and reproduction of mule deer. Wildlife Society Bulletin 31:233-236.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for biodiversity. Pages 342-361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington DC, USA.

Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2006. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934-1943.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the Eastern Sierra Nevada, California. Ph.D. Dissertation. University of California, Berkely, California, USA.

Kucera, T. E. 1991. Adaptive variation in sex ratios of offspring in nutritionally stressed mule deer. Journal of Mammalogy 72:745-749.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122-130.

Kucera, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. Journal of Wildlife Management 61:550-560.

Pease, K. M., A. H. Freedman, J. P. Pollinger, J. E. McCormack, W. Buermann, J. Rodzen, J. Banks, E. Meredith, V. C. Bleich, R. J. Schaefer, K. Jones, and R. K.. Wayne. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. Molecular Ecology 18:1848-1862.

Pierce, B. M. 1999. Predator-prey dynamics between mountain lions and mule deer: effects on distribution, population regulation, habitat selection and prey selection. PhD Dissertation, University of Alaska Fairbanks, Fairbanks, Alaska.

Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533-1543.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000a. Selection of mule deer by mountain lions and coyotes, effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Pierce, B. M., V. C. Bleich, C. L. B. Chetkiewicz, and J. D. Wehausen. 1998. Timing of feeding bouts of mountain lions. Journal of Mammalogy 79:222-226.

Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. Terry Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986-992.

Stephenson, T. R., B. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557-564.

Swift, P. K., V. C. Bleich, T. R. Stephenson, A. E. Adams, B. J. Gonzales, B. M. Pierce, and J. P. Marshal. 2002. Tooth extraction from live-captured mule deer in the absence of chemical immobilization. Wildlife Society Bulletin 30:253-255.

Villepique, J. T., V. C. Bleich, B. M. Pierce, T. R. Stephenson, R. A. Botta, and R. T. Bowyer. 2009. Evaluating GPS collar errors: a critical evaluation of Televilt Posrec-Science ™ collars and a method for screening location data. California Fish and Game 94:155-168.

Table 5. Topics of forthcoming manuscripts from research conducted on mule deer in Round Valley, Bishop, California.

1) Population dynamics and reproductive ecology of mule deer in the Sierra Nevada.

2) Timing of migration of mule deer in the Sierra Nevada: effects of a changing climate

3) Estimating pregnancy, fetal rate, and timing of parturition in mule deer

4) Estimating time and location of parturition using patterns of movement in mule deer

5) Capture and handling techniques of ungulates: animal care and censor interval

6) Resource use and reproductive status: implications for estimating habitat use and selection of ungulates

7) Senescence in reproduction and survival in mule deer

8) Dynamics of an eastern Sierra Nevada mule deer population: top-down or bottom-up regulation?

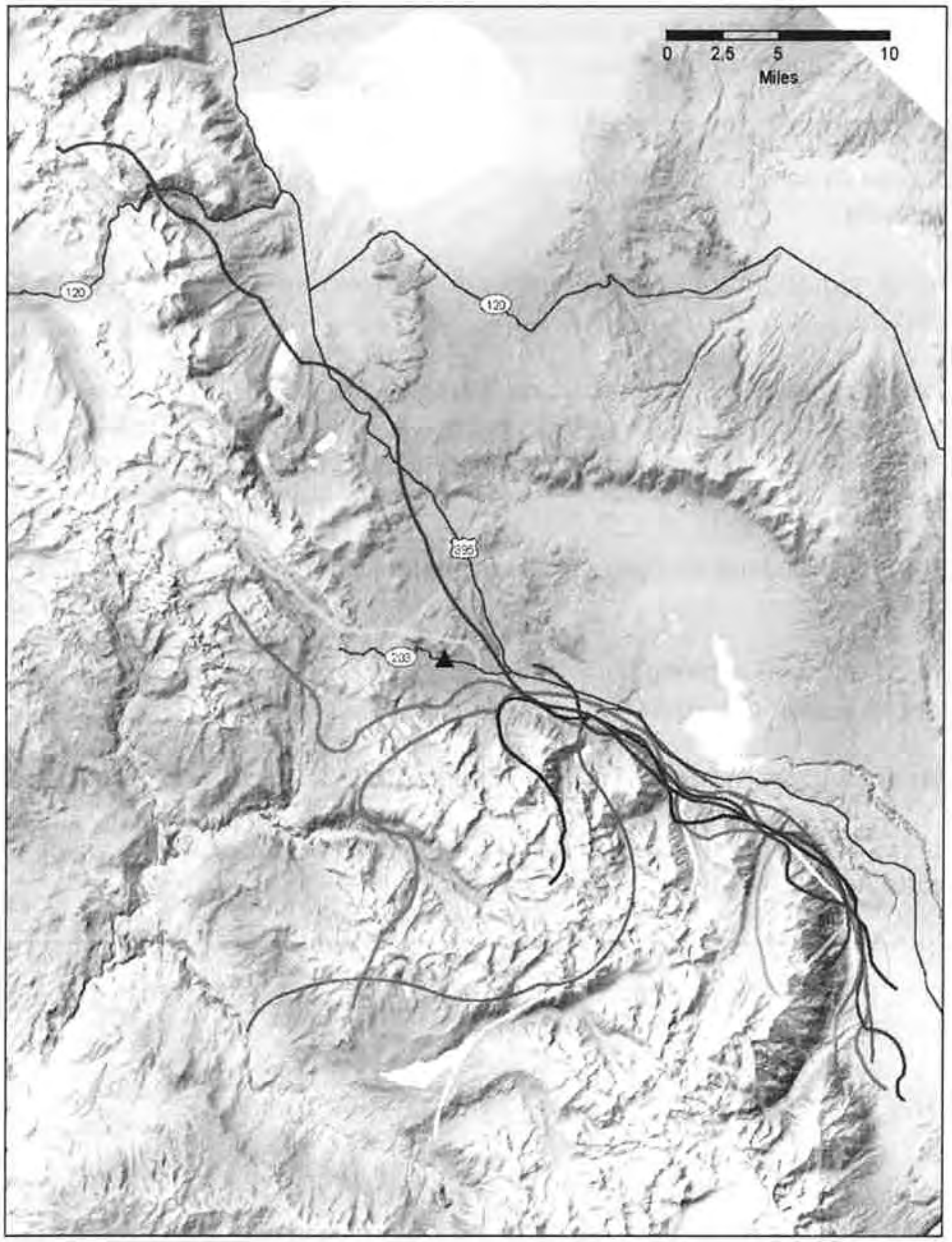

Figure 1. Map of study area displaying some of the primary migration routes utilized by adult female mule deer fitted with GPS collars.

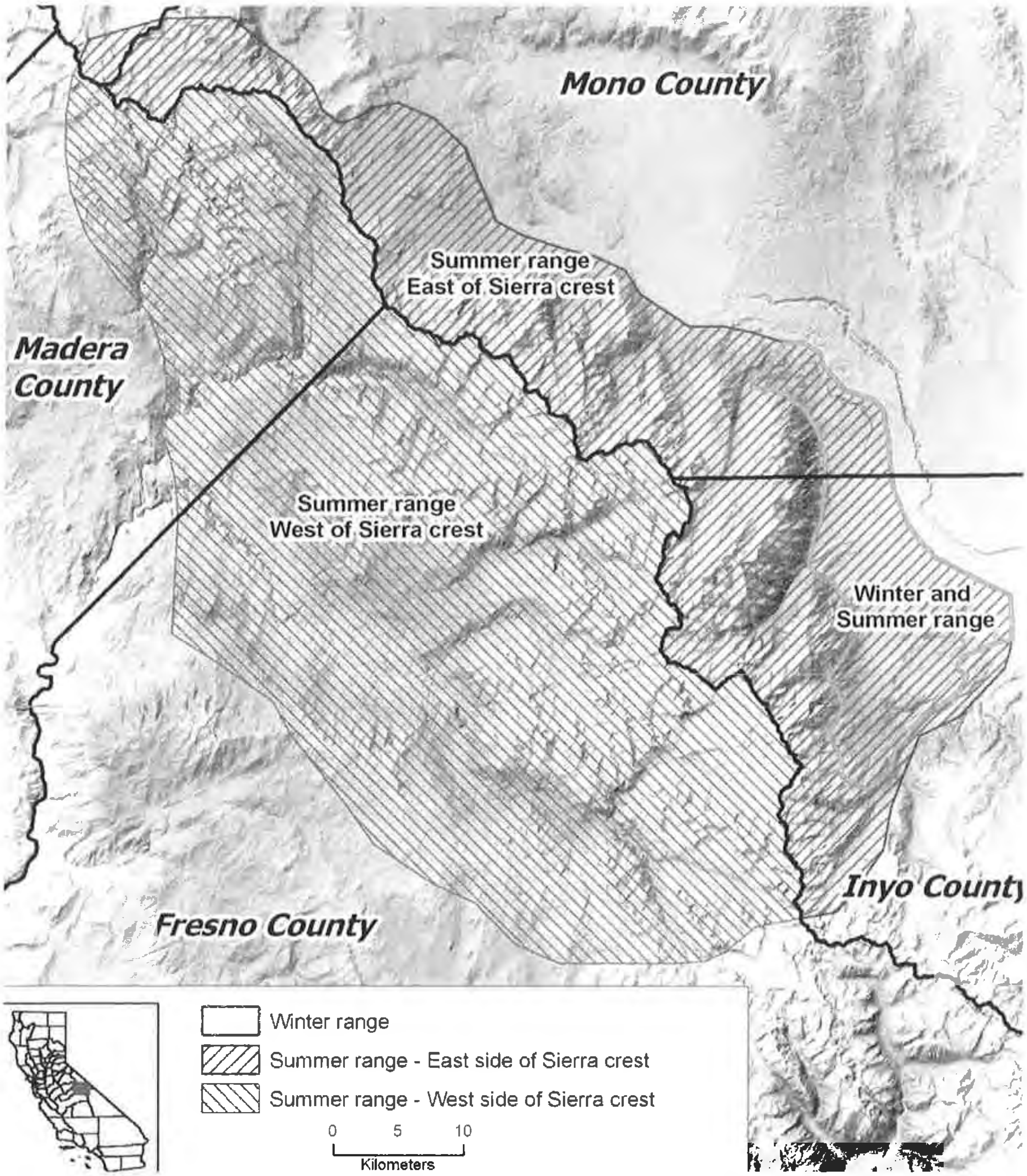

Figure 2. Map of the study area (Madera, Fresno, Mono, and Inyo counties, CA) with west-side summer ranges occurring in the San Joaquin River drainage and east-side summer ranges occurring along the eastern side of the Sierra crest.

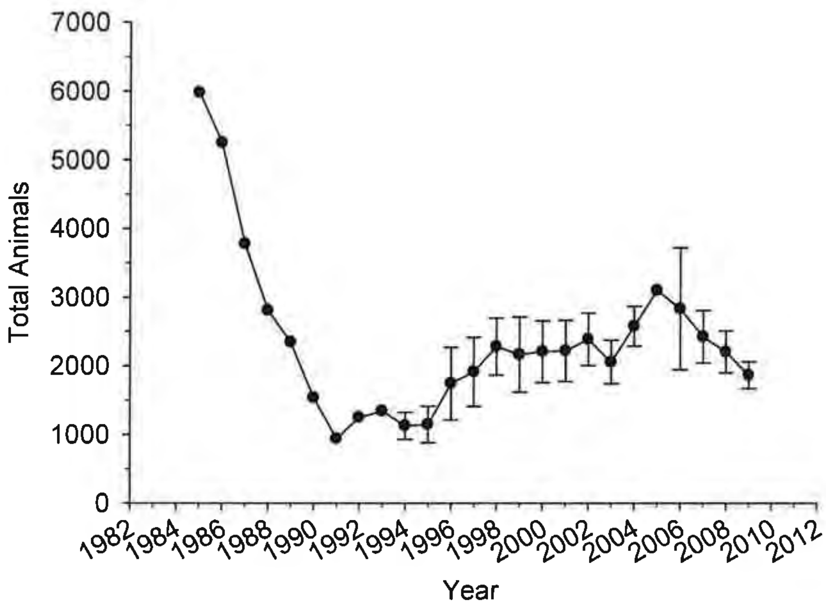

Figure 3. Annual population estimates (±95% CI)of mule deer as determined from total counts prior to 1994 and from mark-resight surveys thereafter, Round Valley, Bishop, California.

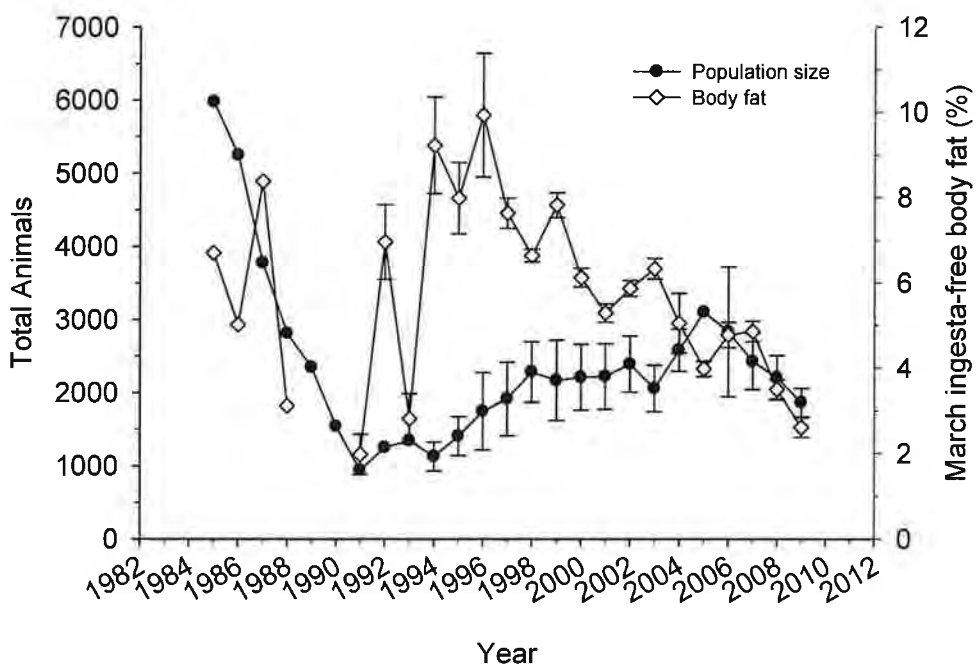

Figure 4. Annual population estimates (±95% CI)of mule deer and March ingesta-free body fat (±SE) of adult female mule deer wintering in Round Valley, Bishop, California.

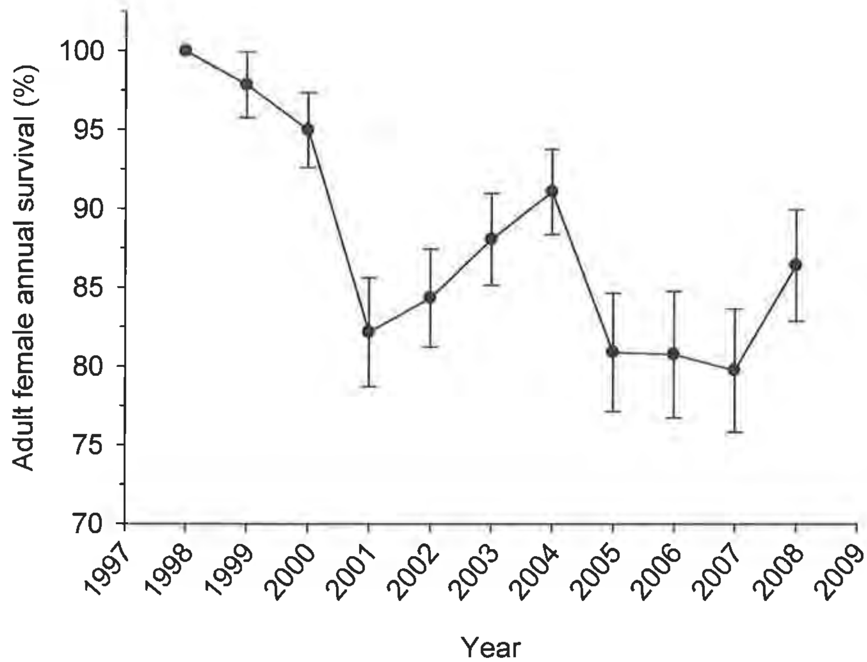

Figure 5. Annual survival (±SE; Jan-Dec) of adult (>1 yr old) female mule deer that overwinter in Round Valley, Bishop, California and summer in the Sierra Nevada, 1998-2008.

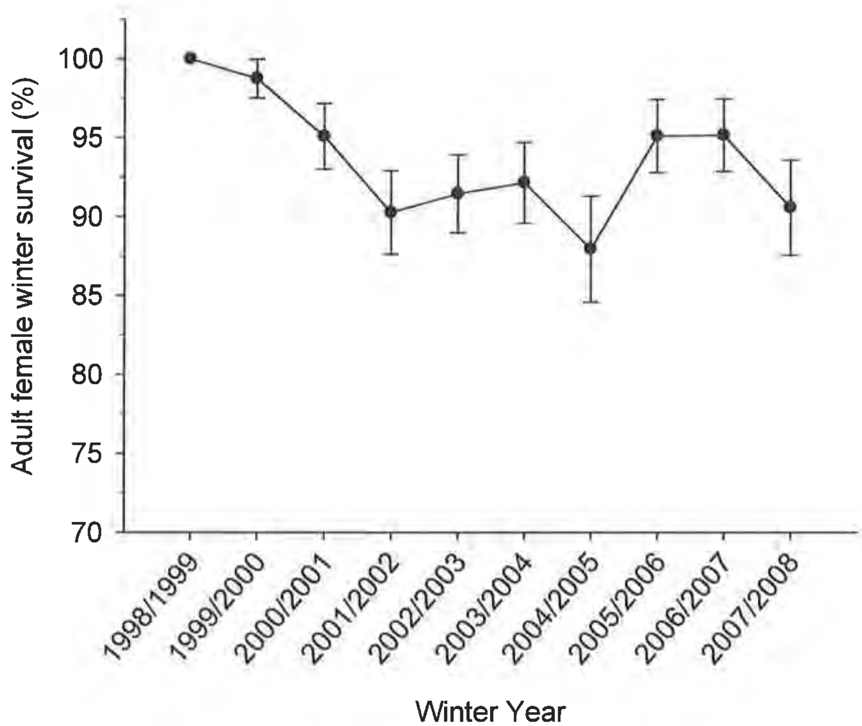

Figure 6. Winter survival (±SE; 16 Oct – 15 April) of adult (>1 yr old) female mule deer in Round Valley, Bishop, California, 1998-2008.

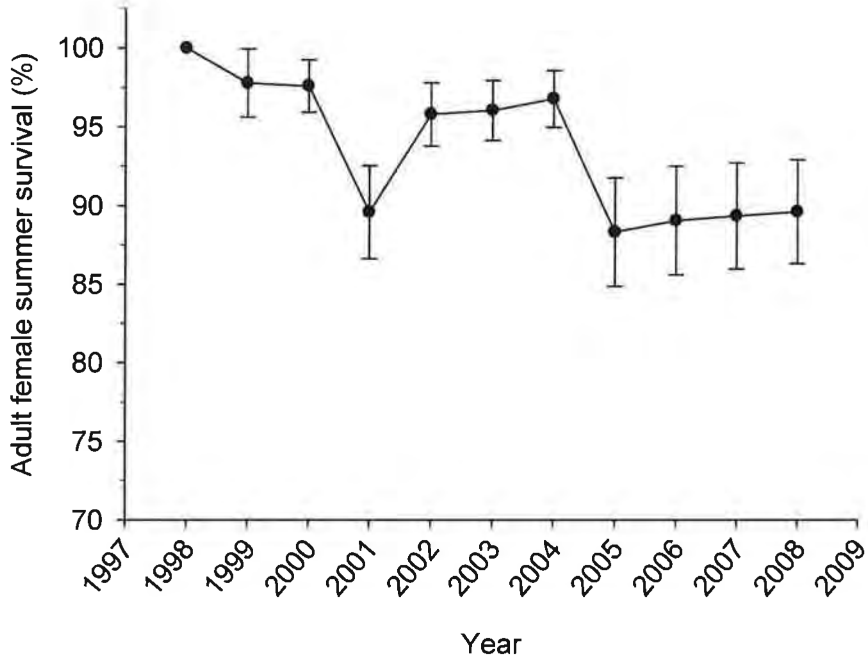

Figure 7. Summer survival (±SE; 16 April – 15 Oct) of adult (>1 yr old) female mule deer in the Sierra Nevada, 1998-2008.

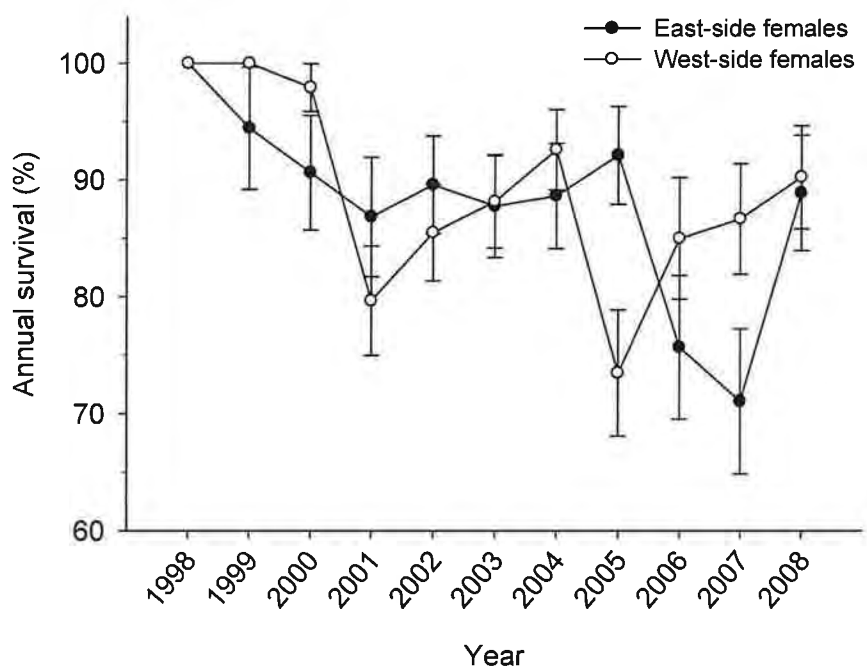

Figure 8. Annual survival (±SE) of adult (>1 yr old) female mule deer with respect to summer residency status in the Sierra Nevada, 1998-2008.

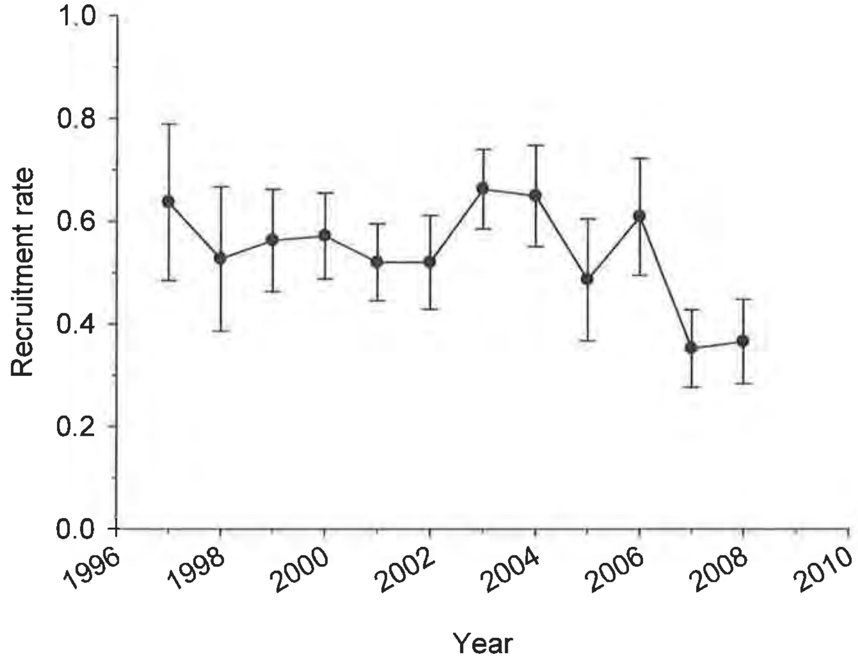

Figure 9. Annual recruitment rate (±SE) in autumn of adult (>1 yr old) female mule deer that were radiocollared, Round Valley, Bishop, California, 1997-2008.

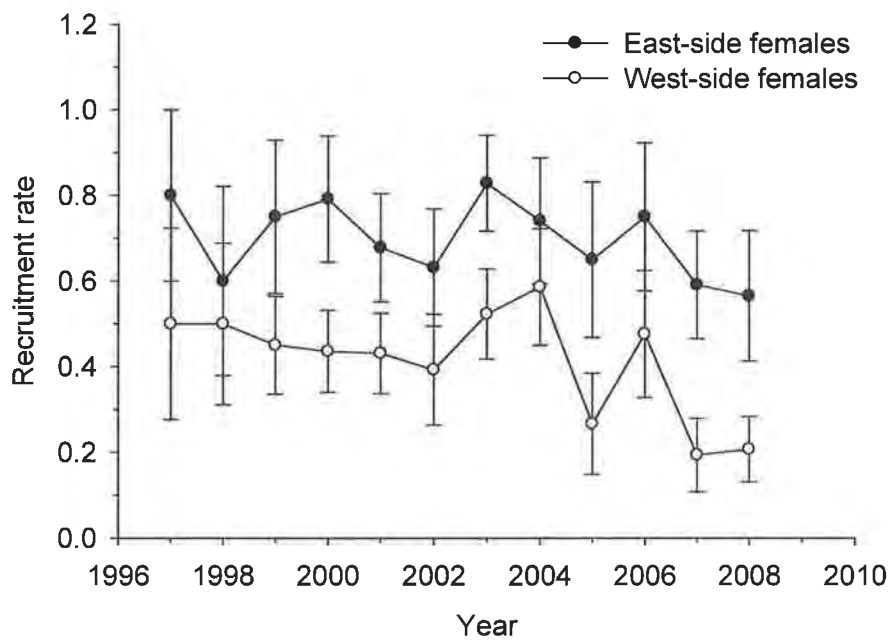

Figure 10. Annual recruitment rate (±SE) of adult (>1 yr old) female mule deer with respect to summer residency (side of Sierra crest) that were radiocollared, Round Valley, Bishop, California, 1997-2008.

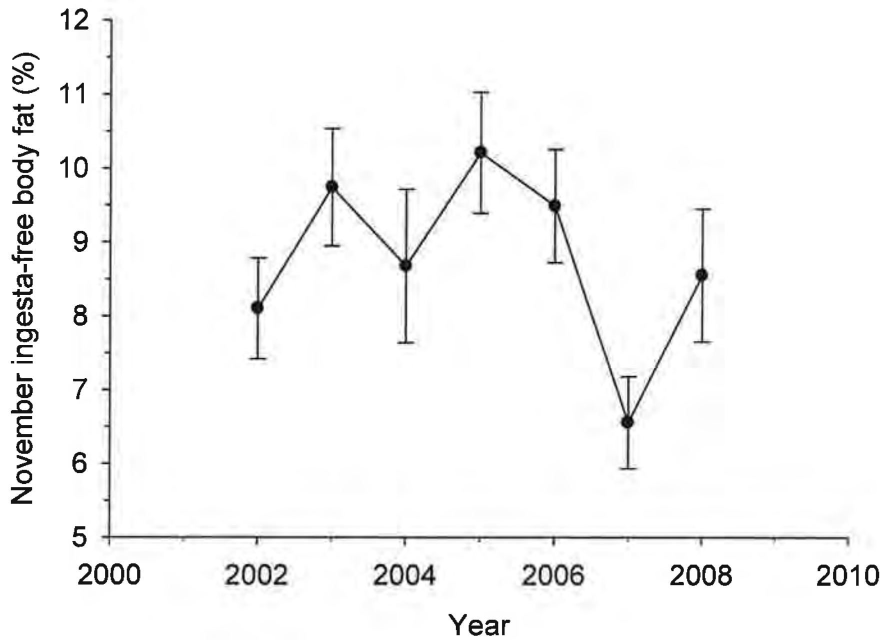

Figure 11. Average ingesta-free body fat (±SE) in November of adult (>1yr old) female mule deer per year, Round Valley, Bishop, California.

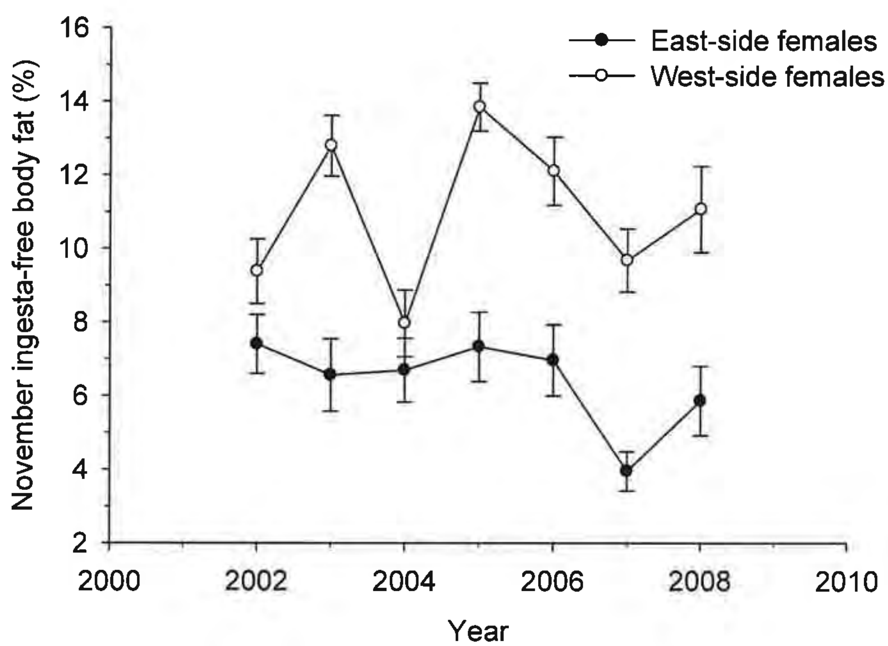

Figure 12. Average ingesta-free body fat (±SE) in November of adult (>1yr old) female mule deer relative to summer residency status (i.e., side of Sierra crest), Round Valley, Bishop, California.

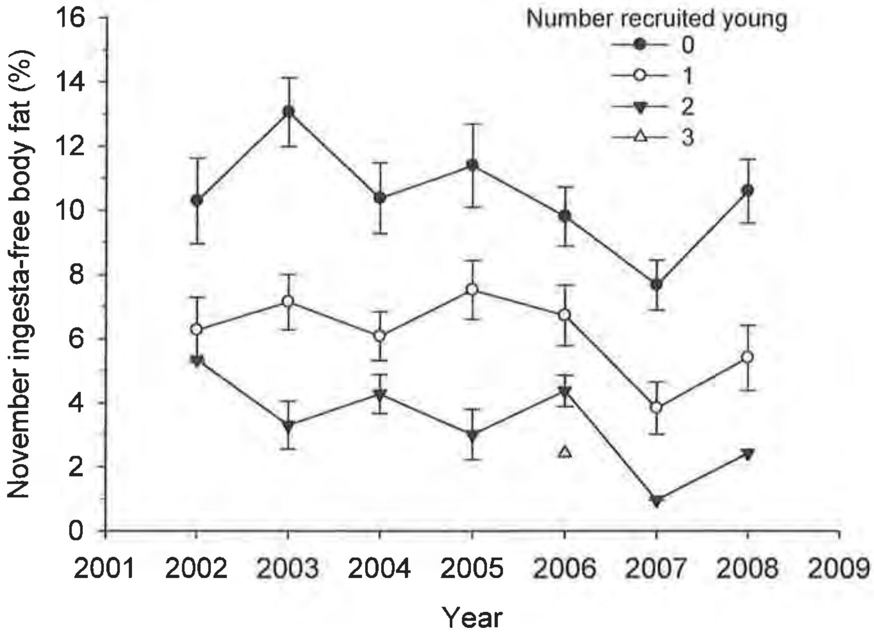

Figure 13. Ingesta-free body fat (%±SE) in November of adult female (>1yr old) mule deer relative to the number of young recruited per year, Round Valley, Bishop, California.

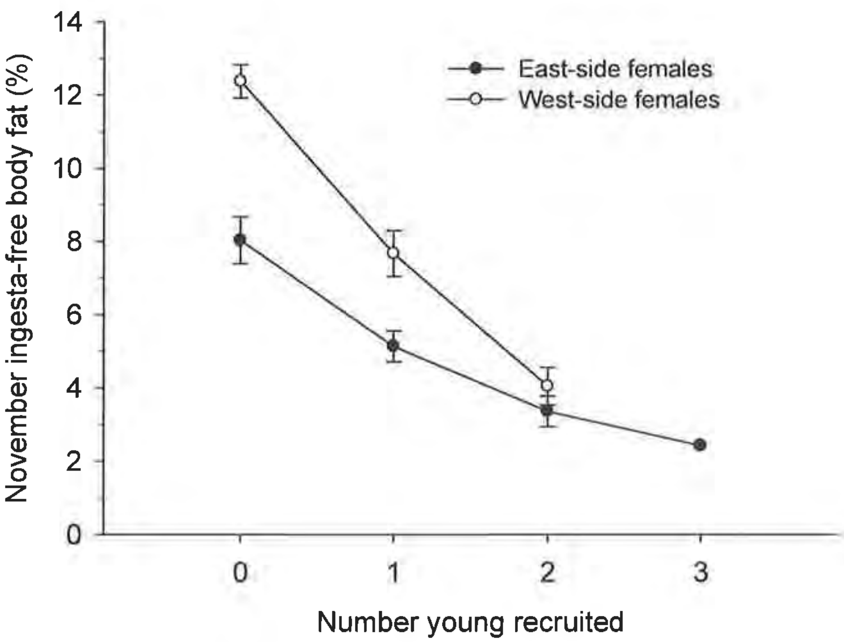

Figure 14. Ingesta-free body fat (%±SE) in November of adult female (>1yr old) mule deer relative to the number of young recruited and summer residency (i.e., side of Sierra crest), Round Valley, Bishop, California.

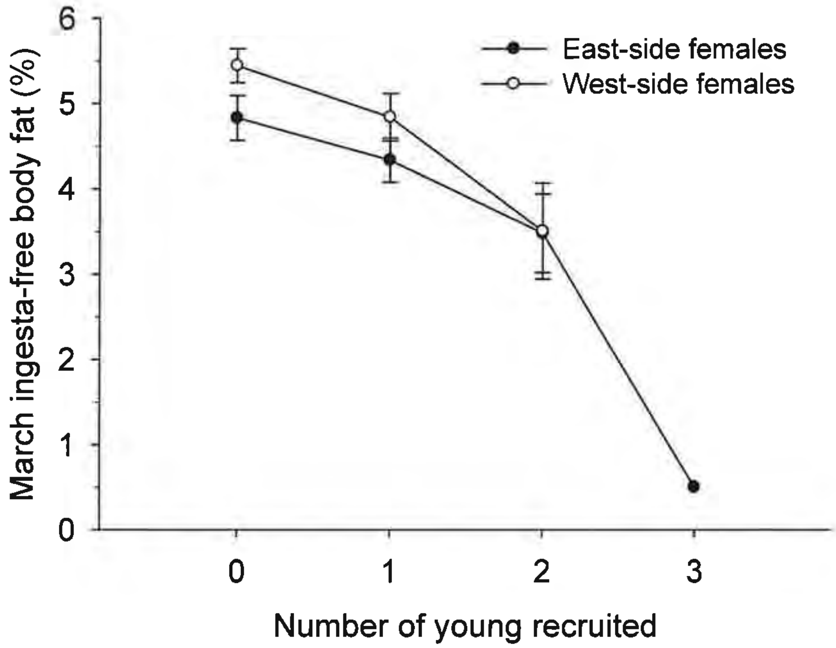

Figure 15. Average ingesta-free body fat (±SE) of adult (>1yr old) female mule deer relative to recruitment status the previous autumn with respect to summer residency status (i.e., side of Sierra crest), Round Valley, Bishop, California.

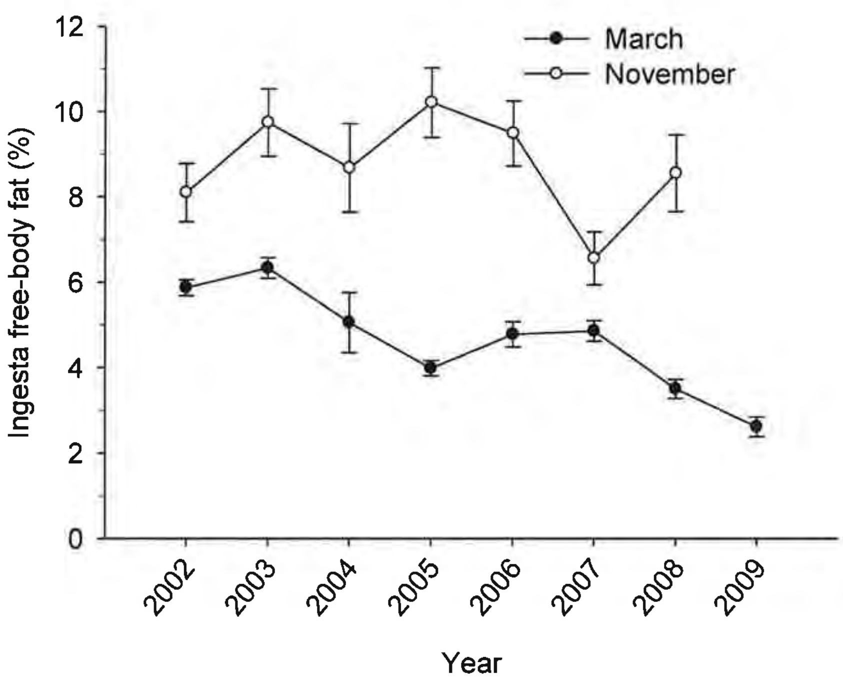

Figure 16. Average ingesta-free body fat (±SE) of adult (>1yr old) female mule deer during March and November 2002-2009, Round Valley, Bishop, California.

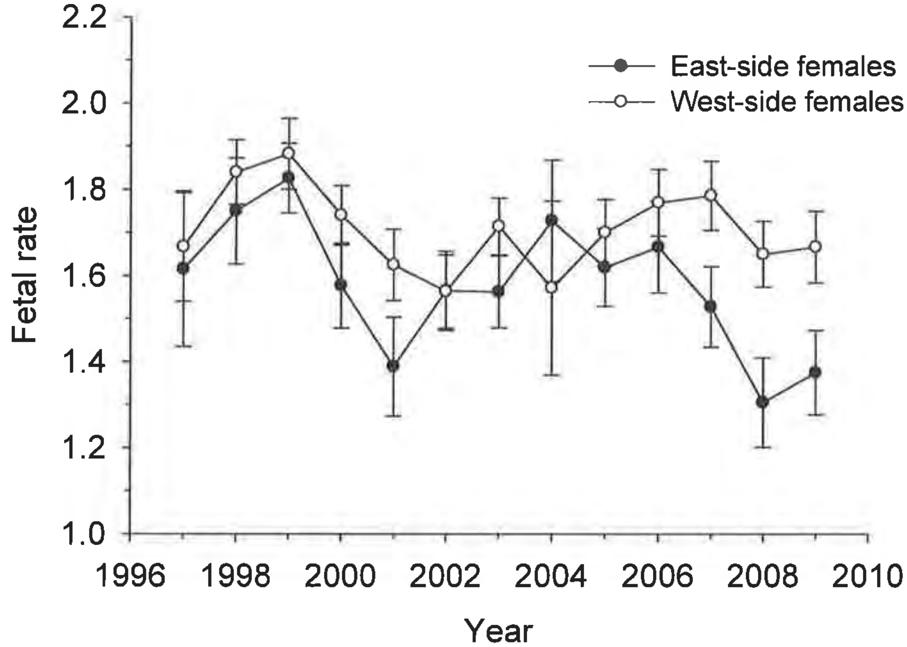

Figure 17. Average number of fetuses per adult (>1yr old) female mule deer during 1997-2009 with respect to summer residency status (i.e., side of Sierra crest), Round Valley, Bishop, California.

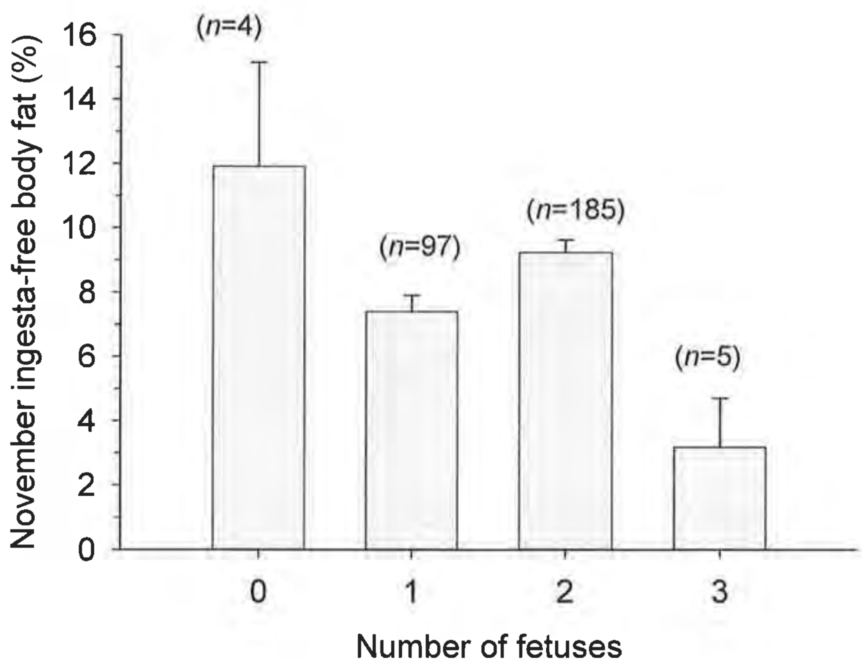

Figure 18. Average ingesta-free body fat (±SE) in November of adult (>1yr old) female mule deer relative to number of fetuses present the following March, Round Valley, Bishop, California. Sample size per group is shown parenthetically.

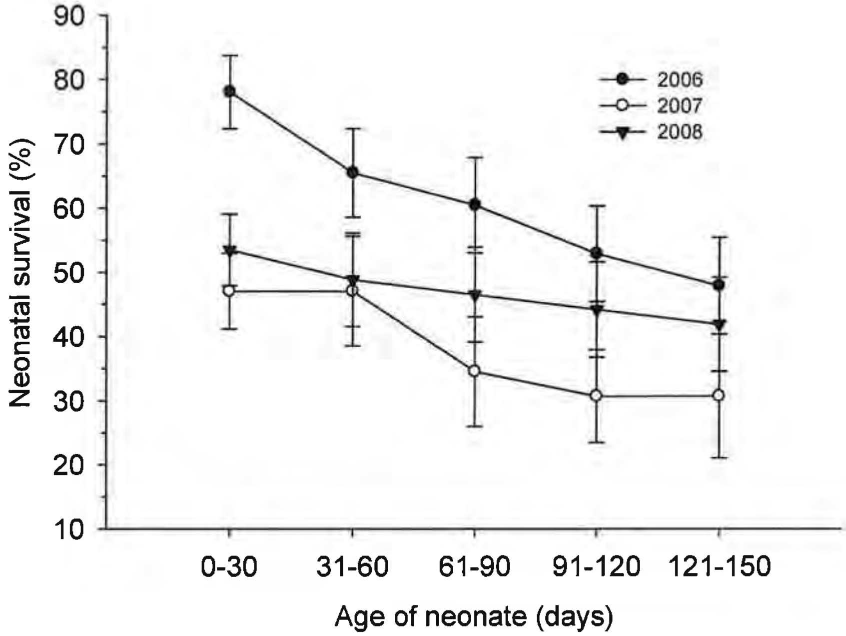

Figure 19. Monthly survival (±SE) of neonatal mule deer from birth to 150 days-of-age in the central Sierra Nevada, 2006-2008.

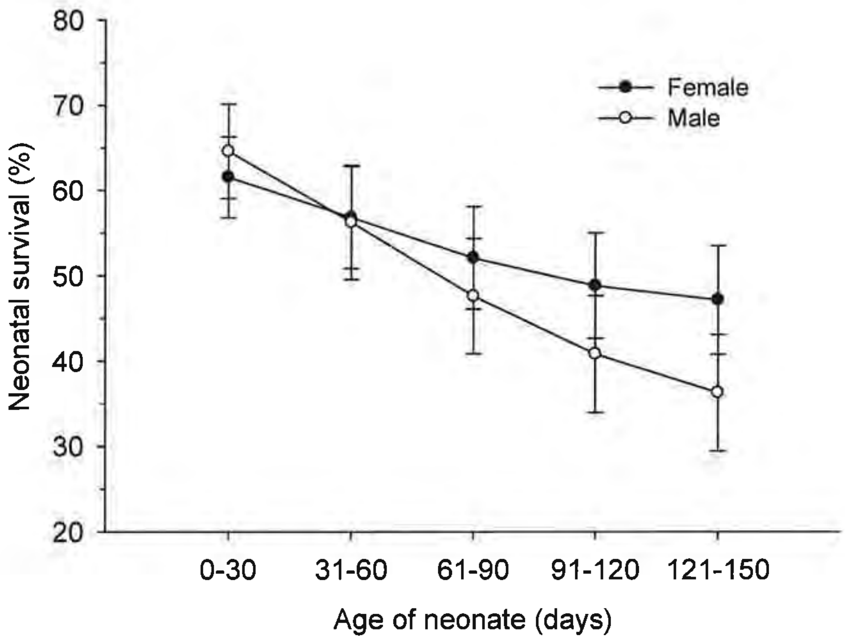

Figure 20. Monthly survival (±SE) of neonatal mule deer by sex from birth to 150 days-of-age in the central Sierra Nevada, 2006-2008.

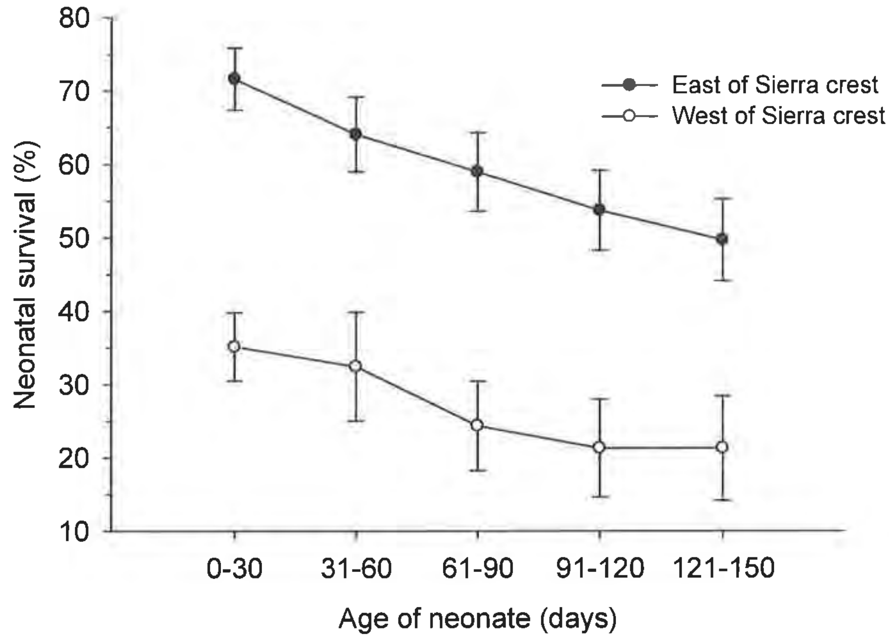

Figure 21. Monthly survival (±SE) of neonatal mule deer from birth to 150 days-of-age in the central Sierra Nevada with respect to which side of the Sierra crest each neonate was born, 2006-2008.

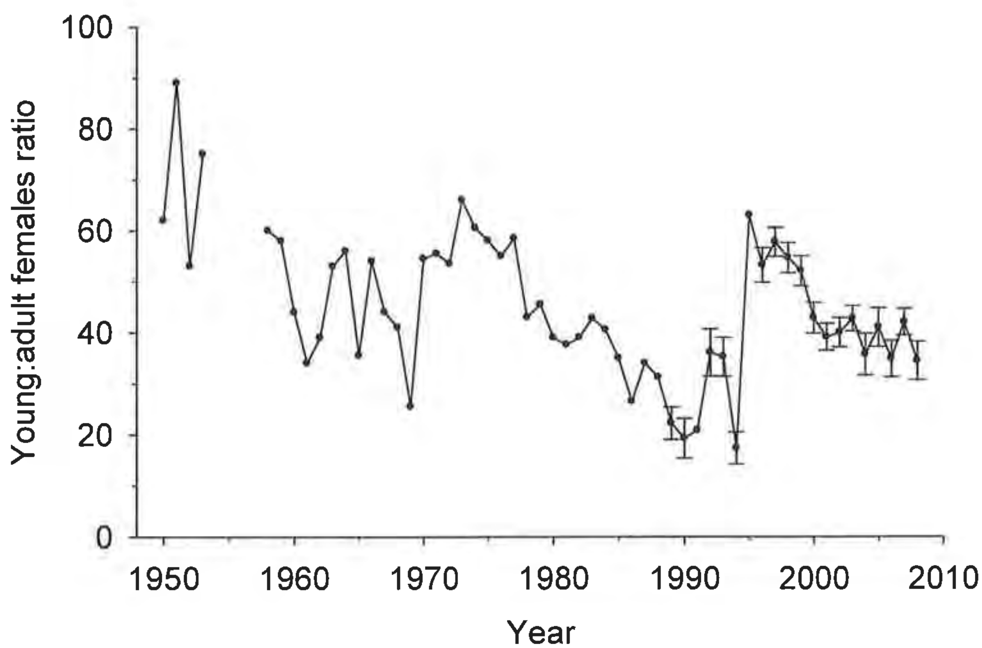

Figure 22. Number of young per 100 females (±95% CI) observed during composition surveys conducted each January in Round Valley, Bishop, California during 1950-2008. Data are reported as the post-season composition of the previous year.

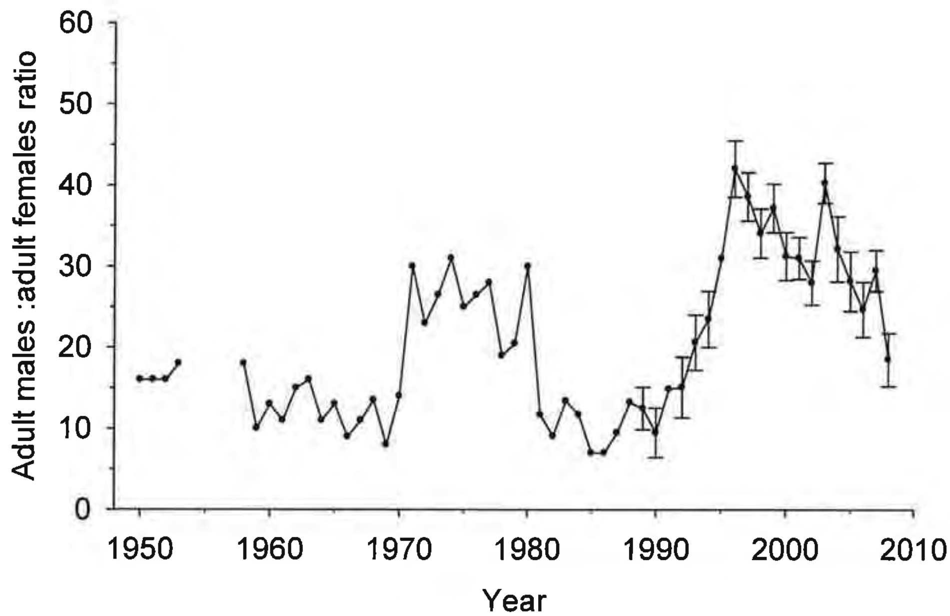

Figure 23. Number of adult males (>1 yr old) per 100 adult females (>1 yr old; ±95% CI) observed during composition surveys conducted each January in Round Valley, Bishop, California during 1950-2008. Data are reported as the post-season composition of the previous year.

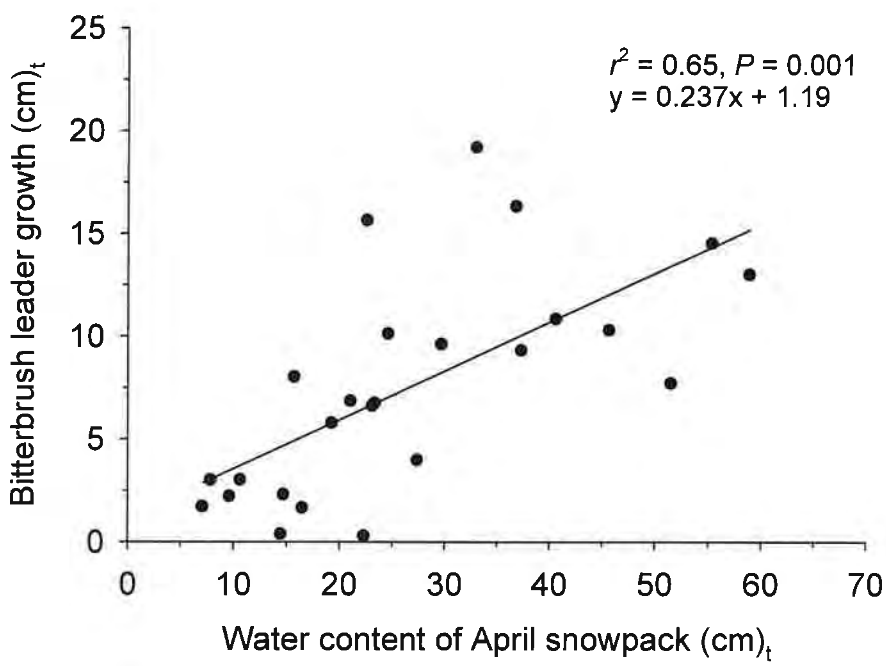

Figure 24. Length of annual growth of bitterbrush leaders relative to water content of snowpack measured in April, 1984-2008, Round Valley, Bishop, California.

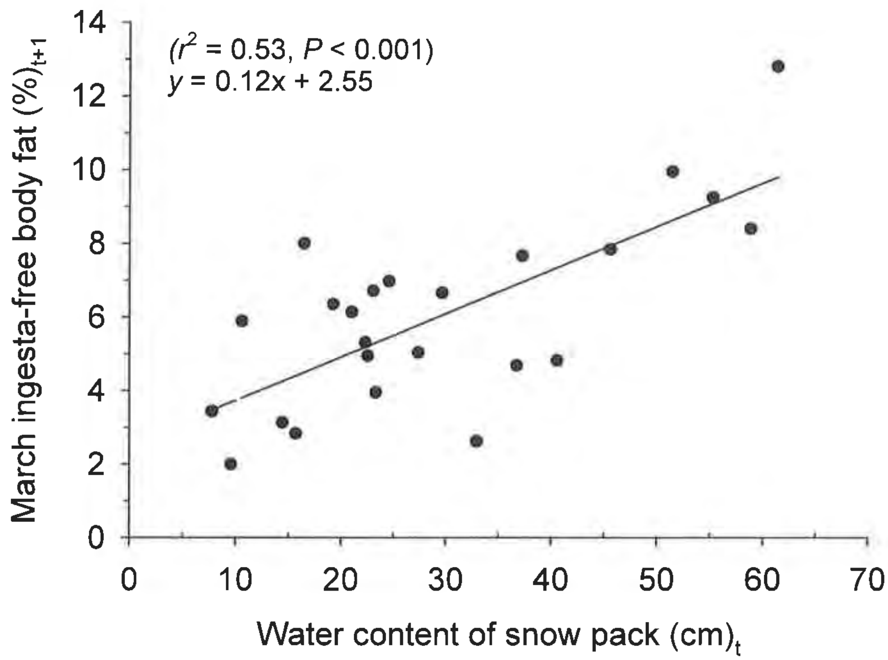

Figure 25. Influence of water content of snow pack on percent of ingesta-free body fat of adult female mule deer the following March in Round Valley, Bishop, California, 1985-2009.

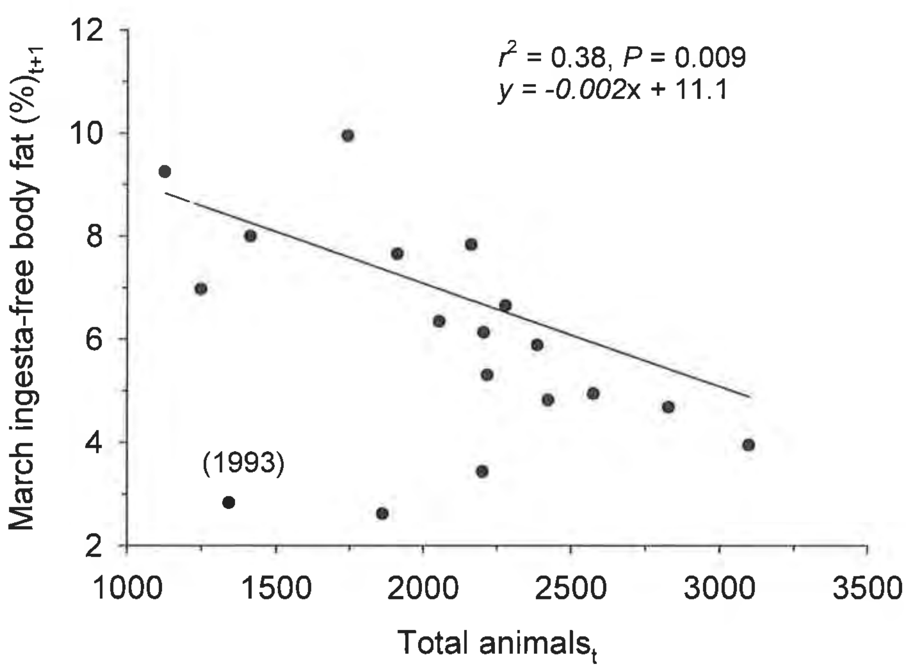

Figure 26. Relationship between population size of mule deer and average percent of ingesta-free body fat of adult females wintering in Round Valley, Bishop, California, following the population crash 1992-2009.

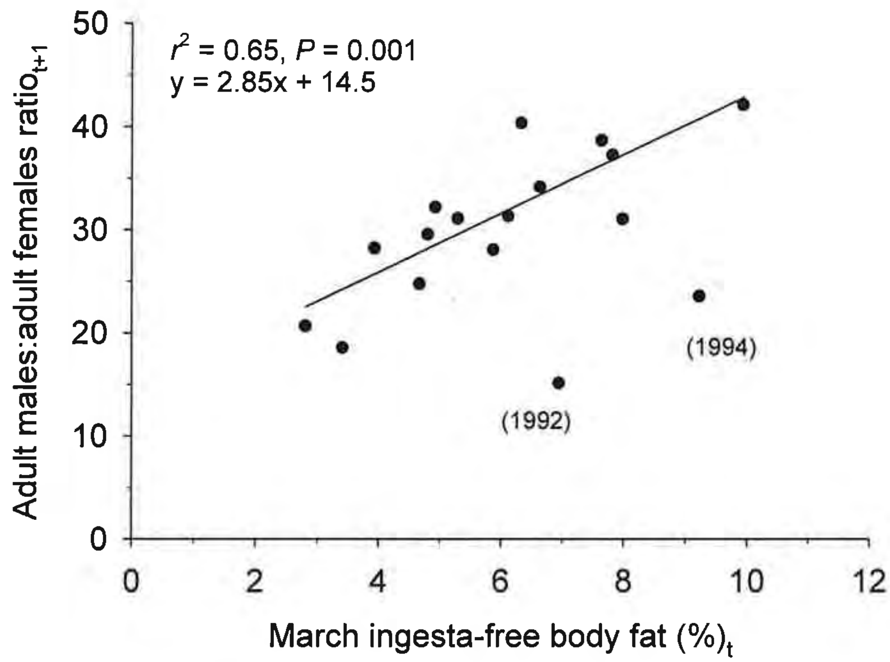

Figure 27. Relationship between ingesta-free body fat of adult female mule deer in March and the number of adult males:adult females the following January, Round Valley, Bishop, California, 1991-2008. Linear regression results are reported with outliers removed (i.e., 1992, 1994).

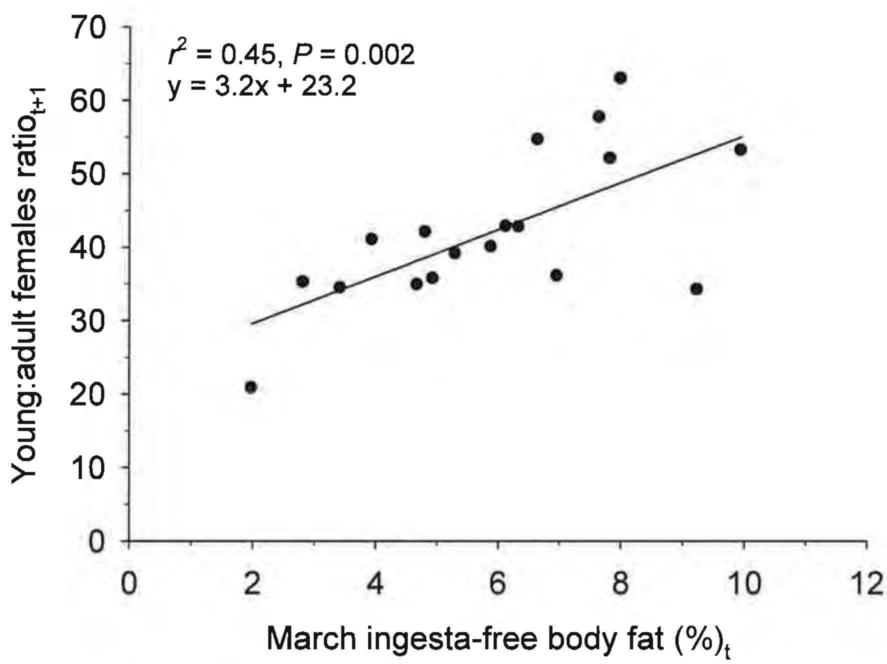

Figure 28. Relationship between ingesta-free body fat of adult female mule deer in March and the number of young:100 adult females the following January, Round Valley, Bishop, California, 1991-2008.

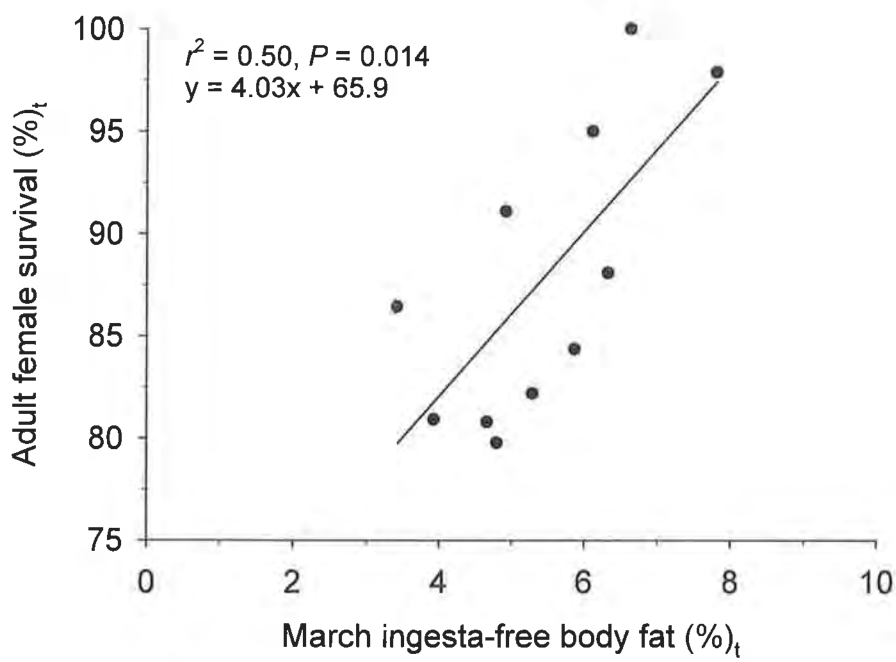

Figure 29. Relationship between ingesta-free body fat of adult female mule deer in March and annual survival of adult females, Round Valley, Bishop, California, 1991-2008.

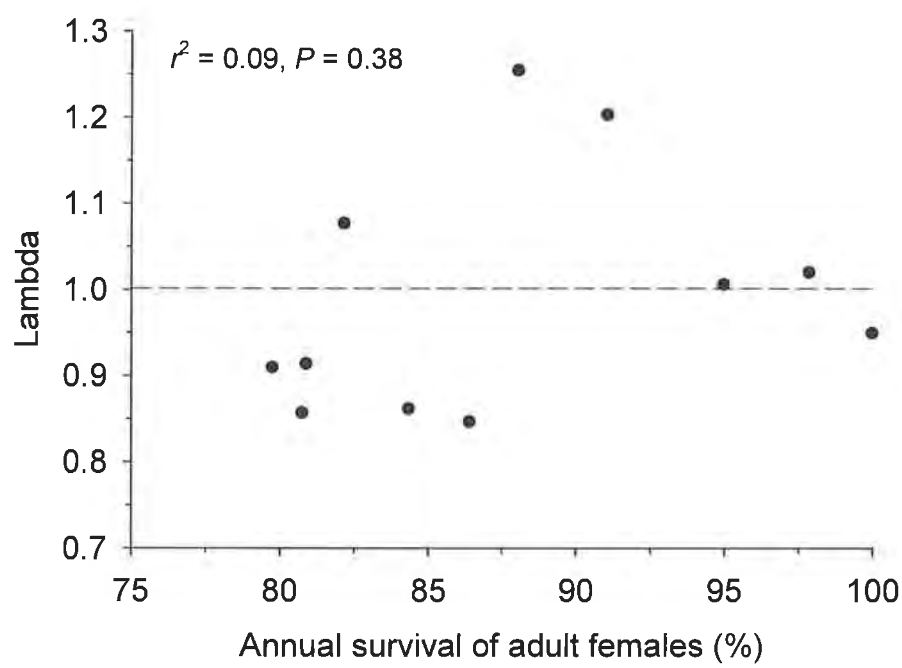

Figure 30. Relationship between annual survival of adult female mule deer (%) and lambda, Round Valley, Bishop, California, 1991-2008.

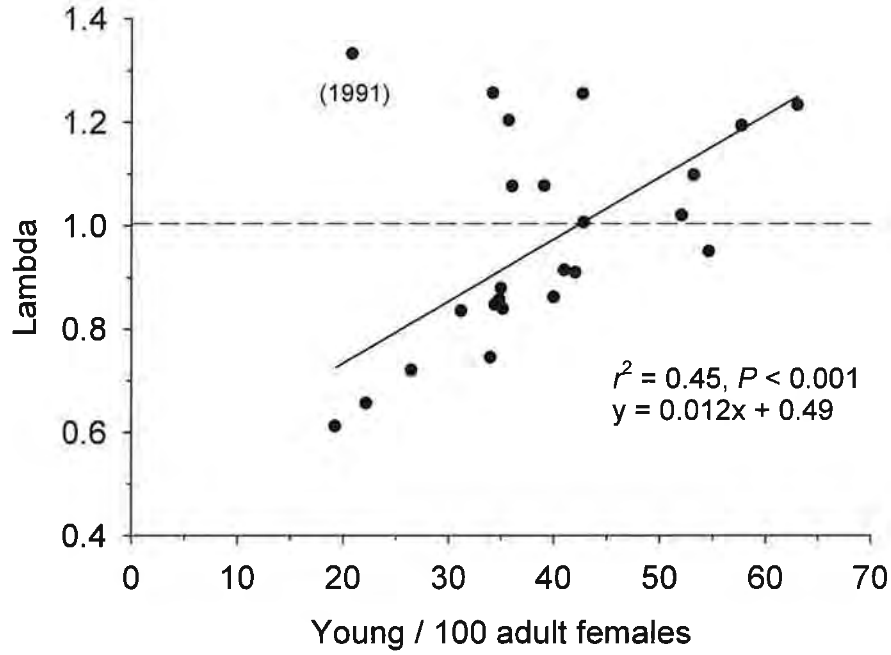

Figure 31. Relationship between number of young:100 females and lambda during the current year, Round Valley, Bishop, California, 1985-2009. Linear regression results are reported with outlier (1991) removed.

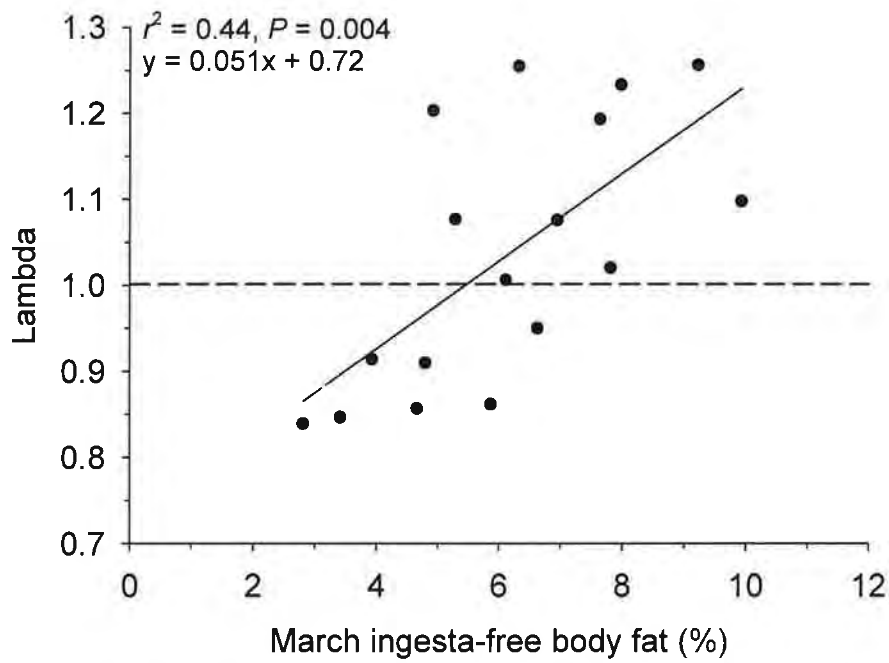

Figure 32. Relationship between ingesta-free body fat of adult female mule deer in March and lambda during the current year, Round Valley, Bishop, California, 1991-2008.

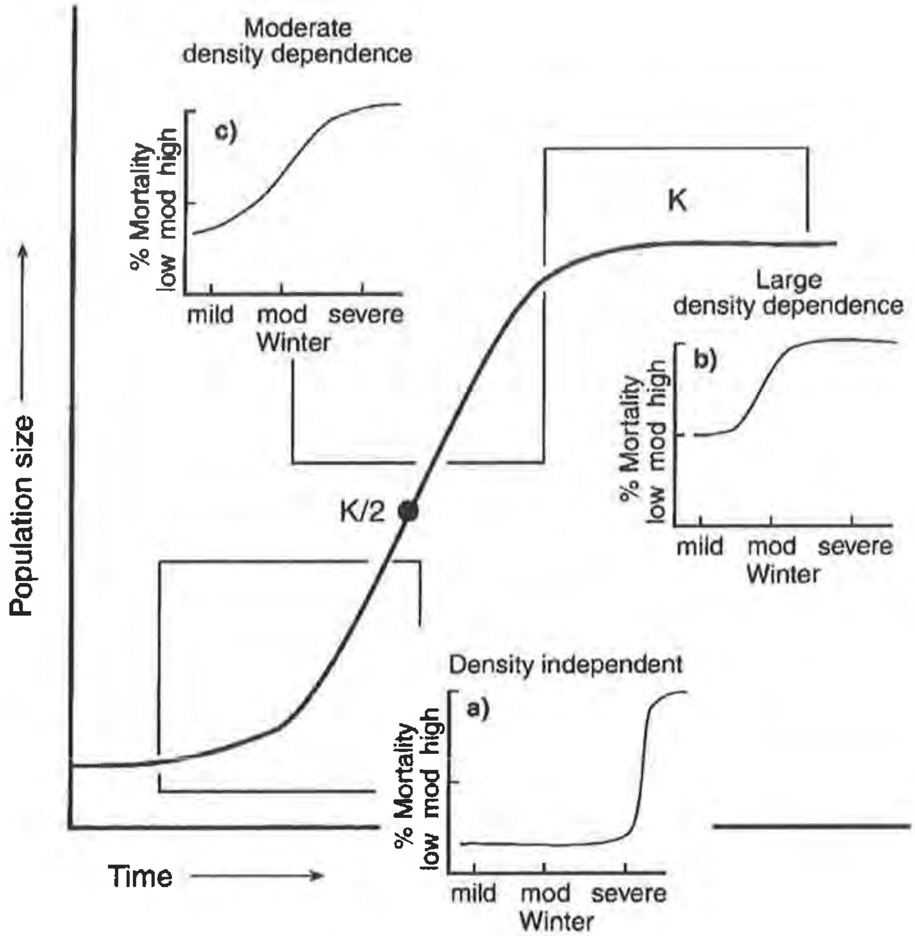

Figure 33. A conceptual model depicting relationships between population density, winter severity, and rate of mortality. Representative curves are provided for (a) density independent, (b) large, and (c) moderate density-dependent effects interacting with winter severity. The lines around the inset graphs show the area on the growth curve to which each inset corresponds. Note that the shape of the population-growth curve need not be symmetrical for the proposed relationships to hold (adapted from Bowyer et al. 2000).

CONTROLLING CHEATGRASS IN WINTER RANGE TO RESTORE HABITAT AND ENDEMIC FIRE

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Abstract. Cheatgrass (*Bromus spp.*), an introduced, invasive, annual grass of the Western rangelands, increases both fire frequency and intensity, competes with native species for water, space and nutrients, and is a primary cause for loss of habitat quality on elk and deer winter ranges. Studies indicate that rangeland with a 5% cheatgrass composition can become dominated by cheatgrass after a fire. When fire enters a landscape, cheatgrass is the first species to colonize after the burn, utilizing moisture before most native vegetation breaks dormancy. Cheatgrass evolved with and responds well to fire, enabling land to burn annually, increasing cheatgrass density. Cheatgrass litter build-up increases fire intensity, temperatures and frequency causing loss of fire tolerant native vegetation. The importance of removing cheatgrass, especially from crucial winter range, is emphasized by death of native shrubs from excessive fire intensity, inability of native species to compete with cheatgrass, and the subsequent rapid cheatgrass domination of the burn area. Four successful scenarios have been devised remove cheatgrass using fire and Plateau® herbicide: 1) Apply fire - wait one growing season - apply Plateau. This scenario generally produces poor conditions for desirable vegetation recovery. Cheatgrass quickly reoccupies the site out competing native plants, and provides the poorest conditions to apply the herbicide. 2) Apply fire - apply Plateau in the same growing season, results in best recovery of existing native vegetation and/or seedbed preparation for revegetation. 3) Apply Plateau - no fire. This scenario is best when cheatgrass litter fuel would cause fire to reach temperatures causing mortality of native species, impeding native plant re-colonization of the site. 4) Apply fire – apply Plateau – revegetate. This scenario is effective when reclaiming cheatgrass monocultures and the area requires replanting of desirable species. By removing cheatgrass prior to or after a burn, crucial winter range species, like true mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), shadscale/Four wing saltbush (*Atriplex spp.*) and sagebrush (*Artemisia spp.*) species can more efficiently and vigorously re-occupy the site or survive the burn. Native grasses and forbs produce 3 to 8 times more biomass with cheatgrass removal. Critical plant inter-space is restored, reducing fire frequency, size and intensity. This information can be used by wildlife/resource managers throughout Western North America to prevent further decline and improve both winter and summer range. Habitat managers can better prepare a program for prescribed burns and wildfire management, to produce maximum forage biomass. For areas consisting of monoculture stands of cheatgrass, this information can be used to re-establish wildlife friendly vegetation (grass, forbs or brush species) into annual grass monocultures, creating sustainable habitat for wildlife summer or winter range.

WESTERN STATES AND PROVINCES DEER AND ELK WORKSHOP PROCEEDINGS 6:20-24

Key words: Artemisia, Atriplex, bitterbrush, Bromus, Cercocarpus, cheatgrass, fire, habitat, mahogany, Purshia, rangeland, sagebrush, shadscale, imazapic

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Fine fire fuel management programs are being implemented by Wyoming Game and Fish Department to reduce loss of big game winter range. Prescribed fire has been an important tool to regenerate brush, improving winter browse. However, severe drought during the late 1990s and early 2000s have favored annual brome species (*Bromus* spp.) and allowed this invasive weed to influence burn area recovery. Critical big game winter range in Wyoming have had an increase of annual brome, such as cheatgrass (*Bromus tectorum*), after wildfire, resulting in decreased desirable vegetation including grass, shrubs and forbs. These results have prompted Wyoming Game and Fish to evaluate areas prior to a prescribed burn to determine if an annual brome component is present and if likelihood of habitat degradation, rather than improvement, may occur. If the site has potential of degradation due to annual brome release, Plateau® herbicide, imazapic, is incorporated into the winter range improvement plan for pre-emergence control of cheatgrass.

Increasing use of the herbicide Plateau, imazapic, for selective control of annual brome in Western wildlands has dictated the need for increased knowledge of tolerant brush species. Western bunchgrass and forb tolerance trials have shown Plateau to be an acceptable tool for release of desirable plant species and renovation of annual brome infested areas[1] (Foy 2003, Rayda 2003). In general, Plateau is not effective at control of brush; however, some brush species exhibit unacceptable injury. Brush tolerance to Plateau is key when considering use of this herbicide for selective control of annual brome prior to a prescribed burn for critical winter range brush regeneration.

In addition, Plateau is gaining recognition and use as a tool to produce aesthetically acceptable fuel breaks and green strips. Plateau can selectively remove the fine annual brome fuel from more fire resistant bunch grasses and shrubs. Removal of the annual brome helps eliminate an ignition fuel as well as eliminating the main fire carrier. Fire modeling of Plateau treated areas utilizing the BehavePlus fire model has shown significant reduction of flammable biomass as well as decreasing flame height and length (Kury 2003). Applications of Plateau are typically broadcast, applied over the top of brush remaining in the green strip for aesthetic, moisture catching or soil stabilizing purposes. Brush tolerance is an important aspect when considering the use of Plateau for enhancing green strips and fuel breaks, as well as an additional tool for habitat improvement.

Tolerance Mechanism

Plateau herbicide, imazapic, is a member of the imidazolinone family. The active ingredient of an imidazolinone herbicide controls susceptible plants by binding to the acetohydroxyacid synthase (AHAS) enzyme and preventing production of three essential amino acids. Plant tolerance to imidazolinones can be due to inherent differences in the AHAS enzyme itself and/or differences in the stability of the enzyme. Some species, such as legumes, tolerance to imidazolinones is contributed to their ability to metabolize the herbicide active ingredient. Mature tissues in plants appear to be relatively unaffected by inhibition of the AHAS enzyme (Shaner 1991). This accounts for the higher susceptibility of annual versus perennial plants, since perennial plants would have a higher percentage of mature tissue. After direct treatment with an imidazolinone herbicide, mature leaves of perennial susceptible plants will remain green for a long period of time, several months, prior to desiccation. Leaves continue to photosynthesis, although amino acid production is arrested. In treated susceptible species, photosynthesis translocation can be disrupted, depriving roots of an energy supply (Shaner 1991). Susceptibility of well-established shrubs may take up to two years to determine.

Results and Discussion

True Mountain Mahogany Tolerance

True mountain mahogany (*Cercocarpus montanus*) trials were conducted on a post-burn site in Douglas, WY. At one year after a wildfire, further loss of mountain mahogany was threatened by competition and additional fine fuel buildup of cheatgrass, tumble mustard (*Sisymbrium altissimum*) and thistle (*Cirsium* spp.) invasion. Plateau treatments were broadcast applied 4 September 2002, prior to cheatgrass emergence. The trial had 7 treatments; 6, 9, and 12 oz of Plateau per acre, with and without methylated seed oil (MSO) surfactant at 1 qt/acre, compared to a non-treated plot. Plot size included 7 to 10 bushes in a 10 x 50 foot area replicated 3 times. The same treatments were conducted on an adjacent area in spring 2003. Treatment goals were to reduce the fine fuel load to prevent further loss of the remaining mountain mahogany population in the event of a wildfire. Data was to be used to aid in plans to prepare similar sites for a prescribed burn.

The spring after application, all fall 2002 treatments showed delayed leaf expansion with some yellowing during the first growing season. This response increased as the Plateau rate increased, with a greater negative response from treatments that included the MSO surfactant. All plots were evaluated the first full growing season after applications on 10 August 2004. Fall treated plots at the typical cheatgrass

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[1] Data on file with BASF Corporation, J.L. Vollmer, Laramie, WY, as "GRASS AND FORB TOLERANCE TO PLATEAU® HERBICIDE – Update July 26, 2006.

recommended application rates of Plateau at 6 or 9 oz/acre and Plateau at 6 oz + MSO had no adverse effects on the true mountain mahogany. Addition of MSO to the Plateau at 9 oz/acre simulated a burn response by stimulating new shoot growth from the base of the plant. The Plateau at 9oz/acre plus MSO treatment could be used to simulate a prescribed burn for habitat enhancement when the cheatgrass population is high enough to threaten mahogany mortality during a wildfire or prescribed burn.

Spring applications showed greater variability in response between plants within a treatment. Plateau at 6oz/acre was the only treatment resulting in mahogany growth similar to the non-treated plot. Plateau at 12 oz/acre + MSO applied in the spring resulted in initial unacceptable stunting of new growth. The observed stunting was viewed as unacceptable due to the decreased amount of vegetation that could be utilized as browse.

New basal growth was evaluated for all treatments as an important source of mahogany regeneration. New basal growth was acceptable for all fall treatments except the Plateau 12oz/acre + MSO. Results suggest that this treatment affected the overall plant system, inhibiting the ability of the plant to recover. For spring-applied treatments, new basal growth, at 16 months after treatment, was not affected by Plateau at the 6 or 12 oz rate or MSO plus Plateau at 9 or 12 oz rate. All other treatments had individual plants that elicited variable shoot growth. Differences in basal growth may be due to individual plant genetics or microclimate including soil type and/or depth.

Fall pre-emergence Plateau treatments without surfactant provided the needed cheatgrass control. The addition of MSO was not needed to achieve adequate cheatgrass control to reduce competition and fire hazard. Spring treatments required the addition of MSO to control the cheatgrass post emergence, but spring treatment is not recommended due to variation in brush response and annual brome efficacy.

Antelope Bitterbrush Tolerance

The antelope bitterbrush (*Purshia tridentata*) tolerance research was conducted on a site prior to a prescribed burn, at 8000 feet east of Laramie, WY. Plateau treatments were broadcast applied 30 September 2003, prior to cheatgrass emergence. The trial had 9 treatments; Plateau at 6, 8, 10 and 12 oz/acre, Plateau at 6 and 8 oz/acre plus non-ionic surfactant (NIS) at 0.25% v/v, and Plateau at 10 and 12oz/acre with MSO surfactant at 1 qt/acre, all compared to a non-treated plot. Plot size included 10 bitterbrush plants in a 10 x 50 foot area replicated three times. Treatment goals were to prevent cheatgrass domination after a prescribed burn.

At the beginning of the first growing season after application, 24 June 2004, bitterbrush showed little response from most treatments. Exceptions were Plateau at 12 oz/acre alone and Plateau 10 and 12 oz/acre plus MSO. The response elicited by these herbicide treatments was a delay in leaf expansion, smaller mature leaves and shortened internodes of new stems (typical imidazolinone symptomology). First year results indicated that later ratings were needed to evaluate long-term herbicide effect on bitterbrush.

At 2.5 years after treatment, 23 May 2006, bitterbrush mortality was evaluated. The 6 and 8 oz/acre rates of Plateau with and without surfactant had no mortality and no evidence of treatment effect (Table 1). The two high rates of Plateau with surfactant resulted in 28% to 43% mortality.

Table 1. Antelope bitterbrush tolerance, leaf expansion and mortality after treatment of Plateau with associated additives.

	Evaluation June 24, 2004	Evaluation May 23, 2006
Treatment	% Injury by leaf Expansion Reduction[a]	% Mortality[a]
Plateau 6oz + NIS	7	0
Plateau 8oz + NIS	8	0
Plateau 10oz + MSO	90	28
Plateau 12oz + MSO	90	43
Plateau 6oz	0	0
Plateau 8oz	0	0
Plateau 10oz	0	27[b]
Plateau 12oz	22	33[b]
Non-treated	0	0

[a]Average over 3 replications

[b] First replication, located on slope with drought tendency had 80% mortality

Surviving plants had no new stem growth and spring leaf growth was severely delayed with the few new leaves displaying typical imidazolinone symptomology, indicating these plants were still under severe stress from the Plateau herbicide. The second and third replications of 10 and 12 oz/acre rate of Plateau without surfactant, showed little to no injury on recovered plants. However, the first replication, located on a drought prone slope, had mortality of 80% for both treatments. This response to adverse environmental factors in combination with a Plateau treatment indicates marginal tolerance of bitterbrush to Plateau at high rates. Of the recovering plants in the second and third replications, first year growth after application was a fifth of the second year growth. Wildlife managers would need to assess bitterbrush recovery potential and browsing demands on these plants to determine if high rates of Plateau were acceptable for their program goals. Rates of 10 and 12 oz of Plateau per acre is rarely needed to achieve acceptable cheatgrass control, allowing managers to adjust rates to achieve antelope bitterbrush selectivity.

Sagebrush Species Tolerance

Sagebrush (*Artemisia* spp.) steppe communities have been severely impacted by fire carried by annual brome species. Restoration of fire-scarred land can be unsuccessful due to competition from annual brome; therefore, a selective herbicide that can be used to preserve remaining sagebrush steppes as well as aid in restoration is very important. Plateau herbicide has been applied over the top of several sage species through research and commercial applications. Table 2 is a summary of tolerance research results and commercial observations made across the western Unites States sagebrush steppe areas.

Table 2. Tolerance summary of sage species to Plateau herbicide at 2 to 12 oz/acre with or without MSO.

Silver Sagebrush (*A. cana*)[a]	no injury
Fringed Sagebrush (*A frigida*)[a]	no injury, new growth greater than in non-treated areas, possibly due to elimination of annual brome competition
Wyoming Big Sage (*A. tridentata*)	
spring applied	no injury
fall applied	no injury, new leader growth often increased compared to non-treated areas, possibly due to elimination of annual brome competition
Seedling Wyoming Big Sage[a]	no injury

[a] Fall applied Plateau herbicide treatment

Sagebrush Case Study

The Johnson Creek Unit of Sybille Canyon, WY suffered the loss of critical bighorn sheep winter habitat in August 2001. An escaped campfire resulted in a 448-acre wildfire. During the fall 2001 cheatgrass dominated the area, out-competing the native vegetation. A rescue/release treatment of Plateau at 8 oz/acre plus MSO was applied in August 2002. Prior to treatment, 100 foot transects were installed on the Wyoming Game and Fish treated area and on an adjacent non-herbicide-treated, burned Bureau of Land Management section. In 2003, post application, belt density transects and nested frequency quadrants were added. Measuring relative cover at 1 year after treatment, cheatgrass increased by 8% in the non-treated area to 75%, while native vegetation decreased a corresponding amount to 25% of the cover (Table 3). In the Plateau treated area, cheatgrass decreased from 84% to 0% with a corresponding increase in native vegetation to 100%.

Table 3. Percent Relative Cover of the Johnson Creek Unit at Sybille Canyon, WY[a]

	Bromus tectorum		Native flora	
Treatment	Pre-treatment	Post-treatment	Pre-treatment	Post-treatment
Non-treated area	67%	75%	33%	25%
Plateau 8oz/acre + MSO	84%	0%	16%	100%

[a]Preliminary data compiled by Wyoming Game and Fish Department[2]

Conclusion

Fall Plateau treatment, prior to cheatgrass emergence, remains the best program for true mountain mahogany tolerance in addition to best cheatgrass control at the lowest herbicide rates. Results indicated that an alternative to fire for mahogany regeneration is Plateau at 9oz/acre plus MSO. This treatment would give wildlife managers a treatment option when annual brome populations prohibit burning due to the increased fire temperatures threatening mahogany survival. A cheatgrass control program in an antelope bitterbrush community should not exceed Plateau at 8oz/acre with or without surfactant. Higher rates can increase the possibility of unacceptable injury to bitterbrush. *Artemisia* spp. exhibited the greatest tolerance with no negative treatment response to the highest label rate of Plateau with or without surfactant.

Plateau has proven to be an effective fire mitigation, release and restoration tool for grass/shrub landscapes. The selective ability of the product gives wildlife and land managers options for improving shrub communities. Specific species tolerance to Plateau is important when choosing rate, timing and additive.

Special Thanks: BASF wishes to acknowledge and thank Ryan Amundson and Keith Schoup, biologists for Wyoming Game and Fish, for bringing the research need of Plateau brush tolerance to our attention, and helping us determine injury acceptability limits dependant on anticipated wildlife utilization.

Literature Cited

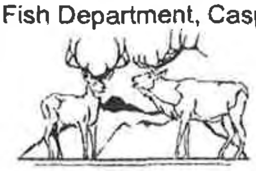
Foy, Lise P., Whitson, Thomas D. and Stevens, Bart W. 2003. Establishment of Native Wildflowers and Grasses for Roadside Re-vegetation Using Imazapic. Western Society of Weed Science Proceedings 25 pp

Kury, Brenda and Vollmer, Jennifer L. 2003. "Data Collection and Fire Modeling Determine the Potential for the use of Plateau ® Herbicide to Establish Fuel Breaks in *Bromus tectorum* - Dominated Rangelands." Western Society of Weed Science Proceedings 24 pp

Rayda, Margaret M. and Miller, Stephen D. 2003. Effect of Imazapic on Crop, Weed and Native Legumes. Western Society of Weed Science Proceedings 77 pp

Shaner, Dale L. and O'Conner, Susan L. 1991. The Imidazolinone Herbicides. CRC Press, Inc. (80, 135 pp)

[2] Data on file with the Wyoming Game and Fish Department, Casper, WY



Comment Letter I9

Methods For Monitoring Mule Deer Populations

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Table of Contents

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PREFACE

Because of their popularity and wide distribution, mule and black-tailed deer (collectively referred to as 'mule deer,' *Odocoileus hemionus*) are one of the most economically and socially important animals in western North America. In a 2006 survey of outdoor activities, the U. S. Fish and Wildlife Service (USFWS) reported nearly 3 million people hunted in the 19 western states (USFWS 2007). Although this included hunters who pursued other species, mule deer have traditionally been one of the most important game animals in the West. In 2006 alone, hunters were afield for almost 50 million days and spent more than $7 billion in local communities across the West on lodging, food, fuel, and hunting-related equipment.

Hunters have contributed millions of dollars through license fees and excise taxes that finance wildlife management and benefit countless wildlife species. These funds support wildlife management agencies, which manage all wildlife species, not just those that are hunted. Mule deer have been an important component of this conservation paradigm and thus are responsible for supporting a wide variety of conservation activities valued by the public, including law enforcement, habitat management and acquisition, and wildlife population management.

The social and economic effects of mule deer declines go far beyond hunters and wildlife management agencies. The mule deer is valued as an integral part of the western landscape by hunters and non-hunters alike. According to the 2006 USFWS survey, 25.6 million residents in 19 western states spent more than $15.5 billion that year "watching wildlife." The value of having abundant populations of such a charismatic species as mule deer cannot be overemphasized. Thus, social and economic impacts of mule deer declines are critical to all agencies that manage mule deer and the habitat they rely on.

To address the multitude of issues impacting recovery of mule deer populations, the Western Association of Fish and Wildlife Agencies (WAFWA) chartered the Mule Deer Working Group (MDWG). The MDWG, comprised of representatives of all WAFWA member agencies, was established to address 3 specific tasks:

1. Develop solutions to common mule deer management challenges;
2. Identify and prioritize cooperative research and management activities in the western states and provinces;
3. Increase communication between agencies and the public who are interested in mule deer, and among those in agencies, universities, and nongovernmental organizations who are interested in mule deer management.

Toward this end, the MDWG has developed strategies to improve mule deer management throughout western North America, and has effectively increased communication among mule deer managers, researchers, administrators, and the public. Increased communication among agency biologists will allow managers to face new resource challenges with the best available science and techniques. This ecoregional and range-wide approach to mule deer conservation will allow natural resource administrators to make science-based decisions and provide up-to-date and accurate information to their stakeholders.

At the first MDWG meeting, members identified issues considered important to mule deer management. These topics included short- and long-term changes to habitat, differences in mule deer ecology between ecoregions, changes to nutritional resources, effects of different hunting strategies, competition with elk (*Cervus elaphus*), inconsistent collection and analyses of data, deer-predator relationships, disease impacts, and interactions that occur among weather patterns and all these issues. The MDWG summarized these issues in a book entitled *Mule Deer Conservation: Issues and Management Strategies* in 2003 (deVos et al. 2003).

In 2004 the MDWG published the North American Mule Deer Conservation Plan (NAMDCP), with an accompanying MOU signed by state and federal agencies. The Plan provides goals, objectives, and strategies for implementing coordinated activities to benefit mule deer. The overall goal of the NAMDCP is *"Ecologically sustainable levels of black-tailed and mule deer throughout their range through habitat protection and management, improved communication, increased knowledge, and ecoregional-based decision making."*

Between 2006 and 2009 the MDWG published habitat management guidelines for all 7 North American ecoregions. These guidelines provide comprehensive recommendations to private, tribal, state, provincial, and federal land managers for maintaining and improving mule deer habitat.

The International Association of Fish and Wildlife Agencies (now the Association of Fish and Wildlife Agencies) joined with the Wildlife Management Institute, U. S. Geological Survey Cooperative Research Units Program, Nevada Department of Wildlife (NDOW), and the MDWG to conduct an Ungulate Survey and Data Management Workshop in 2005. One of the recommendations from that workshop was to develop a handbook of recommended methods for monitoring mule deer populations (Mason et al. 2006).

This handbook provides a comprehensive collection of population monitoring methods for mule deer. We recognize and emphasize that practical, political, and economic factors constrain the ability of wildlife agencies to make dramatic changes in their ongoing monitoring activities. However, when opportunities arise for evaluation or changes to mule deer population monitoring programs, this document should be used to guide that decision-making process.

All publications produced by the MDWG can be found at www.muledeerworkinggroup.com.

INTRODUCTION

This handbook has been prepared to aid mule deer managers and biologists in making better decisions and choices about their monitoring efforts, as well as understanding shortcomings of some commonly used data sets to avoid inappropriate inference. In today's world of escalating operating costs and reductions in human resources, it is absolutely necessary that practitioners select the most efficient monitoring techniques and implement them with the most effective strategies possible. Unfortunately, many monitoring programs simply repeat what has been done previously, with limited scholarly investigation into methods being used. Users of a technique should be aware of the weaknesses and assumptions and the likelihood of obtaining reliable knowledge, and realize the consequences of relying upon a poorly designed or executed method. Modern mule deer management must be based on monitoring methods that are statistically sound and designed to produce data necessary for decision makers.

Previous authors have presented inclusive summaries of mule deer and elk monitoring efforts employed by the western states and provinces (Rupp et al. 2000, Rabe et al. 2002, Carpenter et al. 2003). Carpenter (1998) discussed several obstacles that make regional or landscape-scale research and monitoring difficult. One key obstacle identified was that inter- and intra-agency variation in data collection and monitoring methodologies often complicated and confounded our ability to make inferences about trends and underlying causes of ungulate population fluctuations.

Mason et al. (2006) thoroughly described the need for increased rigor and coordination of monitoring activities for mule deer management in western North America. The authors stated "*We believe there are substantial needs and opportunities to improve interagency and intra-agency coordination and collaboration in data-collection and analysis and to implement better communication and data-sharing strategies.*"

One of the best ways to meet these needs would be a handbook thoroughly describing monitoring methods and their advantages and disadvantages. Mason et al. (2006) called for a steering committee to "*focus on the development of a handbook of recommended field-sampling and statistical-analysis methods for elk and deer population and habitat monitoring.*" As discussed in the Preface, the MDWG, which has a history of developing important and useful documents for mule deer research and management, was the obvious entity to produce a handbook addressing monitoring methods for mule deer. In the following chapters, authors present a variety of monitoring techniques and strategies, including assumptions, advantages, and disadvantages of each.

Obviously, there are a wide range of techniques from which to choose and observers must rigorously select the most appropriate technique for the purpose intended. A call for standardization does not mean doing exactly the same thing in all places. One methodology will not work in all applications. Nor do we imply methods presented here are the only ones to consider. As Mason et al. (2006) explained "*by standardization we do not imply that all states use the same survey system but, rather, that all states should at least employ fundamental* *statistical aspects of random sampling and bias corrections when developing new or applying previously published survey techniques.*"

Nor should this publication constrain further advancements in survey and monitoring approaches. On the contrary, we should aggressively and diligently work toward improvements in accuracy and precision when estimating population parameters, while at the same time reducing excessive costs. Plainly, the need for continued and increased interagency collaboration on monitoring remains as essential today as when the MDWG was first established in 1998.

A key first step is to clearly state and understand management objectives. This will facilitate selection of appropriate monitoring techniques and intensity or frequency of measurement. Sampling all areas in all years may not be necessary. Perhaps focusing monitoring effort on fewer areas, but with greater sampling intensity, will produce more rigorous data on which to base management decisions.

Another important consideration involving standardization is the process of data storage and retrieval. In this era of computers and software packages, all data gathered should be collected and stored with standardized formats so data can be retrieved quickly. One very important advantage of this is cost savings. Human resources spent laboring over poorly stored data result in delays and inaccuracies. The ability to share data among other observers and agencies should also lead to new insights and strengthen our ability to analyze regional trends. Mason et al. (2006) addressed data collection by calling for peer-reviewed, standardized data-collection methods, including a searchable relational database.

Monitoring wildlife populations is one of the most basic elements of wildlife management. Because conducting a census of an entire population is rarely feasible, sampling is required and standard elements of statistical theory must be understood and followed. For the monitoring effort to be useful, resulting estimates should be both accurate and precise. Accuracy is how close an estimated value is to the actual (true) value. Precision is how close the measured values are to each other. However, in practice achieving adequate levels of accuracy and precision may be very difficult.

Among mule deer managers, there is often a strong desire to maintain consistent data-collection methods and parameter estimation techniques over time so estimates are consistent with previous measures. Maintaining data continuity is a worthy goal, but historic approaches may not be the best choice, and continued collection of inappropriate data streams does nothing to promote sound management. However, managers may be able to maintain data continuity when an improved technique is adopted by applying the traditional approach simultaneously for a year or 2 and identifying relationships of new estimates to traditional values. Unfortunately, because many monitoring efforts are poorly designed or implemented, users have no or poor measures of accuracy or precision of resulting estimates. Monitoring efforts must be scientifically sound and applied within an appropriate sampling framework to be useful.

Too frequently, users discover data they worked hard to obtain are not suitable for rigorous statistical analyses. The best way to prevent this situation is to include an assessment of statistical needs in the design phase of the monitoring effort. Consultation with a statistician is an important first step. One key question to address early in a monitoring effort is "what is the power of the test?" The power of the test allows the observer to anticipate the level of sampling necessary to detect a desired difference. In other words, if a management action is designed to reduce the population by 10%, will your sampling intensity allow you to detect this amount of change if it actually occurs? If variability among samples is high, the number of samples required to detect the difference may be quite large.

In some situations, observers may conclude the number of samples required to detect a difference is too large for available resources. The observer then must decide to either increase the difference to be detected or wait until adequate resources are available to appropriately conduct monitoring. Either choice is better than going ahead with measurements only to conclude that, given substantial variability in the data, you cannot possibly determine whether the management action was successful.

This handbook is presented with the intent information contained within is pertinent to many monitoring tasks. The authors all worked under a common vision:

"Collecting and disseminating scientifically defensible and comparable mule deer population information to increase interagency coordination, collaboration, and management capabilities."

We hope you agree we hit the mark.

DEFINITIONS

Accuracy – How closely a sample-based estimate represents the true population.

Bias – A systematic difference between a sample-based estimate and true value.

Census – A complete count of all members of a population in a given area.

Count – Simple tabulation of deer observed in a given area. Counts do not include members of the population that occur in the area but are not detected.

Database – A usually large collection of logically related data organized so one can rapidly search and retrieve desired data.

Database, relational – A relational database contains multiple data tables consisting of different data with a shared attribute. Relationships between records in various tables are strictly defined; data can be accessed or reassembled in many ways without having to reorganize database tables.

Detectability – Probability that a member of a population in a given area will be observed.

Deterministic model - A mathematical representation based on known relationships among items or events with no randomness incorporated into input or output values. A particular model input will produce the same fixed output every time the model is run. See stochastic model.

Metadata – "Data about data." A description or documentation of other data managed within a database. May include descriptive information about the context, quality, condition, or characteristics of the data.

Online analytical processing (OLAP) – Procedure that uses a multidimensional data model ("multidimensional cube") to allow rapid execution of complex analytical and ad hoc queries (typically displayed as a new table on a web site) along any combination of dimensions.

Natality – Ratio of total live births to total population in a specific area and time frame; typically expressed as young/adult female/year.

Precision – Variability associated with an estimate (i.e., how much do estimates deviate from true values). Confidence intervals are a common way of expressing precision of an estimate.

Process variation – Inherent biological fluctuations in a characteristic or process. E.g., the variation in the unknown annual survival rate of a population.

Query – A request for information from a database. Database queries allow users to interactively interrogate a database, analyze data, and update the database. Many database systems require users to make requests for information in the form of stylized queries written in a specific language.

Sample bias – The tendency of a sample to exclude some members of the population and over-represent others.

Sampling frame – A mutually exclusive and all-inclusive list of members of the population to be sampled. E.g., all geographic subunits within a management zone, all wildlife agencies in WAFWA.

Sampling variation – Variability in an estimate due entirely to the way a parameter is sampled (how many and which units). May be measured by quantifying variation between different samples of the same size taken from the same population.

Sightability – Probability that a deer within an observer's field of view will be detected by the observer. Functional synonym of detectability.

Sightability model – Probability functions built from empirical data (typically aerial surveys) that provide an estimated probability of detection of a deer within the observer's field of view for any combination of environmental covariates included in a model. Covariates typically include group size, deer activity, snow cover, and vegetation cover. Sightability correction factors are usually developed based on detectability of radiomarked deer.

Simple random sampling – Drawing a subset of items from a population such that each item has an equal chance of being selected.

Spatially balanced random sampling – Method using hierarchical randomization whereby samples are approximately evenly spread across the spatial sampling frame to prevent clumping.

Spreadsheet – Computer application for data storage and manipulation. Information (data in text or numeric form, formulas, functions) are entered in cells in a row-column matrix and can be manipulated, analyzed, and displayed graphically.

Stochastic model – A mathematical representation which incorporates randomness in some input or output values such that model output is a probability distribution of potential values. See deterministic model.

Stratification – Separation of a population into more homogeneous (similar) sub-populations. Appropriate stratified sampling should reduce sampling variance, improve precision of estimates, and increase efficiency. To be valid, stratification needs to occur prior to data collection (i.e., not after collecting and summarizing observations).

Structured Query Language (SQL) – Database computer language designed for managing data in relational database management systems.

Survey design – A system used to select samples from a sampling frame (population). The design typically invokes a series of formal sampling constructs for the data collection scheme.

Visibility bias – Failure to observe all deer present (in a sampled area) during a survey.

MANAGEMENT OBJECTIVES

Mule deer are managed through a variety of hunt structures designed to attain one or more management objectives. Management objectives can be very simple (e.g., provide for a stated number of hunter days each year) or complex (e.g., provide for a specific buck:doe [B:D] ratio, a specific age structure in the harvest, or a specific level of hunter success). Management objectives are often not simply biological in nature, but rather are generally designed to attain a desired outcome for a specific customer segment. It is overly simplistic to state "hunters only want to hunt." Human dimensions research has demonstrated different segments of the hunting public pursue a wide range of experiences, including simply going afield, spending time with friends and family, seeing wildlife, or harvesting an older age class buck that meets some personal standard.

Management objectives adopted by wildlife management agencies are generally established through a public process that considers desires of hunters and other interested publics, biological limitations, and social values. Social values (best determined via human dimensions research) may include diverse aspects ranging from watchable wildlife interests to tolerance for agricultural damage. Many states and provinces establish broad objectives such as number of hunters afield and number of days they expect hunters to spend hunting. These are important considerations because objectives also factor into expected revenue projections agencies depend on for funding wildlife management activities. Beyond those considerations, hunting opportunity within management units is generally adjusted based on more specific management objectives that may include

1. Population trend.
2. Population abundance objectives (e.g., a specific estimated population with accompanying sex and age structure).
3. Buck:doe ratios (before or after the hunt, or both).
4. Estimated age structure of bucks in the population or age composition of bucks in the harvest.
5. Antler size or conformation of harvested bucks.
6. Number of deer harvested (by sex or age class).
7. Hunter effort or harvest rates (e.g., days afield, success rates, days/harvested deer); or
8. Fawn:doe (F:D) ratios.
9. Habitat condition.
10. Incidence of agricultural depredations or other conflicts.

Harvest and hunting opportunity objectives may be further subdivided among user groups (weapon types or hunter demographics such as youth hunts). Agencies routinely use multiple management objectives (Appendix A) to guide their season structures (which often incorporate multiple hunting seasons).

MONITORING STANDARDS

Monitoring of harvested populations is arguably one of the most important management activities conducted by agencies, but limited revenues preclude intensive monitoring for all or even a majority of populations within each state or province. Depending on intensity, harvest has the potential to influence most mule deer population parameters, including sex ratios, age structure, and abundance (Erickson et al. 2003). Not all populations of mule deer are managed in the same way, and certain population management strategies require more intensive monitoring of population demographics than others. Similarly, different components of the population have differing effects on population trends. For example, buck harvest has little effect on overall population trend, whereas even small changes in doe survival can greatly influence population trend (Bowden et al. 2000, Gaillard et al. 2000). However, adult doe survival shows much less annual variation than does production and survival of juveniles. Because of the high annual variation due to varying environmental influences, production and survival of juveniles accounts for the majority of the annual variation in population size (Gaillard et al. 2000). Consequently, juvenile:adult female ratios are the most common population demographic collected by agencies along with overall population trend. Conversely, despite high sensitivity of population trend to changes in adult female survival (Bowden et al. 2000, Gaillard et al. 2000), high costs of telemetry-based studies, limited agency budgets, and lack of annual variation relative to production and survival of juveniles and hence proportional contribution to population trend, monitoring of adult doe survival is usually undertaken only when needed, as when a decline in population size is indicated.

Monitoring intensity may be driven by both biological and socio-political needs. From a biological standpoint, greater monitoring effort is typically associated with management objectives that maximize buck harvest rates, or control populations with substantial female harvest. In these cases, managers need more information to avoid unintended consequences such as undesired population declines or very low B:D ratios. Conversely, conservative management approaches (e.g., light buck harvest rates used to achieve greater proportions of older age class bucks in the harvest) can be monitored less frequently or with less intensive methods because there is much less risk of creating those undesirable changes in the deer population. For example, in a situation where a management objective calls for a B:D ratio of 40:100, there is no meaningful biological consequence whether the ratio is 30:100 or 50:100. However, periodic assessment of population trend or size should be conducted because populations may be affected by factors other than harvest. Paradoxically, socio-political influences may override this logic and very intensive monitoring may be required to demonstrate a particular strategy is achieving conservative management objectives.

Population status also influences monitoring needs. Populations of small size and uncertain viability require more intensive monitoring than do larger populations under similar harvesting strategies because overharvest or environmental variation can quickly lead to extirpation of small populations. Conversely, populations near or above carrying capacity (*K*) because of inadequate female harvest may also require intensive monitoring (e.g., of deer health, body condition, or recruitment) to measure or demonstrate effects of overpopulation. Because harvesting is essentially a landscape-scale management manipulation for which demographic outcomes are not always known, harvest strategy is another criterion that influences monitoring decisions. Impacts of harvest strategies which are less understood require more intensive monitoring to provide rigorous data on impacts on abundance, sex ratios, and age structure. When possible, agencies should endeavor to understand impacts of harvest strategies through large-scale, experimental manipulation of harvest regulations over multiple areas. Such approaches have greatly clarified the critical components of population dynamics that need to be monitored (Gaillard et al. 2000).

Ideally, harvest strategies and monitoring intensity are linked with agency management objectives and corresponding population demographic variables or controlling processes (e.g., a certain population size will be controlled by female harvest, B:D ratio is controlled by both male and female harvest, and population age structure is controlled by both male and female harvest). Because each management objective helps define an appropriate harvest strategy, the more intensive the management objectives (in terms of population impacts), the more rigorous the degree of monitoring needed to assess responses of the population. Moreover, some harvest strategies may require intensive monitoring for certain objectives (e.g., abundance) but not others (e.g., buck age structure). The following outlines the most common types of harvest strategies employed by agencies and minimum recommended levels of monitoring (see also Table 1).

Doe Harvest Strategies

Independent of buck harvest strategy, does may be harvested at intensities ranging from no harvest to open-entry harvest (most often with some constraint such as primitive weapons, reduced season length or area, or participation limited to youth or senior hunters).

No or light antlerless harvest.— Minimal harvest of antlerless deer limits concerns for population size unless populations are small initially. Lack of substantial antlerless harvest usually assumes populations are well below ecological (i.e., resource-limited) carrying capacity, and thus deer health and antler development are not limited by intra-specific competition. However, if antlerless harvest is low or nonexistent because of socio-political influences, those assumptions may be invalid.

- Requires periodic trend assessment even with little anticipated impact on adult females because populations may change independent of female harvest rates.
- If female harvest is low, but populations are high relative to K, more frequent monitoring of trend or abundance, population productivity or recruitment, or body condition may be needed to demonstrate whether populations are performing poorly and increased female harvest may be beneficial.

Moderate to heavy antlerless harvest.— Includes increased harvest of adult females to control population size or provide increased recreational opportunities.

- Requires annual monitoring of population trend or periodic monitoring of population size to determine impacts of antlerless harvest.
- Requires annual monitoring of population productivity or recruitment to determine appropriate annual antlerless harvest levels. Ideally, monitoring would occur prior to antlerless harvest or account for doe harvest to avoid inflated F:D ratios due to large doe removal.

Buck Harvest Strategies

A variety of harvest criteria and intensities are used in buck management. These include both open-entry (i.e., any hunter can purchase a buck hunting license annually) and limited-entry (i.e., buck permits are available only to a limited number of applicants) systems. Even with limited-entry systems, harvest intensities can range from high buck harvest (total annual mortality rates >70%) to extremely limited (total annual mortality rates <30%). Harvest may also be limited in either system by other selective harvest criteria, such as a minimum or maximum number of antler points.

Very limited-entry buck management (i.e., mature-buck management).— These strategies often severely limit the number of hunters to keep buck harvest mortality rates very low (usually well under 0.50 and frequently <0.30) to produce high B:D ratios and an older age structure among bucks.

- Requires periodic monitoring of buck age structure or B:D ratios to assess success in meeting management objectives. In some cases it may be sufficient to simply monitor success through hunter satisfaction surveys. Socio-political interest may create a need for more intensive monitoring, such as annual assessments.

Limited-entry buck management.— These strategies limit hunter opportunity to reduce buck harvest and annual buck harvest mortality rates (usually to <0.50) and consequently increase B:D ratios and buck age structure. In rare cases, a few agencies have employed antler-point restrictions such as 3- or 4-point minimum strategies to increase escapement of younger bucks in limited-entry hunts (almost exclusively under socio-political influence).

- Requires periodic or annual monitoring of buck age structure or B:D ratios to assess success in meeting management objectives. In some cases it may be sufficient to simply monitor success through hunter satisfaction surveys. Socio-political interest may create a need for more intensive monitoring.
- Under minimum point regulations, periodic monitoring of buck survival rates may be necessary to identify or quantify rates of unlawful harvest (hunters mistakenly or intentionally kill sub-legal bucks that are not retrieved or accounted for in harvest estimates).

Open-entry buck harvest.— Open-entry includes strategies designed to maximize hunter opportunity by allowing all licensed hunters to hunt bucks. These strategies maximize buck harvest and consequently result in lower B:D ratios and a younger buck age structure than most limited-entry systems. Minimum antler-point restrictions are occasionally employed to reduce vulnerability of younger bucks and thus increase post-hunt B:D ratios. However, most increases in escapement of young bucks are usually attributable to voluntary non-participation by hunters, and focused effort on older bucks usually results in a younger or truncated age structure.

- Requires annual monitoring of B:D ratios and periodic monitoring of buck age structure to ensure objectives are met.
- Under minimum point regulations, periodic monitoring of buck survival rates may be necessary to identify or quantify rates of unlawful harvest.

Open-entry spike or 2-point maximum, limited-entry adult buck harvest criteria.— This strategy combines elements of mature-buck management and open-entry buck hunting to maintain high levels of recreation (through open-entry hunts for 1- or ≤2-point bucks) with restricted harvest of adult bucks to allow some escapement into older age classes. Because this strategy is critically dependent upon recruitment of yearling bucks to maintain yearling harvest and allow some escapement into older, lightly harvested, age classes, monitoring of population productivity and buck age structure is needed to determine whether recruitment and escapement of yearling bucks is sufficient to support the limited-entry adult buck harvest.

- Requires annual monitoring of buck age structure and B:D ratios.
- Requires annual monitoring of productivity or recruitment ratios.

Table 1. Recommended population parameters to monitor and frequency of monitoring needed relative to increasing harvest rates for most populations of mule deer. Very small populations of uncertain viability require more frequent and intensive monitoring than levels shown.

Population parameter	→ Increasing harvest rates →			
Harvest	A	A	A	A
Population trend	P	B	A	A
Sex and age composition	P	B	A	A
Population abundance		P	P	A[1]
Fawn survival	If concerns[2]	If concerns	If concerns	If concerns
Adult female survival	If concerns	If concerns	If concerns	If concerns
Examples				
Doe harvest	None	Light	Moderate	Heavy
Buck harvest	Very limited	Limited	Open entry	Open entry 2-pt + very limited adult

A = monitor annually; B = monitor every 2-3 yr; P = monitor at least once every 5 yr; If concerns = investigate if monitoring data suggest concerns over population health (e.g., trends indicate declining population, very low productivity or recruitment, etc.).

[1] If low density population; otherwise B.

[2] If population trend, abundance, or productivity rates show declining trends, agencies may choose to intensively investigate production and survival of juveniles, or adult survival. Most frequently, most annual variation in changes in abundance is driven by high annual variability in production and survival of juveniles (Gaillard et al. 2000), so this demographic should be evaluated first.

Monitoring intensity may vary from levels displayed in Table 1 based on monitoring approach. For example, agencies relying heavily on population modeling, rather than trend or abundance estimates, may need more information on fawn and doe survival rates to populate models. In some cases, managers may desire consecutive annual abundance estimates in order to estimate population rates of change.

PARAMETER ESTIMATION TECHNIQUES

Harvest

Estimating harvest and hunter success rates are major parts of managing mule deer populations. This information is needed to address biological and social aspects of mule deer management. Mule deer populations are difficult to estimate and mathematical models used by managers depend on accurate harvest mortality estimates (as well as other demographic data) to predict population numbers. Hunter success has social and biological importance and is an important factor in setting season structure and hunting opportunity. Many harvest survey methods are similar and only vary in how questions and replies are delivered; thus, many of these methods share limitations and biases. Minimally, hunters are asked to provide data about effort expended (hunter days); where they hunted (e.g., game management unit); and if successful, sex and antler size of harvested deer, harvest date and location, and weapon used.

For sample-based techniques, sample size requirements should be identified before surveys begin so adequate accuracy and precision are obtained. Mandatory harvest reporting, although appealing at first glance, likely never accounts for all harvest or harvest effort. Therefore, additional effort and cost is needed to estimate parameters for non-respondents. Some level of bias is common to all harvest estimation techniques and deer managers need to identify acceptable levels for their program. Carpenter (2000) presented a thorough review and summary of big game harvest surveys.

Web-based surveys.— Web-based surveys are becoming more popular with increased use of personal computers. The proportion of hunters using the Internet increased from 20% in 2001 to 34% in 2002 (Miller 2003). Use of Internet resources by hunters is likely much higher today.

Most agencies now have an online application process that can capture applicants' e-mail addresses. These addresses become a potential e-mail survey list. Utah recently conducted a mule deer hunter opinion survey to help in drafting a statewide mule deer management plan. In this example, e-mails were sent to a randomly selected subsample of all hunters who provided an e-mail address when applying for a permit. The e-mail asked hunters to log on to a web site and complete a survey. Response rate was moderate; only 47% of hunters contacted returned a usable survey after an initial invitation and 2 follow-up e-mails (A. Aoude, Utah Division of Wildlife Resources, unpublished data).

Many agencies have implemented, or are considering, mandatory harvest reporting and web-based surveys are the most cost-effective way to accomplish this for a large population of hunters. There has been little research published on the use of the Internet for conducting harvest surveys, but web-based surveys likely have the combined limitations of mail and phone survey methods. Shih and Fan (2008) found mail surveys usually generate greater response rates than web-based surveys. Kaplowitz et al. (2004) reported comparable response rates for mail and web-based surveys when advance notification preceded surveys, but they noted a significant difference in respondent age by survey type (mail solicited greater returns from older respondents). Given the current older age distribution of hunters, survey designers should be cognizant of this potential bias.

Advantages

- Reduced cost is the greatest advantage of web-based surveys, especially when conducted by agency staff (as opposed to outside contractors).
- E-mails are relatively inexpensive to send, regardless of sample size, and the primary cost is initial programming time (Lukacs 2007).
- Electronically collected information has less potential for transcription error.
- Web-based surveys provide surveyors more control through the use of text validation and logic rules, thus reducing occurrence of incomplete or incorrect answers.

Disadvantages

- Not all hunters have Internet access or use e-mail.
- Surveys may need to be designed for slow transmission speed (because users may access the Internet via a 56K modem) or small e-mail size limits. Therefore, large pictures or maps cannot be included. However, links to web sites that contain additional information can be provided in e-mails.
- E-mail addresses can change frequently.
- Return rates may be variable.

Assumptions

- The main assumption is those hunters who supply e-mail addresses or those who have Internet access are representative of the population of hunters.

Techniques

This survey method is more similar to mail surveys in its biases for response and non-response (see below).

Telephone surveys.— Telephone surveys are currently used by some agencies in the West to estimate harvest of big game species. Response and non-response bias seem to be reduced using this method (Steinert et al. 1994, Unsworth et al. 2002). Sampling designs similar to those used for mail surveys can be used. Random sampling or a complete census can be used depending on size of the hunter pool and return rate.

Advantages

- Allows you to continue calling randomly selected individuals until a predetermined number of samples is reached.
- Allows use of more complex questionnaires (Aney 1974).

Disadvantages

- Costs and non-contact rates for this method can be high (Aney 1974).
- Many people now have caller identification and may disregard calls from unknown sources. This development in technology will likely increase time and costs needed to obtain sufficient sample sizes.
- Caller identification may also exacerbate non-response bias.

Assumptions

- The main assumption is the sample truly reflects the entire population. This assumption is met if a random or systematic sampling scheme is used and if corrected for associated biases.

Techniques

Telephone surveys have been used as an effective way to almost eliminate non-response bias, because ability of the surveyor to contact a hunter was typically unrelated to the way that hunter would answer survey questions. However, this may no longer be the case with increased use of caller identification. Successful hunters may choose to take the call if they recognize caller identification information, whereas unsuccessful hunters may not (Lukacs 2007). Steinert et al. (1994) reported minimal response bias from a telephone survey (compared to previous check station results).

Sample size determination should be based on desired precision for specific groups of hunters (e.g., weapon type) or geographic areas (e.g., management unit). Protocols for operators should be identified in advance and applied rigorously (e.g., number of call backs, completion of all questions, level of data validation, whether surrogates can provide answers for targeted hunters, etc.).

Mail surveys.— Mail surveys have been used by many states and provinces to estimate harvest of big game species. This method can be effective when limitations are considered and correction factors are developed to deal with common sources of bias. There are 2 main sampling schemes when using this method: random sampling and a complete census. Random sampling is the most cost-effective method and can be used when the hunter pool is large and return rates are high. If return rates are low, you may need to conduct follow-up mailings or increase sample size to obtain a statistically valid sample to estimate harvest. However, simply increasing sample size will not solve problems associated with non-response bias. A complete census may be necessary for hunts that are limited to a few hunters or when sample size needed for adequate accuracy is a very large proportion of the entire population.

Advantages

- Likely to reach a large proportion of hunters (regardless of age, economic status, etc.).

Disadvantages

- More costly and labor intensive than Internet-based surveys.
- Potential for bias may be greater than with telephone surveys.
- Data entry from returned surveys can be time consuming and a source of error.
- Questionnaires need to be relatively short and simple.
- Some returned surveys are unusable because they are illegible, incomplete, or contain incorrect information.
- May require multiple contact letters to achieve adequate sample size, which may lengthen the time needed to generate estimates.

Assumptions

- The primary assumption is the sample truly reflects the entire population. This assumption is met if a random or systematic sampling scheme is used and if corrections for associated biases are applied.

Techniques

There are several potential sources of bias associated with mail surveys. Some sources are only applicable when multiple deer can be taken during the season (uncommon for mule deer). These include prestige bias (hunters claim a higher season bag), Type I-memory bias (memory failure causes hunters to overstate their bag by rounding up), and Type II-memory bias (hunters recall small numbers better than large numbers and tend to understate harvest due to large bag limits over a long season) (Geis and Taber 1963).

The 2 primary sources of bias that apply to big game are non-response and response bias (MacDonald and Dillman 1968). Non-response bias is a result of differences in hunting activity or success between respondents and non-respondents. You can correct for non-response bias by telephone sampling a sub-group of non-respondents to determine whether their responses differ significantly from those who responded by mail. If responses are significantly different, data gathered will help you create a correction factor to apply to the mail survey. Non-response bias generally declines with increasing return rates, but minimum response rates needed to avoid bias have not been established. Non-response bias in mail surveys can vary from minor (Atwood 1956, Smith 1959, Taylor et al. 2000) to substantial (Barker 1991). Thus non-response bias should be examined at least periodically.

Response bias is a result of respondents incorrectly reporting their hunting activity. Often the largest response biases come from prestige bias. The most common prestige bias is hunters reporting they have killed a deer when in reality they did not. MacDonald and Dillman (1968) found hunters overstated buck harvest by 6.0% and doe harvest by 11.1%. Other potential examples of prestige bias could include reports of greater body or antler size or points, or claiming harvest of a buck rather than a doe (primarily under either-sex bag limits). Correcting for prestige bias is difficult. One method to estimate and correct for this bias is to send surveys to hunters who were checked at check stations or other mandatory harvest check-ins, and compare survey data with known harvest or hunting activity (MacDonald and Dillman 1968, Steinert et al 1994). More recently, some western managers have identified intentional underreporting by buck mule deer hunters as a bias (M. Cox, NDOW, personal communication), presumably in response to limited eligibility for permits under limited-entry and preferential draw (point) systems.

Telephone and web-based reporting.— Telephone and web-based reports are currently used by some agencies to estimate harvest of big game species as part of either voluntary or mandatory systems. User-selected web or telephone reporting or questionnaires are likely to result in substantive non-response biases which cannot be assumed to equate to biases from mail or telephone surveys. Thus, to obtain statistically valid estimates, user-selected electronic reporting will regularly require follow-up surveys to estimate non-response bias. The apparent reduced financial costs of user-selected reporting should not be the sole determining factor in their use (Duda and Nobile 2010, Gigliotti 2011). Response rates, even when accompanied by incentives (rewards or penalties), are typically moderate and tend to deteriorate over time.

Advantages

- Provide real-time information during ongoing hunting seasons (more quickly than post-season surveys).
- Data can be used to validate other harvest estimation techniques or biases.
- Reduced costs because hunters do the reporting.
- Occurrence of incomplete or incorrect answers can be reduced through survey design (via text validation, logic rules, drop-down lists).

Disadvantages

- Harvest data will very likely be biased (even if reporting is mandatory, some hunters will not respond).
- Non-response bias surveys are usually required.
- Hunters must have access to either a telephone or the Internet.

Assumptions

- Self-reported harvest and hunting activity are representative of respective populations.
- Information provided by hunters is accurate.

Techniques

Hunters are provided with a telephone number or Internet address to report harvest information and hunting effort. Reporting can be either mandatory or voluntary. Telephone operators can be live or automated with differing costs associated with each. Upon completion of a valid report, hunters are typically provided a confirmation number to maintain proof of compliance (for law enforcement, meat processors, taxidermists, license agents, etc.).

Check stations.— Western states and provinces have historically used deer check stations more than they currently do; however, check stations can still provide valuable data about deer populations. Check stations are either required by law or voluntary. Value of harvest data collected at check stations largely depends on intensity of sampling. Even under mandatory check-in, harvest data will likely be biased because some hunters fail to comply. However, such data are often used to provide initial estimates of hunter success and harvest trend from year to year.

Advantages

- Provide real-time information during ongoing hunting seasons (more quickly than post-season surveys).
- Data can be used to validate other harvest estimation techniques or biases (e.g., by comparing known check station data from specific hunters to data collected later from the same hunters with a remote harvest survey).
- Allow for collection of biological measurements and samples (see Body Condition section), including sampling for diseases and parasites.

- Provide opportunities for hunters to interact with biologists, alleviate concerns, and dispel rumors.
- Provide opportunities to explain and promote programs or provide educational materials.
- Can serve as social gathering points for hunters.

Disadvantages

- Even when mandatory, harvest data will very likely be biased.
- Usually labor intensive and expensive.
- May expose staff to potentially dangerous situations.
- May require coordination with or permits from transportation agencies.
- May require specific signage or lighting.
- Mandatory check stations may not be lawful in some jurisdictions.

Assumptions

- Hunters and deer sampled at check stations are representative of the populations.

Techniques

States and provinces vary widely in their use of check stations to estimate harvest trends and evaluate hunting seasons. Nebraska requires all hunters to present harvested deer at a check station. Data collected from this effort allow managers to determine harvest trends for all deer management units. Arizona, Alberta, and California use check stations to obtain harvest information for much smaller areas, such as military bases, wildlife management areas, and wildlife refuges. Harvest data obtained through check stations can include species, sex, age, antler characteristics, success by permit or license type, hunter effort, location of kill, date of kill, and hunter demographics. Most western states and provinces do not use check stations for harvest analysis or population trend information because sampling is nonrandom and subject to potentially large, unknown biases. If unbiased check station estimates of harvest are desired, fishery-access-point survey methods can improve estimates (Unsworth et al. 2002).

Check stations can be operated by trained biologists or trained lay persons depending on data quality needs. If it is necessary to set up check stations at private business locations, operators are typically paid for their cooperation. This payment is usually negotiated prior to the season. Hunters should be provided information about locations of check stations with their licenses or with appropriate signage at local sites of voluntary check stations.

Trends in Population and Demographics

Population trend is the directional movement in relative abundance or other key parameters through time (sensu Skalski et al. 2005). Trend indices are measures that are presumed to correlate with population abundance (or other parameters); thus, trend indices may indicate whether a population has increased, declined, or remained stable over time, if certain assumptions are met. Trend indices are also sometimes used to infer magnitude of annual changes, and, if collected over multiple years, trend indices can also be analyzed to provide a quantitative estimate of magnitude of population change by linear or nonlinear modeling. Trend indices can be either direct (involve direct counts of deer) or indirect (involve counts of indirect evidence of deer presence, such as scat or tracks).

Despite widespread use of trend indices in wildlife management, there is much uncertainty regarding usefulness of these indices (Anderson 2001, Williams et al. 2001, Lancia et al. 2005), including debate as to whether they should be used at all (Anderson 2001, Williams et al. 2001). Also, statistical power of trend indices to detect an actual change in population abundance is often very low. Consequently, changes in population size often have to be quite large (e.g., halving or doubling of the population) to be detected by trend indices. Similarly, statistical theory underlying trend indices has received very little study (Skalski et al. 2005). Despite these questions, trend indices are frequently used, primarily because of cost-efficient application over large geographic areas and challenges involved in developing valid estimates of abundance.

Trend indices are most frequently used to index changes in population abundance, although they may also be used to index trends in age structure, adult sex ratios, or productivity or recruitment ratios. Whereas a great variety of trend indices exist (see below), the underlying assumption of all is there exists a homogenous (across time, habitats, etc.) and proportional relationship between a change in the trend index and a change in abundance or other population parameter. Thus, before using any trend index managers need to consider 3 key questions:

1. Does a change in abundance result in a change in the index?

2. What is the relationship between deer abundance and the index? Frequently, the relationship is assumed to be linear, but often is not.

3. Are the data for the index collected consistently over time and is the sampling representative of the population? Both of these must be true for a trend index to have any real relationship to abundance.

The primary problem with most trend indices is the relationship between the index and abundance has not been determined. Despite this, trend indices are often treated as if they accurately and precisely reflect population abundance even though such a relationship has not been demonstrated. Because of this uncertainty, trend indices are most correctly applied only to determine a relative (as opposed to absolute) change in abundance. A second important problem among trend indices is difficulty in meeting assumptions. Failure to meet explicit assumptions or apply methods to account for unmet assumptions may result in failure of an index to adequately reflect change in populations.

For most trend indices, the relationship between index and deer abundance is not only unknown, but also likely not consistent. Rather, it varies over time and among areas due to changes in environmental factors (season, habitat, weather, deer behavior, etc.), human influences (hunter behavior, differing observers, etc.), and sampling protocols (sampling effort, plots vs. belt transects, etc.). A variety of techniques are used to deal with this variation, which cause violation of the assumption of a homogenous and proportional relationship between abundance and the index. First, sampling strategies are frequently systematic or stratified random as opposed to purely random. These former sampling strategies attempt to account for vegetation type or other environmental attributes varying among survey areas or times. By blocking surveys according to these differences, the overall index should better represent the entire population.

Systematic or stratified random surveys are also often easier to implement than completely randomized designs, especially when surveys are associated with roads or trails which are not randomly located across the landscape. A potential negative effect of systematic sampling is you may not capture all of the environmental variation across the landscape due to your sampling not being random. However, this problem can be overcome by ensuring stratification (blocking) includes all relevant variables in the stratification (e.g., all habitats likely to be used by mule deer). A second way to deal with environmental variables that may affect the relationship between abundance and index includes standardization of survey methodology, which is most often used to account for weather and observer effects. Third, important environmental factors can be included and accounted for in models to relate abundance to the index under "constant" conditions.

Many trend indices (such as pellet-group counts, harvest-per-unit-effort, track surveys,) have been extrapolated to provide estimates of population abundance, creating considerable overlap between trend indices and abundance estimators. Methods most commonly used as abundance estimators require additional assumptions for extrapolation from index to abundance that is beyond this discussion of trend indices and will be covered in the Abundance and Density section.

Minimum aerial counts and classification.— A minimum count represents the absolute minimum number of deer known to be present in a given area (while recognizing an unknown proportion of the population was not seen or counted). Counts and classifications are frequently accomplished through helicopter or fixed-wing surveys; however, several other techniques (e.g., ground counts, spotlight counts, etc.) can also yield minimum counts (see next section). Counts are often standardized to effort, such as numbers seen per hour of flight time or miles of survey route.

Advantages

- Sample sizes obtained from aircraft, and thus minimum estimates, are usually much greater than from ground-based methods.
- Helicopter counts presumably provide more accurate counts and sex and age classification than do ground-based counts because of independence of roads, ability to observe deer in inaccessible areas, longer observation times, closer proximity to deer, and ability to herd deer to provide optimal viewing opportunities (however, observing undisturbed deer from the ground with enhanced optics also allows accurate classification). This may not be true if substantial vegetation cover significantly obscures deer or allows only "fleeting" glimpses of deer.
- A segment of the public strongly favors census and minimum counts over sample-based population estimation. Sample-based estimates are frequently called into question and dismissed by the public if they do not mirror perceptions.
- Provides an absolute minimum population estimate which is understood and accepted by the public (sampling techniques, statistical inference, and probability are poorly understood by many constituents).

Note: the last 2 bullets represent challenges to agencies in educating constituents about the value of sampled-based methods.

Disadvantages

- There are very few cases where mule deer census is possible. Radiomarking studies have shown even very intensive efforts covering 100% of an area fail to account for all individuals due to concealment or observer factors (Bartmann et al. 1986).
- Costs are high compared to most other indices.
- Cost for a census would be prohibitive except for small, mostly confined areas.
- Although presumed to be more accurate than ground-based methods, validation is lacking, particularly for fixed-wing aircraft.
- Significantly more hazardous for biologists than ground-based methods.
- Minimum counts are frequently smaller than annual harvests, causing the public to question survey data and permit allocations.
- Motion sickness or marginally skilled pilots can result in poor viewing opportunities and highly biased data (e.g., large proportions of groups flee to cover before classification).
- Relationship to true population size often unknown or uncertain.

Assumptions

- Census – all members of the population in a given area are detected and accurately counted.
- Minimum count – members of the population counted in a given area are representative of the actual population.
- If minimum counts collected across time, a consistent proportion of the population is counted.
- If population components are separated, sex and age classes are correctly identified.
- Detectability is similar across sex and age classes, or counts are conducted during biological periods where free intermixing occurs between target sex and age classes (Samuel et al. 1987, Bender 2006).

Techniques

Both population censuses and minimum counts are usually conducted from either helicopter or fixed-wing aircraft, with flight protocols (such as airspeed, altitude above ground level, and spacing of transect lines) and observer behavior (including number of observers, direction of observation, and width of transect lines observed) held constant among surveys. Because population census is seldom feasible for free-ranging deer, remote sensing techniques are being evaluated to increase efficiency and improve detection rates (Lancia et al. 2005). Experimental techniques that have been tried include use of aerial photographs to obtain counts of concentrated individuals or thermal imaging. Forward looking infrared (FLIR) sensing has been used for a variety of ungulates with limited success outside of smaller or enclosed areas (Dunn et al. 2002, Drake et al. 2005). Additionally, remotely operated vehicles (ROVs) are being explored as a means to decrease risks to biologists (K. Williams, U.S. Geological Survey, personal communication). However, remote methods seem to have limited applicability, particularly with respect to classification.

Minimum aerial counts are the most commonly used trend index for mule deer. Minimum counts are frequently converted to estimates of population abundance in 1 of 3 ways:

1. Correcting counts for different likelihoods of observing deer based on habitats.
2. Altering size of sampling units based on habitat (Bartmann et al. 1986, Freddy et al. 2004).
3. Assuming all deer along the aerial transect were seen and estimating the width of the transect using distance sampling methods to correct for varying detection probabilities based on habitat, transect width, or other variables.

(See Abundance and Density section for methods used for distance sampling and sightability models). Uncorrected aerial surveys flown with consistent flight protocols to ensure consistent and near total coverage of sampled areas are converted to deer observed/unit area or deer observed/hour to obtain a population index. Aerial counts for population trend, as contrasted with counts used solely for sex and age composition, usually have much more specific survey protocols, similar to those required for abundance estimators such as sightability models. Despite this, as with sightability models and similar methods, estimates will always be negatively biased because topography and other visual barriers will prevent complete observation of survey units.

Spotlight surveys and ground counts.— Spotlight surveys and ground counts are similar, with spotlight surveys representing a special case of ground surveys. Spotlight surveys are conducted at night when deer may be less reluctant to use open habitats or areas adjacent to roads (Harwell et al. 1979, Uno et al. 2006). Both spotlight surveys and ground counts are used to collect minimum count and herd composition data. Typically, routes are standardized, replicated, and usually conducted from motor vehicles (especially for spotlight surveys); ground counts may be conducted on foot or from horseback as well. Surveys can be based on continuous observation along a route or restricted to observation points. Distance sampling methods, including stratification by habitats, are occasionally used to extrapolate minimum counts to abundance estimates.

Advantages

- Easy to conduct, inexpensive compared to aerial surveys, and can cover large geographic areas.
- Produce F:D ratios similar to those from aerial surveys (Bender et al. 2003).

Disadvantages

- Roads do not occur randomly across the landscape and their location likely biases proximity of deer (e.g., may be along a riparian area).
- Buck age structure and sex ratio data likely biased because of poorer sighting conditions and behavior of bucks as compared to helicopter surveys.
- Detection probabilities vary with habitat conditions, weather, observers, disturbance, etc.
- Amount of traffic along trails or roads can affect proximity of deer.
- Sample sizes usually low compared to aerial surveys.

- Low light capability of optics influences results.
- May generate disturbance to adjacent human residents and frequent reports of illegal hunting.

Assumptions
- Sample is representative of the population.
- Index reflects changes in population size rather than changes in deer distribution or detectability.
- Roadsides or trailsides representative of area in general or non-changing over time, or surveys stratified by habitat.
- Deer are equally observable every time the survey is conducted (e.g., vegetation screening between seasons or years is not variable).
- Methods consistent among years and groups counted without error.
- Sex and age classes correctly identified and have similar detectability.
- Observers are equally skilled.
- Extrapolation to population size or density requires further assumptions outlined under distance sampling and sightability models in the Abundance and Density section.

Techniques
Methods used include horseback counts, hiking counts, and counts from motorized vehicles. Ground counts can involve riding, driving, or hiking along a route or between observation points. Surveyors move along a standard route, traveling from one location to another that provides a good vantage point for searching for deer. If using specific observation points, after spending a specified amount of time at an observation point, the observer moves farther along the survey route until the next observation point is reached. Survey data can be interpreted as minimum numbers counted, numbers observed/mile, or used as inputs into distance sampling models to estimate abundance.

Spotlight surveys are usually conducted in habitats that are representative of the unit or area being surveyed. They are conducted shortly after dark, when deer are active and may be less reluctant to use areas close to roads. A driver navigates a vehicle along a permanently established route, while an observer (or 2) shines a spotlight along the side of the route and records all deer seen and classifies deer by sex and age class. Typically, number of deer seen/mile of route serves as an index to deer abundance and sex and age composition provides trend information on population demographics. Data are occasionally used as inputs in distance sampling models. However, managers should recognize deer distribution is likely not independent of roads and a rigorous sampling approach is necessary.

For both ground and spotlight surveys, routes are usually repeated several times each year to account for variability in survey conditions and reduce the chance of an unusually high or low count being used to index population trend. Occasionally, the highest total among replicated surveys is used to index the population as it reflects the minimum number of individuals known to be present.

Harvest per unit effort (HPUE).— Harvest per unit effort scales total harvest by some estimate of hunter effort, most commonly number of hunters or number of hunter-days (i.e., the total number of days hunters actually spent hunting). As the estimate of effort becomes more refined (hunter-days instead of hunters), the trend estimate is considered more sensitive to changes in abundance.

Advantages

- Relatively easy and inexpensive to collect effort data through harvest surveys.
- Presumably more accurate than harvest uncorrected for effort.
- Strong empirical background in fisheries management.

Disadvantages

- Subject to response distortion biases present in social surveys.
- Vulnerable to changes in hunter behavior.
- Influenced by changes in deer vulnerability (e.g., weather conditions, road closures, hunter access, antler restrictions, allocation among weapon types, rutting behavior of bucks, etc.).
- High hunter densities may cause interference in harvest rate and bias HPUE estimates.
- Low hunter densities, limited-entry harvest strategies, and mature-buck management strategies can result in significant hunter selectivity and thus decouple any relationship between HPUE and deer density.

Assumptions

- Harvest and effort data are accurate and unbiased.
- Population closed during hunting season except for harvest removals.
- Probability of harvest constant during the season (can be corrected for differential vulnerability among areas).
- Harvest is proportional to population size.
- Effort measure is constant (i.e., hunters equally skilled).

Techniques

Harvest and effort data are most commonly collected from hunter surveys or check stations. The HPUE index, such as 0.05 deer harvested/hunter-day, is often used as a stand-alone trend index to compare changes within a management unit, and is considered to be more reflective of actual changes in population abundance than harvest alone because of the accounting for hunter effort (Roseberry and Woolf 1991). However, HPUE does not account for variation in harvest rates due to effects of weather or other factors that could impact harvest. Hence, running averages across multiple years are often used to reduce effects of annual variation in these factors. Comparisons among management units differing significantly in habitat is a problem, because HPUE reflects both abundance and vulnerability of deer, and vulnerability can change significantly with the amount of security cover. Roseberry and Woolf (1991) found some HPUE models to be very useful for monitoring white-tailed deer (*O. virginianus*) population trends based on harvest data.

Total harvest.— The simplest trend index is an estimate of total harvest. This index assumes encounters between hunters and deer, and thus harvest, increase as deer abundance increases and decline as abundance declines.

Advantages

- Data easily and frequently collected, primarily from surveys of hunter effort and harvest.

Disadvantages

- Annual variation in harvest estimates can be extremely high and thus provides limited inference for population trend.
- Vulnerability to harvest changes with changes in hunter behavior (e.g., regulation changes, equipment changes, etc.).
- Vulnerability to harvest changes with environmental conditions (e.g., weather conditions, changes in access, habitat changes, etc.).
- Harvest rate varies with hunter and deer density.
- Many potential sources of bias (response distortion) in hunter questionnaires, which are frequently not accounted for.
- Often estimated without variance, thus providing no basis for statistical inference.
- Often of poor or unknown accuracy.
- Generally more effective with very intensive buck harvest strategies such as open-entry seasons.

Assumptions

- Harvest data are accurate.
- Harvest is proportional to population size.
- There is no response or non-response bias if collected through hunter questionnaires.
- Harvest rate (proportion of population harvested) is constant among areas or time periods being compared.
- Population is closed during hunting season except for known harvest removals (e.g., no in-season migratory movements).

Techniques

Harvest data are most often collected via hunter surveys or, less commonly, hunter check stations (see Harvest estimation). If season length and other harvest regulations are the same among seasons, then total harvest alone is often used as a trend index within management units. Because of the substantial influence of habitat on deer vulnerability, total harvest should not be used as an index among dissimilar management units. As limitations on harvest increase relative to deer abundance (e.g., reducing hunter numbers through limited entry), value of harvest as an index declines (Fig. 1). Thus, because female harvest is often more limited, harvest indices are generally based on buck harvest. If season lengths vary, harvest may be modified to harvest/day or daily harvest modeled as a function of season length or numbers previously harvested, with the latter used to estimate population abundance (Davis and Winstead 1980, Lancia et al. 2005). Age-at-harvest data are used in many population reconstruction models (Williams et al. 2001, Gove et al. 2002, Skalski et al. 2005).

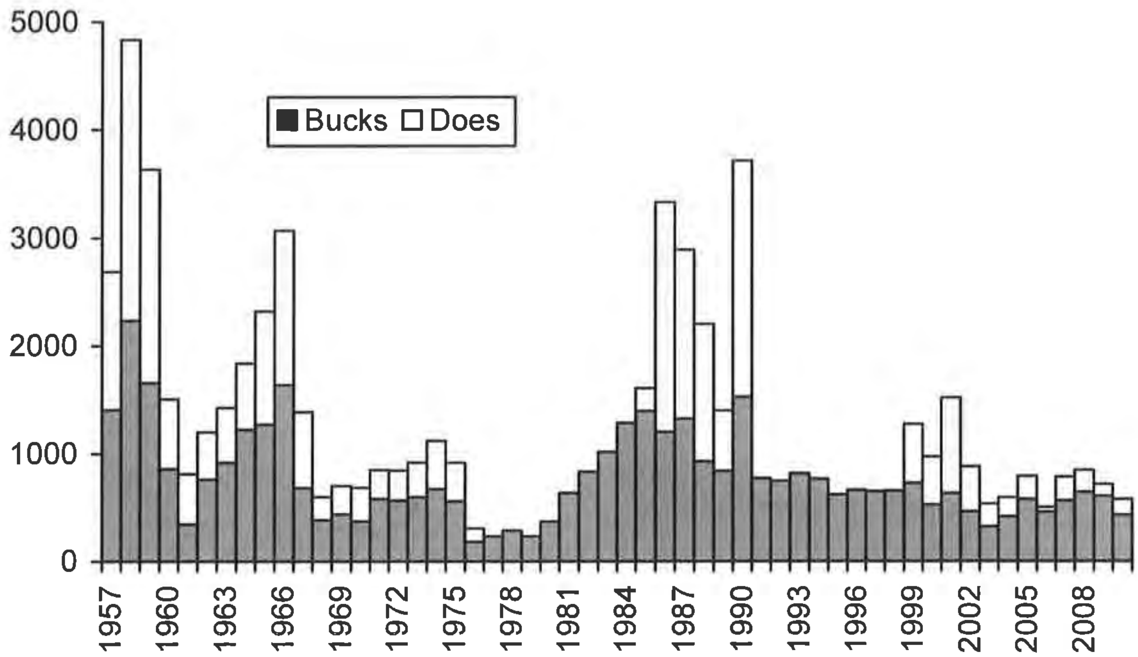

Figure 1. Estimated mule deer harvest, Kaibab Plateau, Arizona, 1957-2010. Limited-entry buck harvest since 1971 and erratic doe harvest severely limit the value of harvest as a population trend index for this area. Figure courtesy of Arizona Game and Fish Department (AGFD).

Track surveys.— Track surveys involve counting numbers of individual tracks or track sets that cross a road or trail, usually with direction of movement limited to 1 way to reduce double counting (McCaffery 1976). Surveys are usually conducted following clearing of roads or trails of old track sets by dragging or following snowfall that covers previous tracks. Data are used most commonly as a relative index or minimum count, but can be used to calculate densities (Overton 1969).

Advantages

- Simple to conduct, relatively inexpensive, and cover a large geographic area.
- May be used for preliminary sampling to implement a more robust method.

Disadvantages

- Limited rigorous validation.
- Difficulty in distinguishing among individuals or species if several ungulate species are present.
- Dependent on activity levels and movement patterns.
- Very dependent upon proper weather or substrate conditions for accurate counts.
- Multiple counts of the same individuals very likely.

- Mild weather conditions that minimize use of winter ranges in some years may result in unreliable data.
- Number of individuals may be indiscernible when deer travel in groups.

Assumptions

- Methods consistent among years and groups counted without error.
- Index reflects changes in population size rather than changes in deer distribution or activity levels.
- Extrapolation to population density requires further assumptions (Overton 1969).

Techniques

Tracks are most commonly counted along dirt or sand roads, which are dragged before counting, or during deer migrations, usually when leaving winter ranges. In the former, roads are dragged to obliterate any tracks that are present; then routes are revisited after some time period (often 1 week, assuming no disturbance to survey substrate, e.g., rain that washes away tracks, etc.) and number of track sets counted. The index is usually presented as number of track sets/mile if collected over the same amount of time annually, but can be converted into density by making several assumptions about deer movement patterns (Overton 1969).

For winter range counts, survey routes are established so they run essentially perpendicular to travel routes between winter and spring ranges. These survey routes are then counted periodically after the start of migration to spring ranges (WGFD 1982). Only deer tracks moving away from winter ranges are counted, with counts run after fresh snowfall or after dragging routes to clear existing tracks. The index in this case is usually presented as the minimum number of individuals counted or number of tracks/mile if routes are run for the same time period each year (usually the entire migration period).

Pellet counts.— Pellet group surveys involve counting the number of fecal pellet groups encountered in plots or belt transects. Mean number of groups can be used as a trend index or is occasionally converted to estimates of population size by integrating defecation rates and number of days indexed (Marques et al. 2001). Pellet group counts for population trend are most frequently conducted on winter ranges. Because habitats are not uniform and pellet group distribution depends on relative habitat use, pellet group transects are most often stratified among vegetation types (Neff 1968, Härkönen and Heikkilä 1999). For greatest accuracy, permanent transects that are cleared of old pellet groups after each survey should be used to eliminate confusion in aging pellet groups.

Advantages

- Easy to conduct, little equipment needed, can cover a large geographic area.
- Have been correlated with other trend indices including aerial counts and hunter observations (Härkönen and Heikkilä 1999).
- Can provide data on relative use of habitats (Leopold et al. 1984).

Disadvantages

- Power to detect trends frequently low, particularly for low density populations.
- Size and shape of plots (e.g., belt transects vs. circular plots) and sampling effort strongly affect results (Härkönen and Heikkilä 1999).
- Bias associated with inclusion or exclusion of groups lying along plot boundaries.
- Difficult to distinguish species in the field if several species of ungulate are present.
- More appropriate for areas of seasonal concentration such as winter ranges.
- Degradation of pellets varies in different environmental conditions and with populations of scavengers such as dung beetles.
- For abundance estimation, there is little validation of most commonly used daily defecation rates which undoubtedly vary with season, diet, etc.
- Labor intensive to conduct over large area.
- Potential for observer bias in aging pellet groups if transects not cleared after each counting.

Assumptions

- Methods consistent among years and groups counted without error.
- Index reflects changes in population size rather than changes in deer distribution, activity levels, or behavior.
- Extrapolation to population abundance requires further assumptions including 1) constant defecation rates, 2) exact knowledge of time of use in days, and 3) population density uniform throughout range.

Techniques

This method involves clearing permanent plots or belt transects of accumulated pellet groups and returning after a specified time period to count the number of new pellet groups. Number of pellet groups/unit area or transect serves as the index to abundance. Pellet group surveys are often used on winter ranges at the end of winter. Pellet group counts are commonly converted to densities by dividing by number of times a deer defecates/day and number of days plots were exposed. For example, if you assume a deer defecates 10 times/day and after 10 days you find 700 pellet groups/acre, it is assumed 7 deer were present (7 deer × 10 days × 10 pellet groups/day/deer) (Neff 1968, Härkönen and Heikkilä 1999). Although used as a trend index or abundance estimator, pellet group counts are usually more valuable in determining relative habitat use patterns (Neff 1968, Leopold et al. 1984, Härkönen and Heikkilä 1999).

Pellet group data are inherently non-normal in distribution, so more complex analysis techniques are useful in teasing out inferences. The negative binomial distribution (Bowden et al. 1969, White and Eberhardt 1980) is particularly useful for examining pellet group data.

Hunter observation surveys.— Hunter observation indices involve having hunters record the number, and occasionally sex and age classes, of deer seen during hunts. Because hunter numbers and effort can be extremely large and are confined to a relatively narrow time frame, numbers of animals seen and herd composition samples collected by hunters can be large and have been correlated with other independent estimates of population size, trend, and composition (Ericsson and Wallin 1999).

Advantages

- Tremendous number of person-days of effort with little cost to agencies.
- Extremely large sample sizes in some cases.
- Have been correlated with other trend indices and with aerial survey data (for other species).
- Provides hunting public with a sense of "ownership" of population data.
- Provides a method requiring little agency time to corroborate other trend indices.

Disadvantages

- Sensitive to response distortion biases of hunters.
- Untrained observers may not count or classify deer accurately
- Independence of observations unknown (but can be accounted for if double counts are assumed when constructing confidence intervals around ratio estimates).
- Detection of target species varies among habitats and thus changes in distribution may be confused with changes in population size unless stratified by habitat.
- Relationships between abundance and observation index vary among areas.
- Precision of estimates low or undefined.

Assumptions

- Numbers of deer observed and recorded without bias.
- Sex and age classification correctly identified and reported.
- Number of hunter-days is consistent or observations are standardized per hunter-day.
- Hunters equally skilled in detecting deer (for abundance trend only).

Techniques

Hunters are provided data forms and asked to record numbers and sex and age classes of deer seen during their hunts and number of days (or similar measure of effort) hunted. Data are usually converted to a standard measure of effort such as deer seen/hunter-day for the trend index (Ericsson and Wallin 1999). Data for deer seen/hunter-day are usually compared within an area between years to estimate annual rate of change in population size. Because ability to detect (observe) deer varies among habitats, this index (as well as all other direct indices) should not be used to compare management units differing in habitats. Although infrequently used for mule deer, estimates of annual population change and calf:cow ratios obtained from this method have been shown to be similar to aerial survey counts for moose (*Alces alces*, Ericsson and Wallin 1999). These data are much less expensive to collect, suggesting this method may provide a useable index for mule deer management with further development of the technique.

Abundance and Density

Estimates of abundance or density (i.e., abundance per unit area) over broad geographical areas are often desired to empirically manage mule deer populations. Because mule deer are widespread and often inconspicuous, total counts have proven to be impractical, even when localized and in fairly open habitats. As a result, statistically-based sampling methods offer the only realistic way to estimate mule deer numbers on the scale of most management units. Cover and terrain often make deer inconspicuous; therefore, methods used to estimate abundance must account for incomplete detectability of deer in the sampling areas. Based on studies with radiomarked deer and counts of known numbers of deer in large enclosures, detectability is often considerably less than 100% even when the census effort is very intensive (McCullough 1979, Bartmann et al. 1986, Beringer et al. 1998). To help address problems related to widespread distribution and incomplete detectability, abundance and density estimates are usually made during winter when mule deer are more concentrated and more visible against snow cover. Estimates of mule deer abundance and density are further complicated because numbers are dynamic and populations are seldom geographically discrete. Deer are born, die, immigrate, emigrate, and frequently move back and forth across management unit or sampling frame boundaries. Methods for estimating abundance and density must take into account whether the population of interest is assumed to be geographically and demographically closed or open during the sampling period.

Population modeling offers an alternative to sample-based population estimation by using demographic parameters such as harvest mortality, sex and age ratios, and survival estimates to predict population numbers. Unfortunately, the public can sometimes be highly skeptical of credible model-based population estimates that do not conform to their perceptions because actual deer are not being counted (Freddy et al. 2004).

Sample-based Methods

Distance sampling.— Distance sampling can be used to estimate number of deer within a fixed distance away from a line or from a point based on distribution of decreasing detection probabilities as distance increases (i.e., deer farther away are harder to see) (Buckland et al. 2001, 2004; Thomas et al. 2010). Distribution of detection probabilities can be estimated based on the assumptions that 1) all deer on the line of travel will be detected or accurately estimated, 2) detection will decrease as distance from the line increases, and 3) deer distribution is independent of sampling design. Population size can be extrapolated from numbers of deer in a sample of line transects or plots that can be stratified by deer density or habitat. Distance sampling for ungulates is usually done along transects from a fixed-wing airplane or helicopter and has been used primarily for species such as pronghorn (*Antilocapra americana*) that occur in relatively flat, open habitats (Johnson et al. 1991, Guenzel 1997, Whittaker et al. 2003, Lukacs 2009). A similar method has been evaluated for mule deer in pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) habitat in a large enclosure with relatively small bias found (White et al. 1989). Use of distance sampling for roadside surveys or spotlight surveys is not recommended because the assumption that deer distribution is independent of transect location is unlikely to be valid when roads are used as transects. Violating the assumption of independent distribution can result in highly biased estimates.

Advantages

- Robust method with relatively few constraining assumptions compared to other methods.

- Provides a probabilistic estimate that accounts for detectability and does not require marked deer if all deer on the line of travel are assumed to be 100% detectable.
- Can be relatively inexpensive if used in fairly open and flat areas where use of fixed-wing aircraft is practical.
- Relatively easy to design and conduct using geographic information system (GIS) software and global positioning system (GPS) units.
- Can be applied to ground mortality transects as well as aerial population surveys.

Disadvantages

- Only realistic in open areas with little terrain relief where deer close to the line of travel are almost 100% detectable. For mule deer, this method would probably be limited to habitats such as upland plains, open agricultural areas, or perhaps some sagebrush (*Artemisia tridentata*)-steppe winter ranges. Even in these habitats, a helicopter would often be required as the sighting platform to achieve acceptable detectability.
- Confidence intervals can be wide (e.g., 95% CI > ±25%) when there is high variability in deer densities between transects within a stratum.
- Dependent on assigning individual deer or clusters of deer to the correct distance interval or accurately determining distance from the line of travel. This can sometimes be problematic, especially with high deer densities.
- Observer fatigue can become an issue during prolonged surveys.
- Can be relatively expensive if a helicopter is used.

Assumptions

- All deer on the line of travel are detected or accurately estimated.
- Distances are accurately measured or deer are recorded in the correct distance band.
- Detection probability decreases as distance from the line of travel increases.
- Deer distribution is not related to transect distribution.
- All deer within a detected group are accurately counted (if group or cluster is the sampling unit). If the individual is the sampling unit, this assumption no longer applies.
- Deer are detected in their original position before any movement related to the survey effort. Deer are not recounted during the survey.

Techniques

Aerial distance sampling for ungulates usually involves

1. Establishing a set of lines of known length across the area of interest that delineate centerlines of a set of fixed-width transects.
2. Flying along each line while maintaining height above ground level (AGL) as constant as possible (with fixed-wing aircraft the flight path may be offset from the line to compensate for the blind spot directly below the aircraft).
3. Accurately assigning individual deer or clusters of deer to fixed-width bands that delineate specific distance intervals away from and perpendicular to the line of travel.

Transects are usually parallel and systematically spaced across the area of interest with a random starting point. Stratification based on deer density or habitat can be used to help reduce variance. As an alternative to 2 and 3 above, actual distances of deer or clusters perpendicular to the line can be determined using a laser range finder and the sighting angle. However, for species such as mule deer that often occur in numerous, small groups, use of distance intervals rather than actual distances is a much more practical method (Guenzel 1997). Fortunately, little bias usually results from assigning deer to distance intervals as opposed to measuring actual distances (Thomas et al. 2010). Distance intervals can be delineated using strut markers (fixed-wing aircraft) or window markers (helicopters) that have been calibrated for a specific AGL (e.g., usually between 75-300 ft [25-100 m] depending on aircraft type, cover, and terrain) to demarcate distance intervals perpendicular to the line of travel using a specific eye position (Guenzel 1997). The AGL can be accurately measured using a digital radar altimeter or a laser rangefinder mounted on the belly of the aircraft. For each observation, AGL should be automatically saved to a computer to allow distance measurements to be corrected, if necessary, for actual AGL. Effective transect width (i.e., truncation limits) and width of distance intervals depend on predicted detectability (i.e., narrower widths are used as detectability decreases). Four or 5 distance intervals are typically used to estimate an adequate detection function.

Program DISTANCE was specifically designed to estimate population size from distance sampling data (Thomas et al. 2010). This software

1. Models detection probabilities as a function of distance from the line of travel when 100% detectability is assumed on the line of travel.
2. Allows covariates (e.g., cluster size, habitat, weather conditions, etc.) to be considered in the distance model.
3. Allows mark-recapture data to be incorporated when detection is <100% on the line of travel.

When detection on the line of travel is not certain, simultaneous double counts using 2 independent observers or a sample of radiomarked deer can be used to correct for incomplete detectability (e.g., Kissling et al. 2006). See mark-resight and mark-recapture for more discussion on simultaneous double counting methods. Cluster size bias can occur using distance sampling because, as distance from the line increases, deer in large groups (i.e., clusters) are more easily detected than individual deer or small clusters. Program DISTANCE can correct for cluster bias using regression methods based on the number of deer counted in each cluster relative to their distance from the line.

Strip-transect sampling.— In areas where cover and terrain make distance sampling infeasible, fixed-width (strip) transect sampling can still be used to obtain a minimum count that can be adjusted using generic or survey-specific detection rates based on detectability of marked deer. Population size can then be extrapolated from the sample of strip transects corrected for detection rates. Helicopter line transects have been evaluated for mule deer and white-tailed deer with satisfactory results (White et al. 1989, Beringer et al. 1998). However, Freddy (1991) compared quadrat sampling to transect sampling for mule deer in sagebrush habitat and reported estimates >200% larger when transects and detection probabilities were used compared to quadrat sampling with a generic sightability correction, leaving doubt as to which method was more biased.

Advantages

- Allows transect sampling to be used in some situations where distance sampling is not feasible because of low detectability or terrain.
- Transect sampling designs are relatively easy to lay out with GIS and are easy to fly with GPS units.
- Provides a probabilistic estimate of the number of detectable deer that can be adjusted using detection probabilities.
- Usually does not require handling and marking of deer.

Disadvantages

- Detection probabilities often must be determined using a sample of radiomarked deer which can substantially add to costs. Depending on diversity of habitats being sampled, different detection probabilities may be required for different strata, transects, and even within individual transects.
- Relatively expensive because an aircraft is required and considerable flying may be needed depending on size of the sampling frame, deer distribution, cover, and desired precision. In areas with substantial cover and terrain, transect widths must be reduced.

Assumptions

- Transect width can accurately be determined and deer can be correctly identified as being in or out of the transect.
- Deer do not move out of a transect before detection and they are not recounted in subsequent transects.
- Detection rate estimates are unbiased and accurately represent actual detection rates. Marked deer have the same probability of being sighted as unmarked deer.

Techniques

Transect counts for mule deer are usually flown using a helicopter. Transect width can be delineated by tape on the windows that has been calibrated for a specific AGL. Unlike distance sampling, there is no need to demarcate distance intervals. Similar to distance sampling, sample transects usually run parallel, are evenly spaced across the area to be surveyed, and have a random starting point. Stratification based on deer density or habitat can be used to help reduce variance. Habitat should be fairly homogenous within each stratum to minimize the number of unique detection probabilities required.

Plot sampling using quadrats.— Quadrat sampling is similar to transect sampling except population size is extrapolated from a sample of randomly selected polygons that are often square and, prior to GPS technology, usually laid out using cadastral coordinates (e.g., section lines). Small (i.e., usually ≤1 mi^2 [2.6 km^2]), intensively surveyed quadrats are used as sampling units in an attempt to improve detectability. Quadrats are usually stratified based on habitat or prior deer density information. Sampling designs can include random, random spatially balanced, and hybrid census and sampling combinations. Quadrat sampling methods for mule deer were described by Kufeld et al. (1980) and Bartmann et al. (1986).

Advantages
- Provides a probabilistic estimate of number of detectable deer.
- Fairly straightforward design that can be laid out with GIS (prior knowledge of deer distribution is very helpful) and flown using GPS.
- Does not require handling and marking of deer.

Disadvantages
- Relatively expensive because a helicopter is usually required and considerable flying may be needed depending on size of the sampling frame, deer distribution, and desired precision.
- Confidence intervals can be wide (e.g., 95% CI > ±25%) irrespective of sample size, especially when deer occur in an unpredictable or clumped distribution.
- Does not include an inherent detectability correction, so actual population size is unknown. Generic sightability factors can be used to adjust the population estimate, but they can be of questionable value because a number of variables can influence sightability (e.g., group size, cover, terrain, snow cover, time of day).
- When deer densities are high, it can be difficult to keep track of deer that have already been counted.
- Deer may move out of a quadrat in response to the aircraft before they are counted.

Assumptions
- Each quadrat within a stratum that may contain deer has a known (often equal) probability of being selected for sampling.
- Deer are detected at a fairly high rate (e.g., >60%), are not double counted, are not erroneously accounted for by being forced into or out of a quadrat, and are accurately identified as being in or out of a quadrat when close to the perimeter.
- Generic sightability factors accurately represent actual detection probabilities.

Techniques
Quadrat methods often use sampling polygons with small areas (0.25-1 mi^2 [0.65-2.6 km^2]) to increase detection rates. Smaller quadrats are used in areas with considerable cover such as pinyon-juniper woodlands, whereas larger quadrats can be used in more open areas such as sagebrush-steppe. Using similar-sized quadrats tends to decrease among-quadrat variation, but is not required. In the past, sampling designs were usually based on cadastral section lines, but GIS and GPS units have greatly increased design flexibility. Use of GPS units has also made quadrat sampling much more practical because quadrats can be accurately flown without landmarks. Stratification can be useful for increasing precision and for optimally allocating sampling effort based on expected deer density. When there is sufficient prior knowledge of deer distribution, stratification can most effectively be achieved on a quadrat by quadrat basis rather than by geographical area.

Quadrat methods for estimating mule deer numbers can require considerable helicopter time (e.g., 20-40 hours is typical for management units in western CO, Kufeld et al. 1980). Extensive amounts of flying can cause observer fatigue and result in prolonged surveys because of weather and conflicting work assignments. Use of multiple helicopters and crews is recommended to finish counts in a timely manner under preferred conditions when snow cover is present. Quadrats should be flown by first following the perimeter to identify deer close to the boundary as being in or out. The interior of the quadrat should then be flown with sufficient intensity to count all detectable deer.

Even though the quadrat method attempts to maximize detectability compared to sampling using transects or larger area units, unknown detectability remains an obvious issue. Survey-specific detection probabilities could be determined by including a sample of radiomarked deer or using sightability covariates (see area sampling using sightability models), but the small size of the quadrats and high cost of the quadrat method make this impractical in many cases. In lieu of specific detection probabilities, generic sightability factors developed using radiocollared deer in similar habitats have been used to adjust quadrat population estimates. In Colorado, a sightability factor of 0.67 is typically used for quadrats in pinyon-juniper winter range and 0.75 is used for sagebrush-steppe (Bartmann et al. 1986; Colorado Division of Wildlife [CDOW], unpublished data). For generic sightability factors to be applicable, quadrats should be flown with as many variables as possible similar to those that occurred when sightability factors were developed (e.g., high percentage of snow cover, same number of observers, quadrats with the same area, etc.). However, even when effort is made to keep survey protocols as consistent as possible, the validity of using generic sightability factors can be questionable because of the number of variables that can affect detectability (e.g., group size, deer activity, time of day, cloud cover, type of helicopter, experience of observers, etc.).

Plot sampling using sightability models.— This method is similar to quadrat sampling except that 1) it includes a model developed using logistic regression methods to account for undetected deer based on a variety of sightability covariates, 2) size of sampling units can be considerably larger than those typically used for quadrat sampling, and 3) sample unit boundaries can be based on terrain features such as drainages instead of cadastral units or GPS coordinates (Ackerman 1988, Samuel et al. 1987, Freddy et al. 2004). A sightability model is developed for a specific survey intensity (i.e., survey time at a given elevation and airspeed per sampling unit area) by relating detectability of radiomarked deer to variables such as habitat, group size, deer activity, screening cover, terrain, snow cover, type of helicopter, and observer experience. Sightability models account for a more comprehensive set of detectability variables than generic sightability factors often used with intense quadrat sampling and allow the contribution that each variable makes to detectability to be evaluated using a stepwise approach. Once the sightability model is developed for a specific survey intensity, covariates supplant the need for determining detection probabilities using radiocollared deer. Even when survey intensity is kept relatively constant, sampling units should be similar in size to help eliminate variables such as increased observer fatigue when larger units are surveyed. Population size can be extrapolated from a set of representative sampling units.

Advantages

- Provides a probabilistic population estimate that includes a sightability correction.
- Once established, sightability covariates are easier and less expensive to measure than detection probabilities.
- Larger sampling units can be flown than with quadrat sampling as long as the sightability model was developed using sampling units similar in size to those being flown and sampling intensity is consistent.
- Larger sampling units are usually less affected by some potential sources of error than small quadrats (e.g., pushing deer out of the sample unit before they are detected, determining whether a deer is in or out of the sample unit, double counting the same deer when densities are high).
- Stratified random sampling of sample units produces precise estimates for lowest costs.

Disadvantages

- High initial costs to develop sightability models. Radiomarked deer must be used to develop different sightability functions for a wide variety of habitats and conditions.
- Relatively high ongoing costs due to extensive helicopter time required to conduct surveys on a management unit basis.
- A sightability model only applies to the specific conditions for which it was developed. Transferability of sightability models to habitats, survey intensities, and conditions different than those used to develop the models is not recommended and could result in highly biased results.
- Variance is likely to increase as detectability decreases.
- Population size can be underestimated if all deer in detected groups are not accurately counted (Cogan and Diefenbach 1998).
- Sampling units based on geographical features such as drainages may not be random, but drawing sampling units under stratified random sampling produces unbiased estimates.

Assumptions

- Probability of detecting deer is >0 and detectability can accurately be predicted using sightability covariates under a variety of circumstances (i.e., model captures all significant variation in sighting probabilities where it will be used).
- Sampling units are representative of the overall sampling frame and those sampling units are analogous to randomly distributed units.
- Deer in detected groups are accurately counted.

Techniques

Unlike quadrat methods that rely on small sampling units to increase sightability, use of sightability covariates allows sampling units to be larger and less intensively flown as long as applicable models have been developed. Sampling units are often defined based on geographical features such as drainages instead of constant-sized quadrats. Similar to quadrat and transect methods, precision of population estimates using sightability models can often be increased by stratifying the sample area by habitat and deer density. Ideally, sampling units should be selected at random or spatially balanced. However, when terrain features such as drainages are to be used as sample units, sample units should be selected to be as representative as possible of each stratum. Population size can be extrapolated from a set of representative sampling units. Sampling units may be stratified according to deer density, thereby reducing variability of a population estimate. All deer in detected groups must be accurately counted to avoid underestimating population size (Cogan and Diefenbach 1998). Sightability survey techniques were described in detail by Unsworth et al. (1994, 1999*a*).

Mark-resight and mark-recapture.— Mark-recapture methods use the ratio of marked (i.e., identifiable) to unmarked deer in population samples to estimate population size (Thompson et al. 1998). The population of interest must be defined in time and space and identified as being geographically and demographically closed or open. Basic mark-recapture models include the Petersen or Lincoln Index (Caughley 1977) for closed populations and the Jolly-Seber Model (Jolly 1965, Seber 1982) for open populations. These basic models have limited practical value because the assumptions required are usually violated when applied to field situations. To address the need for more practical assumptions, a variety of more complex and flexible mark-recapture models have been developed that often require computer-assisted solutions (i.e., no closed form estimator is available). The programs MARK and NOREMARK have been specifically developed for this purpose (White 1996, White and Burnham 1999).

More traditional mark-recapture methods are usually based on sampling without replacement whereby the method of recapture (i.e., being caught in a trap) effectively prevents an individual from being counted more than once per sampling occasion. Although these methods can be very useful for small, inconspicuous, or furtive species, actual recapture is seldom feasible or desirable for more conspicuous large mammals such as deer. As a result, mark-recapture methods that use resighting, with or without replacement, instead of recapture have been developed for more conspicuous species. These mark-resight methods allow relatively non-invasive monitoring instead of actual recapture and subsequent marking of unmarked deer, thereby reducing stress on the deer and costs.

Mark-resight methods have been used to effectively estimate localized mule deer numbers (Bartmann et al. 1987, Wolfe et al. 2004) and newer mark-resight models that incorporate maximum likelihood have improved this method and its potential application to mule deer (McClintock et al. 2009*a*, *b*). Unfortunately, mark-resight methods may not be practical for estimating deer abundance on a large scale (e.g., management unit) because of the cost and time required to mark adequate numbers of deer and conduct resighting surveys. As an alternative, quasi mark-resight approaches have been developed that use mark-resight data to calculate correction factors (i.e., detection probabilities) for incomplete counts (Bartmann et al. 1986, Mackie et al. 1998) or that use simultaneous double-counting to obviate the need for marking deer (Magnusson et al. 1978, Potvin and Breton 2005).

Advantages

- Usually considered one of the most reliable methods for estimating abundance of wildlife populations when sample sizes are adequate and assumptions are not critically violated.
- Unlike most other sampling methods, mark-resight methods explicitly account for detectability (even deer with essentially no detectability).
- Multiple resighting surveys (aerial or ground) can be done over time to increase precision and allow modeling of individual heterogeneity in detection probabilities among individual deer (Bowden et al. 1984, Bowden and Kufeld 1995, McClintock et al. 2009*a*, *b*).
- Provides a probabilistic estimate of population size and, with some more advanced models, allows some demographic parameters to be estimated.
- Can be applied using a wide variety of distinct marks (e.g., tags, collars, radio transmitters, paint, DNA, radioisotopes, physical characteristics, simultaneous duplicate counts) and resight methods (e.g., motion-triggered infrared cameras, hair snags, pit tag scanners, hunter harvest).

Disadvantages

- Can be expensive and labor intensive to achieve an adequate sample of marked deer, ensure marks are available for resighting, and conduct resighting surveys.
- Usually not practical over a large geographical area with a widely distributed species such as mule deer.
- Although the precision of mark-resight estimates is determined by a variety of factors (e.g., number of marks, detection probabilities, number of resight occasions), confidence intervals can be wide (e.g., 95% CI > ±25% for practical applications.
- Dependent on a variety of assumptions (see below), that if violated, can result in spurious results. Methods with less restrictive assumptions may result in reduced precision and accuracy.
- Marked deer may become conditioned to avoid resighting.
- Some quasi mark-resight methods such as simultaneous double-counts can be much less reliable and inherently biased because of individual deer heterogeneity.

Assumptions (Assumptions vary depending on the estimator being used [White 1996]). Basic assumptions include

- Population in the area of interest is to a large extent geographically and demographically closed unless gain and loss are equal or can be reliably estimated.
- Each deer in the population has an equal probability of being marked and marks are distributed randomly or systematically throughout the population of interest.
- Number of marks available for resighting in the sampling area is known or can be reliably estimated.
- Each deer in the population, marked or unmarked, has an equal probability of being sighted or individual sighting probabilities (i.e., resighting heterogeneity) can be estimated.
- Marks are retained during the resight sampling period.
- Deer are correctly identified as being marked or unmarked when sighted.

Techniques

Most mark-resight population estimates of wild ungulates use radiomarked animals. Radiomarks have the advantages of allowing confirmation of the number of marked deer available for resighting within the area of interest and identification of individual deer. Radiomarks have some disadvantages however (e.g., deer usually need to be captured to attached radios, equipment is expensive, radios can fail). In lieu of radiomarks, a variety of other marks have been used with mixed success for deer including ear tags, neck bands, a variety of temporary marks (e.g., paint balls, Pauley and Crenshaw 2006), and external features such as antler characteristics (Jacobson et al. 1997). Regardless of the marking method, marked deer should not be more or less visible than unmarked deer (e.g., fluorescent orange neck bands could make marked deer stand out more than unmarked deer). Nor should the marking method influence the resighting probability of marked versus unmarked deer (e.g., deer captured and marked using helicopter netgunning may avoid a helicopter more than unmarked deer during resighting surveys). Marks can be generic or individually identifiable. The latter has the advantage of allowing estimation of individual detection probabilities which can greatly improve some models.

Collection of DNA from scat or hair has become an increasingly popular method for identifying individual animals in mark-recapture studies. Use of DNA has the major advantages that deer do not need to be handled for marking, sampling is non-invasive and relatively easy, and the technique can be applied to situations where sighting surveys are not feasible (e.g., densely vegetated habitats or furtive species). Potential downsides include genotyping errors and variable relationships between the DNA source (e.g., fecal pellets) and the deer. Brinkman et al. (2011) used DNA from fecal pellets to estimate free-ranging Sitka black-tailed deer (*O. h. sitkensis*) abundance using the Huggins closed model in Program MARK.

Model choice should be carefully considered before beginning mark-resight surveys because different models are based on different assumptions. Mark-resight models that have been used over the years include the joint hypergeometric estimator (JHE, Bartmann et al. 1987), Bowden's estimator (Bowden 1993, Bowden and Kufeld 1995), and the beta-binomial estimator (McClintock et al. 2006). Bowden's estimator has been one of the most useful mark-resight models for deer and other wild ungulates. Unlike some other models, Bowden's estimator does not assume all deer have the same sighting probability (i.e., allows for resighting heterogeneity), populations can be sampled with or without replacement (i.e., individual deer can be observed only once or multiple times per survey), and all marks do not need to be individually identifiable. More recently, maximum likelihood estimators have been developed with similar practical assumptions. These estimators include 1) the mixed logit-normal model (McClintock et al. 2009*b*) when sampling is done without replacement and the number of marks is known, and 2) the Poisson-log normal model (McClintock et al. 2009*a*) when sampling is done with replacement or the exact number of marks is unknown. These maximum likelihood methods have the major advantage of allowing information-theoretic model selection based on Akaike's Information Criterion (Burnham and Anderson 1998).

Program NOREMARK was specifically developed to calculate population estimates based on resight data when animals are not being recaptured (White 1996). The program includes the JHE (Bartmann et al. 1987), Minta-Mangel (Minta and Mangel 1989), and Bowden's (Bowden 1993, Bowden and Kufeld 1995) estimators. More recently, the mixed logit-normal (McClintock et al. 2009*b*) and the Poisson-log normal (McClintock et al. 2009*a*) mark-resight models have been included in Program MARK along with a variety of other mark-recapture models (White and Burnham 1999, White et al. 2001, White 2008).

A quasi-mark-resight method that can be more effectively applied on a management unit scale, particularly when deer are fairly detectable, is to correct minimum counts for the resight rate of a sample of marked deer (Bartmann et al. 1986, Mackie et al. 1998). This approach does not use the ratio of marked to unmarked deer to estimate population size per se, but rather the ratio of observed marked deer to total marked deer to adjust sample-based estimates for incomplete detectability similar to methods used for correcting transect and sample area counts discussed previously. Mark-resight adjustment factors can be survey-specific (i.e., based on resight of marked deer during the survey) or generic (i.e., based on previous resight probabilities under similar conditions).

Simultaneous double-counting is another quasi form of mark-resight whereby a population estimate is derived based on the ratio of total number of deer counted (marked deer) to number of duplicated sightings (resighted deer) using independent observers (Magnusson et al. 1978, Potvin and Breton 2005). For ungulates, simultaneous double-counting is usually done from a helicopter or fixed-wing aircraft and can be applied to a wide area because it has the obvious advantage of not requiring marked deer. Two observers in the same or different aircraft independently record the location, time, and group characteristics of all deer observed. For population estimation, this method assumes all deer are potentially detectable and observers are independent. Both assumptions are often questionable and there is inherent bias towards underestimating true population size to an unknown extent, which raises substantial concern about the appropriateness of this approach. In cases where sighting probabilities of deer are low (<0.45, Potvin and Breton 2005) or unknown, simultaneous double-counts are more appropriately interpreted as adjusted minimum counts rather than population estimates. To adjust for the inherent bias of the simultaneous double-count method, the method can be used in combination with a known sample of marked deer or sightability covariates to adjust the estimate for sighting probabilities (Lubow and Ransom 2007).

Thermal imaging and aerial photography.— Thermal imaging and aerial photography frequently appeal to the public as ostensibly practical methods to census wild ungulates. Although these methods have some potential for estimating mule deer numbers under the right conditions, they have often failed to show much advantage over standard counting methods because of highly variable detection rates (Haroldson et al. 2003, Potvin and Breton 2005).

Advantages

- Create a visual record that can be reviewed, analyzed, and archived.
- Do not rely on real time observations that could be in error.

Disadvantages

- Potential inability to 1) detect deer under cover, 2) differentiate deer from the background, and 3) differentiate mule deer from other species.
- Highly variable results that can be influenced by a wide variety of factors.
- Require relatively expensive equipment and flight costs, but often result in little or no benefit over standard counting methods.
- Thermal imaging flights must be conducted within a narrow range of environmental conditions.

Assumptions

- A high percentage of deer can be individually detected and accurately differentiated from other species and inanimate objects

Techniques

Thermal imaging typically uses a wide-angle FLIR system mounted on a helicopter or airplane. Random or systematic transects are most commonly flown, but a variety of sampling designs are possible. The system can make a video record of the flight that can be reviewed and analyzed at a later date. Thermal imaging cannot penetrate dense vegetation and differentiating deer from inanimate objects is sensitive to temperature gradients and heat loading. Night flights when deer are more likely to be in the open and heat loading is minimal are seldom practical from a safety standpoint. Surveys using FLIR are usually relegated to a narrow window of time after daybreak. Species identification can be problematic in areas where there are other large species such as livestock, elk, white-tailed deer, pronghorn, and bighorn sheep (*Ovis* spp.). Although FLIR surveys often assume detection probabilities approaching 1, actual detection rates can be highly variable (Haroldson et al. 2003, Potvin and Breton 2005). Therefore, FLIR surveys can have little advantage over visual counts because both methods usually must be corrected for incomplete detectability.

Population estimation using aerial photography involves making a photographic record of the area of interest from an altitude that does not cause disturbance to the deer. Use of aerial photographs has had little utility for deer because they are relatively small and seldom in areas with little or no cover. An attempt to use aerial photographs in Colorado to quantify elk numbers in open areas during winter was unsuccessful because individual elk could not be reliably identified (CDOW, unpublished data).

Population Modeling

Population modeling can be used to provide biologically realistic, mathematical simulations of mule deer populations based on demographic parameters that can be estimated using routinely collected field data. Modeling allows populations to regularly be estimated at a scale that would seldom be feasible with sample-based population methods. There are 2 basic types of population models: cumulative and point-estimate. Cumulative models use a balance sheet approach of adding (recruitment and immigration) and subtracting (mortality and emigration) deer over time from an initial population, whereas point-estimate models predict population size at a single point in time independent of prior history. Cumulative models can be evaluated using objective model selection criteria based on how closely model predictions align with field observations over time and how many parameters are used. Evaluation of point-estimate models is generally more subjective or requires comparison with sample-based estimates.

Cumulative models allow multiple sources of data to be integrated and considered over many successive years. This can result in a much more data-rich estimate of population size than single-point estimates because all relevant sources of data over time are considered. Because initial population size and the numbers of deer to add and subtract annually are seldom known, cumulative models rely on parameters that are more easily estimated to allow population gain and loss to be calculated. These parameters typically include harvest and wounding loss, post-hunt sex and age ratios, natural survival rates, and, in some cases, immigration and emigration rates. In practice, field estimates of some of these parameters are often not available, and even when they are measured, they often contain sampling error as well as process variance (White and Lubow 2002, Lukacs et al. 2009). Therefore, it is usually necessary to roughly estimate or adjust some parameters to better align model outputs with observed values. Most cumulative population models for mule deer are based primarily on alignment of modeled and observed post-hunt B:D ratios (Fig. 2). Cumulative models work the best when 1) the data set extends over several years, 2) field data are unbiased, and 3) adult male harvest rates are fairly high.

All models are dependent on the quantity and quality of data utilized. As the saying goes, "garbage in is garbage out." The public and some wildlife professionals can often be highly skeptical of modeled population estimates for mule deer (Freddy et al. 2004). Although there can be legitimate reasons for this skepticism, it is too often focused on how models work rather than quality of data going into models, with the latter being a crucial component.

In addition to their use for estimating population size, mule deer population models can also be useful for predicting outcomes of different management actions, evaluating density-dependent effects, and understanding effects of stochastic events on mule deer population dynamics.

Optimally Fitted Cumulative (OFC) population models.— These models objectively align predicted and observed parameter estimates using mathematical algorithms that are often based on an ordinary least-squares estimator (which is a maximum likelihood estimator when a normal distribution is assumed, White and Lubow 2002). Alignment is accomplished by allowing some parameters (e.g., survival rates and initial population size) to be adjusted within biologically realistic constraints to minimize relative deviation between fitted and observed values (i.e., squared differences adjusted for precision of field estimates). Multiple OFC models with various assumptions and parameter sets can be objectively evaluated and compared based on fit and parsimony using Akaike's Information Criterion (AIC, Burnham and Anderson 1998, White and Lubow 2002). Recently, Bayesian methods have been developed to provide probabilistic population estimates using OFC modeling (Lukacs et al. 2009, Johnson et al. 2010).

Although OFC models are primarily based on alignment of modeled and observed post-hunt B:D ratios, sample-based population estimates, minimum counts, and trend data can also be simultaneously used for, or considered in, alignment (Fig. 3). Occasional use of sample-based population estimates for alignment help give greater credibility to OFC models and allow population estimates over time to be considered in a more comprehensive context.

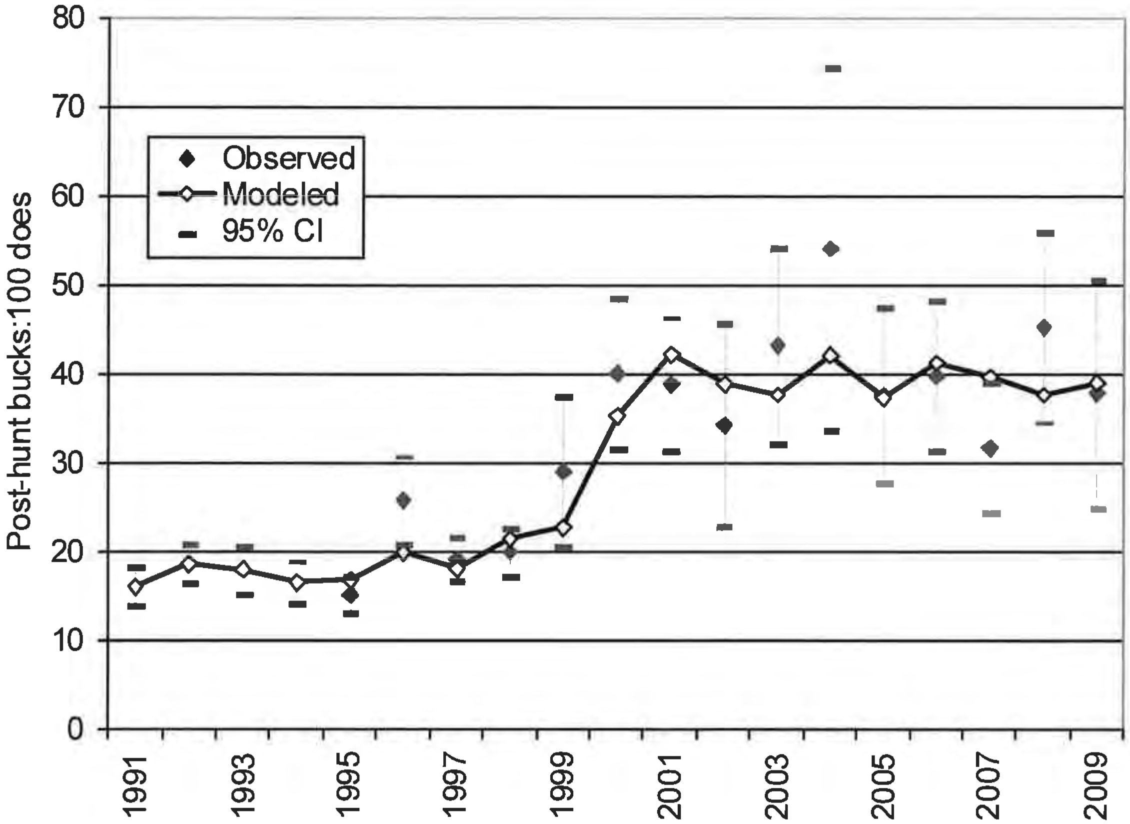

Figure 2. Modeled versus observed (with 95% confidence intervals) post-hunt mule deer B:D ratios using an optimally fitted cumulative population model, DAU D-9, Middle Park, Colorado, 1991-2009. Figure courtesy of CDOW.

At a minimum, OFC models require annual harvest estimates by sex and age (adult or juvenile) and reasonably regular field estimates of post-hunt sex and age ratios. Generic (i.e., determined in representative monitoring areas) or unit-specific field estimates of winter fawn survival rates and annual adult survival rates are also highly recommended (White and Bartmann 1998, Bowden et al. 2000). An example of an optimally fitted, cumulative population model for mule deer was described by White and Lubow (2002).

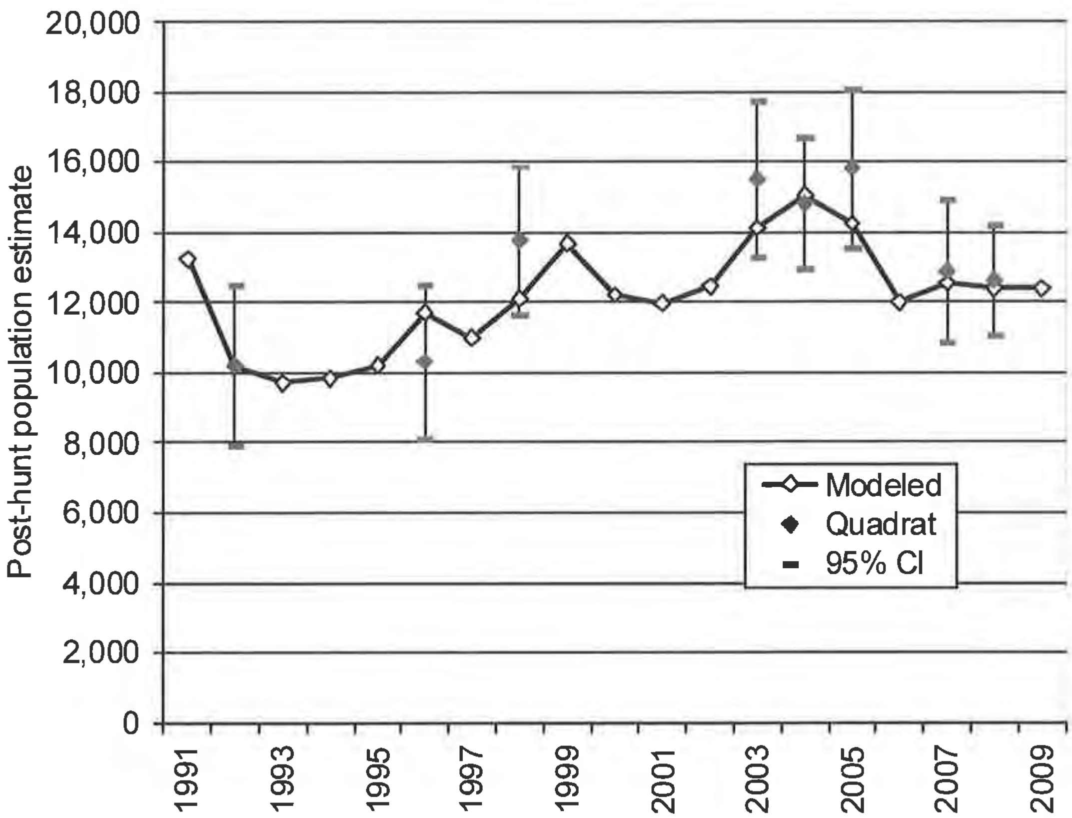

Figure 3. Modeled versus observed mule deer population estimates using an optimally fitted cumulative population model, DAU D-9, Middle Park, Colorado, 1991-2009. Quadrat population estimates were corrected for detectability using a generic sightability factor for sagebrush-steppe winter range. Figure courtesy of CDOW.

Advantages

- Relatively inexpensive compared to sample-based population estimate methods.
- Practical alternative for estimating deer numbers in multiple management units on a regional or statewide basis.
- Highly transparent when spreadsheet-based. All formulas can easily be viewed.
- Can incorporate multiple sources of data over time in a comprehensive context.
- Accounts for precision of field estimates.
- In some cases, Bayesian modeling can be used to obtain probabilistic estimates of population size.
- Not highly dependent on an accurate initial population estimate. Dependence on an initial population estimate decreases as quantity and quality of data in the model increase.
- Very flexible. Additional variables and calculations can easily be added or modified.
- Model solutions are determined using an objective mathematical process rather than by subjective manipulation.

- Allows various model solutions to be evaluated using objective model selection criteria such as AIC.

Disadvantages

- Does not provide a probabilistic estimate of population size unless Bayesian modeling approaches are used (see Techniques below).
- At a minimum, unbiased, relatively accurate harvest estimates and unbiased sex and age ratios are required. Biased data obtained using some common methods (e.g., voluntary hunter harvest reports) would not be appropriate for OFC modeling.
- Credibility of an OFC model is ultimately based on alignment with unbiased, sample-based, population estimates which can make this approach impractical for statewide implementation unless it is assumed that, given adequate, relatively unbiased field data, models can satisfactorily represent population size without corroborating population estimates.
- May lack sufficient data for developing credible models. Data-poor models can have little value except to put harvest estimates into a population context.
- Biologically unrealistic assumptions and constraints can lead to spurious results.
- Users can inadvertently modify formulas in error.

Assumptions

- Parameter estimates are unbiased (or bias can be corrected) and consistently estimated over time (see sections on Harvest, Survival, and Age and Sex Composition for more discussion of potential bias in these parameters).
- To reduce the number of variables, harvest and F:D ratios are usually assumed to be estimated without error. Variance of these estimates can be considered in more complex, data-rich models, however.
- Population being modeled is geographically closed over time or immigration and emigration rates are equal or can be reliably estimated.
- Constraints and constants (e.g., 50:50 fawn sex ratio) are biologically realistic based on available data.

Techniques

Optimally fitted cumulative models can be built and effectively run using spreadsheet software that incorporates an optimization program such as Solver (Frontline Systems, Incline Village, NV, USA). Optimization programs have a target cell, decision variables, and constraints. The optimizer minimizes or maximizes the target cell by iteratively adjusting the decision variables within specified constraints. Optimization of OFC models is accomplished by minimizing a target cell which is the sum of all deviances and penalties in the model. Deviances apply to parameters that are fitted (e.g., B:D ratios) whereas penalties apply to other parameters that might be adjusted (e.g., F:D ratios). Deviances and penalties are calculated relative to the standard error (SE) of each observed value:

$$\text{Deviance or Penalty}_i = [(\text{Observed Value}_i - \text{Modeled Value}_i)/\text{SE of the Observed Value}_i]^2$$

Decision variables in OFC models usually include winter fawn survival rates, annual adult survival rates, and initial population size. While it is also possible to include F:D ratios and harvest estimates as decision variables this can result in excessive complexity and increase the amount of play in the optimal solution. Use of male survival rates as decision variables can be justifiable if there are data indicating differential survival rates between adult males and adult females. However, allowing male survival rates to be adjusted can effectively wash out other variables when aligning sex ratios. Therefore, male survival rates should only be allowed to vary if reliable male survival estimates are available or if they are expressed as a function of adult female survival rates. Performance of OFC models can be improved by removing sampling variation from survival estimates and using process distribution of survival parameters to make more informed adjustments in these decision variables when they have not been measured (Lukacs et al. 2009).

Because population size is treated as a decision variable, OFC models are not highly dependent on entering an accurate estimate of initial population size. However, an optimal solution will be determined much more efficiently if a reasonable initial population estimate is entered. This can be accomplished by determining the relationship between OFC model estimates and buck harvest across management units (data analysis units [DAU] are used for this purpose in Colorado) and years. For example, after all deer hunting became limited in Colorado in 1999, an initial post-hunt population estimate for most DAUs can be approximated by multiplying average buck harvest for the first 3 years of the model by 17.3 (CDOW, unpublished data; Fig. 4). Prior to 1999 when buck licenses were unlimited, an estimate of initial population size can be approximated by multiplying initial buck harvest by 11.4 (CDOW, unpublished data; Fig. 5).

Fit will often improve as additional parameters are added to OFC models or constraints are relaxed. However, the model with the best fit may not provide the best representation of reality. Therefore, evaluation of OFC models should not only take into account goodness of fit between observed and modeled values, but also how many parameters and assumptions are used and biological legitimacy of all parameters, constants, and constraints. Model selection criteria such as AIC can be very helpful for balancing fit and parsimony, but cannot explicitly identify illegitimate constraints or assumptions.

Population reconstruction methods.— Population reconstruction uses cumulative age-specific harvest and mortality data to estimate population structure and size using a bookkeeping approach for all known mortalities by cohort. In their simplest form, population reconstruction models for deer would only have practical application if almost all mortality is assumed to be accounted for using harvest surveys or for small, contained populations where all mortalities can be detected (McCullough 1979). Reconstruction based primarily on harvest data usually underestimates population size and requires mortality recovery rate estimates by cohort to be more realistic (Roseberry and Woolf 1991). More complex reconstruction methods such as the statistical age-at-harvest model incorporate survival rates estimated with radiomarked deer to include non-hunting mortality (Gove et al. 2002).

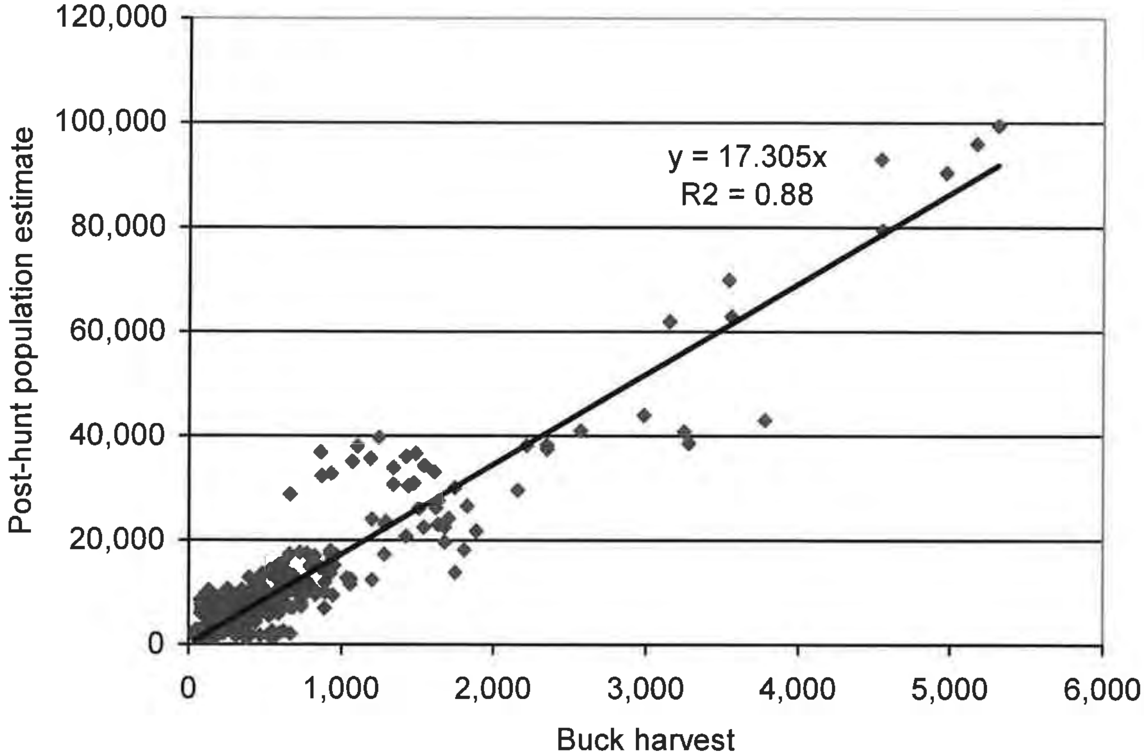

Figure 4. Relationship between buck harvest and modeled post-hunt population estimates for 55 deer DAUs in Colorado using optimally fitted cumulative population models, 1999-2006. All deer licenses in Colorado were limited in 1999 and statewide post-hunt B:D ratios increased from an average of 17:100 prior to limitation to 32:100 after limitation. Figure courtesy of CDOW.

Advantages

- Only requires age-specific harvest or other mortality data.
- Can provide a detailed record of population sex and age structure including age-specific survival rates.

Disadvantages

- Requires age-specific harvest and mortality data which can usually only be reliably obtained by collecting tooth samples from adult deer.
- Population size can only be estimated after all deer alive in that year have died unless assumptions are made to predict future mortality. Such assumptions reduce reliability of population estimates.
- Non-hunting mortality, particularly of fawns, is known to be a major source of mortality in most mule deer populations. Mule deer population reconstruction that does not take into account non-hunting mortality would be of questionable value.

Assumptions

- Usually assumes mortality is primarily due to harvest and the proportion of mortality accounted for is relatively constant over time by cohort.
- Age-specific mortality can accurately be estimated based on harvest surveys and field data. That is, age structure in the harvest is representative of age structure of the population.

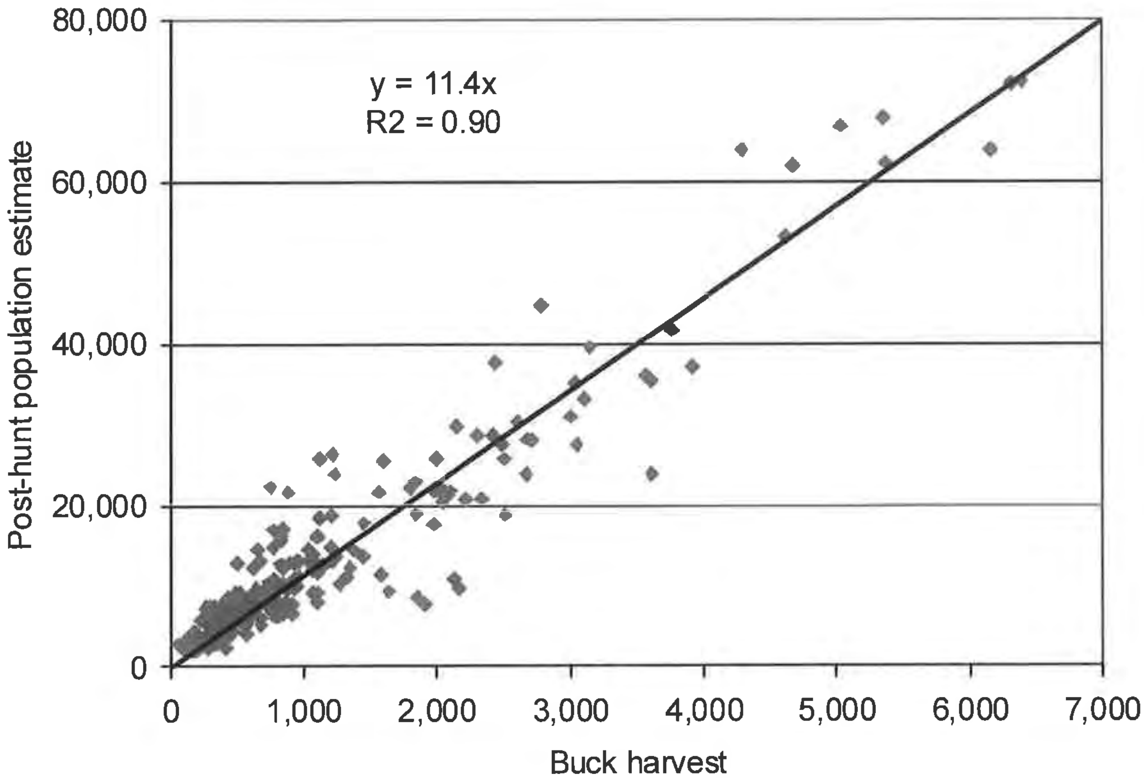

Figure 5. Relationship between buck harvest and modeled post-hunt population estimates for 33 deer DAUs in Colorado with unlimited buck licenses, 1990-1998. Post-hunt B:D ratios averaged approximately 17:100. Figure courtesy of CDOW.

Techniques

Population reconstruction uses year of death and age of known mortalities to populate a post hoc bookkeeping model that follows each cohort over time. Given that mule deer in the wild can potentially live ≥12 years, simple population reconstruction methods usually have limited application for management purposes. Models that predict future mortality to allow more timely reconstruction and include estimated mortality recovery rates introduce additional uncertainty into estimates.

Sex-Age-Kill (SAK) models.— This type of model is used by some states in the Midwest and East to provide a post hoc, pre-season point estimate of white-tailed deer numbers and to project a pre-season population estimate for the following year (Millspaugh et al. 2009). Pre-season population estimates are based on estimating adult male (≥1.5 years) abundance from harvest data and an estimated harvest rate and then estimating total population size based on sex and age ratios.

Advantages

- Uses routinely collected data (harvest by sex and age to calculate pre-hunt sex and age ratios) to estimate density or population size.
- Cost efficient to collect the minimum data typically used.
- Simpler than accounting methods when data are available.

Disadvantages

- Proportion of buck mortality associated with harvest is not empirically estimated. Therefore, adult male harvest rate is modeled based on harvest age structure (units with high hunter pressure and exploitation have lower non-harvest loss) or roughly estimated.
- Fawn:doe ratios are based on opportunistic observations made prior to hunting season. This would seldom be possible with any confidence for many mule deer populations that occupy remote, mountain summer ranges. Pre-hunt F:D ratios for mule deer would be more effectively estimated based on post-hunt aerial classification and adjusted to pre-hunt ratios by accounting for harvest and wounding loss.
- Adult sex ratios are estimated based on proportions of yearling bucks and does in the harvest and the pre-birth sex ratio. For mule deer, adult sex ratios could be more effectively estimated based on post-season aerial classification.
- Model performance can decline as scale is reduced (i.e., statewide vs. management unit basis).
- Sensitive to sudden changes in male harvest rate as may occur with extreme hunting conditions or major changes to hunting rules.
- Model is highly dependent on accurate estimation of the adult male segment.
- Does not usually provide a probabilistic estimate unless all parameter estimates are unbiased and all assumptions are met.
- Not well understood by the public.
- Complicated by antler point restrictions because age structure of harvested bucks is unlikely to represent age structure of bucks in the population.

Assumptions

- Buck harvest is a reliable index of pre-hunt population size and age structure of harvested bucks mirrors buck age structure of the population (i.e., rate of buck harvest is independent of age and size class). This assumption is only likely to be valid when buck licenses are unlimited.
- Population has a stable age structure and is stationary in size for pre- and post-hunt population estimates.
- Model parameter estimates (e.g., F:D ratios, harvest estimates, adult male harvest rates) are unbiased. Generic estimates (e.g., pre-birth sex ratio) are representative.

Techniques

Pre-hunt adult male abundance is estimated by dividing adult male harvest by estimated adult male harvest rate. This rate is calculated as the product of total annual adult male mortality rate and proportion of adult male mortality resulting from harvest. The latter variable is either predicted based on the proportion of 1.5-year-old males in the adult male harvest (a measure of total mortality) or roughly estimated. The assumption of a stable age distribution and stationary size is necessary to calculate total annual adult male mortality rate without bias and to estimate the adult sex ratio. However, a 5-year average of percent yearlings in the buck harvest closely approximates total adult buck mortality under a stable-stationary condition when using uniform hunting rules each year.

Change-in-ratio (CIR) estimators.— This point-estimate method uses changes in sex or age ratios before and after known harvest to estimate population size (Paulik and Robson 1969, Seber 1982). For deer, CIR estimators are usually based on a change in sex ratios after a disproportionately high harvest of bucks compared to does (Conner et al. 1986). Differential harvest between bucks and does is required and the difference should be large enough to result in a substantial change in the sex ratio. In practice, this method is only effective when a large proportion of pre-hunt bucks are harvested.

Advantages

- Relatively inexpensive.
- Uses routinely collected data.

Disadvantages

- Requires unbiased and relatively precise estimates of sex ratios and harvest. Sex ratio variances are often too large to give much confidence in resulting population estimates.
- If harvest does not change the sex ratio relative to the change that can be detected with sex ratio surveys, the estimator fails and does not produce an estimate.

Assumptions

- Harvest and wounding loss by sex are usually assumed to be estimated without error.
- Pre-hunt and post-hunt sex ratios can be estimated with fairly high precision and without bias (i.e., bucks and does are equally detectable during each sex-ratio survey).
- Population is closed between pre-hunt and post-hunt surveys except for known harvest.

Techniques

Change-in-ratio methods rely on unbiased and fairly precise sex-ratio estimates (see Age and Sex Composition). Sex ratios can often be biased because bucks are less likely to be detected than does when male harvest rates are disproportionately high (Roseberry and Woolf 1991). Even if sex ratios are assumed to be unbiased, they often lack enough precision to make CIR population estimates for mule deer very reliable.

POP-II and POP-III models.— POP-II is a commercial, cumulative population modeling program based on the ONEPOP model developed at Colorado State University in the early 1970s (Bartholow 1999). POP-II is similar to OFC models in that it is essentially a bookkeeping program that uses alignment between observed and modeled sex ratios as the basis for adjusting variables in the model. The POP-II model uses parameters generally similar to OFC models and is therefore also highly dependent on unbiased field estimates. However, POP-II is a deterministic model that does not optimally fit observed data, but rather allows the user to manipulate a variety of parameters and assumptions to improve subjective fit. Precision of field estimates is not accounted for in POP-II, nor does the model incorporate sample-based population estimates. Because POP-II is a commercial program, it has much less transparency than a spreadsheet-based model and cannot be customized. POP-III is an extension for POP-II that incorporates stochasticity.

Advantages

- Readily available and turn-key.
- Consistent model framework that cannot be altered by the user.
- Uses an intuitive bookkeeping approach.
- Familiar to biologists in some agencies who have used it for many years.
- Allows "what if" population scenarios and management alternatives to be evaluated.

Disadvantages

- Does not objectively fit observed data using a mathematical algorithm, but rather allows the user to manipulate different aspects of the model to improve fit. Evaluating how the fit of the final model selected compares to a model that is optimally fit is not possible. Model selection can be subjective to conform to expectations.
- Does not provide full transparency to allow the user to understand how parameters are being used and how calculations are being performed.
- Does not have the flexibility of spreadsheet-based models that can be readily customized by the user.
- More dependent on an accurate estimation of initial population size than OFC models. POP-II also requires initial age and sex structure to be entered.
- Does not take into account precision of field estimates.
- Unlike OFC models, outputs cannot be evaluated using model selection criteria such as AIC.
- Requires oldest age class in the field to be specified (older deer are automatically removed). Although contribution of this factor to bias in mule deer models is unknown, specification of the oldest age class has clearly biased some elk models based on longevity of some radiocollared elk.
- Because necessary parameter inputs are rarely empirically measured, incorrect rough estimates can produce large deviations from actual population size.

Assumptions

- Whatever model is selected is representative of the true population.

- Parameter estimates are unbiased (or bias can be corrected) and consistently estimated over time (see sections on Harvest, Survival, and Age and Sex Composition for more discussion of potential bias in these parameters).
- Harvest and F:D ratios are usually assumed to be estimated without error.
- Population being modeled is geographically closed over time, or immigration and emigration rates are equal or can be reliably estimated.
- Constraints and constants (e.g., 50:50 fawn sex ratio) are biologically realistic based on available data.

Techniques

POP-II calculates population size based on a straightforward bookkeeping approach that requires estimates of initial population size and structure and annual estimates of 1) preseason natural mortality, 2) harvest, 3) wounding loss, 4) post-season natural mortality, and 5) birth pulse. Model solutions can be manually manipulated to improve fit between modeled and observed values by changing a number of variables, including natural survival rates, a mortality severity index, harvest effort values, and reproductive rates by group. A correlation coefficient and goodness-of-fit statistic are calculated to help evaluate fit for each simulation. POP-II models are parameter rich and use some data (e.g., age-specific structure, harvest, and reproductive rates) that are rarely estimated in the field for mule deer.

Harvest per unit effort methods (HPUE).— Models employing HPUE are based on an inverse relationship between number of deer harvested or counted for each unit of effort (e.g., per hunter-day, per hour of observation) and population size (Lancia et al. 1996*a*). These models have been used for many years to estimate commercial fish abundance, but have received relatively little use for estimating big game populations. Models incorporating HPUE for estimating white-tailed deer numbers were described by Novak et al. (1991), Roseberry and Woolf (1991), and others.

Advantages

- Relatively inexpensive. When based on harvest per hunter-day or percent success, only hunter survey data are required.

Disadvantages

- Hunter-hours and harvest data are often not available on a daily basis.
- Two or more harvest periods may be required.
- Harvest success must be high enough to cause a significant decline in the population or the slope of HPUE models will not change, and thus not produce an estimate.

Assumptions

- Vulnerability to harvest is constant. Changes in conditions (e.g., weather, snow depth), hunting methods and regulations, and deer behavior during the harvest period are assumed to have little effect on vulnerability or the effect can be reliably estimated.

- Hunters are not highly selective (e.g., hunters do not hold out for larger bucks) and selectivity does not change during the harvest period (e.g., hunters do not become more likely to shoot a small buck or doe later in the season).
- Populations are closed while harvest is occurring.

Techniques

There are several variants of the HPUE method (e.g., 2 harvest periods, Leslie method, direct index, etc.) with different assumptions (Roseberry and Woolf 1991). Relationships between harvest per effort and abundance are determined by regression analysis and are often assumed to be linear. If harvest effort is constant, percent success can substitute for effort in some models. Managers can extrapolate HPUE to estimate population abundance using DeLury non-linear HPUE or similar models (Roseberry and Woolf 1991, Skalski et al. 2005). Currently, HPUE methods have little practical value for estimating mule deer numbers because underlying assumptions are seldom realistic. These methods are more suitable for providing a population index rather than a population estimate and, even then, should be used in conjunction with other methods.

Survival Rates

Finite survival rate is the probability of an organism remaining alive through a specified time period and is usually estimated by the proportion of survivors in a sample. Survival rate estimates, particularly for adult females, are the most sensitive parameters in cumulative mule deer population models (White and Bartmann 1998, Bowden et al. 2000). Although mule deer models are less sensitive to changes in fawn survival, fawn survival rates can also be very influential on model performance because fawn survival can be much more variable (i.e., larger process variance) than adult doe survival (Unsworth et al. 1999*b*, Lukacs et al. 2009).

Survival rates are usually calculated as "natural" survival rates that exclude harvest and, in some cases, wounding loss and illegal kills. Survival rates of adults are usually expressed on an annual basis, whereas, for the purpose of population modeling, fawn survival rates are more practically based on winter survival from the time of post-hunt classification surveys until fawns are recruited as yearlings. Pre-hunt fawn survival is not required for population modeling but can be of interest to better understand population dynamics. Pre-hunt fawn survival is most effectively estimated by locating and radiomarking fawns soon after birth (best accomplished via use of vaginal implant transmitters; Bishop et al. 2007, 2009*b*). Alternatively, but with less accuracy and precision, estimates of pregnancy and fetal rates along with fawn:adult female ratios may be used to estimate pre-hunt fawn survival.

Although annual doe and winter fawn survival rates for mule deer have been commonly monitored, relatively little information is available on natural buck survival rates (Pac and White 2007). This has been because 1) managers often assume doe and buck survival rates are similar (White and Lubow 2002), 2) buck survival is considered to be the least important survival parameter in population models, and 3) placement of radiocollars on adult bucks is problematic because of annual changes in neck circumference. The assumption that doe and buck natural survival rates are similar is probably not valid in many cases and these rates can likely be influenced by buck and doe harvest rates (Mackie et. al 1998; B. Watkins, CDOW, unpublished data). Differential survival can affect model outcomes when B:D ratios are used for alignment.

Most survival rate estimates for mule deer have sampling variation and process variation. Process variation refers to the inherent biological variability (temporal and spatial) in the survival rate across time or space. Survival estimates across multiple years and locations are required to separate process variation from sampling error (White and Bartmann 1998, Bowden et al. 2000, Lukacs et al. 2009). Estimating process variation in mule deer survival rates can improve OFC population model performance, particularly when field data are sparse (Lukacs et al. 2009). Although survival rates can theoretically be estimated based on changes in sex and age ratios, using band recoveries, or using age data to reconstruct populations, by far the most useful method for mule deer is to use samples of radiomarked deer.

Known-fate using radiotelemetry.— With few exceptions, survival rates of wild ungulates are estimated using a sample of radiomarked animals. Using radiotelemetry, survival rates can be efficiently estimated for specific sex and age classes and information can be obtained on cause-specific mortality and spatial distribution. Radiomarks allow the fate (i.e., live, dead, or censored) of marked deer during a specified time period to be known with certainty and allow calculation of survival rates using known-fate models based on simple binomial likelihoods.

Advantages

- Most efficient, direct, and potentially least biased method to determine survival rates.
- Survival probabilities can be continuously estimated over time depending on the frequency of monitoring.
- Allows estimation of survival rates for specific deer groupings (e.g., age class, sex, geographic area, habitat, etc.), potential identification of cause-specific mortality, and estimation of the contribution of specific mortality factors to overall survival.
- Deer with unknown fate can be censored, but still be included in survival rate estimation while they are still known to be alive.

Disadvantages

- Relatively expensive equipment and monitoring costs.
- Infrequent monitoring can be problematic depending on the timeframe of survival estimates.
- Depending on analysis method used, small initial sample sizes can bias survival rates unrealistically low if much mortality occurs early in the survival period.

Assumptions

- Collars are randomly distributed within sex and age classes of interest.
- Date of death can be accurately determined to have occurred within or outside of the period of interest.
- Capture and radiomarking do not affect survival probabilities.

Techniques

Survival studies using radiotelemetry involve

1. Marking a sample of deer with transmitters equipped with mortality sensors.
2. Periodic telemetry monitoring from the ground, from aircraft, or by satellite.
3. Timely field investigation of mortality signals.

4. Estimating date of death when monitoring is infrequent.
5. Censoring deer that cannot be located because of radio failure, shed transmitters, movement out of the study area, or any other reason.

Survival rates can be estimated from known-fate data in a variety of ways. The simplest method is to simply divide the number of deer alive at the end of the period by the number marked. This method has obvious limitations (e.g., censoring is not possible) and is seldom useful. A more common technique is to calculate survival rates using the Kaplan-Meier method (Kaplan and Meier 1958, Pollock et al. 1989). This method

1. Allows staggered entry of fate data (i.e., additional marked deer can be added to the sample at any time during the survival period).
2. Allows available data from censored deer to be considered while their fate is still known.
3. Provides an estimate of precision.

Small initial sample sizes may need to be lumped over time for entry to avoid unrealistically low survival rates when using staggered entry. For example, if only 2 deer are initially radiocollared and 1 dies before other deer are added to the sample, the survival rate using the Kaplan-Meier method will be ≤50% no matter how many additional deer are collared and survive unless appropriate analysis alternatives are used to address this issue.

For more detailed analyses that can take into account specific attributes of known-fates data, program MARK can be used to calculate mule deer survival rates using a variety of models (White and Burnham 1999). A major advantage of MARK is that binomial models based on maximum likelihood estimation can be used to estimate survival, allowing the use of AIC for model selection. Program MARK also includes analysis alternatives for ragged data when deer are not monitored in discrete intervals and exact day of death is unknown.

Adequate sample sizes for survival monitoring depend on rate and timing of mortality and level of precision desired for population modeling. White and Bartmann (1998) recommended samples of at least 40-60 fawns and 20-40 does to achieve reasonable precision in Colorado DAUs. However, replacement or additional doe radiocollars should be deployed each year to help maintain a doe sample that more likely represents age structure of the female population (i.e., younger age cohorts are represented). This approach usually results in a sample of 60-80 does because of relatively high doe survival rates (CDOW, unpublished data).

An attempt should be made to randomly or systematically distribute the radiomarked sample across the area of interest. This can be most effectively accomplished by helicopter net-gunning the deer to be collared. However, to help reduce costs, other less expensive methods (e.g., drop nets, cage traps, chemical immobilization, drive nets) can also be used in combination with net-gunning as long as the sample is spatially well distributed.

For the purpose of population modeling, the beginning of the period for estimating overwinter fawn survival should closely coincide with estimation of F:D ratios. For example, if the survival rate period begins well after age ratio classification, recruitment of fawns to the yearling age class will be overestimated if appreciable mortality occurs during this time interval. To help reduce costs and ensure collars do not become too tight with additional growth, overwinter fawn survival can be estimated using collars designed to drop off in 6-9 months. This can economically be accomplished by cutting collar belting and reattaching the ends using latex surgical tubing that will degrade with ultraviolet light exposure. Another alternative is to use expandable collars, particularly on female fawns, some of which will be recruited into the future adult doe sample.

Band recovery.— Although frequently used for migratory game birds, band recoveries have seldom been used to estimate big game survival rates. White and Bartmann (1983) attempted to use band recoveries to estimate survival of mule deer and concluded the method was generally impractical because of the large sample sizes required and incomplete reporting.

Advantages

- Does not require radiotelemetry equipment and monitoring.

Disadvantages

- Known-fate models do not apply. Survival can be estimated with much higher precision and less bias using radiotelemetry.
- Requires large numbers of deer to be marked which can result in considerable costs.
- Sources of mortality cannot be readily differentiated.
- Requires high band recovery rate to obtain precise estimates.

Assumptions

- Banded and non-banded deer have the same probability of survival.

Techniques

Band recovery methods have been used for many years to estimate survival rates for migratory game birds and fish (Brownie et al. 1985). For mule deer, inexpensive neck bands and ear tags can be used for band recovery studies. However, use of band recovery methods to estimate mule deer survival is seldom justifiable unless large numbers of deer are being marked for other reasons. The only potential advantage of using band recoveries for estimating deer survival is to avoid the expense of radiotelemetry equipment and monitoring. This is seldom justifiable because deer capture costs, rather than telemetry costs, are often the most expensive aspect of survival studies. Program MARK can be used to analyze band recovery data (White et al. 2001).

Change-in-ratio estimators.— This method provides estimates of overwinter fawn and adult survival rates using pre- and post-winter fawn:adult ratios and the estimated age ratio of overwinter mortalities (White et al. 1996). Fawn:adult ratios are used because bucks cannot be readily distinguished from does at a distance in the spring after antlers are shed. The age ratio of overwinter mortalities must be estimated to determine the effect of adult mortality on post-winter fawn:adult ratios. Although theoretically sound, the change-in-ratio method would likely result in very imprecise and likely biased survival estimates for mule deer.

Advantages

- Relatively inexpensive because deer do not need to be captured and marked.

Disadvantages

- Requires accurate and precise estimates of age ratios. Accurate classification of fawns in the spring can be highly prone to error.
- Aerial classification is recommended to achieve a well distributed, representative sample. This adds to the cost and makes accurate age classification more difficult.

Assumptions

- Age-ratio estimates are unbiased or have the same bias in all surveys.
- Deer are not misclassified.
- Fawn mortalities are as likely to be detected as adult mortalities during spring surveys.

Techniques

Pre- and post-winter age ratios can be estimated using ground or aerial surveys. However, aerial surveys are less likely to be biased because bucks are more prone to be segregated from does during post-winter than during pre-winter because of the rut (White et al. 1996). Age ratios of mortalities can be estimated using ground transects in winter range areas.

Population reconstruction methods.— Age-specific annual survival rates can be calculated from reconstructed population data by dividing the number of deer alive in each cohort during year $t+1$ by the number alive in year t. Unlike the use of population reconstruction to estimate population size, survival rate estimates do not require a full accounting of mortalities as long as recovered mortalities are assumed to be representative of total mortalities. This method is equivalent to the cohort life table of the older population dynamics literature. With the possible exception of small, confined populations, population reconstruction methods have little practical value for estimating mule deer survival rates because non-harvest mortality must still be estimated.

Advantages

- Can provide a detailed record of population sex and age structure, including age-specific survival rates.

Disadvantages

- Requires age-specific harvest and mortality data which can usually only be obtained by collecting tooth samples from adult deer.
- Cohort size during years t and $t+1$ can only be estimated after all deer alive in year $t+1$ have died unless assumptions are made to predict future mortality or recovered mortalities are assumed to provide an unbiased representation of total

mortalities. This long time lag makes this method of limited value for adaptive management approaches.
- Non-hunting mortality is difficult to estimate unless deer are in a relatively small enclosure or radiotelemetry is used.

Assumptions
- Age-specific mortality in the population can be accurately estimated based on harvest surveys and field data.
- Population age structure is assumed to be stable.

Techniques
Population reconstruction uses year of death and age of known mortalities to populate a post hoc bookkeeping model by cohort. A variety of methods have been developed for estimating survival rates from age structure data including methods for populations with dynamic age structures (Udevitz and Ballachey 1998).

Age and Sex Composition

Age and sex composition data are simply a classification of relative proportions of bucks, does, fawns within a population. Bucks may be further classified into approximate age or antler-point classes (e.g., 1-2 points or yearling, 3 points, ≥4 points). Ratios of B:D and F:D are generally presented in standardized fashion as bucks:100 does:fawns.

Age and sex composition data can be most useful when adjusting limited entry buck permit numbers among annual seasons, although they are also necessary for population model inputs. As the proportion of surveyed bucks changes, permit numbers can be adjusted accordingly (e.g., reduced permits in response to decreased proportion of bucks in a population). Similarly, buck permits may be adjusted in anticipation of expected recruitment (e.g., increased permits in response to increased proportion of fawns in a population). Because population size can change while B:D or F:D ratios remain stable (Caughley 1974), a population estimate or index to population size (e.g., deer/hour of survey) should be considered with this approach.

Generally, surveys should be conducted within areas accessible for harvest. Surveying areas where hunting is precluded may misrepresent availability of bucks for harvest or fawns for recruitment, although at times these areas may serve as a source from which immigration or recruitment occurs. Decisions regarding including these areas within surveyed habitat should be considered deliberately prior to initiating surveys.

Agencies generally establish a range of acceptable B:D and F:D ratios beyond which managers recommend increases or decreases in permits. These data may be used to determine which type of season may be held (limited entry or open entry, short season or long season) based on similar acceptable ranges. Antlerless harvest may be more difficult to manage with these types of data, except in specific situations (e.g., when F:D ratios drop below a specific threshold, the habitat may be overstocked and reductions in antlerless deer may be recommended to reduce the overall population although weather conditions undoubtedly play an overriding role in many situations).

Composition data are most useful when combined with additional data on population estimates or indices. Without companion data on population trends, age and sex composition data may be misinterpreted because populations can increase or decrease without any associated change in ratios (Caughley 1974). If collected shortly before and shortly after a buck-only harvest, the change in ratio can be used to infer population size (however, this approach is expensive and rarely used for management-level monitoring).

Timing of surveys used to collect age and sex composition can affect the sample. Bucks are generally associated with does and more visible during the breeding period, probably allowing more reliable estimation of actual B:D ratios. Surveys outside of the breeding period generally result in lower B:D ratios. Even during the breeding period, B:D ratios are more variable than F:D ratios (McCullough 1992, Carpenter et al. 2003). Observers should recognize that although antler morphometry is correlated with buck age (Anderson and Medin 1969), differentiating yearlings from adults in the field based on antler characteristics is subjective and, in some cases, unreliable (D. Lutz, WY Game and Fish Department [WGFD], unpublished data). Fawn:doe ratios differ substantially by time of year because fawn survival differs substantially from adult survival. Detectability of various age and sex classes differs by time of year as well. To be useful for comparative purposes, these surveys must be conducted at the same time each year. The later in the winter that surveys are conducted, the greater the difficulty in differentiating among fawns, does, and yearling bucks that have shed antlers. Further, a substantial doe harvest can cause apparent changes in these ratios because both B:D and F:D ratios depend on the denominator of does.

Bias in sex and age ratio estimates

Observer bias in ratio estimation can result from an observer's inability to correctly classify by sex or age, or tendency to select for 1 population segment over another. A common classification error is to incorrectly distinguish between juveniles and yearlings (Downing et al. 1977). This bias can potentially increase or decrease age ratios, but probably most often results in lower F:D ratios. This source of bias can be minimized by using only trained personnel to conduct classifications. Classification by less experienced personnel (those being trained) should be verified by experienced observers. Accuracy of classification and efficiency during aerial surveys are improved by using experienced pilots who know what characteristics the biologist must observe to classify deer. Some aerial observers are finding that viewing animals with image-stabilized binoculars enhances their ability to classify sex and age (however, incidence of motion sickness may increase). Ideally, observers from different areas and jurisdictions should go through periodic training or conduct classifications with experienced observers to improve consistency. When possible, observers should use a consensus approach for classification of deer groups when initial individual classifications differ or simply to ensure a greater level of consistency among and within observers. Although somewhat challenging to obtain from aircraft, photographic documentation of groups may provide an opportunity to verify classifications following the survey.

Another classification error is classifying males with small or shed antlers as adult females (Downing et al. 1977). In some areas, observers may misclassify yearling bucks that have shed antlers as juveniles. Antler loss in mule deer begins in December and continues through April and is typically earlier in northern latitudes than in more southerly locales (Heffelfinger 2006). However, antler loss varies locally and biologists should identify onset of antler loss in their specific area. The later in winter classification surveys are conducted, the more biased (i.e., lower than actual) B:D ratios will become. Deer classification in late January will likely have some inherent bias in northern states and provinces due to shed antlers, whereas in more southerly habitats this may not occur until late February. This source of bias can be reduced by restricting deer classification to periods prior to antler drop and by training observers to look closely for small-antlered males. Again, photographs of observed herds can allow closer scrutiny following the survey. Bias resulting from an observer's tendency to select 1 population segment over another usually relates to preferentially classifying mature males over females, juveniles, and small males. This source of bias can be reduced by classifying large groups of deer in a systematic manner (e.g., from left to right, from back to front, within a specific field of view, etc.) rather than preferentially classifying obvious large males first.

Sampling bias results from not taking a representative sample of a population. This bias can result from surveying only part of a population area, concentrating only on 1 habitat, only surveying specific locations where deer are known to occur, classifying too few deer, or classifying only part of some groups (if subgroup composition is nonrandom). Sampling bias is likely to be more of an issue with sex ratios than age ratios, but both can be affected. Sampling bias can be reduced by using random sampling designs or by making an attempt to broadly survey across a population area, including all habitats where deer could occur. Because nonrandom subgroup composition is common (e.g., bucks tend to lead or follow, fawns tend to clump together), only entire groups should be classified. Appropriate sample sizes should be specified before surveys begin (based on previous or expected variation and desired precision). Identifying a target sample size can also reduce costs in a random sampling framework if surveys are terminated upon acquiring the needed sample, and a spatially balanced sample has been obtained.

Detection bias arises from differential detectability of different population segments (e.g., 1 population segment is more or less detectable than another). This is primarily an issue with adult males because they often form bachelor groups and occupy different habitats than other segments (particularly outside of breeding season). These small groups often have much lower detectability than larger groups of females, juveniles, and young males. Detection bias for deer can be reduced by flying during the peak of breeding season when bucks and does are more likely to be together. However, conducting surveys during the rut can be disruptive and unpopular with the public if concurrent with big game hunting seasons. Further, sampling during mule deer breeding season should still encompass the full range of habitats available to deer (i.e., avoid sampling bias). Considerable post-rut segregation may occur depending on snow depth and winter concentrations.

Redundancy bias occurs when the same deer are unknowingly classified more than once. This bias is more prevalent when large numbers of deer occupy dense vegetation or large groups mix and shift during classification. Redundancy bias can be considered a form of sampling with replacement and addressed with appropriate statistical methods.

Aerial observations.— Aerial observations are conducted to reduce biases typically associated with ground surveys. Aerial surveys provide observers the ability to traverse large tracts of broken terrain using a random or systematic sampling design which is impossible to deploy from the ground, where vehicles and foot surveys are limited by accessibility. Aerial surveys also provide a platform from which observers effectively can look through even relatively dense vegetation because of the improved vantage point (Fig. 6). Because most wildlife will flee from low-level flights, increased detection rates are also possible due to movement of deer.

Figure 6. Helicopters can provide useful platforms for classifying sex and age of mule deer. Photo by T. Keegan, Idaho Department of Fish and Game (IDFG).

Advantages

- Aerial surveys allow use of robust sampling designs, such as systematic or random grids.
- Allow for an improved observer platform that provides improved visibility through vegetation from above.
- Wildlife often move in response to low-level aircraft, which can increase their detectability.
- Helicopters can hover or maintain wildlife within view to improve classification time and position for observers.

- Because aircraft can cover relatively large areas in relatively short periods of time, sample sizes can be large.

Disadvantages

- The primary challenge associated with aerial surveys is increased cost. Helicopters are generally the preferred aircraft for most surveys, but are the most expensive on an hourly basis. Fixed-wing aircraft are less expensive, but not appropriate for areas with rugged terrain and more dense habitats.
- Low-level aerial survey is probably the most dangerous work-related activity for wildlife biologists (Sasse 2003), even though safety is a constant focus of survey pilots.
- Aerial surveys generate bias associated with misclassification because deer are typically moving when classified. Bucks with small antlers or spikes may be misclassified as does, yearling bucks with shed antlers and yearling does may be misclassified as fawns, and older fawns may be misclassified as adult does. This misclassification influences estimates of both sex and age ratios.
- Mountainous terrain requires modification to sampling grids. Helicopters are not able to follow a straight grid line and remain at a constant elevation above ground level in rugged terrain. Fixed-wing aircraft must be relegated to flat terrain with relatively open vegetation.
- Motion sickness can limit observer ability, and survey flights should end immediately if an observer develops motion sickness.

Assumptions

- The primary assumption of aerial survey techniques is the sample is representative of population of interest.
- Aerial surveys not corrected for differential visibility bias assume all age and sex classes are equally observable, which is generally untrue, so such surveys should not be conducted.

Techniques

Classification of sex is typically based on presence or absence of antlers. Observers must see the forehead of each deer to eliminate the possibility that small spike antlers are present. Large ears of mule deer can obscure relatively large spikes if viewed only from the side. If the forehead is not visible, that animal should be noted as "unclassified." Further, depending on area and timing, observers should be aware that some bucks may have shed antlers. Pedicles are typically not obvious, but may be visible under close scrutiny. Other features such as a larger, stockier body; dorsal bridge or curve of the rostrum; and greater contrast between a dark forehead and lighter muzzle provide further evidence that one is observing a buck that has already shed antlers.

Identification of fawns should be based on several characteristics. The following scenario is based on a helicopter survey in which the aircraft approaches from the rear of moving deer and flies by on a parallel path, but many of the characteristics can also be observed during ground observations. The first characteristic to observe is the shape of the rump, which appears more rounded in fawns than adults. The overall appearance of a fawn's hair is often described as "fuzzy," which likely contributes to the more round and stocky appearance. Fawns may also display a "dorsal stripe," a darker looking strip of hair along the back (Fig. 7). However, lack of a dorsal stripe does not conclusively identify an adult. As the helicopter moves alongside, observers should note a deer's gait; fawns tend to have a more erratic or "choppy" gait than adults and often appear to move in a confused or panicked manner in contrast to the deliberate movements of adults. Also note the ratio of neck length and girth to head length. Length of a fawn's neck will appear similar to head length, making the neck appear relatively thick, whereas an adult doe's neck appears longer than the head and relatively thin. Lastly, length of the rostrum relative to the head is the primary characteristic used for separating fawns from adults. A fawn's rostrum appears short and stout compared to that of an adult doe (Schroeder and Robb 2005, Fig. 8), giving a fawn's head a more-triangular shape when viewed from the side (Fig. 7). Note that relative body size can be a misleading characteristic and should not be used alone to differentiate age. For example, a large buck fawn may appear larger than a small yearling doe.

By following the above approach, observers should be able to develop a relatively strong preliminary conclusion about classification of each animal and derive final confirmation from viewing the rostrum. If the rostrum does not confirm initial classification, the helicopter should be turned back so biologists can further observe individuals and obtain definitive classification of all deer in the group.

Typically, observers should count total deer in a group from some distance away; before deer begin moving or when moving slowly. The helicopter can then move closer so observers can conduct actual classification in which only fawns and bucks are counted. Afterward, fawns and bucks are simply subtracted from the total number to obtain the number of does.

Figure 7. The rounded rump, dark dorsal stripe, stout neck, and "fuzzy" appearance help identify the fawn (right). Photo by T. Keegan, IDFG.

Survey design should take into account desired outcomes in terms of adequate sample size, expected precision, and deer distribution. Sample size requirements can be calculated based on expected or previous variance. Alternatively, assuming adequate geographic coverage, graphic representation of cumulative age or sex ratios can be examined to identify approximate numbers of groups beyond which ratios tend to stabilize (Ockenfels 1983, Fig. 7). Typically some form of stratified random sampling that takes into account differential distribution of bucks and does is needed to adequately estimate sex ratios. Although ad hoc surveys can often yield large sample sizes, they should be avoided because of unknown biases, particularly in sex ratios. Surveys require an aircraft that provides adequate visibility for observers, is capable of following a predetermined survey route, and can safely operate in the terrain and conditions in the an aircraft that provides adequate visibility for observers, is capable of following a predetermined survey route, and can safely operate in the terrain and conditions in the survey area. Pilots for deer surveys should have experience with the specific survey methods, herding deer, and flying in the type of terrain being surveyed. Some agencies have initiated protocols for observer experience and training to enhance consistency among observers. For example, primary observers for IDFG undergo annual training, must have 100 hours experience conducting similar surveys, and must have spent 30 hours on similar surveys during each of the most recent 3 years.

Figure 8. Relative rostrum length ranges from shortest in fawns (right) to longest in adults (left). The middle doe displays the intermediate length rostrum of a yearling. Photo by T. Keegan, IDFG.

Limited use of technologically advanced detections systems, such as FLIR scanners, has been attempted (e.g., Naugle et al. 1996). However, these techniques greatly increase costs of conducting surveys and have generally been inadequate for sex and age classification (Wakeling et al. 1999).

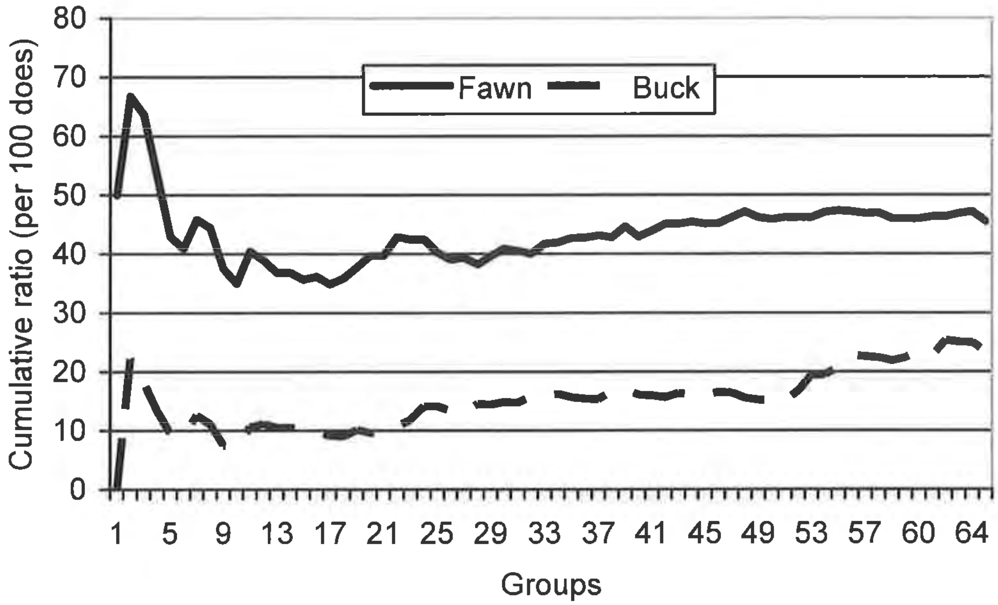

Figure 9. Cumulative sex and age ratios obtained in a stratified random sample within a large mule deer population management unit in east-central Idaho, Dec 2009. Stabilization of cumulative F:D ratio occurred at approximately 45-50 groups, whereas B:D ratios did not stabilize. This survey was designed to obtain only accurate F:D ratios; a different stratification and likely additional groups would be needed to accurately estimate B:D ratios. Using this approach to estimate sample size requires adequate geographic coverage of the population area. Data courtesy of IDFG.

Ground observations.— Ground observations may be obtained from a variety of platforms, including on foot or from livestock or motor vehicles; and may consist of continuous observation routes or fixed-point observation surveys. These types of surveys require relatively little financial resources when compared with aerial surveys. Ground observations generally are less likely to result in disturbance typical of low-level aircraft, and wildlife generally remain visible for greater periods of time than with aircraft, although substantial disturbance is possible during ground surveys as well. Observing undisturbed deer may enhance an observer's ability to correctly classify individuals when using optics such as binoculars or spotting scopes. However, obtaining adequate sample sizes can be difficult. Ground observations are influenced by the same annual breeding cycle observation biases for bucks as are aerial surveys.

Advantages

- Ground observations are less expensive to obtain and usually pose much less risk to observers than aerial surveys.
- Observers viewing undisturbed wildlife are likely to have more time to use optics and may be able to more accurately classify deer they observe (compared to aerial platforms).
- Observers can record additional information about deer habitat condition (e.g., condition of browse, intensity of grazing, availability of water, etc.) while conducting ground surveys.

Disadvantages

- Ground observations are limited by terrain and accessibility. Vehicles cannot access many portions of occupied deer range, especially during breeding season when buck classification may be best accomplished.
- Livestock or foot surveys are limited by speed and area that may be covered. Many areas may be too inaccessible for foot surveys, and access may be limited for even all-terrain vehicles.
- Detectability of deer and ability to count and classify individuals may be limited in areas with dense vegetation or under some weather conditions.
- Observer biases may differ for some portions of age and sex classes.
- Difficulties associated with speed, access, and visibility reduce the ability to obtain adequate sample sizes, which can lead to estimates with large confidence intervals.
- Conducting surveys from roads and trails introduces bias because these features are not randomly distributed across the landscape.
- Most ground-based surveys have been criticized in the literature because of biases that are impossible to detect, correct, or overcome. Nevertheless, many agencies continue to use ground surveys because of the low cost of these data.
- Despite lower overall cost compared to aerial surveys, actual cost per deer observed may be greater for ground surveys than aerial surveys (A. Fuller, AGFD, unpublished data).

Assumptions

- The primary assumption of ground survey techniques is the sample is representative of population of interest.
- Ground surveys assume all age and sex classes are equally observable.

Techniques

Classification techniques for sex and age are generally the same as those described above under aerial observations. However, ground observers may have difficulty observing all the characteristics for classifying fawns. Ground surveys may be employed from virtually any means of traversing habitat so long as it is done consistently among years. Periodic stops in which optics are used to systematically scan visible terrain are generally employed. Undisturbed observations are desired because this provides the greatest potential for accurate classification. Ground surveys should be implemented using a random sampling scheme to reduce biases.

Age determination from teeth.— Determining ages of a large sample of individuals provides information on age structure of a population and helps direct appropriate management actions. Age structure of a deer population tells us much about effects of harvest strategies (e.g., Wakeling 2010). Only rarely do biologists have the opportunity to observe teeth in living deer; inferences from deer teeth are primarily limited to teeth collected from harvested deer via hunter check stations and field checks, or via an alternate tooth collection system.

Deer teeth can provide estimates of age in 2 ways. First, changes in tooth eruption, replacement, and wear of the lower jaw are well-correlated with the age of the deer, particularly through 2.5

years. Second, deer also acquire annual rings in the cementum (cementum annuli) of their teeth (Larson and Tabor 1980). Counting cementum annuli provides accurate age estimates for deer of all ages, but tooth eruption and wear (field aging) for deer is generally only accurate for deer <3.5 years of age (Dimmick and Pelton 1994). However, field aging techniques can be used to assign older deer into age classes (e.g., 3.5-5.5, ≥6.5).

Advantages

- Tooth eruption and wear patterns may be observed and readily compared with published guides (e.g., Larson and Taber 1980).
- Tooth extraction is simple and relatively inexpensive to analyze in a laboratory, although care must be used during extraction (Dimmick and Pelton 1994).
- Relatively large numbers of samples may be compiled during routine hunter checks.

Disadvantages

- Sufficient sample sizes to determine age structure can be derived economically only from harvested deer at check stations or by asking successful hunters to mail or turn in incisors (or other samples) for subsequent analysis.
- Tooth eruption and wear patterns may be used to develop age structure information from live deer, but this requires capture and handling of many deer in a population, which substantially increases cost.
- Tooth eruption and wear patterns can be subjective to some degree, and wear patterns differ depending on primary forage consumed. Regional differences in wear are common.
- Cementum annuli analysis and reporting often requires 3-5 months.
- Extracting teeth from live deer is often not practical or desirable.

Assumptions

- The sample is representative of the population or segment of interest. When sampling from harvested deer, care must be used when extrapolating to the entire population because of bias in hunter selection and differential vulnerability by age to harvest.
- Observers correctly assign classifications of age when assessing tooth eruption and wear.
- Observers correctly remove the proper incisor (I_1), or correctly identify and label alternate teeth.
- Laboratory personnel correctly enumerate cementum annuli.

Techniques

Knowledge of the arrangement and numbering of teeth is essential to evaluate age. Deer have 3 pairs of lower incisors (I_1, I_2, I_3) which are pressed against a hard upper palate (there are no upper incisors). The lower canines (C_1) are incisor-like (incisiform). Upper canines are absent except in rare cases. The lower jaw has 3 premolars (P_2, P_3, P_4) and 3 molars (M_1, M_2, M_3) on each side. There is no P_1. Fawns are born with all lower incisiform teeth (I_1, I_2, I_3, C_1), all 3 premolars (P_2, P_3, P_4), and 1 molar (M_1) on each side. All incisiform teeth and premolars are replaced with adult teeth before the age of 2 years, but molars are permanent (never replaced). This pattern of tooth replacement allows for very accurate aging through the 2.5 year-old age class. After all adult teeth erupt, tooth wear can be examined to estimate age. Inexperienced observers should be trained by experienced observers to learn key attributes on which to focus.

Techniques for determining age from tooth eruption and wear or from cementum annuli are described within most wildlife textbooks (e.g., Larson and Taber 1980, Dimmick and Pelton 1994). When applying tooth eruption and wear in field situations, age is typically recorded in classes (e.g., yearling, 2.5, 3.5-5.5, ≥6.5) because assessing wear is subjective and overlap among age classes in common. Because most deer observed in the field or at check stations display rigor mortis, a simple jaw spreader made from 0.5-in (1.25 cm) rebar or similar material (Fig. 8) can be used to pry the mouth open, which facilitates examination of teeth. Simply insert the flat end between the jaws in front of the premolars and rotate the tool to spread the jaws. Cutting through cheeks (with approval of the hunter) also enhances ability to evaluate tooth eruption and wear. If cheeks can not be cut, a flashlight or other bright light source may be needed to adequately observe molars.

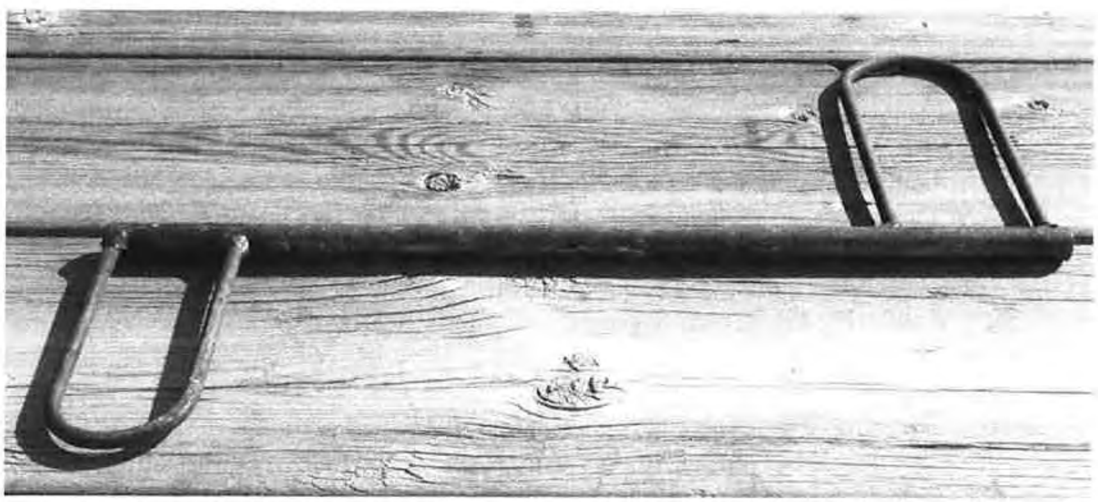

Figure 10. This simple jaw spreader allows biologists to quickly and easily pry open a deer's mouth to examine tooth eruption and wear. The smaller end (approx. 2.75 x 5.5 in [7 x 14 cm]) is used for deer and the larger end (approx. 3.5 x 7 in [9 x 18 cm]) for elk. Overall length is approximately 20 in (51 cm). Photo by T. Keegan, IDFG.

Cementum annuli can provide accurate age estimates, and the preferred tooth for age estimation is I_1 because it is the first incisor replaced with a permanent tooth. This method requires the root tip be intact, so personnel must be careful to not break teeth during extraction. A tooth can be removed by cutting through the gum tissue alongside the tooth and gently pulling and twisting with pliers. Teeth are typically placed in a small paper envelope to allow drying. The tooth is then submitted to a laboratory where technicians cut a cross section of the tooth, stain it, and determine the number of cementum annuli by examining the stained section microscopically.

Mathematical models.— The utility of mathematical models is primarily in evaluation of possible and probable outcomes that may result from proposed management actions. Evaluation of model performance can be achieved through comparison of predicted values to empirically derived data (e.g., population size, harvest, age and sex ratios). Mathematical models include change-in-ratio estimators, published population models, agency-developed models, and population reconstruction models. Although models are routinely criticized for inaccuracies in predictions or being overly complex, mathematical foundations for most models are relatively simple. The challenge lies in obtaining accurate and realistic inputs for these models. Because most estimates of age and sex classifications may be biased and imprecise, the best models incorporate a component of variability. However, other necessary inputs include estimates of survival for specific age and sex classes in the population, and these estimates are generally even less well quantified than age and sex classification data.

Advantages

- Mathematical models are inexpensive to use (although precise and accurate data are often expensive to obtain), as many require few human resources once model runs have been initiated.
- Models allow managers to consider multiple management scenarios and use reasonable rationale to predict effects of management actions.
- The greatest benefit in comparing models with survey data is in developing an understanding of factors most likely to contribute to observed differences.

Disadvantages

- Mathematical models are limited by accuracy and precision of data input into the model. With a perfect knowledge of natality, cause-specific mortality, emigration, and immigration, and effects of weather and habitat changes on these factors, modeling deer populations would be straightforward and more useful.
- Because of the imprecision of mathematical modeling, most models require constant comparison and recalibration with empirical field data.
- Some models, like the change-in-ratio estimator, require ≥2 surveys within a relatively short time frame.
- All models yield predictions for next year based on assumptions that are difficult to quantify.
- When discrepancies between observed and modeled age and sex ratios occur, biologists routinely disagree about which values are less accurate: the empirical input data or the empirical comparative data.

Assumptions

- Input data needed to drive a model (e.g., initial population size, age and sex composition, birth rate, survival rates, and immigration and emigration rates) are accurate and, often, precise.
- When comparing predictions from models to observed data, those observed data are also accurate.

Techniques
The techniques, and assumptions, associated with each model differ somewhat. However, in practice periodic comparisons with empirical data are needed to gauge performance and test inferences derived from models.

Body Condition

Body condition is the term used to describe the physical parameters of a mule deer as it relates to age, skeletal growth, antler growth, mass, and muscle and fat levels. Indices or measurements of those parameters, in carefully designed monitoring programs or research projects, can provide a better understanding how harvest, nutrition, weather, and habitat influence mule deer populations (Harder and Kirkpatrick 1994). Typically, measures of body condition parameters are used as surrogate measures of nutritional quality of mule deer habitat.

Researchers have investigated a variety of measurements and indices of fat deposition and body condition to identify effective predictors of overall deer and habitat condition. Techniques have run the gamut from simple, minimally invasive methods (e.g., Riney 1955) that usually produce relatively low or untested correlations with body condition to intensive techniques requiring specialized equipment (e.g., ultrasonography) that provide strong predictive capability.

There are 2 main categories of body condition measures: measures of body fat (such as body condition score, rump fat depth, and kidney fat), and morphometric measures such as skeletal size (e.g., hind-foot length), chest girth, and body mass. Some techniques can only be applied to dead deer (carcass scores, kidney fat, marrow fat), whereas others can be applied to living or freshly dead deer (skeletal measures, body mass, body condition scores, ultrasonography; see Riney, 1955, Kistner et al. 1980, Wallmo and Regelin 1981, Austin 1984, Stephenson et al. 2002, Cook et al. 2005). When using any condition index, the relationship of a measurement or index to body condition should be well validated. In particular, care should be taken to recognize limitations or sensitivity of different indices, as some are only valid within specific ranges of body condition due to their curvilinear relationships with condition (such that small differences in a measurement can produce large differences in estimated body condition). Further, some body condition measurements are not easily measured in the field, and personnel must be trained (sometimes extensively) to take these measures consistently (Cook et al. 2007).

When choosing indices or parameters to measure, it is important to recognize some measures have been validated against whole body composition in the laboratory. In particular, predicting body fat allows comparisons across studies that use different techniques (e.g., data from a kidney fat index obtained via hunter collections with data from ultrasound from live deer). Estimation of body fat also allows users to make predictions about health and productivity of deer based on published values (e.g., probability of breeding) that would otherwise be less objective if simply using index values (R. Cook, National Council for Air and Stream Improvement [NCASI], personal communication).

Seasonal variation in nutritional quality (and quantity) of forage plants and foraging efficiency of ungulates is evident in the annual cycle of fat deposition and catabolism (Kistner et al. 1980, Wallmo and Regelin 1981, Austin 1984). The role of fats in life histories of mammals was reviewed by Young (1976). As deer gain condition, fat deposition occurs first in the marrow;

then the viscera, including kidneys, heart, and omentum; and finally in subcutaneous depots (Cederlund et al. 1989). Deposited fat is utilized in the reverse sequence (Harris 1945). In general, fat deposition typically peaks in early fall for buck mule deer and early winter for does (Anderson et al. 1972), but consideration should be given to variation in fat deposition cycles throughout mule deer range. For example, mule deer in the Rocky Mountains should be in prime or close to prime condition during the fall hunting seasons, whereas mule deer in the Southwest Desert ecoregion may be coming out of the dry summer and into a period of nutritional abundance. Therefore, standard or consistent timing of data collection for some measures of body condition is necessary for valid comparisons through time.

Body condition scores.— Body condition score (BCS) methods were initially developed to evaluate live domestic animals and later adapted to wild mammals. A BCS involves evaluating fat and muscle amounts through palpation at different places on the body and assigning condition scores (Gerhart et al. 1996, Cook 2000). Proper use of these techniques requires various amounts of training; but if carefully applied, this approach can yield consistent and predictable results.

Advantages

- Method is representative of whole body fat measures, particularly when combined with other measures (e.g., fat depth, see below).
- Non-invasive and usable on live deer.
- Requires little time.
- Validated models exist.

Disadvantages

- Requires training (sometimes extensive) for consistent application.
- Potential for measurement bias.
- Not all methods are widely documented in the literature.

Assumptions

- No measurement error.
- Age of deer is known or estimated accurately.

Techniques

Unfortunately, specific scoring criteria for the most recent versions of the BCS technique for mule deer (e.g., Cook et al. 2007) have not been made widely available (because of the authors' contention that the procedure cannot be used without training; R. Cook, NCASI, personal communication). To date, most biologists using the BCS technique developed by Cook et al. (2007) have obtained direct or indirect training from those authors.

Gerhart et al. (1996), from which succeeding techniques were modified, developed a body condition scoring system for caribou (*Rangifer tarandus*). The procedure developed by Gerhart et al. (1996) evaluated fat and muscle on a scale of 1 (emaciated) to 5 (obese) at 3 points: withers (shoulders), ribs, and rump-hips. However, this technique has not been validated for other species.

Ultrasound.— Ultrasonography is one of the most reliable methods for determining body composition in live deer prior to depletion of subcutaneous fat reserves (Cook et al. 2007, 2010). This method allows direct measurement of fat and muscle thickness at specific locations that can be used to predict percent body fat and gross energy (Cook et al. 2007, 2010; Bishop et al. 2009*a*). Subcutaneous rump fat thickness (MAXFAT, determined by ultrasonography, Stephenson et al. 1998) can be mathematically combined with BCS to produce an index referred to as LIVINDEX (Cook et al. 2001). Cook et al. (2007, 2010) found a combination of rump condition score and fat depth was superior to BCS or MAXFAT taken individually and provided high correlations with total body fat over the entire range of body condition.

Advantages

- Objective measurements that are highly correlated with fat and gross energy composition determined by whole body analysis (when body fat is >6%).
- Relationships between measurements and body condition are nearly linear.
- Non-invasive and usable in live deer.

Disadvantages

- Equipment is expensive.
- Training is required. Inexperience can result in measurements being taken in incorrect locations, measurement errors, or measuring incorrect tissue layer.
- Deer must be captured and handled.
- May be difficult to use under some field conditions.
- At body fat levels <6%, rump fat is no longer present, so ultrasonography alone will not detect differences in condition.

Assumptions

- Ultrasound measurements are made at the correct location, on the correct tissue layer, and without measurement error.

Techniques

Ultrasound measurement techniques have been described by Cook et al. (2007). Measurements usually include longissimus dorsi muscle (loin) thickness (as a possible threshold index for extreme protein catabolism) and subcutaneous rump fat thickness. When ingesta-free body fat is <6%, ultrasonography must be replaced with BCS or other methods to accurately predict body composition.

Kistner index.— This index (Kistner et al. 1980) has proven quite useful for estimating body condition and displayed relatively strong correlation with total body fat when slight modifications to the original scoring system were made (Cook et al. 2007). The technique is only applicable to dead deer and requires several internal organs to complete the assessment. The Kistner scoring system evaluates fat deposition at 6 sites (heart, pericardium, kidney, omentum, rump, and brisket) and body musculature. Scores can range from 0 to 95 (or 100 as modified by Cook et al. 2007). However, subsets of the full Kistner score provide predictions nearly as robust as using the entire score (Cook et al. 2007).

Advantages

- High correlation with total body fat (r^2 = 0.92 when modified by Cook et al. 2007).
- Relatively easy to assign scores with moderate training and appears repeatable across observers.
- Requires no specific tools or equipment.

Disadvantages

- Body muscle and fat assessments are somewhat subjective.
- Requires internal organs typically removed by hunters (generally not available at check stations).
- Relationship is somewhat curvilinear at very high condition levels.

Assumptions

- Body muscle mass and fat deposition are accurate indicators of body condition.

Techniques

The Kistner index is a summation of body musculature assessment and body fat assessment scores. Body musculature (as modified by Cook et al. 2007) is rated as either 0 (bony), 5 (moderate musculature), or 10 (full musculature). Each of the fat depot sites is scored from 0 to 15 in increments of 5 (0 = none, 5 = slight amounts, 10 = moderate amounts, 15 = heavy amounts) in the original score and in increments of 1 as modified by Cook et al. (2007). To be scored as heavy amounts (score = 15), subcutaneous rump and brisket fat should be ≥0.75 in (2 cm) thick (Kistner et al. 1980). Subset scores (e.g., pericardium plus kidneys scores) can provide robust predictive measures of body fat if the entire deer is not available for assessment (Cook et al. 2007).

Femur marrow fat.— Marrow fat (in particular from the femur) has been studied and used as an index to body condition in cervids for many years (Cheatum 1949, Neiland 1970, Verme and Holland 1973, Torbit et al. 1988). Methods developed to assess femur marrow fat from dead deer range from cursory field methods based on color and texture to more quantitative methods utilizing wet and dry mass differences as a measure of fat content. Because marrow fat is the first to be deposited and the last to be mobilized (Cheatum 1949), this technique does have limitations and should be combined with some other measure of body condition to assess deer carcasses above 6% body fat. Cook et al. (2007) mathematically combined femur marrow fat and a kidney fat index (total fat mass) to create a separate index referred to as CONINDEX (Connolly 1981), which provided a robust predictor of mule deer body fat (r^2 = 0.92). Perhaps the greatest value of femur marrow fat alone as a condition index is to determine whether certain thresholds of body fat depletion have been reached (i.e., whether fat reserves are depleted to the point where marrow fat is being mobilized and whether marrow fat is mostly gone indicating most mobilizable fat reserves have been used).

Advantages

- Specimen collection is often relatively easy.
- Visual inspection can be done in the field without laboratory work.
- Laboratory processing techniques are fairly simple.
- Reliable indicator of malnourishment (when marrow fat is being mobilized).

- When combined with a kidney fat index, can provide a useful predictor of body fat over a larger range of body condition than when either is used alone.

Disadvantages

- Relationship to body fat is curvilinear and provides no predictive value when body fat levels are >6% (very narrow range of usefulness).
- Relatively low predictive value for body fat ($r^2 = 0.79$, Cook et al. 2007).
- Visual inspection techniques are typically not sufficiently robust for quantitative use.
- Can be difficult to collect on frozen carcass.

Assumptions

- Any depletion in marrow fat (<85%) indicates body fat is <6%.

Techniques

Remove the femur from the deer; if possible, estimate age of the deer. The bone can then be sampled or frozen for later examination. If the femur will be stored in a freezer for a long period, whole bones should be sealed in an air-tight bag to prevent desiccation. To assess marrow fat, break or saw the femur so as to remove a section of marrow. Examine marrow for color and texture as described by Cheatum (1949). Color and texture ranges from almost white and firm (prior to mobilization) to a red, jelly-like stage (poor condition). Texture and firmness, determined by feel, often provide more accurate determination than color in field examinations. The same sample can be used in the drying technique described by Neiland (1970) or chemical extraction methods described by Verme and Holland (1973). A common use of femur marrow fat examination is as an aid in assessing contribution of malnutrition in studies of cause-specific mortality.

Kidney fat indices (KFI).— A variety of measurements of fat deposition around kidneys have been developed as indices to body condition (see Riney 1955, Anderson et al. 1972, Cook et al. 2007). Different KFIs vary primarily with respect to what portion of the perirenal fat is measured (e.g., trimmed or whole fat mass) or whether a ratio is used that includes mass of the kidney (i.e., instead of using the fat mass as a stand-alone index). These indices provide moderately accurate estimates of total body fat in mule deer (Torbit et al. 1988; $r^2 = 0.81$-0.87, Cook et al. 2007). Cook et al. (2005) indicated KFI was a moderately useful technique, but had a limited range of usefulness, at least in elk. However, when combined with femur marrow fat into a CONINDEX (see femur marrow fat above), the value of KFIs can be improved.

Advantages

- Measurements can be collected in the field with simple equipment.
- Moderate correlation with body condition.

Disadvantages

- Curvilinear relationship to total body fat limits the range over which KFIs are considered sensitive to changes in body condition.
- Small measurement errors could have large effects on body fat estimation.
- Some KFI scores are subjective and may be influenced by observer effects.

- Accuracy and consistency of sample collection can be poor because identifying fat associated with kidneys is subjective.

Assumptions

- Measurement errors are very small and unbiased.
- Scores are consistent within and among observers.
- Age of deer is known or estimated accurately.

Techniques

Wide variation in kidney mass and KFIs have been noted by some investigators, so KFI should be determined consistently (use right, left, or an average of both; not a mixture). Techniques were described by Anderson et al. (1972) and Cook et al. (2007). Basically, kidneys and associated fat are removed from a carcass and weighed (to the nearest 0.1 g). For developing the KFI, perirenal fat can either be trimmed as per Riney (1955) or kept intact as per Anderson et al. (1972). To avoid issues with seasonal fluctuations in organ mass, mass of the fat alone can also serve as an index to condition. No matter which variation is used, log-transformed indices tend to provide greater correlation with total body fat (Torbit et al. 1988; Cook et al. 2001, 2007).

Wyoming index.— This index provides a quick and easy technique to use in the field or at a check station that requires only the typical field-dressed carcass. In deer, subcutaneous body fat is deposited along the spine starting on the rump, then over the kidneys, and finally over the shoulders. Thus, a deer in excellent condition will have fat along the entire length of the spine. A deer in fair or poor condition will only have fat over the rump. This technique is an assessment of body condition that incorporates the index of muscle condition developed by Kistner et al. (1980) and an index of subcutaneous body fat deposition along the spine (Lanka and Emmerich 1996, Lutz et al. 1997).

Advantages

- Can be used on harvested deer.
- No internal organs needed.
- Easily applied in the field and at check stations with only the carcass.

Disadvantages

- Body muscle assessment is subjective.
- Inexperienced observers can mistake connective tissue for fat.
- Even with modifications, only moderately correlated with total body fat in mule deer due to the categorical nature of this index ($r^2 = 0.75$, Cook et al. 2007).
- Relationship to total body fat is highly curvilinear when deer are at higher levels of body condition (limited range of use).

Assumptions

- Body muscle mass and fat deposition are accurate indicators of body condition.

Techniques
The Wyoming index is a summation of body musculature assessment score and body fat assessment score. Scores range from 0 (poor) to 20 (excellent) in increments of 5. Rump fat on deer in excellent condition (body fat score = 15) should be ≥0.75 in (2 cm) thick (Kistner et al. 1980). Because of the limited range of use and moderate correlative value, use of the Wyoming index should be limited to broad scale evaluations (e.g., herd unit).

Body Musculature (Maximum score = 5) – Ocular assessment of muscle mass of the deer. If body is bony, score = 0; body musculature is full, score = 5.

Body Fat (Maximum score = 15) – This parameter is obtained by making incisions in the deer's hide to assess whether or not fat is present at 3 locations over the spine: 1) just above the base of the tail, 2) above the kidneys, and 3) above the front shoulders (Fig. 9). If

No visible fat at point 1, score = 0;
If fat visible at point 1, score = 5;
If fat visible at point 2, score = 10;
If fat visible at point 3, score = 15.

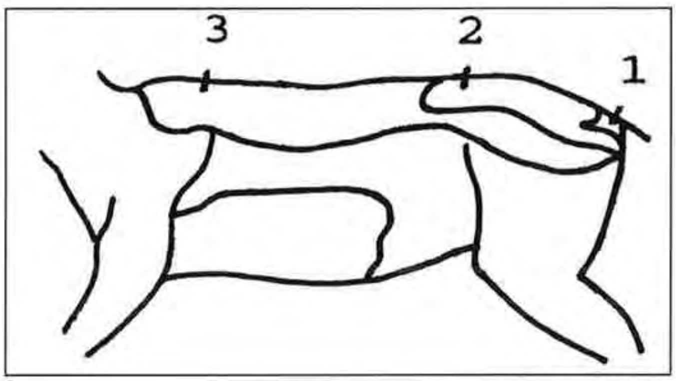

Figure 11. Body fat scoring incision locations and representative fat deposition. Figure courtesy of WGFD.

Xiphoid fat.— Xiphoid fat depth can be used as an index to overall body fat, and therefore body condition (Austin 1984). Body fat in northern mule deer is at a maximum in late fall and reflects the annual nutrition cycle (Wallmo and Regelin 1981). Thus, body fat can be inferred as a measure of summer habitat quality (Kistner et al. 1980). Xiphoid fat is deposited subcutaneously and thus is deposited last and used first (Harris 1945). Austin (1984) found xiphoid fat was most sensitive in yearling bucks, with fat deposition varying more in older deer.

Advantages
- Can be gathered at check stations or during field contacts.
- Minimally invasive to a carcass.
- Detects gross differences in condition.

Disadvantages

- Has not been validated against whole body fat.
- Does not reflect fine scale changes in overall body condition well.
- Usefulness generally limited to yearling bucks.
- Need ≥100 samples for useful comparisons.
- Measurement bias can be a problem.
- Can only be measured on dead deer.
- Fat depth may be obscured or altered by hunters during field dressing.
- Some hunters do not want their deer cut across the xiphoid process.

Assumptions

- Measurement is accurate and consistent.
- Fat deposition on the xiphoid is representative of the rest of the deer.

Techniques

Begin by making a 2-in (5-cm) incision through the hide to the base of the sternum and through the xiphoid process. Use a clear plastic rule to measure depth of fat between the skin and the process perpendicular to the sternum at several points along the first 0.75-1.25 in (2-3 cm) of sternum without deforming the layers. There is a thin layer of muscle <1 mm thick that lies beneath the fat layer; use that layer as a boundary for the measurement. Measure to the nearest millimeter and calculate a mean of multiple measurements. Occasionally there are multiple layers of fat, in which case, only the top layer should be measured (Austin 1984). Xiphoid fat depth is generally considered to have limited usefulness because of difficulty in obtaining accurate measurements and lack of sensitivity.

Metabolic indicators.— A variety of blood, urine, and fecal compounds have been investigated as potential indicators of nutritional status and body condition in deer (e.g., Saltz and White 1991*a*, *b*; Saltz et al. 1992; Saltz et al. 1995). Of all these compounds, serum thyroid hormone concentrations appear to have the most potential for evaluating the metabolic status of mule deer if used under the right conditions (Bishop et al. 2009*a*). Although serum thyroid hormone concentrations can be used to predict percent body fat, their greatest potential value is for evaluating relative condition of deer populations over time and by area. Mule deer does that received supplemental feed during winter in Colorado could be readily differentiated from does that did not based on their serum thyroid hormone concentrations (Bishop et al. 2009*a*).

Advantages

- Relatively easy and inexpensive to obtain if deer are being captured for other reasons, such as radiomarking.
- Applicable to live deer with minimal handling.

Disadvantages

- Deer must be captured to obtain blood samples.
- Thyroid hormones are only useful indicators when deer are in a catabolic state during late winter (limited range of usefulness).

- Samples must be taken during the same time of year and from the same sex and age classes to be comparable.
- Metabolic indicators are rate variables as opposed to state variables and can be highly influenced or confounded by nutritional status (diet), season, and sex and age of a deer.

Assumptions

- Serum thyroid hormone concentrations are related to long-term metabolic status rather than circannual patterns and short-term fluctuations or nutritional status (diet).

Techniques

The optimal time to take blood samples for thyroid hormone analysis is in late February and early March when deer are catabolizing their body reserves. Thyroid hormones can have little relationship to body condition when deer are in an anabolic state (i.e., during fat accretion) and can vary seasonally. Does are recommended for sampling over fawns and bucks because they will likely show a greater range of body condition and thyroid hormone concentrations in late winter. Bishop et al. (2009*a*) found total thyroxine (T4) and free T4 had higher correlations with body fat than total triidothyronine (T3) and free T3 in mule deer does, whereas Watkins et al. (1991) found T3 to be the best indicator in white-tailed deer fawns.

Skeletal size.— Skeletal size measures can be used as an index to growth, and thus nutrition, of deer when they were fawns. Skeletal measures have long been used as an index to age, growth rates, and body condition as a function of growth (Verme and Ozoga 1980). Common skeletal measures include total length, chest girth, femur length, hind-foot length, and metatarsal length. Hind-foot or metatarsal length measurements have been found to represent age and overall growth of mule deer fawns (e.g., Robinette et al. 1973) and can be more accurately measured than total length. Chest girth can be confounded by subcutaneous body fat, particularly in adults, and thus should be used in conjunction with other measures. Combinations of hind-foot length, chest girth, and body mass were used to assess winter fawn size and condition (M. Hurley, IDFG, unpublished data)

Advantages

- Skeletal measures are easy to obtain on live-captured or harvested deer.
- Measurement error for most variables is a minor issue with minimal training (however, chest-girth measurements may be prone to inconsistency).
- Skeletal growth can index nutritional quality of habitat during the period when most growth occurred (e.g., fawn measurements in early winter reflect summer nutrition; M. Hurley, IDFG, unpublished data).

Disadvantages

- Measurement errors can bias data, especially for longer measurements when a tape must be repositioned to complete the measurement.
- Requires large sample size and multiple years of data in order to make inferences about annual differences in body condition.

- Limited value unless used in conjunction with mass measurements for analysis.

Assumptions
- Systematic relationship between body condition and skeletal measurements.
- Ages and lactation status are estimated accurately.
- No measurement errors.

Techniques
Skeletal measurements should be made with a soft measuring tape (e.g., cloth, fiberglass) that will conform to body contours (when applicable) and not stretch or shrink under field conditions.

Total length – Measure is taken from the end of the nose to the tip of the tail by contouring along the spine.

Chest girth – Measured around the chest immediately behind the front shoulder and perpendicular to the spine. The tape end is then pulled firmly alongside the tape and length is measured on the exhale (Fig. 10). When measuring chest girth, tape tautness should remain as consistent as possible across deer and measurers in an effort to minimize measuring error.

Figure 12. Measuring chest girth of a mule deer fawn. Photo by T. Keegan, IDFG.

Hind-foot length – Measured from the tip of the calcaneus to the tip of the hoof along the lateral side (Fig. 11).

Figure 13. Measuring hind foot length of a mule deer fawn. Photo by C. Austin, IDFG.

Metatarsal length – Best measured with a large caliper starting at the tip of the calcaneus forward to end of the metatarsal with the hoof bent at 90 degrees to the metatarsal bone.

Body mass.— Body mass is a function of the combined mass of musculature, skeleton, viscera (with contents), and body fat of a deer. Monitoring differences and changes in mass can be a useful tool for examining body condition. For a small ungulate like mule deer, body mass is a relatively simple measure to obtain. Mass can be measured in terms of total body (alive or dead) or eviscerated carcass. Gerhart et al. (1996) used mass in combination with a body condition score to obtain a body reserve index for caribou. However, Cook et al. (2007) found mass did not improve predictive value of condition scores for mule deer.

Advantages

- Relatively easy to obtain.
- Small measurement error.
- Can be measured on live deer.
- May have potential for combination with other body condition measures to create condition indices.

Disadvantages

- Body mass is only moderately correlated with body composition in mule deer (Cook et al. 2007, Bishop et al. 2009*a*) and what mass alone indicates may be ambiguous.
- Ingesta mass and products of conception can greatly influence live body mass.
- Measures of eviscerated carcasses can be biased depending on which organs and other tissues are removed from the carcass.
- Differences in individual scales can bias data.
- Deer must be physically handled.

Assumptions

- All scales are calibrated the same.
- All measurements are accurate.
- Organs and tissue removed from eviscerated carcasses are the same.

Techniques

Body mass measure is taken by weighing the deer with a scale. Scales can vary from spring scales (most commonly used) to strain gauges (mechanical and electric). To obtain accurate measurements, the range of scales must completely overlap the range of expected deer body masses, while maximizing sensitivity of the measure. For example, if weighing deer neonates where maximum expected mass will be 15 lb (7 kg), biologists should use a 20-30-lb (9-14-kg) scale with ≤0.1-lb (0.5-kg) graduations, rather than a 300-lb (136-kg) scale with 5-lb (2-kg) graduations.

To obtain masses on un-sedated mule deer, they must be adequately restrained to reduce excessive movement. One of the easiest restraint methods is wrapping a nylon hobble around the 4 legs. Most wildlife veterinarians recommend weighing hobbled deer in a sternally recumbent position in a cloth or nylon bag. Maintaining sternal recumbency during the procedure helps prevent aspiration of rumen contents and gut torsion. For weighing neonates or young fawns, a small cloth or nylon bag that will securely hold the deer works well. Another acceptable method is to suspend the deer below a scale on a cradle or stretcher. Tare weights of restraining materials should be taken into account. When possible, someone other than those lifting the scale and deer should read the scale to ensure accuracy of measurements.

To provide useful information, mass measurements must be collected and reported by sex and age class. Mass of fawns and yearlings should be most reflective of recent environmental variation and thus more important in identifying relationships among habitat and weather conditions.

Antler size.— Antler size is directly related to 3 factors: age, nutrition, and genetics. Males on a higher nutritional plane are more likely to approach their maximum genetic potential for antler growth. Antler growth has been linked to nutrition in captive white-tailed (French et al. 1955) and mule deer (Robinette et al. 1973). Anderson (1981), using data from Snyder (1959), identified significant differences in yearling buck antler beam diameter between years of substantially different rainfall and attributed increases to increased nutrition. Similarly, several authors noted declines in proportions of spike-antlered yearling bucks under improved habitat conditions (Swank 1958, Snyder 1959, Wallmo 1960). Conversely, Anderson and Medin (1969) found antler growth did not change with changes in forage quality and availability during years of extreme difference in moisture in Colorado, but suggested antler growth was an accurate predictor of age for mule deer <40 months of age.

Although attempts have been made to use antler growth as an index to condition by age class throughout mule deer range, antler growth appears to be a poor or inconsistent predictor of body condition in free-ranging mule deer. Use of antler growth measures as an index to mule deer body condition may be limited because of the large degree of variation in antler growth across regions, probably in relation to differences in climate, habitat, and soil mineral content. Further, antler growth may only correspond to nutrition during a portion of the year. Antler measurements are typically collected from harvested deer.

Advantages

- Data can be easily gathered at check stations or in the field.

Disadvantages

- Only applies to males.
- To date, little, if any, quantitative relationship to forage quantity and quality (nutrition) has been documented for mule deer.
- Potential for measurement errors if data collectors are not properly trained.
- Reflective of only nutritional conditions before and during antler growth period and may not reflect current body condition.
- Age, genetics, and regional differences in nutrition exert a substantial and highly variable influence on antler growth.

Assumptions

- Ages accurately estimated.
- Antler development of local deer is similar and something less than the maximum genetic potential.
- Antler growth changes with buck age.

Techniques

Several different measures have been taken by researchers, including a main beam length, basal circumference, inside spread, number of points, and symmetry (Lindsdale and Tomich 1953, Anderson and Medin 1969, Robinette et al. 1973). Other researchers have measured antler volume using water displacement, antler mass, and combinations of tine length and diameter measurements (e.g., scoring systems developed for record keeping) to measure antler growth. As with body mass, data should be reported by age class, with yearling antler growth having the most potential to reflect nutritional conditions during the previous spring and summer. At this time, we recommend against use of antler size as a measure of body condition.

DATA STORAGE AND RETRIEVAL

Much has been written about study design, data collection, statistical analysis methods, and computer programs for population analyses (e.g., Bookhout 1994, Anderson 2001, Braun 2005, this handbook). But the wildlife literature is surprisingly deficient in describing methods for effectively storing and managing wildlife data. Organized and cost-effective data management, coupled with appropriate retrieval systems, is critical for efficiently synthesizing information and answering questions about mule deer populations.

Most mule deer managers are accustomed to storing and analyzing data they collected at a local level. However, demands and expectations for data typically exceed local needs. To be useful for jurisdiction-wide or regional management of mule deer, data must be shared and analyzed at those scales. Technical aspects of data management at such large scales, such as design of relational databases, may exceed the expertise of many mule deer managers and fall under the purview of information technology specialists or biometricians. But managers and biologists need to understand requirements and processes for correct data collection and storage as well as those for retrieving, analyzing, and reporting data.

There exist a number of common challenges in using and storing data. In this section, we address how to store your data in the most effective and efficient ways, now and in the future. Given the tremendous rate of change in computer technology, tools available in the future may be very different than what we have today, but we must ensure our data (past and present) are stored so their value is maintained in perpetuity.

Standardization

Carpenter (1998) identified the lack of standardized inventory methodologies and data management among agencies as an obstacle to understanding deer population status and management. He and others (e.g., White and Bartmann 1998, Bowden et al. 2000, Carpenter et al. 2003) recommended types of data that should be collected to monitor mule deer populations. Similarly, Ballard et al. (2002) were unable to conduct a synthetic analysis of deer radiotelemetry data from several western states because original data were often unavailable or irretrievable; they made a compelling case for integrating such data into centralized archives.

Mason et al. (2006) made a case for standardizing ungulate surveys and data management in the West and articulated a need for more research and monitoring at regional scales. Among their recommendations were:

- Review existing agency monitoring and management strategies to increase consistency and data sharing.
- Explore inconsistencies that impede greater interagency cooperation.
- Develop practical methods for statistically reliable deer and elk population monitoring and guidelines for data collection, storage, and sharing.
- Have each agency's results stored in a searchable relational database.
- Develop a regional archive of scientifically defensible data.

- Use interagency data to study trends and causes of population changes at landscape scales.
- Improve research and monitoring at regional scales.

Mason et al. (2006) concluded combining data among agencies will leverage increasingly scarce resources and lead to more efficient management and cost-effectiveness for each agency. They also suggested development of a regional data archive would strengthen credibility of agencies, broaden public support of harvest regulations, and reduce potential for legal problems caused by differences among agency management regimes. Rupp et al. (2000) suggested future challenges to population survey results would likely be based on statistical arguments about deficiencies in deer data. Consistent, long-term data are very valuable for adaptive management of wildlife species (e.g., Lancia et al. 1996*b*, Enck et al. 2006).

To aid in meeting recommendations of Mason et al. (2006), we suggest the following goals for any mule deer inventory or research project:

1) Collect high quality data (important and measured without error).
2) Ensure data are correctly and accurately entered into an electronic format.
3) Store data appropriately so information can be easily accessed when needed.
4) Store data securely to ensure integrity.
5) Provide access to data for everyone who needs or wants it (now and into the future).
6) Ensure data are easily comparable across subareas within your jurisdiction and across time, as well as among states and provinces.

Data Collection (Goal 1)

Previous chapters focused on appropriate data collection methods for mule deer. However, there are some basic aspects of data collection that can enhance data storage and retrieval. Raw data should be collected and stored at the lowest level possible, along with summarized or interpreted results (Huettmann 2005). Raw data can always be recombined or summarized, but the reverse is not possible. Maintaining raw data allows application of new or improved correction factors, statistical procedures, data groupings, or other analyses.

Widespread availability of GPS-enabled systems has been a boon to mule deer monitoring, allowing managers to record spatial locations with relatively high accuracy. However, inconsistent or erroneous use of geodetic datums and coordinate systems can reduce accuracy of such data (O'Neil et al. 2005). Ideally, all staff within an agency should use a single standard. At the very least, geodetic datum must be recorded and included with all records. Although conversion among datums is not difficult, for compatibility with current GIS, recommended datums are North American Datum of 1983 (NAD 83) or World Geodetic System of 1984 (WGS 84) (FGDC 1998, O'Neil et al. 2005). For ease in data entry and usage, latitude and longitude coordinates should be recorded as decimal degrees.

Data Entry (Goal 2)

Data must be accurately entered into a database or spreadsheet and double-checked for accuracy. Entry should be governed by data validation rules to help prevent erroneous, invalid, or duplicate data from being entered and uploaded. Data entry should be kept as simple, efficient, intuitive, and well-defined as possible. Most database programs allow constraints on data being entered to prevent out-of-range values, incorrectly formatted entries, or missing data. Spreadsheet entry provides an option for uploading large data sets as long as validation occurs during entry and upload.

Data Storage (Goal 3)
Most wildlife agencies have trained professional database managers (e.g., information technology specialists) who manage large databases of financial transactions such as license sales and budgets, and other specialists who develop web sites and user applications. But it is field staff who collect data describing deer populations, and this is typically where problems arise in data management.

The following scenarios characterize effective data management systems in keeping with recommendations of Mason et al. (2006):

- All similar data are combined into 1 large database (e.g., relational, hierarchical), covering all years and areas of the state or province.
- All data of a given type are in a single format.
- The database contains metadata which describe source, contents, and limitations of the data.
- The database is stored at a central location on a common network drive.
- All agency staff are networked together and use the same software (and same version) so they can all access central network drives.
- The network is protected by a firewall, virus scanners, and other security features.
- Network databases are backed up automatically (daily, weekly, monthly) and updated to account for new versions of software and hardware.
- Important datasets are password-protected and read-only, so only authorized users can make changes or view sensitive data.

Data Security (Goal 4)
Data security falls into 2 broad categories: maintenance of correct biological data and protection of personal information. Data maintenance begins with field data collection. Whether data are recorded on paper or electronically, care must be taken to protect the media until data can be replicated and transferred to permanent storage. Any number of mishaps can cause loss of data (e.g., theft, physical damage, or loss of equipment or storage media; accidental or malicious computer problems; large-scale disasters), so data must be replicated and stored in several locations to ensure integrity. In concert with an appropriate storage system, data security can be enhanced at various levels through read-only access protection, password protection, firewalls, and protective programs (e.g., against viruses, malware, spyware). Any changes to a database should be recorded as part of the metadata (see below).

Although security of biological data is integral to mule deer management, security of personal information has more far-reaching legal and social ramifications due to potential for identity theft and other fraudulent uses. Most agencies have developed policies and procedures for protection of personal information, but some information may still be widely available to agency personnel (e.g., lists of license holders with personal information, harvest reports). Personal information, particularly Social Security or driver's license numbers, should not be transferred from agency databases to portable computers or storage media or unsecure computers. If such transfer is required, data should be password protected and encrypted.

Data Accessibility (Goal 5)
Data (raw and summary) should be made easily accessible so it can be provided to other users in your own agency, agency managers, other agencies, and stakeholder groups (Huettman 2005). Although wide access to data may be a cause for concern (e.g., misinterpretation, misuse, pre-publication release), data collected by government employees are essentially public property and thus available to anyone through various public records laws. In the case of sensitive or draft data, access can be controlled through a variety of security measures.

Access to data may take several forms: collaboration and analyses among agency staff; information needs of policy makers (directors, commissioners, legislators); requests from stakeholders; and legal requirements (reports to funding agencies, legal challenges). Thus, requests for information can range from simple to extremely complex. Regardless of complexity, the process of providing answers is facilitated through use of queries and well-organized databases.

An important aspect of data management, access, and queries is database structure. Data must be structured so as to allow efficient queries. Required products might include a sub-set of data records, summary table, graphic representation, statistical analysis, or GIS map. Producing these items usually requires exporting data into a statistical or graphics software package. Therefore, data should be structured to enhance extraction and be flexible in a number of different formats. Relational or hierarchical database structures offer several advantages in accessing, managing, and summarizing data. In some cases, connections can be designed to directly access a database and transfer specific data on demand. Professional credibility is enhanced by having and providing high quality data in an appropriate format with advanced analyses when requested.

For some assessments, different types of data from several sources must be compiled. For example, harvest, GIS, and license data are usually kept in separate databases from inventory data, but might be used together to assess harvest success by management unit. Similarly, multiple data sets might be needed for population modeling. Ability to integrate multiple datasets for applications should be considered when designing a database system. Most database programs allow data from many sources to be easily connected.

Positive attributes of data accessibility include

- Accessible via commonly available software (others could find and access data in your absence).
- Easy to understand (e.g., simple formats and clearly labeled variables).
- Metadata available to describe the database.
- Easy to summarize (e.g., within and across years, geographic areas).
- Easy to analyze (using queries, statistical packages, etc.).
- Ability to generate automatic analyses and summaries for users (including those who collected and entered the data).

- Data tables can be exported directly into other programs (statistical packages, graphics software).
- Data can be linked to or easily uploaded to an agency website.
- Data can be linked to other applications (e.g., on-line hunter assistance programs).
- System is adaptable to take advantage of new technologies.

An important feature of centralized databases with well-designed access is cost savings. Cost of data storage is now so low that there is very little expense involved in storing and backing-up the largest data files (possibly excluding high-resolution photographs and GIS maps). A much greater expense would likely arise from inefficiently finding, managing, and comparing many separate smaller data files on different computers. Further, a single database approach is more efficient with regard to back-up procedures and software updates and conversions.

Data Comparability (Goal 6)
The most important requirement for ensuring data are comparable is standardization. Each user should record data in the same format, across years and management units, and have them stored in the same location. Ideally, raw data collected in one jurisdiction would be similar to data collected in nearby jurisdictions. Object-oriented data storage models (e.g., eXtensible Markup Language [XML]) provide a flexible structure to store and transport data in different formats and across different systems and may facilitate information exchange among agencies via the Internet. This approach allows comparison and collaboration among jurisdictions, resulting in more rigorous scientific results, more appropriate policy decisions, and hopefully, the ability to withstand social and legal challenges. Numerous benefits derive from being able to compare data collected by different methods in the same or similar locations (e.g., Unsworth et al. 1999*b*, Freddy et al. 2004). Vast amounts of data have been collected across the range of mule deer, and we would all benefit from regional or range-wide analyses of this information (e.g., Ballard et al. 2002).

Most large organizations are moving toward standardized and centralized data management. There are many advantages:

- Data are much more secure. Likelihood of data loss due to accidental erasure, computer breakdown, corrupted data files, stolen hardware, retirement or death of an employee, power surges, natural disasters, etc. is significantly reduced. Files can be password protected or placed behind firewalls.
- Datasets are all-inclusive through time and space, facilitating summary and analysis at multiple scales.
- Data can be backed up more efficiently.
- Data can be jointly viewed by many different users, in different locations, at the same time.
- Software upgrades, and corrections and improvements to data can be done once and provided to everyone (e.g., revision of DAU groupings).
- Purchasing power of entire government agencies allows use of similar computers and software packages which enhances computer maintenance and reduces training needs.
- Consistent data formats and management can be applied to multiple species.

However, no system is without some negative aspects. Potential disadvantages for centralized data management include

- Some agency staff may resist due to perceived loss of control over data, concerns about ability to access data, or unfamiliarity with software.
- Conversion may require strong leadership to convince everyone involved to use standard formats and central storage. Clear agency policies on data management are essential.
- May require a dedicated database manager and additional specialists to manage data and run complicated queries.
- May require multiple back-up methods (e.g., tape, server, CD-R) and locations (on-site and off-site).
- The need for automated queries or programming usually requires additional staff time.
- Networks can occasionally suffer from technical problems (low speed, service disruptions), particularly for remote users.

Computer Technology
There have been incredible changes in computer technology since approximately 1986, when many biologists began using personal computers. White and Clark (1994) described in detail software and hardware available at the time and noted "computer use had exploded" in the previous 20 years. They went on to state computer use was the fastest developing part of the wildlife profession and predicted huge changes in the future. Some 15 years later, some of the technology they described is now obsolete.

And yet, many problems identified by White and Clark (1994) are still with us: entering, storing, and documenting data for effective use; backing up data to prevent loss; obtaining appropriate, affordable software; and staying current with computer technologies. Perhaps surprisingly, there is little mention of these topics in the most recent wildlife techniques manual (Braun 2005).

Keeping up with technology is just as large a problem for us now. For example, by the time this document was published, there was a new version of the software used to produce it. In the near future, computers, servers, networks, and storage devices may barely resemble current technology.

Older media (e.g., floppy disks, diskettes, tape drives, and now CD-Rs), once standard technology, are rapidly becoming outdated and data backed up on those media may already be difficult to retrieve. Stability of various digital storage media are not well understood, but failures of CD-Rs within 5 years have been noted and stability varies among different types and manufacturers (Slattery et al. 2004, Bradley 2006). Further, CD-Rs may become obsolete as technology advances (Bradley 2006). In contrast, portable hard drives and flash drives can inexpensively store enormous amounts of data (e.g., 1 terabyte = 1 million megabytes or approximately 1 million 3.5-in diskettes). Regardless of the storage media, managers must develop specific plans for updating storage as technology advances.

Software
Making recommendations about specific software is difficult and such recommendations can quickly become obsolete. The computer industry is very competitive and there are numerous

similar products available to serve a specific purpose, often at a range of prices. In many cases, agency staff have computers and software purchased as a package through government purchasing (lowest bid), and therefore not under direct control of individual staff. Therefore, for simplicity, we will speak generically of several kinds of software.

Microsoft (Redmond, WA) products (e.g., Excel, Access, SQL Server) are the most widely purchased programs running on personal computers. However, there are other similar products available, with different features or prices, including open source counterparts available through the Internet at no cost. Users should look for products that allow for simple exchange of data among various software programs.

A variety of statistical packages are available, both as stand-alone commercial software (e.g., SAS [SAS Institute, Cary, NC], SPSS [Chicago, IL], Statgraphics [Statpoint Technologies, Warrenton, VA], Systat [Systat Software, Richmond, CA]), or freely downloadable programs (e.g., R-Project, www.r-project.org/). R is a free software language and environment for statistical computing and graphics that provides a wide variety of statistical (e.g., linear and nonlinear modeling, classical statistical tests, time-series analysis, classification, clustering) and graphical techniques.

Either spreadsheet or database software can be used for managing and analyzing a dataset (entering data; combining, comparing, and manipulating these data; joining with other data sets; and backing them up). Which is more appropriate depends on size of the dataset and types of manipulations to be applied. If you can store and analyze all of your data on 1 worksheet of a spreadsheet, then a spreadsheet may be a practical alternative to a database program, although spreadsheets have limitations. Conversely, a database program is the best way to store and manage large amounts of complicated data, particularly when data must be combined from multiple sources or files to conduct analyses.

Spreadsheets (for use as a database)

Advantages

- Relatively simple to learn and use.
- Best for small datasets (e.g., <1,000 records).
- User can easily conduct complicated arithmetic (including population modeling) and moderately advanced statistical procedures.
- Producing charts and graphs is convenient.
- Easy to print simple reports and lists of records.
- More efficient for a one-time analysis.
- Easy data duplication.
- Many diverse plug-ins available.

Disadvantages

- Unable to check data validity during entry.
- Creating subsets of data can be challenging.
- Difficult to join or compare 2 lists.
- Data records (cells) are not linked and can be scrambled by improper sorting.

- Difficult to conduct complicated queries or analyze across multiple groups.
- Known to produce mathematical errors under some circumstances, particularly when there are missing data values (Powell et al. 2008). Difficult to check math for large spreadsheet calculations.
- Difficult to print records in complex formats (e.g., reports).
- Lack database security features.
- Limited capacity.
- Only available to 1 user at a time, which can lead to creation of multiple versions.

Relational databases

Advantages

- Capable of efficiently storing and manipulating large, complicated databases (thousands to millions of records).
- User can create data input forms with constraints on data input, which reduces invalid entries (e.g., prevent missing values, ensure correct format, specify bounds, limit entries to drop-down lists).
- Allows user to develop and save powerful queries (e.g., sort and group records, select subsets of records, join several subsets of records to create a new table for analysis, conduct arithmetic and simple statistical procedures).
- Flexibility in specifying export content and format; allows use in many other programs.
- Data records are unique entities that cannot be scrambled by sorting procedures.
- Ability to develop automated queries for common data analysis questions.
- Allows for online analytical processing to conduct real-time, easily customized, or complex queries.
- Allows for advanced security.
- Can be accessed by multiple users at the same time.

Disadvantages

- More difficult to learn and use.
- May need a technical specialist for more complicated queries or specialized uses.
- Limited graphics capabilities, so user must export data to other software packages to create charts and graphs.
- Limited capability for statistical analysis, so user must export data to other software packages.

Data Continuity and Metadata

Guaranteeing availability and maintenance of datasets through time is a critical aspect of mule deer management. As databases grow through time, so does reliability of estimates derived from the data and ability to conduct more complicated analyses. Many attempts to retrieve and analyze important, expensive information have failed because data have been lost or stored in unusable or obsolete formats (e.g., Ballard et al. 2002). Provisions for data continuity and compatibility should be a foremost goal in the design of data management systems. Although determining likely future data formats is challenging, these actions will enhance future compatibility and continuity:

- Upgrade files and data to newer data storage media as they become available (but maintain older versions as well).
- Update software (e.g., database, spreadsheet) to newer versions as they become available.
- Store data media in ≥2 safe places (e.g., network server, office, home).
- Name files clearly with appropriate dates so someone else can find them.
- Provide metadata to describe files, their sources, and their purposes.

What do you wish you knew about data collected by your predecessors 30 years ago? What will your successors want to know about data you collected, 30 years from now? A large proportion of wildlife managers are nearing retirement age (McMullin 2004) which may result in a significant loss of institutional knowledge. In the context of database management, this knowledge is equivalent to metadata.

Metadata are information which describe and document data in a dataset. A data file is simply a set of numbers or words unless there is documentation to identify what values mean and how they can be used. O'Neil et al. (2005) noted the importance of metadata to document contents of a dataset, as well as how data were created, how to use data efficiently and effectively, and how to prevent loss of critical information, especially when staff move to other positions or retire. Inclusion of metadata is particularly important if data are made available to other people (within or outside your agency).

Over time, methodologies and personnel involved in mule deer monitoring will gradually change. Tracking those changes can preserve the value of data, either by maintaining consistent protocols or documenting transitions. Correct use of metadata can prevent problems such as loss of information with staff changes, data redundancy (multiple similar versions, sometimes conflicting), misapplication of data, and improper decisions based upon poorly documented data. As with all data, metadata need to be stored securely in a central location, in one format, following standard protocols (e.g., Kimball 1998), and backed up.

Metadata documentation is required of any spatial datasets created with federal funding (Huettman 2005, O'Neil et al. 2005). The Federal Geographic Data Committee (FGDC) provides detailed standards for spatial data sets and justification for their use (www.fgdc.gov/metadata). These standards should be applied to all mule deer datasets.

Typical metadata include

- Why data were collected and how they should be used.
- Who collected the data.
- What is included in the dataset.
- Definitions of variables and data fields, including units of measure.
- Clear definitions of any codes, labels, or specific terms (e.g., 1=male, 2=female).
- Methods used to collect data: where, when, and how collected (e.g., aircraft type).
- Conditions under which data were collected (e.g., weather).
- For spatial data: geodetic datum, coordinate system, and format (e.g., NAD 83, latitude-longitude, decimal degrees).
- When data entry occurred.

- How any secondary calculations were made.
- Known biases or other issues inherent in the data.
- Where data are stored (including back-up) and how they can be accessed.
- What software and statistics were used to create the database and analyze data.
- Who has permission to use, edit, and distribute data to others.
- Location of any summaries, reports, or publications.
- For data acquired elsewhere, a description of its origin and how it was obtained.

Images

Photographs, slides, and digital images represent unique and valuable data that cannot be stored in the same ways as typical data. Although many of the same principles of storage and accessibility apply, images must be cataloged to allow efficient retrieval and use. A first step is developing a system for naming files of digital photographs, including important identifying information (metadata) such as photographer's name, date, location, subject, and direction or aspect of view. Physical photographs and slides should be scanned to produce digital images and stored in a central repository, as well as saving physical originals.

Commercially available software is available for managing images. Images can be stored within databases, but usually require additional software or computer programming to allow for uploading files. Additionally, images stored in databases may be difficult to view or be viewable in limited software packages. A preferable alternative to storing images in databases may be to store images in a central filing system, then add locations of files to the database.

SUMMARY

The importance of designing monitoring efforts in the framework of statistically sound sampling cannot be over-emphasized. Many monitoring efforts fall short because they lack this critical component. Sampling designs allow the investigator to determine precision (reliability or repeatability) of resulting estimates. Measures of precision are necessary to determine the probability that implemented management approaches will achieve desired outcomes. The importance of statistically sound sampling must be recognized from the beginning of any monitoring effort, not at the end, by seeking advice of a statistician early in the design phase.

We present and discuss a wide variety of monitoring techniques organized by monitoring topic. Numerous population indices are discussed, with special attention given to weaknesses of correlating indices to actual changes in population abundance. Discussions of individual techniques are accompanied by descriptions of principal advantages and disadvantages of each. In addition, critical assumptions about techniques are presented, with pertinent literature sources provided for further investigation. Our intent is that readers of this document will find it essential to become informed on mule deer monitoring techniques.

Management Objectives
Before any monitoring data are collected, it is important to clearly state and understand your mule deer management objectives. Which type of data and technique are needed to meet objectives of the management effort? Management objectives are a combination of biological and social needs and are arrived at after considerable discussion and debate.

Some management objectives are easier to achieve than others and may require considerably less intensive monitoring than more complex objectives. You must understand what your management system is designed to do and critically evaluate what information is needed to reach those objectives. The section on recommended monitoring standards is designed to help the reader better understand what type of data and what intensity of measurement will be needed given a variety of typical mule deer harvest systems. As population management moves closer to maximized harvest objectives, monitoring intensity should increase to ensure harvest levels are appropriate. Developing a monitoring approach to provide data to ascertain if and when you have reached stated objectives is highly critical to efficient and successful management. A table is presented that identifies potential population parameters and the frequency at which measures should be made as management intensity increases. This analysis and synopsis is a very useful tool and deserves careful review and understanding. The first 2 sections in this handbook address these important topics and are a "must read" before moving on to selection of specific techniques.

Parameter Estimation Techniques
As would be expected, the meat of the document resides in the section on parameter estimation techniques. The reader is provided with a thorough discussion of a wide variety of mule deer monitoring techniques to estimate harvest, population trend, abundance and density, survival, age and sex composition, and body condition. A brief description of the purpose and use of each technique is presented. References to key literature sources for each technique are also provided. Following the introductory material, bulleted lists of advantages and disadvantages, including

critical assumptions that must be made with each technique, are presented. To the uninitiated, this array of techniques may at first seem overwhelming. However, having these concise and succinct descriptions available in 1 document is an advantage and serves a need that has existed for some time.

This document is titled "Methods for Monitoring Mule Deer Populations." The reader will be exposed to a variety of methods presented to inform and assist in selection of the most appropriate approach for a given monitoring objective. Considering the wide variability in terrain, vegetative cover, and weather conditions across the range of mule deer, recommending any one approach is difficult and perhaps presumptive. However, the methodologies that have proven to be most reliable and dependable are recommended.

No single method can be expected to perform in superior fashion for every situation. Unfortunately, the adage "you get what you pay for" is pertinent to choosing monitoring approaches, and often methods that require the largest investments, either in human or fiscal resources, provide the most "bang for the buck." A key challenge in choosing a monitoring technique is to first decide the level of precision or accuracy required to answer the questions you are asking. That decision will then provide the basis for determining the most appropriate technique and level of investment required. However, users have demonstrated certain methods, if applied appropriately, will produce robust data. To aid the investigator in making these choices we have selected the methodology that we judge to be the most reliable and preferred approach for each basic parameter estimation process.

Harvest

Delays in obtaining harvest data prior to making future harvest decisions have haunted mule deer managers for decades. Mail or telephone surveys have been the gold standard for many years, but changing computer technologies are rapidly altering the landscape for estimating mule deer harvests. Development and access to the Internet opens doors to surveying hunters more easily and quickly. Concomitantly, improved software packages enhance the ability of a manager to analyze harvest data without having to handle the data. Recently, wildlife agencies have incorporated web-based surveys with telephone surveys (Lukacs 2007). Results of these efforts are promising, and with continued development this approach will likely be the preferred technique of the future. However, these probability-based surveys should not be confused with user-selected web or telephone reporting or questionnaires which are likely to result in substantive non-response biases.

Trends in Population and Demographics

Historically, one of the most common measures for assessing mule deer populations and demographics was some index of population trend. The underlying assumption of a trend index is that there exists a homogenous (across time, habitats, etc.) and proportional relationship between a change in the trend index and a change in abundance or other population parameter. The primary problem with trend indices is the relationship between an index and the population parameter in question has not been determined and is most likely not consistent.

Consequently, recommending any single trend index is difficult. We thoroughly describe advantages, disadvantages, and assumptions for a wide variety of indices that have been used. If a trend index is to be used, it will only be valid if employed with a sound sampling framework and when assumptions are met or addressed statistically. Historically, indices such as pellet group counts, minimum aerial counts, and harvest per unit effort, when applied appropriately, have provided useful information. Minimum aerial counts and classifications are the most commonly used indices. If an index is chosen as a method to monitor population trajectory or performance, it is imperative that the user investigate and determine the relationship between the index and the population parameter in question.

Abundance and Density – Sample-based Methods
One of the most desired measures of any wildlife population is an estimate of abundance. In all likelihood, more fiscal resources are allocated to estimating abundance than any other parameter. Estimates of abundance over broad geographical areas are often desired to manage mule deer populations. Given that obtaining total census counts of mule deer is impractical, development of statistically-based sampling systems becomes necessary.

There are a plethora of methods that have been employed, and most are based on the likelihood that deer can be observed from an aerial-based platform. The fact that detectability of mule deer is typically <100% has been widely demonstrated. Further, detection rates vary across habitats and result in underestimates of total deer present and the need to calculate some measure to account for this bias. The most common approach to estimate these biases includes variations and combinations of mark-resight, distance sampling, and sightability models. We present a thorough discussion of the advantages, disadvantages, and assumptions of each approach and it appears use of detection rates is appropriate.

The variability in detecting mule deer over widely differing habitats makes it necessary to develop correction factors by determining detectability of deer related to variables such as group size, overstory cover, terrain, snow cover, type of aircraft, observer experience, and survey intensity. Correction factors may be developed through a variety of techniques, although using radiomarked deer is the most common approach. Once an investigator develops a sightability model for a specific situation based on relevant covariates, future surveys can be conducted without the need for radiocollared deer. This approach, when applied under a sample-based system, seems to be the most robust and should be the template for obtaining mule deer abundance estimates.

Population Modeling
Various models have been used for years to provide mathematical simulations of mule deer populations. All models are dependent on the quantity and quality of data utilized. Earlier population models essentially allowed the user to manipulate a variety of parameters and assumptions to improve "fit" between observed and modeled data. These models were not very transparent and a major disadvantage was that users frequently did not understand or appreciate how data were being manipulated.

Optimally Fitted Cumulative models align predicted and observed parameter estimates using an objective mathematical algorithm based on an ordinary least-squares estimator. These models can be objectively evaluated and compared based on fit and thrift and appear to have several advantages over previous models. Advent of these models and associated software programs have greatly improved population modeling and brought greater credibility to this approach. We do not recommended use of population modeling alone as a method to make management decisions about mule deer populations, but OFC models can be valuable tools to better understand and evaluate population measures.

Survival Rates

Survival rates of adult females and fawns are the most important parameters influencing mule deer populations and very useful data for population models (Lukacs et al. 2009). A variety of approaches have been used to estimate survival rates, but use of radiotelemetry is the most efficient and direct method. A disadvantage is the relatively expensive equipment and monitoring costs. Software to analyze survival data has greatly increased utility of such data. Considering the costs of this approach, we recommend a subset of management areas be chosen to serve as "representative" of other areas, thereby avoiding the need to sample all populations of concern. The utility and robustness of data obtained from radiotelemetry renders it the method of choice when the observer is measuring survival.

Age and Sex Composition

Knowledge about the age and sex composition of a mule deer population is an important consideration in mule deer management. Various approaches have been utilized to determine these parameters. Bias in data obtained is a significant concern and can come from several causes such as observer error, or inadequate or improperly designed samples. Having well-trained, experienced observers who are able to accurately identify age and sex categories is highly important to obtaining valid data. The most common and recommended approach is to obtain composition data via observers in aircraft, preferably helicopters. Under some circumstances, observers might be more accurate if classifying deer during ground observations. However, the ability to sample larger and more inaccessible areas and obtain more observations from the air makes aerial measurements most efficient. Detection biases by age or sex class are major problems and must be accounted for. Generally, improved sampling designs that cover all habitat aspects are recommended.

Body Condition

Growing concerns and interest in the condition of mule deer habitats have spawned efforts to improve measures of mule deer body condition. There are 2 main types of body condition measures: morphometric measures such as skeletal size and body mass, and measures of body fat. Some measures are suited only to dead deer whereas others can be applied to living or dead deer. Once again, measures of body condition are indices and concerns about reliability of an index discussed earlier also apply here. Many of the body condition measures are somewhat subjective and rely upon observer training and consistency to be meaningful. Others, such as ultrasonography, produce more objective and repeatable measures of body composition. Few methods are robust across the entire range of mule deer body condition, so combinations of measures are often necessary and improve reliability of estimates. Combinations of more direct measures of body fat, supplemented by morphometric measures, seem to be the most promising approaches. As always, sound sampling approaches must be implemented.

Data Storage and Retrieval
Any monitoring effort is only as good as the data obtained. Considerable effort and care must go into planning how data will be recorded, transcribed, analyzed, stored, reported, and updated as media technology changes. Any break in this chain of events risks the loss of very expensive and perhaps irreplaceable information. Efforts directed at improving the data gathering process at the beginning of the monitoring effort will return great dividends once field work is done.

Stages of data handling are presented to help break the process into important components. To maximize benefits, data must be standardized and consistent in format, widely available to other users, secure, and safely backed up at multiple sites. Efficiencies of today's hardware and software allow data to be statistically analyzed and immediately reported. The ability to immediately construct summary tables and graphics must be maximized. How to organize and store data so these important steps can be realized is covered in considerable detail in the section on data storage and retrieval.

This handbook is designed to provide all mule deer investigators with useful reference information. The intent is to foster more informed and potentially consistent approaches to mule deer monitoring among investigators across the range of mule deer and lead to enhanced data sharing within and among states and provinces.

Finally, an important, but often overlooked, factor is the level of training of observers and, in the case of aerial monitoring, pilots. Data obtained using an appropriate technique, which has been implemented correctly, but collected by inexperienced or inadequately trained practitioners may suffer in quality. Time spent ensuring observers are familiar with the entire monitoring experience before actual data collection begins will pay great dividends.

As professionals, we owe the magnificent mule deer and the many publics who enjoy them our very best efforts in our monitoring work. The decisions we make can only be as good as the information we collect. This document should be a valuable link in this important process.

LITERATURE CITED

Ackerman, B. B. 1988. Visibility bias of mule deer census procedures in southeast Idaho. Dissertation, University of Idaho, Moscow, USA.

Anderson, A. E. 1981. Morphological and physiological characteristics. Pages 27–97 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. Wildlife Management Institute, Washington, D. C., and University of Nebraska Press, Lincoln, USA.

Anderson, A. E., and D. E. Medin. 1969. Antler morphometry in a Colorado mule deer population. Journal of Wildlife Management 33:520–533.

Anderson, A. E., D. E. Medin, and D. C. Bowden. 1972. Indices of carcass fat in a Colorado mule deer population. Journal of Wildlife Management 36:579–594.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Aney, W. W. 1974. Estimating fish and wildlife harvest: a survey of methods used. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissioners 54:70–99.

Atwood, E. L. 1956. Validity of mail survey data on bagged waterfowl. Journal of Wildlife Management 20:1–16.

Austin, D. D. 1984. Fat depth at the xiphoid process – a rapid index to deer condition. Great Basin Naturalist 44:178–181.

Ballard, W. B., J. C. deVos, Jr., J. F. Kamler, and H. A. Whitlaw. 2002. A need for an integrated radiotelemetry database. Wildlife Society Bulletin 30:263–264.

Barker, R. J. 1991. Nonresponse bias in New Zealand waterfowl harvest surveys. Journal of Wildlife Management 55:126–131.

Bartholow, J. M. 1999. POP-II system documentation. Fossil Creek Software, Fort Collins, Colorado, USA.

Bartmann, R. M., L. H. Carpenter, R. A. Garrott, and D. C. Bowden. 1986. Accuracy of helicopter counts of mule deer in pinyon-juniper woodland. Wildlife Society Bulletin 14:356–363.

Bartmann, R. M., G. C. White, L. H. Carpenter, and R. A. Garrott. 1987. Aerial mark-recapture estimates of confined mule deer in pinyon-juniper woodland. Journal of Wildlife Management 51:41–46.

Bender, L. C. 2006. Uses of herd composition ratios in ungulate management. Wildlife Society Bulletin 34:1225–1230.

Bender, L. C., W. L. Myers, and W. R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. Wildlife Biology 9:199–205.

Beringer, J., L. P. Hansen, and O. Sexton. 1998. Detection rates of white-tailed deer with a helicopter over snow. Wildlife Society Bulletin 26:24–28.

Bishop, C. J., D. J. Freddy, G. C. White, B. E. Watkins, T. R. Stephenson, and L. L. Wolfe. 2007. Using vaginal implant transmitters to aid in capture of mule deer neonates. Journal of Wildlife Management 71:945–954.

Bishop, C. J., B. E. Watkins, L. L. Wolfe, D. J. Freddy, and G. C. White. 2009*a*. Evaluating mule deer body condition using serum thyroid hormone concentrations. Journal of Wildlife Management 73:462–467.

Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009*b*. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172.

Bookhout, T. A., editor. 1994. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Bowden, D. C. 1993. A simple technique for estimating population size. Technical Report 93/12, Department of Statistics, Colorado State University, Fort Collins, USA. <http://www.stat.colostate.edu/research/Technical%20Reports/1993/93-12%20Bowden.pdf>. Accessed 17 Nov 2009.

Bowden, D. C., A. E. Anderson, and D. E. Medin. 1969. Frequency distributions of mule deer fecal group counts. Journal of Wildlife Management 33:895–905.

Bowden, D. C., A. E. Anderson, and D. E. Medin. 1984. Sampling plans for mule deer sex and age ratios. Journal of Wildlife Management 48:500–509.

Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

Bowden, D. C., G. C. White, and R. M. Bartmann. 2000. Optimal allocation of sampling effort for monitoring a harvested mule deer population. Journal of Wildlife Management 64:1013–1024.

Bradley, K. 2006. Risks associated with the use of recordable CDs and DVDs as reliable storage media in archival collections – strategies and alternatives. Memory of the World Programme, UNESCO, Paris, France. <http://portal.unesco.org/ci/en/files/22734/11571181531CD_DVD_for_UNESCO_final__2006.pdf/CD%2BDVD%2Bfor%2BUNESCO%2Bfinal%2B%2B2006.pdf>. Accessed 12 Nov 2009.

Braun, C. E., editor. 2005. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Brinkman, T. J., D. K. Person, F. S. Chapin III, W. Smith, and K. J. Hundertmark. 2011. Estimating abundance of Sitka black-tailed deer using DNA from fecal pellets. Journal of Wildlife Management 75:232–242.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data – a handbook. Second edition. U.S. Fish and Wildlife Service Resource Publication 156, Washington, D.C., USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, United Kingdom.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, United Kingdom.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference. Springer-Verlag, New York, New York, USA.

Carpenter, L. H. 1998. Deer in the West. Pages 1–10 *in* J. C. deVos, Jr., editor. Proceedings of the 1997 Deer/Elk Workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

Carpenter, L. H. 2000. Harvest management goals. Pages 192–213 *in* S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Carpenter, L. H., D. Lutz, and D. Weybright. 2003. Mule deer data types, uses, analyses, and summaries. Pages 163–175 *in* J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Caughley, G. 1974. Interpretation of age ratios. Journal of Wildlife Management 38:557–562.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, USA.

Cederlund, G. N., R. J. Bergstrom, and K. Danelli. 1989. Seasonal variation in mandible marrow fat in moose. Journal of Wildlife Management 53:587–592.

Cheatum, E. L. 1949. Bone marrow as an index to malnutrition in deer. New York State Conservationist 3(5):19–22.

Cogan, R. D., and D. R. Diefenbach. 1998. Effect of undercounting and model selection on a sightability-adjustment estimator for elk. Journal of Wildlife Management 62:269–279.

Conner, M. C., R. A. Lancia, and K. H. Pollock. 1986. Precision of the change-in-ratio-technique for deer population management. Journal of Wildlife Management 50:125–129.

Connolly, G. E. 1981. Assessing populations. Pages 287–345 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. Wildlife Management Institute, Washington, D. C., and University of Nebraska Press, Lincoln, USA.

Cook, R. C. 2000. Studies of body condition and reproductive physiology in Rocky Mountain elk. Thesis, University of Idaho, Moscow, USA.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973–987.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson (deceased). 2005. Nutritional condition indices for elk: the good (and less good), the bad, and the ugly. Pages 102–112 *in* M. J. Wisdom, technical editor. The Starkey Project: a synthesis of long term studies of elk and mule deer. Reprinted from the 2004 Transactions of the North American Wildlife and Natural Resources Conference, Alliance Communications Group, Lawrence, Kansas, USA.

Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. McCorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoeneckerj, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. Journal of Wildlife Management 74:880–896.

Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934–1943.

Davis, D. E., and R. L. Winstead. 1980. Estimating the numbers of wildlife populations. Pages 221–245 *in* S. D. Schemnitz, editor. Wildlife management techniques manual. Fourth edition. The Wildlife Society, Washington, D.C., USA.

deVos, J. C., Jr., M. R. Conover, and N. E. Headrick, editors. 2003. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Dimmick, R. W., and M. R. Pelton. 1994. Criteria of sex and age. Pages 169–214 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Downing, R. L., E. D. Michael, and R. J. Proux, Jr. 1977. Accuracy of sex and age ratio counts of white-tailed deer. Journal of Wildlife Management 41:709–714.

Drake, D., C. Aquila, and G. Huntington. 2005. Counting a suburban deer population using Forward-Looking Infrared radar and road counts. Wildlife Society Bulletin 33:656–661.

Duda, M. D., and J. L. Nobile. 2010. The fallacy of online surveys: no data are better than bad data. Human Dimensions of Wildlife 15:55–64.

Dunn, W. C., J. P. Donnelly, and W. J. Krausmann. 2002. Using thermal infrared sensing to count elk in the southwestern United States. Wildlife Society Bulletin 30:963–967.

Enck, J. W., D. J. Decker, S. J. Riley, J. F. Organ, L. H. Carpenter, and W. F. Siemer. 2006. Integrating ecological and human dimensions in adaptive management of wildlife-related impacts. Wildlife Society Bulletin 34:698–705.

Erickson, G. L., J. R. Heffelfinger, and J. H. Ellenberger. 2003. Potential effects of hunting and hunt structure on mule deer abundance and demographics. Pages 119–138 *in* J. C. deVos, Jr., M .R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

Ericsson, G., and K. Wallin. 1999. Hunter observations as an index of moose *Alces alces* population parameters. Wildlife Biology 5:177–185.

Federal Geographic Data Committee (FGDC). 1998. Geospatial positioning accuracy standards, part 1: reporting methodology. FGDC-STD-007.1-1998. <http://www.fgdc.gov/standards/projects/FGDC-standards-projects/accuracy/part1/chapter1>. Accessed 24 Dec 2009.

Freddy, D. J. 1991. Elk census methodology. Colorado Division of Wildlife, Wildlife Research Report, Jul:59–72.

Freddy, D. J., G. C. White, M. C. Kneeland, R. H. Kahn, J. W. Unsworth, W. J. deVergie, V. K. Graham, J. H. Ellenberger, and C. H. Wagner. 2004. How many mule deer are there? Challenges of credibility in Colorado. Wildlife Society Bulletin 32:916–927.

Gaillard, J-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Geis, A. D., and R. D. Taber. 1963. Measuring hunting and other mortality. Pages 284–298 *in* H. S. Mosby, editor. Wildlife investigational techniques. Second edition. The Wildlife Society, Blacksburg, Virginia, USA.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Estimating fat content of caribou from body condition scores. Journal of Wildlife Management 60:713–718.

Gigliotti, L. M. 2011. Comparison of an internet versus mail survey: a case study. Human Dimensions of Wildlife 16:55–62.

Gove, N. E., J. R. Skalski, P. Zager, and R. L. Townsend. 2002. Statistical models for population reconstruction using age-at-harvest data. Journal of Wildlife Management 66:310–320.

Guenzel, R. J. 1997. Estimating pronghorn abundance using aerial line transect sampling. Wyoming Game and Fish Department, Cheyenne, USA.

Harder, J. D., and R. L. Kirkpatrick. 1994. Physiological methods in wildlife research. Pages 275–306 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Härkönen, S., and R. Heikkilä. 1999. Use of pellet group counts in determining density and habitat use of moose *Alces alces* in Finland. Wildlife Biology 5:233–239.

Haroldson, B. S., E. P. Wiggers, J. Beringer, L. P. Hansen, and J. B. McAninch. 2003. Evaluation of aerial thermal imaging for detecting white-tailed deer in a deciduous forest environment. Wildlife Society Bulletin 31:1188–1197.

Harris, D. 1945. Symptoms of malnutrition in deer. Journal of Wildlife Management 9:319–322.

Harwell, F., R. L. Cook, and J. C. Barron. 1979. Spotlight count method for surveying white-tailed deer in Texas. Texas Parks and Wildlife Department, Austin, USA.

Heffelfinger, J. 2006. Deer of the Southwest: a complete guide to the natural history, biology, and management of southwestern mule deer and white-tailed deer. Texas A&M University Press, College Station, USA.

Huettmann, F. 2005. Databases and science-based management in the context of wildlife and habitat: towards a certified ISO standard for objective decision-making for the global community by using the internet. Journal of Wildlife Management 69:466–472.

Jacobson, H. A., J. C. Kroll, R. W. Browning, B. H. Koerth, and M. H. Conway. 1997. Infrared-triggered cameras for censusing white-tailed deer. Wildlife Society Bulletin 25:547–556.

Johnson, B. K., F. G. Lindzey, and R. J. Guenzel. 1991. Use of aerial line transect surveys to estimate pronghorn populations in Wyoming. Wildlife Society Bulletin 19:315–321.

Johnson, H. E., L. S. Mills, J. D. Wehausen, and T. R. Stephenson. 2010. Combining ground count, telemetry, and mark-resight data to infer population dynamics in an endangered species. Journal of Applied Ecology 47:1083–1093.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Kaplowitz, M. D., T. D. Hadlock, and R. Levine. 2004. A comparison of web and mail survey response rates. Public Opinion Quarterly 68:94–101.

Kimball, R. 1998. Meta meta data data: making a list of data about metadata and exploring information cataloging tools. DBMS Magazine March 1998. <http://www.ralphkimball.com/html/articles_search/articles1998/9803d05.html>. Accessed 4 Nov 2009.

Kissling, M. L., and E. O. Garton. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. Auk 123:735-752

Kistner, T. P., C. E. Trainer, and N. A. Hartmann. 1980. A field technique for evaluating physical condition of deer. Wildlife Society Bulletin 8:11–17.

Kufeld, R. C., J. H. Olterman, and D. C. Bowden. 1980. A helicopter quadrat census for mule deer on Uncompahgre Plateau, Colorado. Journal of Wildlife Management 44:632–639.

Lancia, R. A., J. W. Bishir, M. C. Conner, and C. S. Rosenberry. 1996*a*. Use of catch-effort to estimate population size. Wildlife Society Bulletin 24:731–737.

Lancia, R. A., C. E. Braun, M. W. Collopy, R. D. Dueser, J. G. Kie, C. J. Martinka, J. D. Nichols, T. D. Nudds, W. R. Porath, and N. G. Tilghman. 1996*b*. ARM! for the future: adaptive resource management in the wildlife profession. Wildlife Society Bulletin 24:436–442.

Lancia, R. A., W. L. Kendall, K. H. Pollock, and J. D. Nichols. 2005. Estimating the number of animals in wildlife populations. Pages 106–153 *in* C. E. Braun, editor. Techniques for wildlife investigation and management. The Wildlife Society, Bethesda, Maryland, USA.

Lanka, R., and J. Emmerich. 1996. Fat deposition measurements as an index to mule deer body condition and spring/summer habitat conditions. Wyoming Game and Fish Department, Cheyenne, USA.

Larson, J. S., and R. D. Taber. 1980. Criteria of sex and age. Pages 143–202 *in* S. D. Schemnitz, editor. Wildlife management techniques manual. Fourth edition. The Wildlife Society, Washington, D.C., USA.

Leopold, B. D., P. R. Krausman, and J. J. Hervert. 1984. Comment: the pellet-group census technique as an indicator of relative habitat use. Wildlife Society Bulletin 12:325–326.

Lindsdale, J. M., and P. Q. Tomich. 1953. A herd of mule deer: a record of observations made on the Hastings Natural History Reservation. University of California Press, Berkeley, USA.

Lubow, B. C., and J. I. Ransom. 2007. Aerial population estimates of wild horses (*Equus caballus*) in the Adobe Town and Salt Wells Creek Herd Management Areas using an integrated simultaneous double-count and sightability bias correction technique. U.S. Geological Survey Open-File Report 2007-1274, Reston, Virginia, USA.

Lukacs, P. M. 2007. Development and analysis of joint internet-telephone hunter surveys. Human Dimensions of Wildlife 12:263–273.

Lukacs, P. M. 2009. Pronghorn distance sampling in Colorado. Unpublished report. Colorado Division of Wildlife, Fort Collins, USA.

Lukacs, P. M., G. C. White, B. E. Watkins, R. H. Kahn, B. A. Banulis, D. J. Finely, A. A. Holland, J. A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. Journal of Wildlife Management 73:817–826.

Lutz, D., J. Emmerich, B. Lanka, T. Christiansen, L. Jahnke, B. Rudd, J. Nemick, and J. Bohne. 1997. Big game management – strategies to quantify body condition, mortality and the effects of weather. Wyoming Game and Fish Department, Cheyenne, USA.

MacDonald, D., and E. G. Dillman. 1968. Techniques for estimating nonstatistical bias in big game harvest surveys. Journal of Wildlife Management 32:119–129.

Mackie, R. L., D. F. Pac, K. L. Hamlin, and G. L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Fish, Wildlife and Parks, Helena, USA.

Magnusson, W. E., G. J. Caughley, and G. C. Grigg. 1978. A double-survey estimate of population size from incomplete counts. Journal of Wildlife Management 42:174–176.

Marques, F. F. C., S. T. Buckland, D. Goffin, C. E. Dixon, D. L. Borchers, B. A. Mayle, and A. J. Peace. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38:349–363.

Mason, R., L. H. Carpenter, M. Cox, J. C. deVos, Jr., J. Fairchild, D. J. Freddy, J. R. Heffelfinger, R. H. Kahn, S. M. McCorquodale, D. F. Pac, D. Summers, G. C. White, and B. K. Williams. 2006. A case for standardized ungulate surveys and data management in the western United States. Wildlife Society Bulletin 34:1238–1242.

McCaffery, K. R. 1976. Deer trail counts as an index to populations and habitat use. Journal of Wildlife Management 40:308–316.

McClintock, B. T., G. C. White, M. F. Antolin, and D. W. Tripp. 2009*a*. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237–246.

McClintock, B. T., G. C. White, and K. P. Burnham. 2006. A robust design mark-resight abundance estimator allowing heterogeneity in resighting probabilities. Journal of Agricultural, Biological, and Ecological Statistics 11:231–248.

McClintock, B. T., G. C. White, K. P. Burnham, and M. A. Pryde. 2009*b*. A generalized mixed effects model of abundance for mark-resight data when sampling is without replacement. Pages 271–289 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

McCullough, D. R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor, USA.

McCullough, D. R. 1992. Concepts of large herbivore dynamics. Pages 967–984 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Science Publishers, London, United Kingdom.

McMullin, S. L. 2004. Demographics of retirement and professional development needs of state fisheries and wildlife agency employees. Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, USA.

Miller, C. A. 2003. Hunter use of the Internet: defining the market. Human Dimensions of Wildlife 8:307–308.

Millspaugh, J. J., J. R. Skalski, R. L. Townsend, D. R. Diefenbach, M. S. Boyce, L. P. Hansen, and K. Kammermeyer. 2009. An evaluation of sex-age-kill (SAK) model performance. Journal of Wildlife Management 73:442–451.

Minta, S., and M. Mangel. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecology 70:1738–1751.

Naugle, D. E., J. A. Jenks, and B. J. Kerhohan. 1996. The use of thermal infrared sensing to estimate density of white-tailed deer. Wildlife Society Bulletin 24:37–43.

Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. Journal of Wildlife Management 32:597–614.

Neiland, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. Journal of Wildlife Management 34:904–907.

Novak, J. M., K. T. Scribner, W. D. Dupont, and M. H. Smith. 1991. Catch-effort estimation of white-tailed deer population size. Journal of Wildlife Management 55:31–38.

Ockenfels, R. A. 1983. An evaluation of age and sex ratio data. Wildlife Digest 15. Arizona Game and Fish Department, Phoenix, USA.

O'Neil, T. A., P. Bettinger, B. G. Marcot, B. W. Luscombe, G. T. Koeln, H. J. Bruner, C. Barrett, J. A. Pollock, and S. Bernatus. 2005. Application of spatial technologies in wildlife biology. Pages 418–447 *in* C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Overton, W. S. 1969. Estimating the numbers of animals in wildlife populations. Pages 403–456 *in* R. H. Giles, Jr., editor. Wildlife management techniques. Third edition (revised). The Wildlife Society, Washington, D.C., USA.

Pac, D. F., and G. C. White. 2007. Survival and cause-specific mortality of male mule deer under different hunting regulations in the Bridger Mountains, Montana. Journal of Wildlife Management 71:816–827.

Pauley, G. R., and J. G. Crenshaw. 2006. Evaluation of paintball, mark-resight surveys for estimating mountain goat abundance. Wildlife Society Bulletin 34:1350–1355.

Paulik, G. J., and D. S. Robson. 1969. Statistical calculations for change-in-ratio estimators of population parameters. Journal of Wildlife Management 33:1–27.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Potvin, F., and L. Breton. 2005. From the field: testing 2 aerial survey techniques on deer in fenced enclosures – visual double-counts and thermal infrared sensing. Wildlife Society Bulletin 33:317–325.

Powell, S. G., K. R. Baker, and B. Lawson. 2008. A critical review of the literature on spreadsheet errors. Decision Support Systems 46:128–138.

Rabe, M. J., S. S. Rosenstock, and J. C. deVos, Jr. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. Wildlife Society Bulletin 30:46–52.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. New Zealand Journal of Science and Technology 36 (section B):429–463.

Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. Journal of Wildlife Management 37:312–326.

Roseberry, J. L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117.

Rupp, S. P., W. B. Ballard, and M. C. Wallace. 2000. A nationwide evaluation of deer hunter harvest survey techniques. Wildlife Society Bulletin 28:570–578.

Saltz, D., and G. C. White. 1991*a*. Urinary cortisol and urea nitrogen responses in irreversibly undernourished mule deer fawns. Journal of Wildlife Diseases 27:41–46.

Saltz, D., and G. C. White. 1991*b*. Urinary cortisol and urea nitrogen responses to winter stress in mule deer. Journal of Wildlife Management 55:1–16.

Saltz, D., G. C. White, and R. M. Bartmann. 1992. Urinary cortisol, urea nitrogen excretion, and winter survival in mule deer fawns. Journal of Wildlife Management 56:640–644.

Saltz, D., G. C. White, and R. M. Bartmann. 1995. Assessing animal condition, nutrition, and stress from urine in snow: a critical view. Wildlife Society Bulletin 23:694–698.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. Journal of Wildlife Management 51:622–630.

Sasse, D. B. 2003. Job-related mortality of wildlife workers in the United States, 1937-2000. Wildlife Society Bulletin 31:1015–1020.

Schroeder, M. A., and L. A. Robb. 2005. Criteria for gender and age. Pages 303–338 *in* C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.

Seber, G. A. F. 1982. Estimation of animal abundance. Second edition. Griffin, London, United Kingdom.

Shih, T., and X. Fan. 2008. Comparing response rates from web and mail surveys: a meta-analysis. Field Methods 20(3):249–271.

Skalski, J. R., K. E. Ryding, and J. J. Millspaugh. 2005. Wildlife demography. Elsevier, Burlington, Massachusetts, USA.

Slattery, O., R. Lu, J. Zheng, F. Byers, and X. Tang. 2004. Stability comparison of recordable optical discs – a study of error rates in harsh conditions. Journal of Research of the National Institute of Standards and Technology 109:517–524.

Smith, R. H. 1959. A hunter questionnaire for compiling hunt statistics. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissioners 39:213–218.

Snyder, W. A. 1959. Deer harvest information. Job completion report, P-R W-75-R-6. New Mexico Game and Fish Department, Santa Fe, USA.

Steinert, S. F, H. D. Riffel, and G. C. White. 1994. Comparisons of big game harvest estimates from check station and telephone surveys. Journal of Wildlife Management 58:335–340.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Swank, W. G. 1958. The mule deer in Arizona chaparral, and an analysis of other important deer herds; a research and management study. Wildlife Bulletin number 3. Arizona Game and Fish Department, Phoenix, USA.

Taylor, C. E., D. L. Otis, H. S. Hill, Jr., and C. R. Ruth. 2000. Design and evaluation of mail surveys to estimate deer harvest parameters. Wildlife Society Bulletin 28:717–723.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, New York, New York, USA.

Torbit, S. C., L. H. Carpenter, R. M. Bartmann, A. W. Alldredge, and G. C. White. 1988. Calibration of carcass fat indices in wintering mule deer. Journal of Wildlife Management 52:582–588.

Udevitz, M. S., and B. E. Ballachey. 1998. Estimating survival rates with age structure data. Journal of Wildlife Management 62:779–792.

Uno, H., K. Kaji, T. Saitoh, H. Matsuda, H. Hirakawa, K. Yamamura, and K. Tamada. 2006. Evaluation of relative density indices for sika deer in eastern Hokkaido, Japan. Ecological Research 21:624–632.

Unsworth, J. W., N. F. Johnson, L. J. Nelson, and H. M. Miyasaki. 2002. Estimating mule deer harvest in southwestern Idaho. Wildlife Society Bulletin 30:487–491.

Unsworth, J. W., F. A. Leban, E. O. Garton, D. J. Leptich, and P. Zager. 1999*a*. Aerial survey: user's manual. Electronic edition. Idaho Department of Fish & Game, Boise, USA.

Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: user's manual. Second edition. Idaho Department of Fish and Game, Boise, USA.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999*b*. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.

U.S. Fish and Wildlife Service [USFWS]. 2007. 2006 national survey of fishing, hunting, and wildlife-associated recreation. <http://library.fws.gov/Pubs/nat_survey2006_final.pdf>. Accessed 10 Jun 2009.

Verme, L. J., and J. C. Holland. 1973. Reagent-dry assay of marrow fat in white-tailed deer. Journal of Wildlife Management 37:103–105.

Verme, L. J., and J. J. Ozoga. 1980. Effects of diet on growth and lipogenesis in deer fawns. Journal of Wildlife Management 44:315–324.

Wakeling, B. F. 2010. Mule deer antler growth and hunting management on the North Kaibab, Arizona. Pages 271–276 *in* C. van Riper III, B. F. Wakeling, and T. D. Sisk, editors. The Colorado Plateau IV: shaping conservation through science and management. University of Arizona Press, Tucson, USA.

Wakeling, B. F., D. N. Cagle, and J. H. Witham. 1999. Performance of aerial forward-looking infrared surveys on cattle, elk, and turkey in northern Arizona. Proceedings of the Biennial Conference of Research on the Colorado Plateau 4:77–88.

Wallmo, O. C. 1960. Big Bend ecological survey. Job completion report, P-R project W-57-R-8. Texas Game and Fish Commission, Austin, USA.

Wallmo, O. C., and W. L. Regelin. 1981. Rocky Mountain and Intermountain habitats. Part 1: food habits and nutrition. Pages 387–398 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. Wildlife Management Institute, Washington, D. C., and University of Nebraska Press, Lincoln, USA.

Watkins, B. E., J. H. Witham, D. E. Ullrey, D. J. Watkins, and J. M. Jones. 1991. Body composition and condition evaluation of white-tailed deer fawns. Journal of Wildlife Management 55:39–51.

White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. Wildlife Society Bulletin 24:50–52.

White, G. C. 2008. Closed population estimation models and their extensions in program MARK. Environmental and Ecological Statistics 15:89–99.

White, G. C., and R. M. Bartmann. 1983. Estimation of survival rates from band recoveries of mule deer in Colorado. Journal of Wildlife Management 47:506–511.

White, G. C., and R. M. Bartmann. 1998. Mule deer management – what should be monitored? Pages 104–118 *in* J. C. deVos, Jr., editor. Proceedings of the 1997 Deer/Elk Workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.

White, G. C., R. M. Bartmann, L. H. Carpenter, and R. A. Garrott. 1989. Evaluation of aerial line transects for estimating mule deer densities. Journal of Wildlife Management 53:625–635.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–139. <http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm>. Accessed 10 Jun 2009.

White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of program MARK. Pages 368–377 *in* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.

White, G. C., and W. R. Clark. 1994. Microcomputer applications in wildlife management and research. Pages 75–95 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

White, G. C., and L. E. Eberhardt. 1980. Statistical analysis of deer and elk pellet group data. Journal of Wildlife Management 44:121–131.

White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66:300–309.

White, G. C., A. F. Reeve, F. G. Lindzey, and K. P. Burnham. 1996. Estimation of mule deer winter mortality from age ratios. Journal of Wildlife Management 60:37–44.

Whittaker, D. G., W. A. Van Dyke, and S. L. Love. 2003. Evaluation of aerial line transect for estimating pronghorn antelope abundance in low-density populations. Wildlife Society Bulletin 31:443–453.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wolfe, L. L., M. W. Miller, and E. S. Williams. 2004. Feasibility of "test-and-cull" for managing chronic wasting disease in urban mule deer. Wildlife Society Bulletin 32:500–505.

Wyoming Game and Fish Department (WGFD). 1982. Handbook of biological techniques. Wyoming Game and Fish Department, Cheyenne, USA.

Young, R. A. 1976. Fat, energy and mammalian survival. American Zoologist 16:699–710.

APPENDIX A

OBJECTIVES AND PRACTICES APPLIED TO MULE DEER MANAGEMENT IN 18 WESTERN STATES AND PROVINCES

The following tables are based on survey responses from 18 of 23 wildlife agencies that are members of the Western Association of Fish and Wildlife Agencies and manage mule deer.

Table 1. Objectives applied to mule deer management in 18 western states and provinces.

Management objective	Jurisdiction	Percent
Population trend	AK, AZ, ID, KS, MT, NE, NV, ND, SD, SK, TX, YK	67
Population abundance	AB, AZ, CO, ID, MT, ND, OR, SD, SK, TX, UT, WY	67
Pre-season B:D ratio	ND, SD, SK, TX	22
Post-season B:D ratio	AB, AZ, CO, ID, MT, NE, NV, OR, TX, UT, WY	61
Buck age structure	AZ, KS, MT, NE, NV, SD, TX	39
Antler composition of harvested bucks	AZ, ID, MT, NV, OR, TX	33
Fawn:doe ratio	AZ, MT, NV, SK, TX	28
Hunter days	AK, AB, AZ, ID, KS, NV, ND, SD, YK	50
Habitat considerations	AK, AB, AZ, CO, ID, KS, MT, NV, SD, TX, UT, WY	67
Min. or max. buck harvest	AK, MT, NE	17
Min. or max. doe harvest	NE	6
Conflict management	AB, CO, ID, KS, MT, NE, ND, SD, SK, TX, UT, WY	67

Table 2. Harvest frameworks for any-weapon mule deer seasons in 18 western states and provinces. Does not include archery, muzzleloader, and special situations.

Harvest framework	Jurisdiction	Percent
Limited entry buck	AB, AZ, CO, ID, MT, NE, NV, NM, ND, OR, SD, UT, WY, YK	78
Limited entry either sex	CO, KS, NE, NV, OR, SD, SK, WY	44
Limited entry doe	AB, AZ, CO, ID, KS, MT, NE, NV, ND, OR, SD, SK, UT, WY	78
Unlimited buck	AK, ID, MT, NM, OR, TX, WY	41
Unlimited either sex	AK, ID, MT, SK, TX, WY	33
Unlimited doe	SK,WY	11

Table 3. Methods used to estimate mule deer harvest in 18 western states and provinces.

Management objective	Jurisdiction	Percent
Mail		
Random survey	AK, AZ, KS, ND, SD, SK, TX, WY	44
Complete survey	AZ, ID, NV, YK	22
Telephone		
Random survey	AB, CO, ID, MT, OR, TX, UT	39
Complete survey	AZ, NM, OR	17
Web-based		
Random survey	CO, KS, OR, WY	22
Complete survey	ID, NV, NM, OR, UT	28
Check station	AZ, MT, NE, ND, TX, UT, WY, YK	44

Table 4. Methods used to estimate mule deer population trend in 18 western states and provinces[a].

Method[a]	Jurisdiction	Percent
Helicopter		
Double count	AZ	6
Targeted (no detectability correction)	AB, MT, NM	17
Random sample (no detectability correction)	TX	6
Distance sampling	OR	6
Fixed-wing aircraft		
Double count	AZ	6
Targeted (no detectability correction)	MT, ND	11
Ground-based		
Count	AZ, KS, MT, SK	22
Pellet count	AK	6
Modeling		
Change-in-ratio	MT	6
Sex-age-kill	NM	6
POP-II	AZ, OR, WY	17
Agency model	AB, AZ, MT, SD	22
Population reconstruction	AZ, MT, NM	17
Harvest per unit effort	AZ	6
Monitor harvest	AK, AB, AZ, CO, ID, KS, MT, NE, NV, ND, SK, TX, WY	72

[a] The following methods were not used by any jurisdiction: helicopter sightability or mark-resight; fixed-wing sightability, mark-resight, random sample without detectability correction, or distance sampling; ground-based mark-resight or track counts.

Table 5. Methods used to estimate mule deer abundance in 18 western states and provinces[a].

Method[a]	Jurisdiction	Percent
Helicopter		
Sightability	ID, MT, OR, WY	22
Mark-resight	MT	6
Double count	AZ, MT	11
Targeted (no detectability correction)	MT, NM	11
Random sample (no detectability correction)	AB, CO, SK, TX	22
Fixed-wing aircraft		
Sightability	MT	6
Mark-resight	MT	6
Double count	AZ, MT	11
Targeted (no detectability correction)	MT, ND	11
Ground-based count	AZ, KS, MT, OR	22
Modeling		
Change-in-ratio	MT, WY	11
Sex-age-kill	NM	6
POP-II	AZ, NM, OR, UT, WY	28
Agency model	AB, AZ, CO, ID, MT, NV, SD, SK	44
Population reconstruction	AZ, MT, NV, NM	22
Harvest per unit effort	AZ	6

[a] The following methods were not used by any jurisdiction: helicopter or fixed-wing distance sampling; fixed-wing random sample without detectability correction; ground-based mark-resight, pellet counts, or track counts.

Table 6. Methods used to estimate survival of mule deer in 18 western states and provinces[a].

Management objective	Jurisdiction	Percent
Telemetry	AK, AZ, CO, ID, MT, OR, WY	39
Modeling		
Change in ratio	MT, UT, WY	17
POP-II	AZ, OR, UT	17
Agency model	AB, AZ, CO, ID, NV, SD	33
Life table analysis	AZ	6

[a] The following methods were not used by any jurisdiction: sex-age-kill or weather-based models.

Table 7. Methods used to estimate age and sex composition of mule deer populations in 18 western states and provinces[a].

Method[a]	Jurisdiction	Percent
Helicopter		
Sightability	ID	11
Double count	AZ	6
Targeted (no detectability correction)	AZ, CO, MT, NV, NM, WY	33
Random sample (no detectability correction)	AB, AZ, CO, ID, OR, TX	33
Fixed-wing aircraft		
Double count	AZ	6
Targeted (no detectability correction)	AZ, MT, ND	17
Random sample (no detectability correction)	AZ	6
Ground classification	AZ, ID, KS, MT, NE, NV, OR, SK, TX, UT, WY	61
Modeling		
Change-in-ratio	MT	6
POP-II	AZ, OR	11
Agency model	AB, AZ, SD	17
Population reconstruction	AZ, MT	11
Harvest per unit effort	AZ	6

[a] The following methods were not used by any jurisdiction: helicopter mark-resight or distance sampling; fixed-wing sightability, mark-resight, or distance sampling; SAK models.

Table 8. Methods used to estimate body condition of mule deer in 18 western states and provinces[a].

Method	Jurisdiction	Percent
Xiphoid fat	ID, UT	11
Body mass	CO, ID, MT, TX, WY	28
Antler growth	AZ, ID, MT, TX, UT	28
Skeletal growth	ID, MT	11
"Cook" method	ID	6
Femur marrow	WY	6

[a] The following methods were not used by any jurisdiction: kidney-fat index, Kistner score, ultrasound, blood indices, or urine indices.

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Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife
Idaho Department of Fish and Game
Kansas Department of Wildlife and Parks
Montana Department of Fish, Wildlife and Parks
Nebraska Game and Parks Commission
Nevada Department of Wildlife
New Mexico Department of Game and Fish
North Dakota Game and Fish Department
Oklahoma Department of Wildlife Conservation
Oregon Department of Fish and Wildlife
Saskatchewan Department of Environment and Resource Management
South Dakota Department of Game, Fish and Parks
Texas Parks and Wildlife Department
Utah Division of Wildlife Resources
Washington Department of Fish and Wildlife
Wyoming Game and Fish Department
Yukon Department of Environment

GEOTHERMAL EXPANSION PROJECT

MAMMOTH LAKES, CALIFORNIA

DEER TRACK-COUNT SURVEY RESULTS

MACTEC PROJECT NO. 4306080009

Prepared by:

MACTEC

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Senior Environmental Scientist

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June 2011

Table of Contents

Figures

Tables

Appendices

1.0 Introduction

The purpose of this report is to summarize the movement of the Round Valley mule deer (*Odocoileus hemionus*) herd through the area of the Casa Diablo 4 Geothermal Expansion Project. The area is considered a herd summer range and migration corridor. The California Department of Fish and Game (CDFG) deer surveys and other authorities indicate that a portion of the Round Valley deer herd migrate through the proposed Project area in late April through the third week of May, depending on snow conditions.

There have been several deer surveys/studies performed in the Project area over the years, including track counts, pellet counts, radio collar, and other methods. The most recent deer study (1997-2000) estimates the Round Valley herd at 2,200 to 2,300 individuals (Quad Knof 2004). Associate Biologist Mr. Tim Taylor of the CDFG recommended that deer track-count surveys be conducted in the area of the Casa Diablo C4 Geothermal Project. The track-count methodology is described in Section 3.0 below. Data collected during May 2011 track-count surveys was used to summarize the results described in this report.

2.0 Setting

2.1 Location/Project Area

The Project is located on the Old Mammoth, 7.5' USGS Quad (1994) in portions of Sections 25, and 36 of T3S, R27E and Sections 30, 31, and 32 of T3S, R28E, Mount Diablo Baseline & Meridian (MDB&M), east and west of the intersection of U.S. Highway 395 (U.S. 395) and State Route 203 in Mono County, California (Figure 1). The western portion of the project is located east of Mammoth Lakes, California at Shady Rest Park. Elevation ranges from 2237 (7339 feet) to 2376 meters (7795 feet) above mean sea level (amsl). The majority of the Project area is open space with well pads and pipelines located in selected areas.

2.2 Weather Conditions

The winter snow fall of 2010-2011 stayed well into spring with snow fall continuing during the survey period. Portions of the survey routes, in the Jeffrey pine forest, were covered in snow and could not be surveyed during the early part of the survey period. The deep snow pack at higher elevations also remained through the month of May.

2.3 Biological Habitat

The habitat/vegetation in the Project area consists of sagebrush (*Artemisia tridentata*) and Jeffrey pine (*Pinus jeffreyi*) components, as described in the California Wildlife Habitat Relationships System. The most abundant is the Jeffrey pine. The dominant species found in the canopy is Jeffrey pine, forming a pure stand. Where a shrub component exists under the canopy it is dominated by sagebrush. The sagebrush community is dominated by dense sagebrush with other shrubs, perennials, and grasses.

3.0 Methodology

Consistent with CDFG recommendations, deer track-count surveys were conducted Between May 4 and June 1, 2011 by MACTEC Engineering and Consulting, Inc. (MACTEC) biologists Nancy Santos and Carter Schleicher. Survey dates included: May 4-5, 9-10, 12-13, 16-17, 18-19, 23-24, 26-27, and 31-June 1.

Roads originally selected to be surveyed were located on both sides of U.S. 395 (Figure 2 below). A reconnaissance of the roads was conducted prior to the actual surveys to determine the conditions of the roads. The roads to the east of U.S. 395 were determined to be in poor condition (ditched like a gully or overgrown with vegetation) and could not be dragged. The road to the east of Shady Rest Park was not surveyed as originally intended. Due to a long winter and cold spring all the snow had not melted off portions of the roads in the Jeffrey pine habitat. This prevented the dragging of the last section of Sawmill, Poleline, the 4WD Road off Poleline Road, and the east road adjacent to Shady Rest Park. This only lasted until the snow melted at which time all portions of the three main roads were part of the survey route. The 4WD Road adjacent to U.S. 395 was also part of the survey route.

On the evening of day one, the selected survey roads were dragged with a metal mesh-like net behind the vehicle. The drag was done as late as possible before dark, to clear the roads of existing tracks including vehicle, human, dog and deer. The morning of day two, deer track-count surveys were conducted, by vehicle and on foot, on all sections of roads dragged the previous night. It was not uncommon to find vehicle tracks and footprints (human and dog) already on top of the freshly dragged areas from the night before. Visual observations of deer were noted both during the drag and deer track-count survey periods.

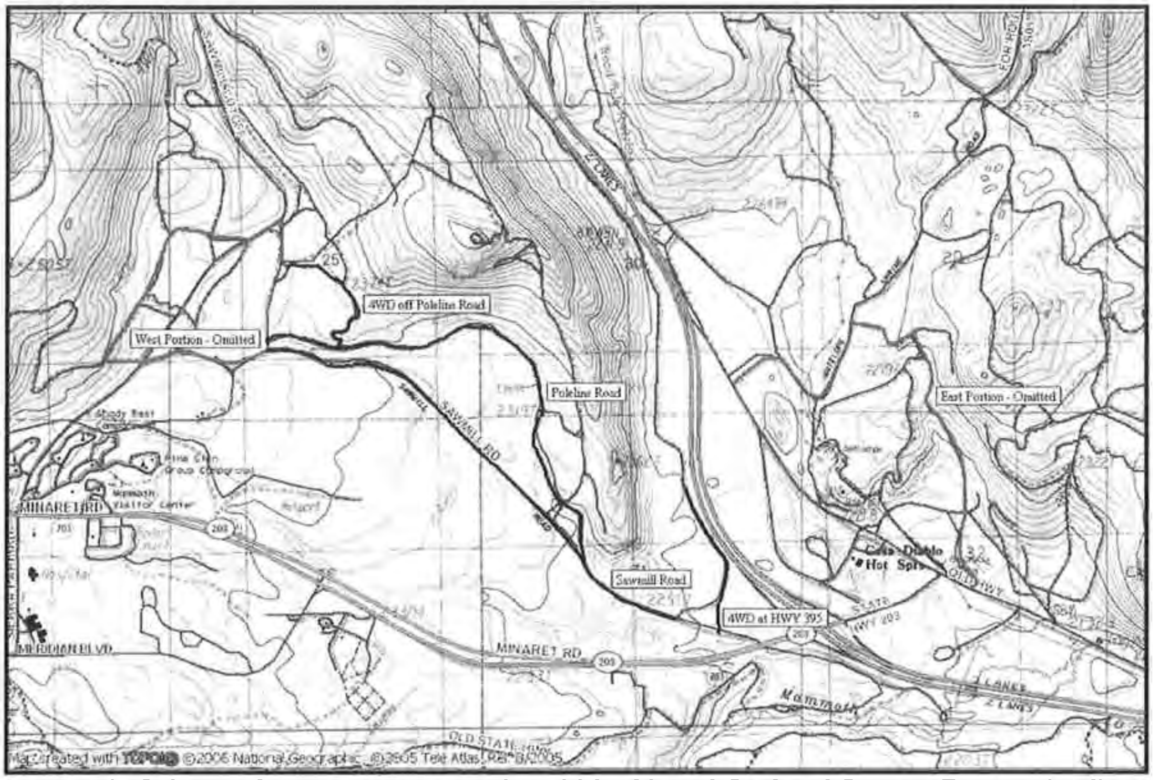

Figure 2. Original Survey Routes (red and black) and Omitted Survey Routes (red)

Deer track-count surveys included the collection of GPS data on the location of deer and deer tracks, where the deer entered the road, where the deer exited the road, and what direction the deer were coming from and going to. The data was collected and compiled into a spreadsheet (Appendix A) and used to determine the area of use by the deer, quantity of deer passing through the area, and direction of the deer.

Deer track-count survey methodologies were based on personal communications and review of previous studies, and are listed below:

- Assessment of Deer Utilization of the Mammoth Pacific, L.P., Geothermal Exploration Areas: Basalt Canyon, Upper Basalt, and Rhyolite Plateau
- Casa Diablo Geothermal Development Project: Deer Study Final Report, 1987,
- Personal communications with Tim Taylor CDFG (2011)
- Personal communications with Richard Perloff, US Forest Service, Mammoth Lakes RD (2011)

4.0 Track-Count Survey Results

Deer from the Round Valley herd are said to move through the Project area during spring migration and are assumed to move in a northerly direction towards summer range and fawning grounds. The results of the track-count surveys are summarized in Table 1 below.

Table 1. Deer Observations and Track-Counts s Detected Moving in Each Direction

Date	North	South	East	West	Total
May 4*	0	0	0	0	0
May 5	1	5	0	0	6
May 9*	0	0	0	0	0
May 10	10	2	0	0	12
May 12*	0	0	0	0	0
May 13	13	10	1	9	34
May 16*	0	0	0	0	0
May 17	2	5	5	1	13
May 18*	0	0	0	0	0
May 19	0	3	0	4	7
May 23*	0	0	0	0	0
May 24	6	5	0	2	13
May 26*	0	0	0	0	0
May 27	22	11	3	5	41
May 31*	3	4	0	0	7
June 1	10	4	3	1	17
Total	**67**	**49**	**12**	**22**	**170**

Note: * = drag days only where deer observations were recorded. Totals do not include deer were direction of movement was not known.

The greatest period of deer use in the Project area was the week of May 27, followed closely by the week of May 13. The total number of deer tracks observed moving through the Project area during those two time periods was 43 and 34, respectively.

A total of 170 deer or tracks were observed during the entire survey period, May 4 through June 1. This is the maximum number of deer that could have used the area. It is more likely the actual number of deer is lower due to the possibility that tracks of the same deer could have been counted more than once. At most .07 percent (170/2300) of the Round Valley herd used the Project area over a period of eight days in May 2001.

The number of deer moving (migrating or foraging) in a northerly direction (N, NW, NE, NNW, and NNE) was limited to 67 deer or .04 percent (87/2300) of the 2,300 animals that migrate out of Round Valley. The remainder of the deer, more than one-half the total, was observed traveling to the south, east and west. Figure 3 illustrates the location of each deer visual or track-count observation for the duration of the survey period.

Sawmill Road was the most heavily deer tracked during the survey period (approximately 60 deer) and the deer tended to parallel or cross the road in the sagebrush portion of the habitat. The majority of the traffic on Sawmill Road was deer crossing the road in a direct manner or walking along the road for a time and then crossing the road to the other side.

Nearby and almost parallel to Sawmill Road is Poleline Road, which was utilized by deer but to a lesser degree then Sawmill Road. Approximately 35 deer were identified as having used Poleline Road during the survey period and the majority of them were heading northwest along the road.

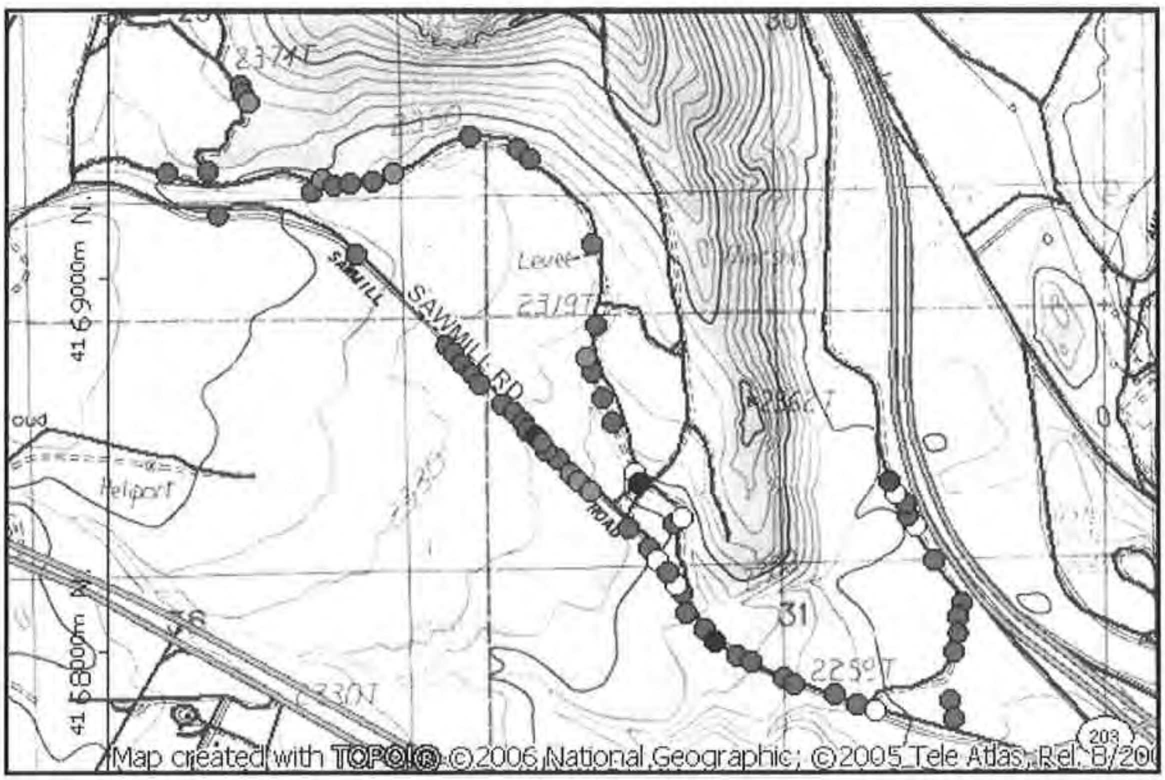

Figure 3. Deer Locations along All Survey Routes
Color key: Red = 1 deer, yellow = 2 deer, Green = 3 deer, blue = 4 deer, purple = 5 deer and white = 7 deer

The 4WD Road off Poleline Road was traveled little by the deer. It appears the deer moved through the area to the east of the 4WD Road or turned around and went south or east again when they realized the snow pack was still too deep to traverse.

The 4WD Road off U.S. 395 was also travelled by the deer and the majority of those deer were traveling to the north or northwest, taking another road west towards Poleline and Sawmill Roads.

5.0 Conclusions and Recommendations

5.1 Conclusions

Based on literature review, data collection, and communication with Mr. Tim Taylor, the following conclusions have been made.

The Round Valley mule deer herd utilizes the habitat in the area of the Casa Diablo CD4 Geothermal Expansion Project site. The mule deer use the area for migration, foraging and cover, including both the sagebrush and Jeffrey pine habitats. It is unclear from this study, how much of the deer use was migration and how much was a resident population foraging back and forth.

Evidence shows that all roads included in the study were used by the deer during the survey period to access or leave the Project area. Sawmill Road was used most often by the deer in the open sagebrush country.

The results of the track-count data show that the deer were milling about in the Project area waiting for snow at higher elevations to clear, foraging as a resident population, or a combination of both.

5.2 Recommendations

Due to the late winter and cold spring the deer appear to have delayed their departure for the higher elevations of their summer range and fawning grounds. Therefore, should the Project be approved and operational, Mono County may wish to revisit mule deer mitigation measures and request additional data collection on deer use in the area of the Casa Diablo 4 Geothermal Expansion Project.

6.0 Summary

In summary, the foregoing survey indicates that a minimal number (.07 percent) of individuals from the Round Valley deer herd used the Project area for foraging or migration over a period of eight days in May, 2011.

7.0 References

Perloff, Richard, 2011. USDA Forest Service, Mammoth Lakes Ranger District, Inyo National Forest. Pers. Com.

Quad Knopf. 2004. Revised Environmental Impact Report, Pine Creek Communities Development Project. (SCH #1998041020) Prepared for Inyo County Board of Supervisors, Inyo County, CA.

Taylor, Tim, 2011. California Department of Fish and Wildlife, Bishop, CA. Pers. com.

APPENDIX A

Deer Track-Count Survey Results

MEMORANDUM

December 29, 2011

To: Ron Leiken
Ormat Corp.

From: Jim Paulus
Principal, Jim Paulus Ph.D.

RE: Interaction Between Fall 2011 Migrating Deer and the Basalt Canyon Pipeline at the CD4 Project

This memorandum is an addendum to recent reports regarding deer use of the CD4 Project area near Mammoth Lakes. One area of study, specifically the forested section of Transect EE between sites 12-31 and 55-27, was highly used by migrating deer and was also consistently blanketed with snow during the latter part of deer surveys reported in the December 28, 2011 document, "Fall 2011 Migratory Deer Survey for the M-1 Project Site at the Casa Diablo Geothermal Area." This coincidence was exploited by performing additional off-transect tracking during the period November 11 to December 2 to determine how migrating deer got across the existing Basalt Canyon Pipeline.

The Basalt Canyon Pipeline, in existence since 2006, is an aboveground linear structure, a 36-48 inch diameter pipe suspended about one foot off the ground, which crosses through relatively dense Jeffrey Pine Forest vegetation and lies perpendicular to the identified migration corridor. Deer could jump over it readily, as has been documented. About 200 ft of this particular section is a double barrel, having two pipes spaced within a few inches of each other but otherwise constructed in a fashion that is identical to the (single) pipes that continue upstream and downstream. Given the habitat and human activity seems to be unvarying in this general area, I can see no other reason deer might choose or reject crossing at any place along this section of the Basalt Canyon Pipeline, other than their reaction to the pipeline itself. The locations of crossings, the length of travel parallel to the pipeline prior to crossing, and direction of travel were mapped.

Analysis is necessarily limited by small sample size, as in total only 23 deer were mapped over the 13 sample dates. The first clear trend is refusal to cross at the double barrel. Crossings were concentrated at the western end of the double pipe section, where it merges into a single pipeline. Tracks indicated deer were diverted an average 100 ft upon encountering the double barrel. All 7 deer mapped there crossed to the west of the double barrel. A second clear trend was discovered among the remaining 16 crossings, which occurred well to the east of the double barrel. 70% of deer mapped there came across the pipeline at one 20 ft pipeline length. There is a visibly greater gap under the pipe at this point due to a small variation in topography. The ground to pipe gap is 36 inches at its greatest, so adult deer would have to stoop but not crawl to pass. It was also noted that the coyotes that are common in this area routinely traveled to this gap. It is possible the animals using the passage were simply following tracks left by others. In support of this, the track map shows almost zero diversion of deer along the pipeline at the "overhead" gap.

These trends would be in agreement with the hypothesis that deer will use an alternative to double barrel pipeline if provided, in this case the alternative being the nearest single pipeline section. Also, the tendency to use the only overhead pipe available within the habitat type chosen for migration strongly supports the hypothesis that passages provided for migration will be used regularly in the years soon after pipeline completion. Deer use of this unintentional, rather cramped overhead bodes well for any intention to provide overhead-style passages for migrating deer that might be included in the upcoming CD4 Project.

Comment Letter I9

33

Pages 873-897 *In* Clait E. Braun, Editor. 2005.
Techniques for Wildlife Investigations and Management.
The Wildlife Society, Bethesda, Maryland, USA.

MANAGING RANGELANDS FOR WILDLIFE

Vernon C. Bleich, John G. Kie, Eric R. Loft, Thomas R. Stephenson, Michael W. Oehler, Sr., and Alvin L. Medina

INTRODUCTION

Rangelands are plant communities dominated by grasses, forbs, and shrubs. Their primary use by humans worldwide is for livestock grazing, but these communities also are habitat for wildlife. Traditionally, wildlife-related concerns of range managers focused on predators of livestock and on wildlife species that are hunted. Today, managers are interested in biodiversity and a wide range of species. Management of public rangelands in the United States is constrained by federal and state laws, which require managers to address the impact of management activities on all wildlife.

The majority of rangelands used by wildlife in the United States are public lands administered by the U.S. Forest Service and Bureau of Land Management, both of which have multiple-use mandates. With existing laws such as the Endangered Species Act and Clean Water Act, and ecosystem management and ecosystem health policies of the major land management agencies in the United States, there is expanding need to address the ecology of rangelands as it relates to plants, soils, water, wildlife, and livestock.

Photographs, videos, Internet web sites, agenda-driven "science," opinion pieces, the growth of advocacy groups, legal challenges (and threat of legal challenges), and society's changing sentiments about use and condition of public rangelands have generated an abundance of confusion and uncertainty about rangeland management. What formerly was a field primarily limited to understanding livestock-big game species relationships is now open to examination of livestock impacts on all native flora and fauna, and the communities and ecosystems in which they exist.

The single greatest change influencing wildlife on western rangeland management during the 1990s has been the shift of concern from competition of livestock with big game such as deer (*Odocoileus* spp.) and elk (*Cervus elaphus*), to concern for all wildlife, and biodiversity in general. For terrestrial wildlife species, the fate of species such as the willow flycatcher (*Empidonax traillii*) and sage-grouse (*Centrocercus* spp.) now dominate livestock and wildlife issues in montane meadow-riparian systems and sagebrush (*Artemisia* spp.) steppe, respectively, in many areas of the western United States. In California for example, ungulates aren't mentioned in a recent decision to amend management of >1.7 million ha on 11 national forests (U.S. Department of Agriculture 2001). Aquatic, riparian, and meadow system rangeland management would, instead, be heavily influenced by habitat needs of the willow flycatcher, mountain yellow-legged frog (*Rana muscosa*), Yosemite toad (*Bufo canorus*), and great gray owl (*Strix nebulosa*).

Effectively managing rangelands for wildlife requires achieving a specified level of habitat structure as represented by vertical and canopy cover, food items as represented by species composition, and adequate water quality and availability. Additionally, where livestock grazing is involved, there is a need to understand and manage for interspecific and social interactions between livestock and wildlife, as well as strategies to mitigate adverse effects. These interactions may be in the form of behavioral avoidance or attraction, direct mortality caused by livestock, or habitat modifications, and indirect mortality caused by disease transmission. Wildlife-livestock interactions have greater application at a broad geographic scale rather than a site-specific study area.

Because most state and federal agencies have unique missions and mandates (Salwasser et al. 1987), management philosophies and on-the-ground techniques differ markedly among agencies. Philosophical differences can be further exacerbated when adjacent tracts of land, managed by different agencies, have their own unique designations (e.g., specially designated area). Specially designated areas come in a variety of shapes and sizes, but in the United States they are typically managed by one of a few federal agencies (e.g., U.S. Forest Service, Bureau of Land Management, National Park Service, or U.S. Fish and Wildlife Service), and include such areas as wilderness, special research areas, wildlife refuges, sanctuaries, or any other site where certain activities or management tools (e.g., aircraft, mechanical equipment) may be precluded. These areas are usually small relative to the management prescriptions of adjacent properties and, thus, exist as noncontiguous islands that must be managed differently from surrounding landscapes.

Because of the varied and unique challenges confronting managers in today's world, this chapter is not intended to be an all-encompassing treatise. Rather, it presents a discussion of selected issues and techniques in an effort to provide the reader with a general understanding and appreciation for the complexities associated with managing rangelands. An extensive literature review is included and the reader is encouraged to explore the vast quantity of information that has been published on this subject, some of which is also summarized elsewhere (e.g., Krausman 1996). It is our hope this chapter adequately (1) provides an overview of rangeland management to benefit wildlife species and natural communities, with an emphasis on western North America; (2) identifies some of the topical issues and primary rangeland systems of concern; and, (3) describes some of the techniques for accommodating wildlife and wildlife issues on rangelands.

PLANT SUCCESSION AND WILDLIFE MANAGEMENT GOALS FOR RANGELANDS

Plant succession is the gradual replacement of one assemblage of plant species with others through time until a relatively stable climax community is reached (Clements 1916). As each group of plant species is replaced, the value of the community as habitat to any particular species of wildlife changes. The result is a succession of wildlife species as plant communities and populations of primary consumers undergo successional changes altering the different trophic levels (Kie et al. 1994).

Range Condition and Wildlife Habitat

Only a portion of the vegetation biomass in a rangeland will provide adequate nutrition for an herbivore. As body size decreases, diet selectivity generally increases (Van Soest 1994); consequently, many wild herbivores (which tend to be smaller than domestic livestock) consume much less of the vegetation resource than livestock, particularly cattle. Furthermore, domestic livestock may consume a greater proportion of poorer-quality bulk forages because producers supplement diets of livestock to balance nutritional requirements for growth and reproduction at least for some portion of the year. Proper estimates of carrying capacity for wildlife on rangelands assume that all nutrients will be obtained from the range (Hobbs and Swift 1985).

Rangelands exist in many different successional stages and structural conditions because of the influence of fire, mechanical disturbance, herbicide treatment, and grazing by wild and domestic herbivores. Some plant communities respond to grazing in a predictable manner, depending on the plant species present (Dyksterhuis 1949). Some plant species are dominant in climax communities because they are superior competitors in the absence of disturbance. However, they begin to decline in vigor and abundance with increased grazing pressure (Dyksterhuis 1949). As they decline, other less palatable plants present at the climax stage become more abundant as competition is reduced. If grazing intensity is sufficiently heavy and occurs over a long period of time, new plant species, well adapted to heavy grazing, appear in the community. As a result, many exotic species of plants (e.g., spurges, thistles, brome grasses) become established and overall condition of the range is reduced.

In the past, rangelands have been managed on a concept of how close existing vegetation approximates a climax community using terms such as excellent, good, fair, and poor (Dyksterhuis 1949). This procedure cannot be used on seeded rangelands, however, or those dominated by introduced, naturalized plant species such as the annual grasslands of California (Smith 1978, 1988). Also, range condition terms including excellent, good, fair, and poor are defined in terms of providing forage for livestock–habitat is species specific and differs greatly among species. A site rated as poor may provide excellent habitat for wildlife adapted to early-seral vegetation (e.g., white-tailed deer [*Odocoileus virginianus*]), whereas a site rated as excellent on this scale (e.g., grassland) may not be used at all by that species. More appropriate terms for describing the condition of rangeland vegetation as they relate to wildlife needs are climax, late seral, mid-seral, and early seral (Pieper and Beck 1990).

Additional problems may arise when changes in livestock grazing practices do not immediately produce a change in rangeland vegetation. For example, some grassland sites in southeastern Arizona that had been converted to shrublands by heavy livestock grazing failed to revert to native grasses following 20 years without livestock (Valone et al. 2002). In contrast, other sites that were protected for up to 39 years exhibited an increase in grasses, suggesting that substantial time lags following protection from grazing were necessary (Valone et al. 2002).

Since 1990, range ecologists have been developing models of change in rangeland vegetation based on the concept of multiple steady states (Laycock 1991, 1994). These states are often portrayed as state-transition models (Westoby et al. 1989), wherein "states" are recognizable assemblages of species at a particular site that are stable over time. Such models are useful in understanding why some plant communities fail to respond immediately to changes in management practices. Parameterizing state-transition models, however, often requires large data sets on composition of rangeland vegetation collected over many years. If such data are available, state-transition models can provide more precise predictions about vegetation change (Allen-Diaz and Bartolome 1998) than the classical linear succession model developed by Clements (1916) and may be useful in restoring degraded rangelands (Chambers and Linnerooth 2001).

Models of Rangelands as Wildlife Habitat

The system of classifying wildlife habitats according to potential natural vegetation and seral stage for coniferous forests (Thomas 1979) also has been applied to rangeland vegetation in southeastern Oregon (Maser et al. 1984). Habitat data were assembled for 341 species of vertebrates assessing impacts of different range management activities on those species by equating plant communities and their structural conditions with habitat values for wildlife. The structural conditions were grass-forb, low shrub, tall shrub, tree, and tree-shrub. As a plant community progresses from grass-forb to tree-shrub conditions through succession, changes occur in environmental variables important to wildlife. For example, herbage production tends to be highest in grass-forb communities; browse production highest in low-shrub and high-shrub communities; and canopy closure, canopy volume, and structural diversity highest in tree and tree-shrub communities (Maser et al. 1984). Management actions such as brush and weed control, water development, prescribed burning, seeding and planting, and grazing also can result in changes in structural conditions (Maser et al. 1984).

Accounting for needs of large numbers of wildlife species makes land-use planning difficult. To simplify the process, wildlife can be grouped into life forms based on the relationship of the species to their habitats. In southeastern Oregon, 2 characteristics of each species (where it feeds and where it reproduces) were used to distinguish 16 life forms. For example, dark-eyed juncos (*Junco hyemalis*) and mule deer (*Odocoileus hemionus*) characterize those species that feed and reproduce on the ground. Other examples of such life forms include the long-toed salamander (*Ambystoma macrodactylum*) and western toad (*Bufo boreas*), which feed on the ground, in shrubs, or in trees, and reproduce in water (Maser et al. 1984).

Beyond generalized models of wildlife habitat associations, managers occasionally estimate nutritional carrying capacity of rangelands. Most models of range supply and animal demand sum the available nutrients supplied by forage in the habitat and then divide by the animal's nutritional requirements (Robbins 1973, Hobbs et al. 1982). However, these models are simple and fail to make predictions based on varying levels of nutritional quality required by individuals (e.g., pregnant or lactating females, breeding males, migrating adults, etc.) (Hobbs and Swift 1985). To avoid overestimating the number of animals that existing plant biomass can support, carrying capacity models should consider minimum dietary nutrient concentration (Hobbs and Swift 1985, Hanley and Rogers 1989).

The influence of grazing can also affect wildlife species richness, diversity, density, and abundance. Some conclusions, for example that grazing tends to increase abundance of common species but reduces the overall diversity of species (Bronham et al. 1999, Rambo and Faeth 1999), provide a community approach that may contribute to additional generalizations when other taxonomic groups are considered.

CONTEMPORARY ISSUES IN RANGELAND MANAGEMENT

Key Rangelands of Concern

Riparian, montane meadow, and aquatic habitats continue to remain a high priority for conservation and management on western rangelands. Minimizing soil erosion and maintaining or restoring water quality are paramount in sustaining these systems for the future. Meeting these 2 umbrella objectives may accommodate the needs of some wildlife species that inhabit these systems. Increasing concern now exists for other wildlife habitats that are rangelands. This interest has arisen largely because of growing concern for biological diversity, but also for specific wildlife species that are declining and/or are being petitioned for listing under the federal Endangered Species Act. While there are numerous other plant communities and wildlife habitats that comprise rangelands throughout the world, the following systems or habitats are currently of great issue on public rangelands in the western United States.

Sagebrush Steppe

Foremost of concern among rangeland habitats at present are the expanses of sagebrush/perennial bunchgrass range that dominate much of public land in the west (e.g., Paige and Ritter 1999). From a timing perspective, just as range livestock management has been challenged in the 1990s to work toward avoiding negative impacts to the riparian zone and to more effectively use upland range, livestock use of uplands has now come under scrutiny as well. Recent research indicating that sage-grouse are declining and that they nest most successfully when there is an herbaceous understory at least 18 cm in height (Sveum et al. 1998) has created an additional challenge for livestock managers on public lands–how to avoid impacting riparian zones while ensuring adequate herbaceous cover to meet the needs of at least one nesting species in sagebrush/grass communities. Use and management of fire, herbicides, proximity to urbanization and agriculture, use of off-road vehicles, and power lines also are contributing factors affecting quality of wildlife habitat on these rangelands.

Other habitats of concern geographically associated with sagebrush steppe are browse communities dominated by antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus* spp.), or saltbush (*Atriplex* spp.). Often, these communities serve as a seasonal range for wildlife, such as in winter, but are grazed by livestock in summer.

Desert

Concern about potential impacts to the desert tortoise (*Gopherus agassizii*) from livestock grazing and other uses prompted the Bureau of Land Management to recently issue a grazing decision to help protect this species in California desert systems. These systems are particularly susceptible to impacts of grazing because they require a long time for recovery of vegetation growth and vigor if they are able to recover at all (e.g., Krueger et al. 2002). Additionally, concern exists for native frogs relying on the rare and often heavily impacted riparian and aquatic areas of the desert southwest (Jennings and Hayes 1993).

Aspen

Habitats dominated by quaking aspen (*Populus tremuloides*) support a high diversity of wildlife on western ranges (Debyle 1985). These habitats also serve as valuable grazing (Sampson and Malmsten 1926) areas for livestock because of the proximity of food, cover, and usually water. There is growing concern that this community is on the decline in managed forests and ranges throughout the west because of lack of stand regeneration resulting from browsing by herbivores, fire suppression, and disease (e.g., California Department of Fish and Game 1998, Knight 2001). In turn, succession to dominance by conifers or by shrub communities (e.g., sagebrush) may result, thereby decreasing the value as wildlife habitat or as rangeland for domestic livestock grazing.

Integrating Wildlife Objectives and Range Livestock Management

Livestock grazing results in impacts on rangelands and wildlife species. It can either decrease or improve the conditions for wildlife depending on the species or community attribute of interest. A goal for public land resource managers is to identify the acceptable level of livestock impact, apply appropriate standards and guidelines, and then monitor their impacts. Implementing management decisions to meet wildlife species and habitat objectives, as well as broader goals of ecosystem health on public rangelands, often are emotionally charged socioeconomic (if not sociopolitical) decisions. These decisions often involve reducing use or eliminating livestock in the area of concern for a period of time to allow recovery. Numerous case studies and demonstration areas have illustrated that these actions are effective in some rangeland habitats such as riparian and aspen communities.

Within the field of wildlife–livestock interactions, addressing competition between livestock and large native herbivores was a primary emphasis on western public lands during the 1950s–1980s; during the 1990s the emphasis shifted to developing strategies to protect and restore riparian areas from overgrazing by livestock. Preventing livestock from negatively affecting riparian areas and achieving better distribution of grazing animals throughout upland areas were desired objectives. More recently (mid 1990s to present), there is evidence demonstrating the importance of standing herbaceous vegetation for nesting sage-grouse, a vegetation component that could be difficult to meet without significant change in grazing management strategies. Thus, more encompassing ecosystem-landscape-biodiversity concepts for management of rangelands have evolved in recent years. These have caused further shifts in the directions of many interest groups, government agencies, and academicians.

On public rangelands, recent objectives go beyond achieving and maintaining good to excellent range conditions for livestock and wildlife. Instead, objectives have broadened to conserve biodiversity, improve ecosystem health, and meet habitat requirements of federally listed, or potentially listed, wildlife. These objectives could be represented in many cases by increased herbaceous cover, soil maintenance, reduction in invasive species, and clean water. A more general approach would be to define positive ecological changes through rangeland management actions. Across landscapes, achieving such positive changes likely would satisfy most concerns for wildlife simply because such large-scale changes have been needed for decades.

Examples of species receiving substantial attention at present are the willow flycatcher and great gray owl, which rely on high quality mountain meadow-willow (*Salix* spp.) riparian complexes, and sage-grouse that rely on a combined habitat structure of sagebrush and standing herbaceous vegetation. The former 2 species continue to represent the needs and concerns related to grazing impacts on montane meadow and riparian areas, while the burgeoning sage-grouse issue has been labeled the range equivalent of the spotted owl (*Strix occidentalis*) issue because desired herbaceous cover levels will be difficult to achieve on grazed rangelands.

Investigations of Wildlife–Livestock Relationships

Studies of wildlife and livestock interactions are typically conducted to increase understanding of direct and indirect effects of livestock (as the manipulated perturbation or stressor) on a native species and/or its habitat. Much of the existing work was retrospective, rather than experimental, in that it was conducted with livestock as part of the system rather than as an introduced perturbation with treatments and controls. This difference also reflects one of the fundamental social debates regarding livestock on public lands in the United States: are humans, and the impacts they bring, part of the biotic community or ecosystem (e.g., Box 2000)?

Unquestionably, the science on wildlife-livestock relationships varies in terms of its rigor, thoroughness, results, and applicability to real systems. It indicates the presence of large, non-native herbivores is beneficial to some species and detrimental to others. Some initial investigations of wildlife–livestock relationships examined how cattle and mule deer distributed themselves throughout a common range (Julander and Robinette 1950, Julander 1955, Julander and Jeffery 1964) instead of manipulating cattle to measure how deer responded with and without cattle in the same area. Unfortunately, the ability to conduct replicated experiments at appropriate spatial and temporal scales to assess livestock grazing impacts on a wildlife population is logistically difficult. Conclusions from retrospective studies, that deer or other wildlife species preferred the steeper slopes while livestock preferred the flatter areas, became dogma in range science and suggested that a harmonious coexistence occurs without objective experimental evidence.

Perhaps the most acceptable generalization that can be made is that increasing the grazing level (often termed heavy, uncontrolled, excessive, or severe grazing) above some site-based threshold results in impacts that are not desirable to any interest. Further confounding our ability to generalize among wildlife–livestock investigations is that stocking rates, number of grazing levels (ungrazed or grazed in some studies; none, light, moderate, or heavy grazing in others), time of year grazed, vegetation communities, time lags to examine the response (e.g., Dobkin et al. 1998), and wildlife species of interest are not consistently applied or comparable.

During the 1950s–1980s, the primary wildlife emphasis on public rangelands was competition among large ungulates and livestock. Kie et al. (1994) summarized much of the knowledge in this area, and large herbivores continue to be of interest (e.g., Austin 2000). Rangeland science, however, has broadened to include examinations of livestock impacts on nontraditional wildlife and biodiversity. The body of literature examining the impacts of livestock on taxonomic groups such as amphibians (Jennings and Hayes 1993, Denton and Beebee 1996, Bull and Hayes 2000), reptiles (Bock et al. 1990, Bostick 1990, Kazmaier et al. 2001), birds (Dobkin et al. 1998, Goguen and Mathews 1998, Sveum et al. 1998, Belanger and Picard 1999, Beck and Mitchell 2000), small mammals (Hayward et al. 1997), and invertebrates (Rambo and Faeth 1999, Bronham et al. 1999) continues to grow, as does the number of review papers on livestock grazing impacts on biological diversity and ecosystems (Fleischner 1994, Belsky and Blumenthal 1997, Larsen et al. 1998, Belsky et al. 1999, Jones 2000).

Using livestock as a tool to manage wildlife habitat has been advocated for many years and examples of how this benefits one or more wildlife species do exist (Severson 1990). For example, Leopold et al. (1951) described the benefits of livestock in opening up paths for deer and other wildlife throughout willow-dominated montane meadow systems. Other examples describe the benefits of livestock in helping maintain or enhance vegetation species diversity (Rambo and Faeth 1999, Humphrey and Patterson 2000) or enhancing forage quality for other large herbivores (Clark et al. 2000). Whether the mechanical benefits, or more importantly, ecological benefits are needed every year is rarely, but should be, asked in the context of the entire system affected. Have Leopold et al.'s (1951) willow meadows been opened up "enough," or do they need to be continually grazed summer-long in high mountain ecosystems, such as those in the Sierra Nevada?

Accommodating Wildlife and Habitat Objectives on Rangelands

A common link between the wildlife biologist and the range manager is the vegetation community and the wildlife habitats represented. From a wildlife perspective, perhaps an efficient technique would be to develop habitat objectives such as percent cover, desired plant species composition, and structural conditions of vegetation that are desired for a species, a suite of species, or a community as a whole, rather than a targeted species population objective. This approach leaves the range or livestock manager with the task of identifying potential strategies for managing livestock to achieve wildlife objectives. Identifying how wildlife species respond to livestock grazing might be of value in assessing whether the overall effects of the grazing level are acceptable or not; this process for wildlife would be analogous to characterizing plant species as increasers, decreasers, or invaders in response to livestock grazing (e.g., Stoddart et al. 1975).

The concept of maintaining or enhancing biodiversity on multiple use rangelands should also capitalize on interjecting management diversity in terms of grazing systems used. Interjecting unpredictable changes in habitat structure by resting habitats that normally are grazed continuously adds to this kind of diversity. Additional study and information on how individual species respond would help distinguish between desirable and undesirable trends in species responses.

Historically, land use plans prepared by the U.S. Forest Service and Bureau of Land Management, in collaboration with state wildlife agencies, often developed population objectives for species such as deer, elk, or pronghorn (*Antilocapra americana*). A more measurable approach would involve moving from a specific population target and, instead, focusing on achieving a desired habitat condition across the landscape–at the scale of allotments, resource areas, districts, or entire national forests.

Role of Monitoring and Assessment in Addressing Wildlife–Livestock Issues

> *"The lack of biological data is, without a doubt, one of the greatest single factors in retarding development of a larger conservation program"* (California Fish and Game 1926:28)

Because of the inherent controversy and often-polarized views of wildlife and livestock relationships, difficult management decisions are often tabled in the absence of adequate data on species trends or ecological condition of the system in question. Consequently, among the most valuable activities that can be undertaken for the benefit of wildlife on rangelands is the collection of scientifically defensible data on distribution, abundance, status, trend, and habitat relationships. Ranging from basic inventory, to implementation of long-term monitoring, and experimental investigation of cause-and-effect relationships, scientific data aid management decisions. A meaningful progression of actions to examine and understand wildlife and livestock relationships might involve assessing:

a) wildlife habitat requirements and preferences,
b) livestock use of habitats preferred by wildlife,
c) livestock and wildlife effects on those habitats and vegetation communities,
d) livestock effects on wildlife species, and
e) how wildlife responds over time.

The effects studied range from direct influences of livestock on species (e.g., trampling of frogs) to numerous indirect effects (e.g., effect on prey species or hiding cover). Far more likely than experimental manipulations, however, are study and characterization of habitat conditions including structure and composition of vegetation and how it influences species productivity and abundance. An adaptive element would include mechanisms to change livestock management strategies as information is gained or to test specific hypotheses with an experimental or manipulative approach.

MANAGING LIVESTOCK ON RANGELANDS

Heavy livestock grazing has been detrimental to many wildlife species in western North America (Smith 1977, Gallizioli 1979, Peek and Krausman 1996). Uncontrolled grazing clearly can affect the structure and composition of wildlife habitats. When adverse impacts occur, elimination of livestock can improve habitat conditions, although in many situations changes in livestock management practices can result in similar benefits. When properly managed, livestock grazing can be used to improve habitat for wildlife dependent on early-seral stage plant communities (Longhurst et al. 1976; Urness 1976, 1990; Kie and Loft 1990; Ohmart 1996). Information on relationships between livestock and wildlife is available in a variety of books, symposium proceedings, and review papers (Smith 1975, Townsend and Smith 1977, Schmidt and Gilbert 1978, DeGraaf 1980, Wallmo 1981, Peek and Dalke 1982, Thomas and Toweill 1982, Menke 1983, Severson and Medina 1983, Halls 1984, Severson 1990, Krausman 1996).

The relationship between grazing and wildlife habitat is complex. Livestock influence wildlife habitat by modifying plant biomass, species composition, and structural components such as vegetation height and cover. The impact of livestock grazing on wild ungulates can be classified as direct negative, indirect negative, operational, or beneficial (Mackie 1978, Wagner 1978). An example of a direct negative impact is competition between cattle and deer for a resource such as food or cover (Mackie 1978, Wagner 1978). Competition occurs when 2 organisms use a resource in short supply, or when one organism harms another in the process of seeking the resource (Birch 1957, Wagner 1978). Factors affecting impacts of livestock on wildlife include diet similarity, forage availability, animal distribution patterns, season of use, and behavioral interactions (Nelson and Burnell 1975, Severson and Medina 1983).

Indirect negative impacts of cattle grazing include: (1) gradual reductions in vigor of some plants and in amount and quality of forage produced; (2) elimination or reduction of the ability of forage plants to reproduce; (3) reduction or elimination of locally important cover types and replacement by less favorable types or communities, by direct actions over time or by changing the rate of natural succession; and (4) general alterations and reduction in the kinds, qualities, and amounts of preferred or otherwise important plants through selective grazing, browsing, or other activities (Mackie 1978).

Operational impacts are associated with livestock management (Mackie 1978) and include fence construction, water development (Evans and Kerbs 1977, Wilson 1977, Yoakum 1980), brush control (Holechek 1981), and disturbance associated with handling of livestock. For example, deer may temporarily move from pastures when cattle roundups occur (Hood and Inglis 1974, Rodgers et al. 1978).

Small mammals also influence rangeland vegetation (Moore and Reid 1951, Wood 1969, Batzli and Pitelka 1970, Turner et al. 1973, Borchert and Jain 1978) and compete with livestock for forage (Fitch and Bentley 1949, Howard et al. 1959). Because of their size and susceptibility to predation, rodents, lagomorphs, and other small mammals are highly dependent on the structure of vegetation in their habitats (Grant et al. 1982, Parmenter and MacMahon 1983, Bock et al. 1984). Grazing by livestock influences vegetation structure in those habitats and can significantly affect small mammal populations (Reynolds and Trost 1980).

Livestock grazing adversely affects many grassland birds, although moderate grazing can be neutral or beneficial to some species (Buttery and Shields 1975). Livestock management practices also can affect birds indirectly. For example, an organophosphate insecticide externally applied to cattle to control warbles may kill American magpies (*Pica hudsonia*) and cause secondary mortality among red-tailed hawks (*Buteo jamaicensis*) eating carcasses of the poisoned magpies (Henny et al. 1985).

Livestock management practices that can affect wildlife habitats and populations include livestock numbers, timing and duration of grazing, animal distribution, livestock types, and specialized grazing systems. These practices can be modified to reduce or eliminate adverse effects on wildlife and, at times, to enhance wildlife habitats (Severson 1990).

Livestock Numbers

Livestock numbers, or stocking rates, usually are specified by animal unit months (AUMs). One AUM is one animal unit (one mature cow with a calf, or equivalent) grazed for one month (Heady 1975:117). Livestock effects on wildlife become more pronounced with increasing stocking rates. A few cattle in a pasture may have no discernible effect on wildlife, but beyond some threshold wildlife response may increase rapidly. A range manager's traditional definition of proper grazing is based on maintaining a mix of plant species valuable as livestock forage and preventing soil erosion. Optimum livestock densities for wildlife may occur at different, and often lower, stocking rates. Thus, as with most effects of livestock on wildlife, responses can be difficult to interpret because of inherent site differences (Johnson 1982), and differences in grazing intensity, timing, and duration.

Timing and Duration of Grazing

Moderate cattle grazing of riparian areas in late fall in Colorado had no detectable impact on 6 species of birds dependent on the grass-herb-shrub layer for foraging, nesting, or both (Sedgwick and Knopf 1987). However, summer grazing can eliminate habitat specialists such as willow flycatchers, Lincoln's sparrows (*Melospiza lincolnii*), and white-crowned sparrows (*Zonotrichia leucophrys*) (Knopf et al. 1988).

The time of year that livestock are present can alter the composition of plant communities. Heavy grazing during a period of rapid growth of one plant species will favor other species that grow more rapidly at other times. For

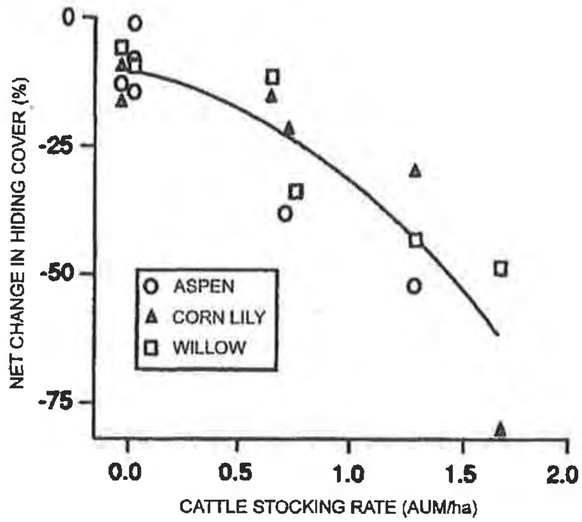

Fig. 1. Net change in mule deer hiding cover between 0 and 1 m in height from beginning of summer until mid-August as a function of cattle stocking rate (AUM/ha = animal unit months per hectare) (after Loft et al. 1987).

example, spring grazing of annual grasslands in California reduces grass cover and encourages growth of summer-maturing forbs such as turkey-mullein (*Eremocarpus setigerus*), the seeds of which are readily eaten by mourning doves (*Zenaida macroura*) (Kie 1988). Conversely, many wildlife species are most susceptible to livestock-induced changes in habitat during their reproductive seasons. Birds that nest on the ground or in shrubs can experience reproductive losses if their nests are trampled or otherwise destroyed by cattle. For example, willow flycatchers in California breed exclusively in riparian deciduous woodlands, and prefer willows as nesting substrate (Valentine et al. 1988). Flycatchers prefer to nest near the edges of willow clumps or along livestock trails (Valentine et al. 1988, Sanders and Flett 1989), where they are susceptible to physical disturbance. In one study, 4 of 20 willow flycatcher nests in a 4-year period were destroyed by cattle before young fledged, and 4 other nests were destroyed after young fledged (Valentine et al. 1988). When cattle stocking levels were reduced and 75% of the remaining cattle were confined to a fenced pasture away from willow flycatcher nest sites until 15 July, no willow flycatcher nests were lost (Valentine et al. 1988).

Excessive grazing can accelerate loss of hiding cover early in summer when mule deer fawns are young (Loft et al. 1987) (Fig. 1). These conflicts can be minimized or eliminated by delaying grazing until later in the year (Kie 1991).

Livestock Distribution

Livestock congregate around sources of water, supplemental feed, and mineral blocks; their impacts are most pronounced in those areas. Riparian zones, because of their abundant forage and water, are good examples of livestock concentration areas. Cross-fencing, developing alternative water sources, and providing feeding supplements on upland sites away from riparian areas more evenly distribute livestock. However, in certain situations, wildlife can benefit from patchy livestock distribution because some areas are lightly grazed. For example, many species of wildlife inhabit ecotonal areas ("edges"), and patchy distribution of livestock across home ranges of those species enables selection of grazed versus ungrazed patches to serve as foraging areas or refugia.

Types of Livestock

Effects of grazing on wildlife depend on the species of livestock. Differences in diet between cattle and domestic sheep dictate the effects they have on plant species composition. Also, cattle usually range within the confines of a fenced allotment, but sheep often are herded. Herded bands of sheep may have enhanced some habitats for mule deer in California (Longhurst et al. 1976) by repeated grazing and browsing that stimulated regrowth of more palatable shrubs and herbaceous vegetation. However, transmission of diseases from domestic sheep to mountain sheep (*Ovis canadensis*) may have eliminated many populations of the latter from California (Wehausen et al. 1987). As a result, professional organizations (e.g., Desert Bighorn Council Technical Staff 1990) and federal agencies have adopted management policies that reduce the probability of contact between domestic sheep and mountain sheep (U.S. Department of Interior 1992, U.S. Department of Interior and California Department of Fish and Game 2002).

Competition between pronghorn and domestic sheep is greater than between pronghorn and cattle because of increased overlap in forage preferences. On overgrazed sheep ranges, insufficient forb growth was available for pronghorn during the critical mid-winter period, and pronghorn die-offs were common (Buechner 1950). In general, domestic sheep are more likely than cattle to affect pronghorn adversely (Autenrieth 1978, Salwasser 1980, Yoakum 1980, Kindschy et al. 1982), and even moderate use by sheep during the winter dormant period can leave range units unsuitable for pronghorn until plant regrowth in spring (Clary and Beale 1983). Cows with calves often exhibit grazing patterns different from those of steers, and differences among breeds of cattle and sheep may occur.

Specialized Grazing Systems

Many specialized grazing systems exist, although most can be classified into 3 types (Heady 1975, Stoddart et al. 1975). *Continuous grazing* allows livestock to graze season-long or year-long. *Deferred grazing* refers to delaying or deferring grazing until after most of the range plants have set seed. Deferred grazing allows plants to grow, store carbohydrates, and reproduce at high rates. *Rotational grazing* involves dividing a range unit and rotating livestock through different pastures.

Combinations of periodic deferment and rotational grazing are called *deferred-rotation* grazing systems. A common one of these is the *4-pasture deferred-rotation* system, in which 4 range units or pastures are used, with 3 being grazed year-long and the fourth being deferred for 4 months. The pastures are then rotated each year.

Rest-rotation grazing is similar to a deferred-rotation system, but the period of rest consists of a full year or more. *Short-duration* grazing systems are similar to deferred-rotation systems, except that ≥8 small pastures are used, stocking rates are high in each pasture as it is used, but livestock are present for only short periods of time. Because timing of livestock grazing is critically important to most rangeland wildlife species, rotational grazing systems designed to consider wildlife have the greatest potential to reduce adverse effects.

Rest-rotation grazing may have the most potential to provide benefits to wildlife. This system often is economically disruptive because it foregoes livestock forage, but such losses may be compensated by benefits derived from wildlife-related recreation on public lands. For example, development of a rest-rotation grazing system in a single deer-hunting zone in California might specify that each range unit would be grazed only 1 of 3 years. The value of unused livestock forage, calculated on the basis of net economic value at $12.82 per AUM, would equal about $71,000 over each 3-year grazing cycle. However, increased deer populations and additional hunting opportunities would be valued at $6.5 million over the same period (Loomis et al. 1991).

Using Livestock to Manage Wildlife Habitat

In some situations, livestock grazing can be used to manage wildlife habitat (Longhurst et al. 1976, 1982; Holechek 1980, 1982; Urness 1982, 1990; Severson 1990). Livestock grazing has been applied to the management of habitat for species as diverse as mule deer (Smith et al. 1979, Willms et al. 1979, Reiner and Urness 1982), northern bobwhites *(Colinus virginianus)* (Moore and Terry 1979), and Canada geese (*Branta canadensis*) (Glass 1988). For example, cattle grazing in late winter and spring on foothill, annual grasslands in California encourages growth of forbs that are valuable to many wildlife species.

In other situations, application of prescribed grazing has met with mixed results. Too often, the intent of using livestock grazing has been to manage habitat for a single species, whereas entire communities actually are affected. Using livestock to maintain a plant community in an early seral stage often will benefit those wildlife species dependent on such habitat, while simultaneously impacting species associated with climax communities (Kie and Loft 1990).

The prescription, or strategy, for grazing is important. Maximizing benefits to wildlife from changes in grazing will involve reductions in livestock numbers and shortening grazing seasons compared to management plans designed to maximize livestock production. Livestock grazing by itself is neither good nor bad for wildlife, but depends on a variety of factors, including wildlife species of concern, livestock numbers, timing and duration of livestock grazing, livestock distribution, and kinds of livestock (Kie and Loft 1990). Wildlife and range managers might consider avoiding generalizations and evaluate the role of livestock on wildlife and their habitats independently for each species, grazing plan, and management situation.

MANAGING RANGELAND BY ANTHROPOGENIC MANIPULATION

Fire

Rangeland species evolved under the influence of fire and, hence, many are fire adapted. The natural occurrence of fire varies among regions as a result of fuels, topography, climate, and ignition source. The effect that fires have on landscapes is further dependent upon fire size, intensity, frequency, time of year during which they occur, and resulting burn patterns (Riggs et al. 1996). The interval at which fire occurs on a landscape varies as a function of active fire suppression, prior fire regime, plant community, and geographic location (Wright and Bailey 1982).

Effects of fire on wildlife populations may be positive or negative depending upon the temporal scale under consideration (short- vs. long-term), species involved, and characteristics of the burn. Fire effects on wildlife may be characterized as those directly affecting diet and those relating to habitat structure. Although effects on forage quality tend to be rather short-lived following a fire (Hobbs and Spowart 1984), structural changes may persist for decades, as is the case when forested and shrub stands are eliminated (Bunting 1986, Everett 1986, West and Yorks 2002). Effects of fire on bird and small mammal populations tend to be related to modifications of vegetation structure (Blake 1982, Bock and Bock 1983, Niemi and Probst 1990, Riggs et al. 1996).

Diet quality may be altered by fire as a result of alterations to floristic composition of plant communities, chemical composition of plant tissues, and structure of the plant canopy (Riggs et al. 1996). Although investigators have observed increases in both crude protein (Hobbs and Spowart 1984, Cook et al. 1994) and in vitro digestibility (Hobbs and Spowart 1984) in forages following fire, some of the greatest nutritional benefits may be derived through increases in foraging efficiency (Hobbs and Spowart 1984, Canon et al. 1987). Fire removes litter and dead standing herbage of low nutritional value (Van Soest 1994) enabling herbivores to more efficiently select nutritious plant material (Hobbs and Spowart 1984). The effects of burning on forage quality and stand composition and canopy among graminoids and herbaceous species persist for 1–3 years (Hobbs and Spowart 1984). Ultimately, effects on animal condition and productivity are most definitive; Svejcar (1989) noted increases in cattle performance when feeding on burned tallgass prairie.

Grazing prior to burning proportionately reduces nitrogen losses in forage (Hobbs et al. 1991), and grazing that precedes fire in tallgrass prairie reduces spatial variability of patches and improves animal performance (Hobbs et al. 1991). However, grazing of dry prairies following fire can inhibit forage recovery, and preference for burns by cattle may require adjustments to stocking rate (Erichsen-Arychuk et al. 2002).

Riggs et al. (1996) discussed the economics of prescribed fire and reported the larger the prescribed fire, the more cost effective, because fixed costs are applied over a greater area. They cautioned, however, that beneficial effects of fire treatments on wildlife habitats and populations should outweigh issues focusing too heavily on the amount of area burned. The role of fire varies from region to region and by ecosystem. Thus, prescriptions should be tailored to specific project areas.

Other Methods of Vegetation Manipulation

In addition to burning and grazing, vegetation manipulation of rangelands may occur through use of hand tools, mechanical equipment, and chemical spraying. The goals, as well as logistic and financial constraints, will affect which method is most suitable for any given area. Mechanical treatments are used to remove undesirable overstory species that inhibit growth of understory forage species (Bleich and Holl 1981, Fulbright and Guthery 1996, Holechek et al. 1998, Stephenson et al. 1998). Herbicide application may be used to control either unwanted brush or herbaceous species.

Although there may be social and legal constraints that affect use of herbicides, their application may be appropriate in some cases. In contrast to mechanical removal of vegetation, application of herbicides over large areas is typically less expensive and time consuming. Herbicides may be applied by hand, or with sprayers mounted to tractors or aircraft (Koerth 1996). The Herbicide Handbook Committee (1994, 1998) provides a thorough review of the types of chemicals available and their known effects.

Mechanical removal of brush from rangelands for the benefit of wildlife tends to be most successful when applied to patches intermixed in a landscape mosaic (Fulbright and Guthery 1996). In contrast, extensive clearing is detrimental to species dependent on woody plants. Major techniques for large scale brush removal include use of roller choppers, shredders (e.g., rotary axe), and crushers for top growth removal or, conversely, whole plant removal by root plowing, chaining and cabling, disking, and bulldozing and power grubbing (Bleich and Holl 1981, Fulbright and Guthery 1996). Additional considerations when selecting mechanical methods include topography, extent of resprouting, soil type, and size of the area to be treated (Holechek et al. 1998).

MANAGING RANGELAND RIPARIAN AREAS

Riparian areas are important habitats for terrestrial and aquatic wildlife (Carothers and Johnson 1975; Thomas et al. 1979*a,c*; Platts and Raleigh 1984; Skovlin 1984; Platts 1990). Their importance is a result of being obligate habitat for many aquatic species, of the uniqueness of their soil and vegetation complexes that produce diverse vegetation structure and concomitant diverse biological communities, and of their limited extent across a diversity of landscapes. Their value for a given species of wildlife is a function of water availability (for example, mule deer in the Sonoran Desert vs. wildlife in the Prairie Pothole Region of North America), life stages, animal movements, weather, and other factors.

Riparian vegetation and its structural arrangement are important for wildlife. Many vertebrate and invertebrate species depend directly or indirectly on riparian vegetation for food, cover, or other life requisites. Some wildlife use riparian zones disproportionately more than any other habitat. For example, of 363 terrestrial species in the Great Basin of southeastern Oregon, 288 depend directly on riparian zones or use them more than other habitats (Thomas et al. 1979*a*). Herpetofaunas also are strongly associated with riparian areas (Jones 1988). Riparian soils and substrates are important to amphibians, reptiles, and small mammals because these wildlife forms often inhabit subsurface environments. The temperate microclimate, availability of moisture, and greater biomass production of these areas provide for complex food webs.

The value of riparian areas to wildlife is only generally described, owing to the difficulty of long-term observations. Mule (Thomas et al. 1979*b*) and white-tailed (Compton et al. 1988) deer select woody riparian vegetation for cover and forage. Selected bird species have demonstrated an affinity for distinct layers of vegetation (Gutzwiller and Anderson 1986). Riparian zones provide migration routes for birds, bats, deer, and elk (Wauer 1977) and are frequently used by deer and elk as travel corridors between high-elevation summer ranges and low-elevation winter ranges. Moreover, riparian habitats are strongly selected by mountain lions (*Puma concolor*) in some areas (Dickson and Beier 2002).

Riparian habitats are of further importance because they comprise only about 1% of the landscape in the United States (Knopf 1988). Further, >70% of the original riparian habitats in the United States have been lost through a variety of land use practices (Megahan and King 1985). Barclay (1978) reported that natural riparian habitats within the Oklahoma grasslands have nearly vanished, and channelization was responsible for conversion of 86% of bottomland forests to other land uses. In the southwestern United States, many historically perennial streams are largely ephemeral watercourses today (Johnson et al. 1989).

Central to development of management strategies for riparian areas are: (1) an understanding of what constitutes a riparian area, (2) their internal functions and processes, (3) the influences on riparian ecosystems, and (4) their importance to wildlife. Elmore (1989) argued that a fundamental understanding of the functioning of riparian ecosystems was initially necessary to evaluate benefits and incorporate management actions into land use plans.

Rivers and streams transport water and sediments (Jensen and Platts 1987). Thus, riparian habitats are unique products derived from the dynamic processes that a given stream produces and are influenced by the interactions of climate, geology, geomorphology, hydrology, pedogenesis, and chemical and biological processes. Little information is available, however, on wildlife/riparian interactions. As a result, wildlife management considerations frequently are excluded from land use plans (Dwyer et al. 1984, Dickson and Huntley 1987). Substantial work has been done on riverine/riparian dynamics (reviewed by Curtis and Ripley 1975; Thomas et al. 1979*a,b*; Brinson et al. 1981, Kauffman and Krueger 1984; Platts and Raleigh 1984; Skovlin 1984; Warner and Hendrix 1984; DeBano and Schmidt 1989; Platts 1990).

Value, Structure, and Function of Riparian Areas

Several authors have proposed riparian terminology; both Swanson et al. (1982) and Johnson and Lowe (1985) suggest that disparity exists among users. They defined riparian areas as the sum of the terrestrial and aquatic components characterized by: (1) presence of permanent or ephemeral surface or subsurface water, (2) water flowing through channels defined by the local physiography, and (3) the presence of obligate, occasionally facultative, plants requiring readily available water and rooted in aquatic soils derived from alluvium. Riparian ecosystems usually occur as an ecotone between aquatic and upland ecosystems, and have distinct and variable vegetation, soil, and water characteristics. Typically, riparian areas are viewed as riverine habitats with perennial surface flows and associated plants and soils. However, surface flows may be ephemeral or periodic, as in desert washes or arroyos of the southwestern United States.

Riparian vegetation typically functions to allow necessary sediment transport and natural erosional processes. It also effectively reduces accelerated erosion that could result in loss of riparian habitats (Miller 1987). Riparian trees supply large organic debris and function to influence the physical (morphology), chemical (nutrient cycling), and biological (flora and fauna) components of the system (Bisson et al. 1987). Changes in stream channel structure and habitat diversity can occur when large organic debris is removed (Bilby 1984). Structural diversity, an important feature of riparian vegetation (Jain 1976, Anderson and Ohmart 1977), is affected by consequences of natural or human-caused habitat disruption.

Management Problems and Strategies

Management of riparian habitats is important because of the role of these ecosystems in water quality and nutrient recycling (Stednick 1988), and because riparian vegetation is considered to be the most sensitive and productive North American wildlife habitat (Carothers and Johnson 1975). Indeed, no other habitat in North America is as important to noncolonial nesting birds; riparian areas are equally important to other terrestrial vertebrates (Szaro et al. 1985).

Riparian zones are easily affected by natural or induced changes on their watersheds, including grazing (Kauffman and Krueger 1984, Skovlin 1984, Chaney et al. 1990). Moreover, problems seemingly related to riparian habitats alone cannot be resolved by considering only that habitat. As a result, management of riparian areas should be considered both onsite (within the riparian zone) and offsite (outside the riparian zone), which accounts for all adjacent uplands that exert influence over the watershed. Onsite activities such as grazing management and vegetation treatments are performed within riparian habitats; offsite activities include logging, road construction, and slash burning. Management activities outside the riparian zone may change the quantity and quality of water entering the riparian area (Stednick 1988). A variety of range management options are available for sustaining health of riparian habitats including complete protection (Stromberg and Patten 1988), multiple-use approaches, and exclusive use.

Livestock grazing is perhaps the greatest biological threat to riparian habitats in the western United States, given that about 91% of the total rangeland is grazed (Chaney et al. 1990). Improper livestock grazing affects all 4 components of the riverine/riparian system–channel, stream banks, water column, and vegetation (Platts 1990). Livestock grazing problems usually are the result of improper distribution of cows and not simply too many (Severson and Medina 1983). Concentrated livestock use results in sparse tree or shrub stands of low vigor, generally with substantial dead material on the ground, a tight, sod-bound soil, and lack of tree or shrub reproduction. Damage occurs in several ways. One is compaction of soil, which reduces moisture infiltration and increases runoff. Another is constant removal of herbage, which allows soil temperatures to rise and increases evaporation from the soil surface. A third is physical damage to the trees or shrubs by rubbing, trampling, and browsing (Severson and Boldt 1978). The primary method for resolving overuse of riparian areas has been modified grazing strategies, which have met with mixed results (Dwyer et al. 1984, Skovlin 1984, Chaney et al. 1990).

Isolated case studies have demonstrated that revised grazing management improved conditions, but also that condition of riparian habitats continues to decline (U.S. General Accounting Office 1988). Myers (1989) reported 74% of the grazing systems evaluated failed to positively improve rangeland health within 20 years; however, riparian vegetation usually improves from grazing relief within 4–6 years, depending on severity of use (Platts and Nelson 1989). Areas with severe overuse require greater periods of time (>15 years) for native species such as sedges (Cyperaceae) to displace species adapted to overuse (Elmore and Beschta 1987).

Conventional grazing systems (Heady 1975) were developed with consideration only for production and maintenance of forage plants, primarily graminoids. Application of these systems to maintain woody streamside vegetation and stream bank integrity likely will not be satisfactory, given the ecophysiology of shrubs and trees. Platts (1990: 6) provided an excellent description of grazing strategies designed to complement restoration objectives with livestock management, and suggested that, "the solution is to identify and develop compatible grazing methods," given our state of knowledge of the functions of riparian systems. Indeed, at least one grazing strategy is available that would provide riparian areas with the necessary rest or protection needed to restore, maintain, or enhance their productivity. The least acceptable option is "no use" by ungulates and this option may be attractive in situations where restoration is a major objective of overall riparian management. Another recommendation is to fence critical reaches of riparian habitats in an effort to maintain the integrity of the streamside zone (Platts 1990).

A good management strategy for sustaining rangeland riparian areas will: (1) maintain the productivity of the vegetation (e.g., structure, species composition), (2) maintain the integrity of stream dynamics (e.g., channel and bank stability), and (3) recognize that several factors (e.g., soils, vegetation, hydrology, and animals) interact to maintain a dynamic equilibrium within the riparian zone. Successful management of riparian areas is dependent on application of knowledge from the physical sciences, such as hydrology and geomorphology, combined with an aggressive program that provides adequate protection to the structure, composition, and diversity of vegetation in such areas.

DEVELOPING RANGELAND WATER SOURCES

Increasing the amount of water available to wildlife has been used to enhance habitat for species inhabiting arid rangelands (Kie et al. 1994). Techniques include improvement of natural springs, seeps, and waterholes, and construction of artificial devices to capture and store rainfall (Tsukamoto and Stiver 1990, Young et al. 1995, Arizona State University College of Law 1997). Recently, development of rangeland water sources has been questioned (Broyles 1995) and become controversial (e.g., Broyles and Cutler 1999, Rosenstock et al. 2001) and will require substantial effort to resolve (Rosenstock et al. 1999).

Many methods have been used to make subsurface water available to wildlife including manual techniques, explosives, prescribed fire, and chemicals. Recently, horizontal well technology has been applied to development of springs and seeps for wildlife (Kie et al. 1994). Handwork, although time consuming and costly, may be the most practical way to accomplish some types of developments (Weaver et al. 1959). Helicopters can be used to transport personnel and hand tools into remote sites, thereby allowing development of those sites (Bleich 1983).

Water sources can be improved with explosives (Weaver et al. 1959), but caution is necessary to ensure that water-yielding subsurface formations are not altered drastically and water flow is not interrupted. When such damage does occur, it is usually the result of a heavy charge opening a crack that allows water to escape. Explosives should be used only on marginal seeps where sufficient water is not immediately available and where it can be used safely. Explosives also are useful in clearing channels to allow storm flows to bypass a spring, or to lay pipe to be used for gravity flow of water to a basin (Weaver et al. 1959).

Prescribed fire can be used to remove phreatophytic vegetation, resulting in a decrease in the transpiration of subsurface water and increased surface flows (Biswell and Schultz 1958, Weaver et al. 1959). Use of prescribed fire requires extreme caution and periodic reburning may be necessary to maintain surface flows. However, the importance of small patches of desert riparian vegetation to a multitude of species makes any substantial reduction in the occurrence of such vegetation undesirable (Bleich 1992). Where prescribed fire can be used to temporarily clear a spring site or seep so that other development may proceed, its use may be desirable, but its role is limited.

Herbicides increase surface flows by eliminating vegetation responsible for evapotranspiration of subsurface water. They can be particularly useful where water is limited; loss of cover or shade may be more than offset by making a permanent water supply available to wildlife (Weaver et al. 1959). The limited distribution of native, riparian vegetation in arid areas makes widespread use of herbicides undesirable. Herbicides can, however, be used to control saltcedar or tamarisk (*Tamarix* spp.) at desert water sources (Sanchez 1975). Control of this exotic species can be successfully accomplished on a small scale by hand cutting and herbicide application (Sanchez 1975, Neill 1990).

Development of Springs

Development of springs should: (1) provide at least one escape route for wildlife to and from the site that takes advantage of the natural terrain and vegetation; (2) provide an alternate escape route where feasible; (3) protect water developments from livestock while allowing access for wildlife; (4) reduce the possibility of wildlife drowning by providing gentle basin slopes or ramps in tanks; (5) maintain or provide adequate natural cover, plantings, or brush piles around the watering area; (6) provide, where applicable, a sign to inform the public of the purpose of the development; (7) provide for development of sufficient capacity to supply water whenever it is needed for wild animals; and (8) provide livestock and public access to water outside the protected water development (Yoakum et al. 1980, Bleich 1992, Kie et al. 1994). If shy animals are involved, water for human consumption can be piped some distance from the wildlife water source. For example, sustained camping should be discouraged within a 1-km radius of water used by mountain sheep.

Ramps or walk-in wells offer a simple and inexpensive method of making water available to wildlife (Weaver et al. 1959). Unless the ramp is cut through rock, however, the sides must be boarded to keep material from sloughing into the excavation. Ramps should be a minimum of 1 m wide to allow large animals to enter and exit easily. Ramps are also important for escape in other types of water developments such as livestock troughs (Wilson 1977) and guzzlers (Andrew et al. 2001).

Construction of small basins or pools at a water source is an effective way to conserve water and make it readily available to wildlife. Basins may be constructed with rock, cement, or masonry, or they may be gouged from solid rock near the source when small seeps originate in a rock stratum. A simple basin, constructed with hand tools, can be chiseled into solid rock and will effectively store water for years. Where appropriate, power tools and explosives may be used to create larger storage basins. When explosives are used, care must be taken not to damage the source of the water, or the rock face so that it cannot be modified to store water. A major advantage of this type of development is that they are nearly indestructible.

Rock basins can be enlarged with cement and rocks or masonry materials. Similarly, these materials may be used to construct diversions to protect a basin from debris caused by storm flows, or to create an artificial basin at a location where the development of a solid rock basin is impractical. Special masonry techniques may be necessary to ensure a bond between the mortar and rock (Gray 1974).

Many springs and seeps occur in canyon bottoms. Even when developed, such springs are subject to damage by water from storms. A method of development that often is satisfactory is to bury a length of perforated asphalt or plastic pipe packed in gravel, at the spring source, and pipe the water to a basin or trough away from the canyon bottom and danger of flooding. Placing large rocks over a source after it has been developed and capping the development with concrete increases protection. Alternatively, a redwood spring box may be installed at a water source allowing access for maintenance with water piped to a trough in a safe location.

Plastic pipe is a good choice for use because it is lightweight, durable, and not subject to rust or corrosion; further, repairs are easily accomplished. Any type of pipe should be buried sufficiently deep to prevent freezing, trampling by livestock and wild ungulates, or damage from floods. A continuous downhill grade will help prevent air locks from developing in the pipe and ensure constant flow of water. When water is to be piped away from excavated springs, a trough constructed of concrete or masonry is preferred because it will not rust. If the trough poses a potential hazard for small animals and birds, a ramp should be installed to facilitate access to the water (Bond 1947).

Horizontal Wells

Traditional techniques used to develop springs and seeps have several disadvantages: (1) flow of water from the source cannot be controlled, (2) variable flow may be inadequate to generate enough water to create a surface source, and (3) exposed spring water and the source may be susceptible to contamination (Welchert and Freeman 1973).. Horizontal well technology can overcome some of these disadvantages (Coombes and Bleich 1979; Bleich 1982, 1990; Bleich et al. 1982*a*).

Horizontal wells have several advantages: (1) success rate, particularly in arid regions where historical sources may have failed, is high; (2) amount of water can be readily controlled, thus reducing waste; (3) the area is not readily subject to contamination; (4) they are relatively inexpensive to develop; and (5) maintenance requirements are low. Horizontal wells also have disadvantages: (1) the initial cost of the equipment necessary to construct them can be high (although private contractors can do the work with their own equipment), (2) transporting the necessary equipment to remote sites can be difficult, and (3) some horizontal wells require a vacuum relief valve to prevent air locks from interrupting the flow.

Site selection is the most important and difficult step in development of a horizontal well. Several factors, including presence of historical springs and seeps, distribution of phreatophytes, and presence of an appropriate geological formation, must be evaluated (Welchert and Freeman 1973). Dike formations (a tilted, impervious formation that forms a natural barrier to an aquifer) and the contact formation (a perched water table over an impervious material) are both suitable for horizontal well development. Developing a dike formation requires the impervious barrier be penetrated to tap the stored water (Fig. 2). A contact formation is developed by penetrating at or above a seep area at the boundary of an impervious layer (Fig. 2).

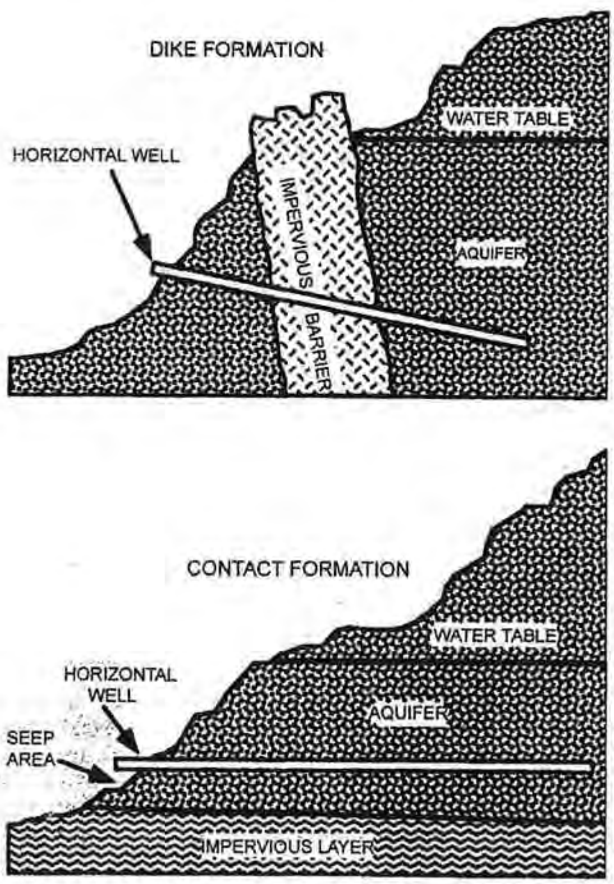

Fig. 2. Horizontal wells can be developed in dike or contact formations. The position of the well relative to the aquifer and impervious barrier is critically important to the success of the well (after Welchert and Freeman 1973).

Tinajas

Tinajas are rock tanks created by erosion that hold water. In some desert mountain ranges, tinajas may provide the only sources of water for wildlife. The capacity of tinajas can range from a few liters to more than 100,000 L of water.

Several techniques are available to increase storage capacity of tinajas. Sunshades can be used to reduce evaporation of water (Halloran 1949; Halloran and Deming 1956, 1958; Weaver et al. 1959). Shades can be constructed by anchoring eyebolts into the canyon walls, installing cables, and attaching shading material such as sheet metal to the cables (Weaver et al. 1959). In Arizona, sunshades have been built with a framework of 5-cm pipe placed into holes drilled into bedrock, with shading material then attached to the framework (Werner 1984).

Some tinajas can be deepened or enlarged with explosives (Halloran 1949, Weaver et al. 1959), but use of this method risks damage to the tinaja. A safer, and potentially more effective, method involves constructing an impervious dam on the downstream side, combined with a pervious structure to divert debris around the tinajas but allowing water to flow into them (Werner 1984). Deep, steep-sided tinajas often pose special problems for wildlife, because individuals can become trapped when water levels are low. Pneumatic equipment or explosives can be used to chisel or blast access ramps in such situations (Halloran 1949). Mensch (1969) used explosives to create an escape ramp at a natural tinaja in which 34 mountain sheep had died within a 2-year period.

Sand Dams

Some of the earliest techniques designed to increase water availability in arid regions involved construction of sand dams or sand tanks (Sykes 1937; Halloran 1949; Halloran and Deming 1956, 1958). These devices originally were constructed by placing a concrete dam across a narrow canyon. One or more pipes that could be capped to prevent water from draining penetrated the dam. The dammed area then filled with sand and gravel washed in by floods. Water soaks into the sand and gravel, and is stored, protected from excessive evaporation (National Academy of Sciences 1974).

Sand dams must be securely anchored in bedrock, and the design and construction of the dam may be the most important aspect of the entire system (Bleich and Weaver 1983). Because seepage at the bedrock interface could be a significant source of water loss, Bleich and Weaver (1983) emphasized that techniques used must result in an efficient bond between cement and bedrock (Gray 1974).

Storage volume of sand dams can be increased in a variety of ways (Sivils and Brock 1981, Bleich and Weaver 1983), but dams should not be too large. Compounds such as calcium aluminate can be added to the concrete to decrease set-up time (Gray 1974); however, sand dams should be no more than 12 m long and 3 m high (Halloran and Deming 1956, 1958). Water stored behind sand dams can be piped to a trough some distance from the dam (Sivils and Brock 1981), or used to flood natural or constructed potholes downstream.

Because precipitation in arid regions often occurs as violent thunderstorms, washes and canyons often flow large amounts of water over a short period of time. These brief flows may not allow sufficient time for storm water to saturate areas behind sand dams, especially if the underground storage capability has been enhanced (Sivils and Brock 1981, Bleich and Weaver 1983). Rock-filled baskets or gabions anchored into bedrock can be placed across a wash or canyon perpendicular to the direction of flow to slow water velocity. Such structures also raise and widen the wash.

Reservoirs and Small Ponds

A reservoir consists of open water impounded behind a dam. Reservoirs can be constructed by building a dam directly across a drainage or by enclosing a depression on one side of a drainage and constructing a ditch to divert water into the resulting basin (Yoakum et al. 1980). They also recommended that reservoirs be designed to provide maximum storage with minimum surface area to reduce evaporation. Major points to consider in selection of reservoir sites include: (1) suitability of soils for dams (clays with a fair proportion of sand and gravel, i.e., 1 part clay to 2–3 parts grit); (2) the watershed area above the dam should be sufficiently large to provide water to fill the reservoir, but not so large that excessive flows will damage the spillway or wash out the dam; (3) channel width and depth with a bottom easily made watertight and channel grade immediately above the dam as flat as possible; (4) easy access for wildlife to the water; and (5) an adequate spillway naturally incorporated into the development.

The base thickness of the dam must be equal to or greater than 4.5 times the height plus the crest thickness. Slopes of the dam should be 2.5:1 on the upstream face and 2:1 on the downstream face. Minimum width of the top of all dams should be 3 m. Fill of the dam should be at least 10% higher than the required height to allow for settling. Freeboard (depth from the top of the dam to the high-water mark when the spillway is carrying the estimated peak runoff) should not be less than 60 cm, and the spillway should be designed to handle double the largest expected volume of runoff. A natural spillway is preferred and it should have a broad, relatively flat cross section. Water should be taken out through the spillway well above the fill, and then re-enter the main channel some distance downstream. Spillways should be wide, flat-bottomed, and protected by riprapping, or by facing with rocks. The entrance should be wide and smooth, and the grade of the spillway channel should be low so the water will flow through without cutting (Hamilton and Jepson 1940).

New reservoirs usually do not hold water satisfactorily for several months. Bentonite spread over the bottom and sides of the basin and face of the dam will help seal the impoundment. The basin also can be lined with polyethylene or another appropriate material, with 15–30 cm of dirt rolled evenly over the top (U.S. Department of Interior 1966). Other artificial materials such as Hypalon® (Water Saver Company, Denver, Colorado, USA) are superior to polyethylene, because of their strength and resistance to ultraviolet radiation. These liners can be custom made for reservoirs of different sizes.

Dugouts

Large earthen catchment basins built to collect water for livestock were commonly called charcos by early settlers along the Mexican border, and dugouts by pioneers in other areas (Yoakum et al. 1980). Dugouts can be placed in almost any type of topography, but are most common in areas of comparatively flat, well-drained terrain. Such areas facilitate maximum storage with minimum excavation. Dugouts can be small, rectangular excavations (Fig. 3). All sides should be sloped sufficiently to prevent sloughing (usually ≤2:1) and one or more relatively flat side slopes (≤4:1) should be provided to facilitate access for large mammals (U.S. Department of Interior 1964).

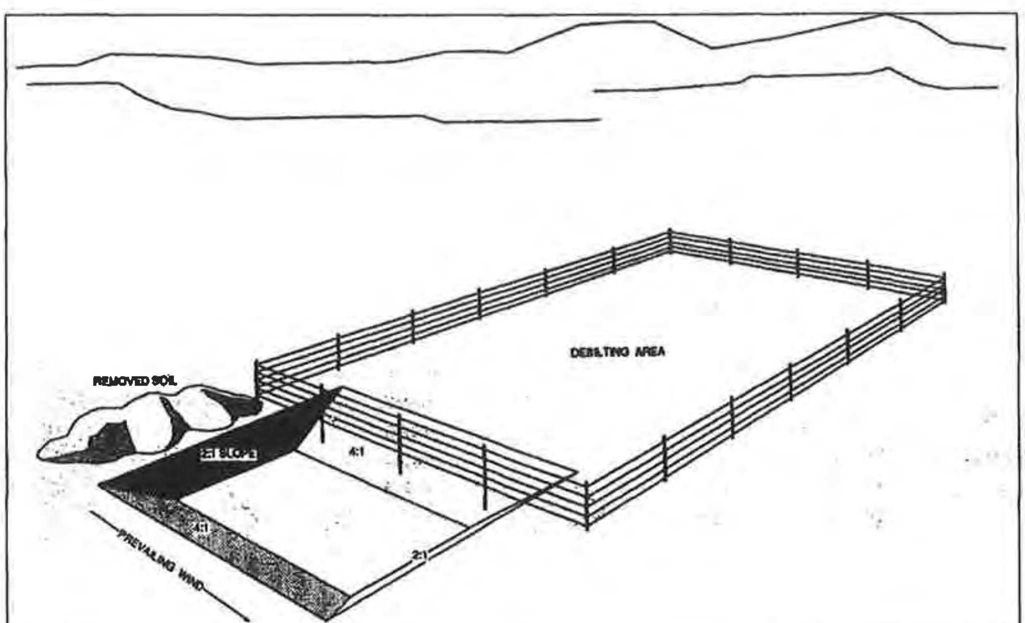

Fig. 3. Dugouts, also known as charcos, can be constructed to provide water for wildlife on rangelands (after Yoakum et al. 1980, Kindschy et al. 1982).

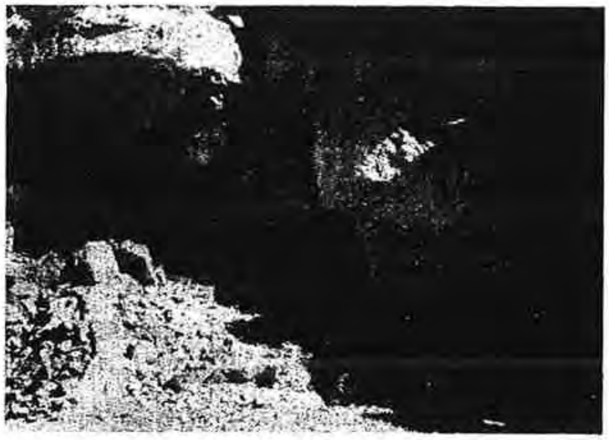

Fig. 4. An adit is a short tunnel that has been blasted into solid rock to store water for wildlife. The entrance to the adit must be at the same elevation as the bottom of the wash in which it is located.

Adits

Adits (Fig. 4) are short, dead end tunnels that extend into solid rock constructed with a downward sloping floor to allow access by wildlife (Halloran and Deming 1956, 1958). Adits have been constructed in Arizona and other western states, primarily to benefit mountain sheep (Parry 1972, Weaver 1973).

Personnel skilled in hard rock blasting techniques should be used to construct adits. These water storage depots should have openings at least 2 × 3 m and be at least 4–5 m in length. The water storage depth should be at least 4 m to ensure a dependable water supply (Halloran and Deming 1956, 1958). Commercial masonry sealers should be used to prevent seepage of water through rock fractures (Halloran and Deming 1956, 1958; Gray 1974; Werner 1984).

Because the opening of an adit must be approximately the same elevation of the wash in which it is placed, it may be necessary to construct a diversion that allows flood waters to enter, yet causes debris, sand, and boulders to bypass the adit. Boulders placed on the upstream sides of adits can be used for this purpose (Halloran and Deming 1956, 1958). Another effective, but simple, technique involves construction of a rock gabion (Werner 1984).

Adits also can be designed to store water from a natural source, such as a seasonal or permanent spring (Werner 1984), and water sometimes can be diverted into adits from natural slick-rock aprons above the site. Adits also can be used to store water that normally would be unavailable, and water can be pumped from the adit into a nearby tinaja (Werner 1984). In such instances, the adit should be covered to reduce evaporation. Shade structures have been used to reduce evaporation at adits in which stored water is directly available to wildlife (Halloran and Deming 1956, 1958).

Guzzlers

Guzzlers are permanent, self-filling, structures that collect and store rainwater and make it directly available to wildlife. Guzzlers can be constructed to provide water for small animals only, or for animals of all sizes.

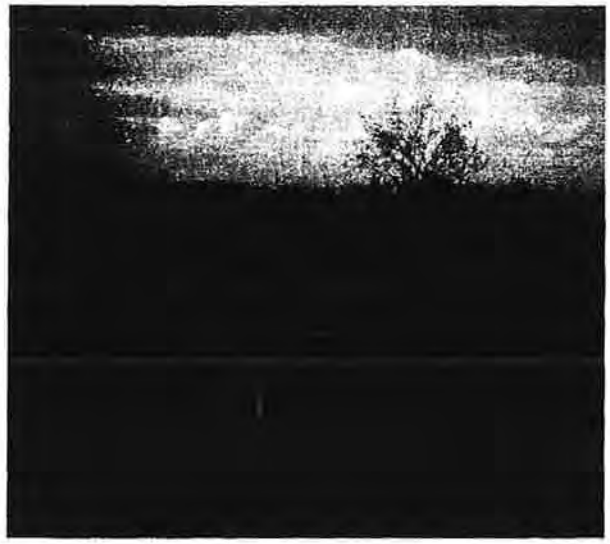

Fig. 5. Contemporary underground guzzlers (Lesicka and Hervert 1995) store up to 40,000 L of water and have no moving parts. Wildlife walk down a ramp to reach stored water.

Several techniques can be used to collect water for guzzlers. Aprons that collect rainfall can be of manufactured or natural materials, including concrete or sheet metal, but asphalted, oiled, waxed, or otherwise treated soil aprons can be used (Glading 1947, Fink et al. 1973, Rauzi et al. 1973, Myers and Frasier 1974, Frasier et al. 1979, Johnson and Jacobs 1986, Rice 1990, Lesicka and Hervert 1995).

Guzzlers useful for wildlife generally store water in underground tanks, and wildlife walk a ramp to enter the guzzler to drink (Halloran and Deming 1956, 1958; Lesicka and Hervert 1995) (Fig. 5). However, water can also be stored in underground or aboveground concrete, plastic, metal, or fiberglass tanks (Garton 1956*a*,*b*; Roberts 1977; Bleich et al. 1982*b*; Remington et al. 1984; Werner 1984; Bardwell 1990; Bleich and Pauli 1990; deVos and Clarkson 1990; Gunn 1990; Lesicka and Hervert 1995). Aboveground tanks (Fig. 6) usually have a float-valve to regulate water at a drinking trough away from the water storage tanks (Roberts 1977, Werner 1984, Bleich and Pauli 1990). Underground tanks generally have no moving parts (Lesicka and Hervert 1995) and are not as subject to mechanical failures as are designs that incorporate a float valve. Moreover, guzzlers that store water for large mammals below the surface of the ground are nearly undetectable by humans more than a few meters from them (Fig. 7); current designs (Lesicka and Hervert 1995) present little risk of drowning to native vertebrates, including desert tortoise (Andrew et al. 2001).

The most important step in installation of a guzzler is locating a suitable site. A guzzler should not be placed in a wash or gully where it may collect silt or sand or be damaged by floodwaters; many guzzlers have been installed in areas lacking critical habitat components (Lewis 1973). When constructing a guzzler for small animals, Yoakum et al. (1980) recommended that: (1) size of the water-collecting apron be proportioned so the storage tank will need no water source other than rainfall to fill it, (2) a site should be chosen where digging is comparatively easy, and (3) the tank should be placed with its open end away from the

Fig. 6. Guzzlers constructed with above ground storage tanks generally have a float valve to control the water level in the drinking trough. Guzzlers of this type store up to 10,000 L of water for use by large mammals in the Mojave Desert, California.

prevailing wind and, if possible, facing in a northerly direction to reduce water temperature, evaporation, and growth of algae.

Tanks usually are made of concrete or plastic. Occasionally, steel tanks are used as are used heavy equipment tires (Elderkin and Morris 1989, Morris and Elderkin 1990). The plastic guzzler is a prefabricated tank constructed of fiberglass impregnated with plastic resin. Only washed gravel aggregates should be used for construction of concrete tanks, or the concrete may disintegrate in several years. Tanks made of steel are used for guzzlers in some areas and give satisfactory service. Use of tanks constructed of other artificial materials is relatively new.

Concrete sealed with bitumul, galvanized metal sheet roofing, glass mat and bitumul, rubber or plastic sheets, asphalt, and plywood have been used successfully for water collecting surfaces. Durable materials such as concrete or metal are least expensive to maintain, although soil cement appears to be a promising material; (Rice 1990) and Lesicka and Hervert (1995) successfully used areas of native desert soil. Efficiency (percent of water collected) and life-spans (years) vary among materials: steel (98%, 25 years) is best, followed by asphalt roofing (86–92%, 8 years), plastic covered with 2.5 cm of gravel (66–87%, 8–15 years), butyl rubber (98%, 15–20 years), asphalt paving (95%, 15 years) and liquid asphalt soil water (90%, 5 years) (Fairbourn et al. 1972).

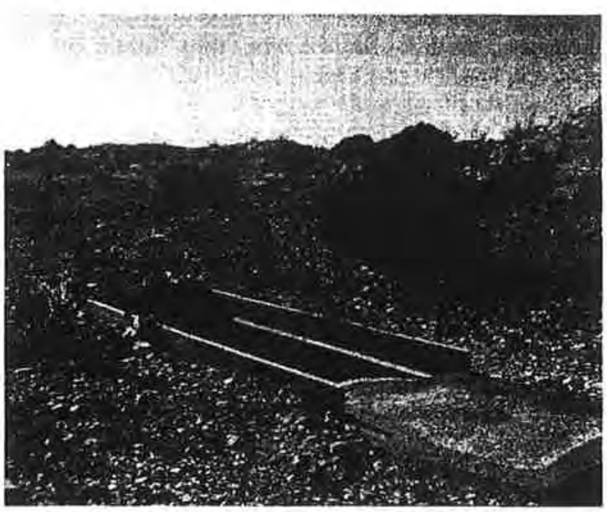

Fig. 7. Underground guzzlers of the design by Lesicka and Hervert (1995) are nearly invisible to humans more than a few meters away, making them especially useful in designated wilderness.

The area of the water-collecting surface needed to fill a guzzler (Fig. 8) depends on the storage capacity of the guzzler, minimum annual rainfall at the site, and type of collecting surface. Each 10 m^2 in apron surface area will result in collection of about 1 liter of water for each centimeter of rainfall. Calculations should be based on minimum precipitation expected, rather than the average or maximum, to prevent guzzler failure during drought years. When different types of aprons are used, required surface area can be calculated from the harvest efficiencies (Fairbourn et al. 1972). Leakage, evaporation, and heavy use by wildlife may also dictate a larger apron.

Big-game guzzlers are designed to collect water from either artificial (Gunn 1990) or natural aprons (Stevenson 1990, Lesicka and Hervert 1995). Using slick-rock catchments to collect runoff from bare rock areas is a common technique (Bleich et al. 1982*b*, deVos and Clarkson 1990, Stevenson 1990). These guzzlers take advantage of the fact that rock surfaces yield nearly 100% of the precipitation falling on them as runoff. Several authors (Bardwell 1990, Gunn 1990, Stevenson 1990, Lesicka and Hervert 1995) provide design specifications and other recommendations for construction of these catchments. Bardwell (1990), Bleich and Pauli (1990), deVos and Clarkson (1990), and Gunn (1990) provide information regarding performance of these units over time. These investigators

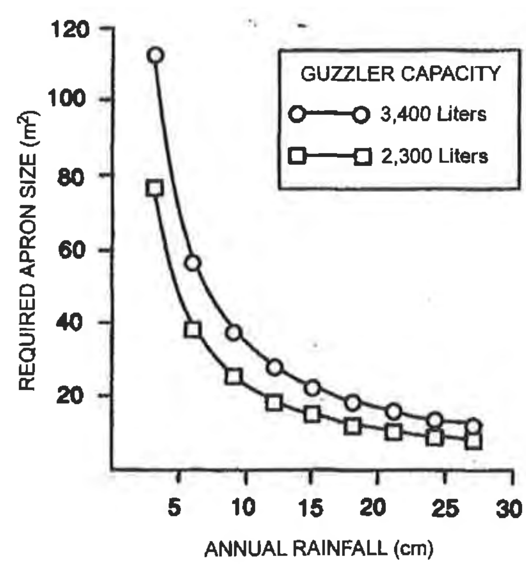

Fig. 8. Size of an apron necessary to fill a guzzler is dependent upon total annual rainfall and storage capacity of the guzzler. The relationship portrayed is based on the assumption the apron yields 100% of rainfall as runoff (after Yoakum et al. 1980).

also evaluated techniques used in the construction of big-game guzzlers and evaluated the reliability of materials.

One of the most important considerations when constructing guzzlers is that all anthropogenic devices are subject to failure; regular monitoring is an essential aspect of any maintenance program. Recently, methods of monitoring the status of water sources that incorporate remote sensing have been developed (Hill and Bleich 1999) for use in areas that are difficult to reach, or that have otherwise restricted access, such as wilderness areas. This technology does not replace biannual visits, which are necessary to detect potential failures, or correct those that already may have occurred (Bleich and Pauli 1990, Hill and Bleich 1999).

The effectiveness and performance of some big-game guzzlers depends on plumbing components. For example, Bleich and Pauli (1990) reported that frozen pipes and fittings accounted for 35 of 98 failures among 22 guzzlers over an 11-year period. Furthermore, of the 98 failures, float-valve malfunction accounted for 31, design and construction flaws for 9, and natural disasters for 6. Other problems, including rusted tanks, rusted drinker boxes, and vandalism, accounted for 17. Overall, each of the 22 guzzlers evaluated averaged 4.4 mechanical failures over an 11-year period, but each was in service an average of 87% of that time. Mechanical failures did not necessarily lead to an inoperative guzzler, but did require effort to repair them.

The most complete guide for construction of guzzlers currently available was prepared by Brigham and Stevenson (1997) and is available on request from the U.S. Department of Interior, Bureau of Land Management, National Applied Resources Sciences Center, P.O. Box 25047, Denver, Colorado, USA.

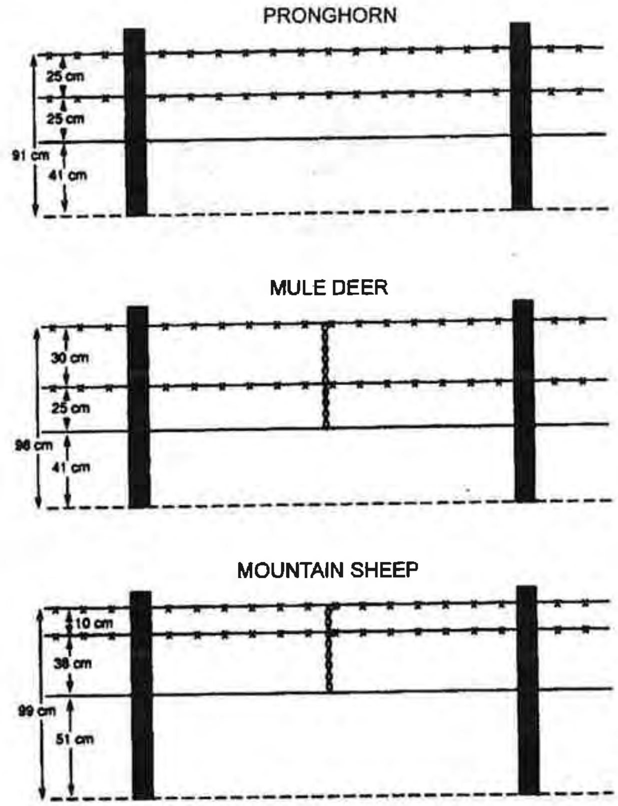

Fig. 9. Recommended specifications for wire fences constructed on ranges used by pronghorn (after Yoakum 1980, Kindschy et al. 1982, U.S. Department of Interior 1985), mule deer (after Jepson et al. 1983, U.S. Department of Interior 1985), and mountain sheep (after Hall 1985, Brigham 1990). Note the use of a smooth bottom wire on all designs and the lack of stays on fences for use on pronghorn ranges.

CONSTRUCTING RANGELAND FENCES

The relationship of fences and wildlife on rangelands in the western United States has been a point of contention for the past century. Fences constructed to control domestic livestock can adversely impact some wildlife species. For example, fences can be major obstacles or traps to pronghorn (Martinka 1967, Spillett et al. 1967, Oakley 1973) and mule deer (Yoakum et al. 1980, Mackie 1981). Proper fence design and use of appropriate construction materials can reduce adverse effects. Details of fence construction on rangelands used by pronghorn, mule deer, elk, bison (*Bison bison*), and collared peccary (*Pecari tajacu*) are available elsewhere (U.S. Department of Interior 1985, Karsky 1988). Preventing the movement of some wildlife species may be desirable, and specific fence designs can accomplish that goal (Longhurst et al. 1962, Messner et al. 1973, deCalesta and Cropsey 1978, Jepson et al. 1983, Karsky 1988).

Fences and Pronghorn

The severity of pronghorn-fence problems varies among areas. Fences are primarily a problem for herds moving seasonally to and from wintering areas on northern rangelands (Oakley 1973). However, seasonal movement problems also were reported in New Mexico (Russell 1964, Howard et al. 1983) and Texas (Buechner 1950, Hailey 1979), especially during drought years.

If fencing is necessary, only that required to provide proper livestock control and minimize hindrance to pronghorn and other wildlife should be used. Unrestricted passage for all age classes during all seasons and all weather conditions should be provided (Yoakum et al. 1980). Fencing watering areas on dry summer rangelands may be as detrimental to pronghorn as fencing migration routes. If a fenced water development is provided specifically for pronghorn, the area should encompass at least 1–2 ha of relatively level terrain (Yoakum et al. 1980).

Fence specifications to control livestock on pronghorn range have evolved over many years (Spillett et al. 1967, Autenrieth 1978, Salwasser 1980, Yoakum 1980, Kindschy et al. 1982, U.S. Department of Interior 1985). Fences should consist of 3 strands of wire, the bottom strand being smooth (Fig. 9). Four- to 6-strand barbed-wire fences limit pronghorn movements and should not be used. The bottom wire should be at least 40 cm above ground. Absence of stays between posts will facilitate the occasional movement of pronghorn through the fence (Yoakum et al. 1980, Kindschy et al. 1982, Hall 1985).

New fences should be flagged with white cloth so pronghorn can become familiar with their locations. By the time a white rag tied to the top of each fence post deteriorates, pronghorn will have become accustomed to the fence (Kindschy et al. 1982). Painting the top of steel fence posts white also helps make the fence more visible to pronghorn (Hall 1985).

Where snow accumulation restricts pronghorn movements, let-down or adjustable fences should be used (Yoakum et al. 1980). A let-down fence can consist of a wooden stay at each fence post to which the wires are attached. The stay is secured to the fence post with a wire loop at the top and either a second loop or a pivot bolt at the bottom.

Let-down fence sections may be designed to permit pulling the let-down sections back against sections of permanently standing fence. Let-down fences should provide for adjustments in wire tension. When the wire is so taut that it does not lie flat on the ground or is so loose that wire loops are formed, a hazard is created for people and animals (U.S. Department of Interior 1985). Adjustable fences (Fig. 10) that allow the movement of one or more wires can allow pronghorn passage during periods when livestock are not present (Anderson and Denton 1980). Adjustable fences are particularly useful when winter snow depths exceed 30 cm (Yoakum et al. 1980).

Pronghorn passes are structures that resemble cattle guards intersecting a fence (Spillett et al. 1967, Mapston and ZoBell 1972, Yoakum et al. 1980, Howard et al. 1983). Suitable locations for pronghorn passes make use of the tendency of individuals to parallel a fence, looking for a way to cross. The pass capitalizes on the ability of pronghorn to jump laterally over obstacles. Pronghorn passes have been built and tested under a variety of conditions (Spillett et al. 1967, Howard et al. 1983). Some adult pronghorn quickly learn to use the facilities, but others do not. Pronghorn fawns often were unable to negotiate the passes. Pronghorn passes are of limited value and should not be used as a panacea for pronghorn access problems (U.S. Department of Interior 1985).

Net-wire fences prevent the movement of pronghorn fawns in particular, and should not be used on public rangelands where pronghorn occur (Autenrieth 1978, Yoakum 1980). However, some adults may become adept at jumping a net-wire fence up to 80 cm high. Higher net-wire fences can be used where the goal is to restrict the movement of animals, such as in live-trapping, control of animals in research projects, decreasing crop depredations, or restricting access to hazardous areas such as highways.

Fences and Mule Deer

The relationship between livestock fences and mule deer has not raised the political furor that it has for pronghorn. However, throughout North America where fences have been built, they likely have caused far greater mortality to deer than to pronghorn. Deer are more apt to be trapped as individuals, whereas large numbers of pronghorn may be restricted. Also, deer frequently are caught in fences in isolated areas not readily witnessed, whereas pronghorn mortalities in open country are easy to observe.

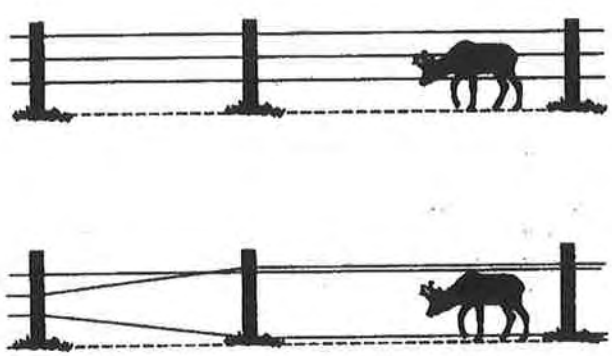

Fig. 10. Adjustable fence modifications to facilitate movement of pronghorn and other ungulates (after Anderson and Denton 1980).

Deer often crawl under fences when not hurried, but jump them when startled or chased (Mackie 1981). When a deer jumps a fence, its feet can become entangled between the top 2 wires, resulting in death. Limiting total fence height to 96 cm can reduce this problem (U.S. Department of Interior 1985) (Fig. 9). If the top wire is barbed, it should be separated from the next wire by 30 cm; otherwise, it should be a smooth wire (Jepson et al. 1983). Unlike fences used on pronghorn ranges, wire stays should be placed every 2.5 m between posts to keep the top wires from twisting around the leg of a deer (Yoakum et al. 1980, U.S. Department of Interior 1985).

The effective height of a fence as a barrier to deer moving uphill is increased on steep slopes. For example, a 110-cm fence on a 20% slope is equivalent to a 140-cm fence on level ground. On a 50% slope, it is equivalent to a 190-cm fence on level ground (Kerr 1979, Anderson and Denton 1980). Thus, height adjustments should be made accordingly.

Let-down fences along seasonal travel routes for deer help ensure free movement. The let-down feature of the fence also helps prevent damage from snow loading during winter. Movements of mule deer also can be aided with an adjustable fence. Net-wire fences no higher than 90 cm allow movement of adult deer but prevent passage of fawns. They should not be placed on summer and autumn migration routes used by deer.

Fences and Mountain Sheep

The construction of wire fences on ranges used by mountain sheep (for example, to exclude livestock from water developments) presents particular problems. Mountain sheep are likely to become entangled in a fence when placing their head through the top 2 wires. This problem is minimized if the 2 top wires are no more than 10 cm apart (Brigham 1990). A 3-wire fence should be used with wires spaced at 51, 38, and 10 cm intervals (Fig. 9), allowing mountain sheep movement under the bottom wire and between it and the middle wire (U.S. Department of Interior 1985, Brigham 1990). Six-wire fence designs (U.S. Department of Interior 1985) are dangerous to mountain sheep and should not be used (Brigham 1990). To minimize the probability of mountain sheep becoming entangled, fences consisting of uprights and 2 parallel rails easily can be constructed (Andrew et al. 1997) (Fig. 11).

Electric Fences

Electric fences often are used to control livestock or feral hoof stock such as burros, and some designs pose little hindrance to movement of wildlife. Electric fences are most effective on moist sites, where 2 wires may be sufficient to control cattle. On sites with at least 60 cm of rain annually, an electric fence can be made of 2 smooth wires at heights of 60 and 90 cm above ground (U.S. Department of Interior 1985, Karsky 1988). The top wire is electrified and the bottom wire serves as the ground. The wires are free running at all posts, and pose little danger of entrap-

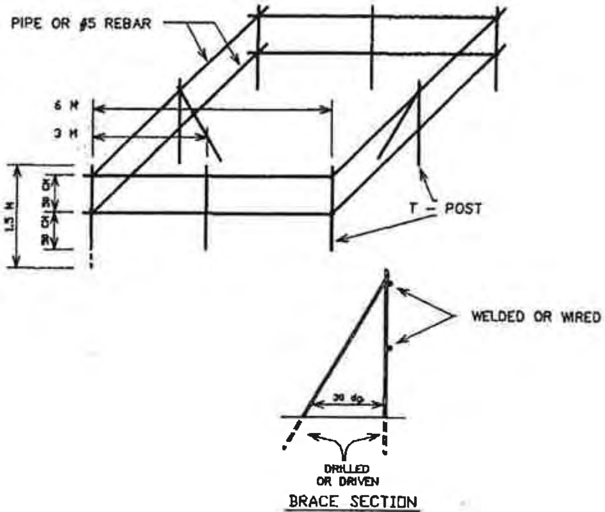

Fig. 11. A simple fence, constructed of metal t-posts and rebar spaced at appropriate intervals effectively excludes feral asses from water sources in desert ecosystems, yet allows passage by native ungulates (after Andrew et al. 1997).

ping mule deer. On drier sites, electric fences require more wires to function effectively (Karsky 1988), and the added wires can adversely affect movements by wildlife.

Wood and Steel Fences

Fences can be constructed entirely from wood posts and rails in a variety of designs with raw materials obtained at the site or manufactured materials (U.S. Department of Interior 1985, Karsky 1988, Andrew et al. 1997). Wood fences are usually expensive but can be attractive and may require less maintenance than wire fences. Construction options include post and pole, log worm, log and block, and buck and pole designs (Karsky 1988). The same principles apply to wood fences as to wire fences in minimizing hindrance to wildlife movements. The top rail or pole of a wooden fence should be kept low to allow mule deer to jump over and the bottom rail or post kept sufficiently high to allow movement of fawns. Andrew et al. (1997) designed an inexpensive rail fence using t-posts and rebar, which was totally effective in reducing access to water sources by feral asses and yet provided unimpeded access by mountain sheep and mule deer.

Rock Jacks

In many areas, soils are too shallow and rocky to allow steel fence posts to be easily driven into the ground (Hall 1985). At such sites, rock jacks are often constructed in the form of wood-rail cribs or wire baskets. The cribs or baskets are filled with rocks and serve as anchors to which wire fences can be secured. Cover and dens for small mammals are provided if the bottom rail of a rock jack is kept 10–15 cm above the ground (Hall 1985). Use of rocks at least 30 cm in diameter will also provide crevasses suitable for use by small mammals (Maser et al. 1979, Hall 1985).

Fences To Exclude Wildlife

Excluding selected wildlife species from certain areas may be desirable. Elk, mule deer, and other species often heavily depredate orchards, vineyards, and other crops; appropriate fence designs can help alleviate such problems. Highways can be hazardous to mule deer and other ungulates that need to reach critically important seasonal ranges. Fences can be used to channel their movement to suitable underpasses and minimize collisions with vehicles. Experimental plots used in research often require exclusion of one or more species of wildlife. Finally, fencing can be used as an alternative to other control measures in reducing predation on livestock.

A 1.8-m upright net-wire fence, or one slanted at 45 degrees to a total height of about 1.3 m, can be used to exclude mule deer (Longhurst et al. 1962, Messner et al. 1973, Karsky 1988). Electric fences with 4–6 wires also discourage deer movements (Karsky 1988).

Fences can be used to reduce or eliminate the need for lethal control of coyotes (*Canis latrans*), which can be excluded from pastures by either woven wire (Thompson 1979, deCalesta and Cropsey 1978, Jepson et al. 1983) or electric fences (Gates et al. 1978, Dorrance and Bourne 1980, Karsky 1988, Nass and Theade 1988). To be effective, a woven wire fence must be at least 170 cm high, have mesh openings no larger than 10 × 15 cm, and have an overhang to prevent jumping and an apron to prevent digging, each at least 40 cm wide (Thompson 1979). A 7-wire electric fence (4 hot wires alternating with 3 ground wires) totaling 130 cm in height also can be used (Dorrance and Bourne 1980). Other electric fence designs are available to deter coyotes (Karsky 1988). In general, fencing to control coyotes is expensive, and probably justified only to protect small areas of high production capacity, such as irrigated pastures.

SUMMARY

Management of livestock on public rangelands has become a divisive and contentious issue. Land management agencies increasingly are criticized for failing to give appropriate consideration to grazing issues that affect wildlife, or wildlife habitat, on public lands. The single greatest change influencing conservation of wildlife on western rangelands during the 1990s has been the shift from an emphasis on competition of livestock with big game to concern for biodiversity in general.

We chose to not criticize current grazing practices but to present a reasonable review of contemporary issues related to livestock management on public lands. Further, we have attempted to: (1) provide an overview of rangeland management to benefit wildlife species and natural communities, with an emphasis on western North America; (2) identify some of the topical issues and primary rangeland systems of particular concern; and (3) describe some of the methods for accommodating wildlife and wildlife-related issues, including habitat enhancement techniques, on rangelands. Students and others making use of information in this chapter are encouraged to further explore the vast literature on management of rangelands and livestock, and to use that information to ensure the persistence of healthy and productive rangeland ecosystems, particularly as they relate to the issue of wildlife conservation.

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LITERATURE CITED

ALLEN-DIAZ, B., AND J. W. BARTOLOME. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. Ecological Applications 8:795–804.

ANDERSON, B. W., AND R. D. OHMART. 1977. Vegetation structure and bird use in the lower Colorado River valley. Pages 23–34 *in* R. R. Johnson and D. A. Jones, technical coordinators. Importance, preservation, and management of riparian habitat. U.S. Department of Agriculture, Forest Service, General Technical Report RM-43.

ANDERSON, L. D., AND J. W. DENTON. 1980. Adjustable wire fences for facilitating big game movement. U.S. Department of the Interior, Bureau of Land Management, Technical Note 343.

ANDREW, N. G., L. M. LESICKA, AND V. C. BLEICH. 1997. An improved fence design to protect water sources for native ungulates. Wildlife Society Bulletin 25:823–825.

———, V. C. BLEICH, A. D. MORRISON, L. M. LESICKA, AND P. J. COOLEY. 2001. Wildlife mortalities associated with artificial water sources. Wildlife Society Bulletin 29:275–280.

ARIZONA STATE UNIVERSITY COLLEGE OF LAW. 1997. Environmental, economic, and legal issues related to rangeland water developments. Center for the Study of Law, Science, and Technology, Arizona State University, Tempe, USA.

AUSTIN, D. D. 2000. Managing livestock grazing for mule deer (*Odocoileus hemionus*) on winter range in the Great Basin. Western North American Naturalist 60:198–203.

AUTENRIETH, R. 1978. Guidelines for the management of pronghorn antelope. Proceedings of the Pronghorn Antelope Workshop 8:473–526.

BARCLAY, J. S. 1978. The effects of channelization on riparian vegetation and wildlife in south-central Oklahoma. Pages 129–138 *in* R. R. Johnson and J. F. McCormick, technical coordinators. Strategies for protection and management of floodplain wetlands and other riparian ecosystems. U.S. Department of Agriculture, Forest Service, General Technical Report WO-12.

BARDWELL, P. P. 1990. Artificial water development design, materials, and problems encountered in the BLM, Carson City District, Nevada. Pages 133–139 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

BATZLI, G. O., AND F. A. PITELKA. 1970. Influence of meadow mouse populations on California grasslands. Ecology 51:1027–1039.

BECK, J. L., AND D. L. MITCHELL. 2000. Influences of livestock grazing on sage grouse habitat. Wildlife Society Bulletin 28:986–992.

BELANGER, L., AND M. PICARD. 1999. Cattle grazing and avian communities of the St. Lawrence River Islands. Journal of Range Management 52:332–338.

BELSKY, A. J., AND D. M. BLUMENTHAL. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. Conservation Biology 12:315–327.

———, A. MATZKE, AND S. USELMAN. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431.

BILBY, R. E. 1984. Removal of woody debris may affect stream channel stability. Journal of Forestry 82:609–613.

BIRCH, L. C. 1957. The meanings of competition. American Naturalist 91:5–18.

BISSON, P. A., R. E. BILBY, M. D. BRYAN, C. A. DOLOFF, G. B. GRETTER, R. A. HOUSE, M. L. MURPHY, K. V. KOSKY, AND J. R. SEDELL. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143–190 *in* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. Contribution 57. Institute of Forest Resources, University of Washington, Seattle, USA.

BISWELL, H. H., AND A. M. SCHULTZ. 1958. Effects of vegetation removal on spring flow. California Fish and Game 44:211–230.

BLAKE, J. G. 1982. Influence of fire and logging on nonbreeding bird communities of ponderosa pine forests. Journal of Wildlife Management 46:404–415.

BLEICH, V. C. 1982. Horizontal wells for mountain sheep: desert bighorn "get the shaft". Transactions of the Desert Bighorn Council 26:63–64.

———. 1983. Comments on helicopter use by wildlife agencies. Wildlife Society Bulletin 11:304–306.

———. 1990. Horizontal wells for wildlife water development. Pages 51–58 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

———. 1992. History of wildlife water developments, Inyo County, California. Pages 100–106 *in* C. A. Hall, Jr., V. Doyle-Jones, and B. Widawski, editors. The history of water: eastern Sierra Nevada, Owens Valley, White-Inyo Mountains. University of California, White Mountain Research Station, Bishop, USA.

———, AND S. A. HOLL. 1981. Management of chaparral habitat for mule deer and mountain sheep in southern California. Pages 247–254 *in* C. E. Conrad and W. C. Oechel, technical coordinators. Proceedings, symposium on dynamics and management of Mediterranean-type ecosystems. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-58.

———, AND A. M. PAULI. 1990. Mechanical evaluation of artificial watering devices built for mountain sheep in California. Pages 65–72 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

———, AND R. A. WEAVER. 1983. "Improved" sand dams for wildlife habitat management. Journal of Range Management 36:133.

———, L. J. COOMBES, AND J. H. DAVIS. 1982*a*. Horizontal wells as a wildlife habitat improvement technique. Wildlife Society Bulletin 10:324–328.

———, ———, AND G. W. SUDMEIER. 1982*b*. Volunteer participation in California wildlife habitat improvement projects. Transactions of the Desert Bighorn Council 26:56–58.

BOCK, C. E., AND J. H. BOCK. 1983. Responses of birds and deer mice to prescribed burning in ponderosa pine. Journal of Wildlife Management 47:836–840.

———, H. M. SMITH, AND J. H. BOCK. 1990. The effect of livestock grazing upon abundance of the lizard, *Sceloporus scalaris*, in southeastern Arizona. Journal of Herpetology 24:445–446.

———, J. A. BOCK, W. R. KENNEY, AND V. M. HAWTHORNE. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management 37:239–242.

BOND, R. M. 1947. Ramps for escape of wildlife from stock troughs. Journal of Wildlife Management 7:122–123.

BORCHERT, M. I., AND S. K. JAIN. 1978. The effect of rodent seed predation on four species of California annual grasses. Oecologia 33:101–113.

BOSTICK, V. 1990. The desert tortoise in relation to cattle grazing. Rangelands 12:149–151.

BOX, T. 2000. Public rangelands without cows? Rangelands 22(4): 27–30.

BRIGHAM, W. R. 1990. Fencing wildlife water developments. Pages 37–43 *in* G. K. Tsukamoto, and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

———, AND C. STEVENSON. 1997. Wildlife water catchment construction in Nevada. U.S. Department of the Interior, Bureau of Land Management, Technical Note 397.

BRINSON, M. M., B. L. SWIFT, R. C. PLANTICO, AND J. S. BARCLAY. 1981. Riparian ecosystems: their ecology and status. U.S. Department of the Interior, Fish and Wildlife Service, FWS/OBS-81.

BRONHAM, L., M. CARDILLO, A. F. BENNETT, AND M. A. ELGAR. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Australian Journal of Ecology 24:199–207.

BROYLES, B. 1995. Desert wildlife water developments: questioning use in the southwest. Wildlife Society Bulletin 23:663–675.

———, AND T. L. CUTLER. 1999. Effect of surface water on desert bighorn sheep in the Cabeza Prieta National Wildlife Refuge, southwestern Arizona. Wildlife Society Bulletin 27:1082–1088.

BUECHNER, H. K. 1950. Life history, ecology, and range use of the pronghorn antelope in Trans-Pecos Texas. American Midland Naturalist 43:257–354.

BULL, E. L., AND M. P. HAYES. 2000. Livestock effects on reproduction of the Columbia spotted frog. Journal of Range Management 53:291–294.

BUNTING, S. C. 1986. Use of prescribed burning in juniper and pinyon-juniper woodlands. Pages 141–145 *in* R. L. Everett, editor. Proceedings of the pinyon-juniper conference. U.S. Department of Agriculture, Forest Service, General Technical Report INT-215.

BUTTERY, R. F., AND P. W. SHIELDS. 1975. Range management practices and bird habitat values. Pages 183–189 *in* D. R. Smith, technical coordinator. Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S. Department of Agriculture, Forest Service, General Technical Report WO-1.

CALIFORNIA DEPARTMENT OF FISH AND GAME. 1926. Editorial. California Fish and Game 12:28.

———. 1998. Report to the Fish and Game Commission: an assessment of mule deer and black-tailed deer habitats and populations in California. California Department of Fish and Game, Sacramento, USA.

CANON, S. K., P. J. URNESS, AND N. V. DEBYLE. 1987. Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. Journal of Range Management 40:433–438.

CAROTHERS, S. W., AND R. R. JOHNSON. 1975. Water management practices and their effects on nongame birds in range habitats. Pages 210–222 *in* D. R. Smith, technical coordinator. Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S. Department of Agriculture, Forest Service, General Technical Report WO-1.

CHAMBERS, J. C., AND A. R. LINNEROOTH. 2001. Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts—the establishment component. Applied Vegetation Science 4:157–166.

CHANEY, E., W. ELMORE, AND W. S. PLATTS. 1990. Livestock grazing on western riparian areas. U.S. Environmental Protection Agency, Denver, Colorado, USA.

CLARK, P. E., W. C. KRUEGER, L. D. BRYANT, AND D. R. THOMAS. 2000. Livestock grazing effects on forage quality of elk winter range. Journal of Range Management 53:97–105.

CLARY, W. P., AND D. M. BEALE. 1983. Pronghorn reactions to winter sheep grazing, plant communities, and topography in the Great Basin. Journal of Range Management 36:749–752.

CLEMENTS, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute Publication 242.

COMPTON, B. B., R. J. MACKIE, AND G. L. DUSEK. 1988. Factors influencing distribution of white-tailed deer in riparian habitats. Journal of Wildlife Management 52:544–548.

COOK, J. G., T. J. HERSHEY, AND L. L. IRWIN. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. Journal of Range Management 47:296–302.

COOMBES, L. J., AND V. C. BLEICH. 1979. Horizontal wells—The DFG's new slant on water for wildlife. Outdoor California 40(6):10–12.

CURTIS, R. L., AND T. H. RIPLEY. 1975. Water management practices and their effect on nongame bird habit values in a deciduous forest community. Pages 128–141 *in* D. R. Smith, technical coordinator. Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S. Department of Agriculture, Forest Service, General Technical Report WO-1.

DEBANO, L. F., AND L. J. SCHMIDT. 1989. Improving southwestern riparian areas through watershed management. U.S. Department of Agriculture, Forest Service, General Technical Report RM-182.

DEBYLE, N. V. 1985. Wildlife. Pages 135–152 *in* N. V. DeByle and R. P. Winokur, editors. Aspen: ecology and management in the western United States. U.S. Department of Agriculture, Forest Service, General Technical Report RM-119.

DECALESTA, D. S., AND M. G. CROPSEY. 1978. Field test of a coyote-proof fence. Wildlife Society Bulletin 6:256–259.

DEGRAAF, R. M., technical coordinator. 1980. Workshop proceedings—management of western forests and grasslands for nongame birds. U.S. Department of Agriculture, Forest Service, General Technical Report INT-86.

DENTON, J. S., AND T. J. C. BEEBEE. 1996. Habitat occupancy by juvenile natterjack toads (*Bufo calamita*) on grazed and ungrazed heathland. Herpetological Journal 6:49–52.

DESERT BIGHORN COUNCIL TECHNICAL STAFF. 1990. Guidelines for management of domestic sheep in the vicinity of desert bighorn habitat. Desert Bighorn Council Transactions 34:33–35.

DEVOS, JR., J. C., AND R. W. CLARKSON. 1990. A historic review of Arizona's water developments with discussions on benefits to wildlife, water quality, and design considerations. Pages 157–165 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

DICKSON, B. G., AND P. BEIER. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66:1235–1245.

DICKSON, J. G., AND J. C. HUNTLEY. 1987. Riparian zones and wildlife in southern forests: the problem and squirrel relationships. Pages 37–39 *in* J. G. Dickson and O. E. Maughan, editors. Managing southern forests for wildlife and fish. U.S. Department of Agriculture, Forest Service, General Technical Report SO-65.

DOBKIN, D. S., A. C. RICH, AND W. H. PYLE. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. Conservation Biology 12:209–221.

DORRANCE, M. J., AND J. BOURNE. 1980. An evaluation of anti-coyote electric fencing. Journal of Range Management 33:385–387.

DWYER, D. D., J. C. BUCKHOUSE, AND W. S. HUEY. 1984. Impacts of grazing intensity and specialized grazing systems on the use and value of rangeland: summary and recommendations. Pages 867–884 *in* Impacts of grazing intensity and specialized grazing systems on use and values of rangelands. National Academy of Sciences, Natural Resource Council, and U.S. Department of the Interior, Bureau of Land Management, Washington, D.C., USA.

DYKSTERHUIS, E. J. 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management 2:104–115.

ELDERKIN, JR., R. L., AND J. MORRIS. 1989. Design for a durable and inexpensive guzzler. Wildlife Society Bulletin 17:192–194.

ELMORE, W. 1989. Rangeland riparian systems. Pages 93–95 *in* D. L. Abell, technical coordinator. Proceedings of the California riparian systems conference: protection, management, and restoration for the 1990's. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-110.

———, AND R. L. BESCHTA. 1987. Riparian areas: perceptions in management. Rangelands 9:260–265.

ERICHSEN-ARYCHUK, C., E. W. BORK, AND A. W. BAILEY. 2002. Northern dry mixed prairie responses to summer wildfire and drought. Journal of Range Management 55:164–170.

EVANS, K. E., AND R. R. KERBS. 1977. Avian use of livestock watering ponds in western South Dakota. U.S. Department of Agriculture, Forest Service, General Technical Report RM-35.

EVERETT, R. L. 1986. Plant response to fire in the pinyon-juniper zone. Pages 152–157 *in* R. L. Everett, editor. Proceedings of the pinyon-juniper Conference. U.S. Department of Agriculture, Forest Service, General Technical Report INT-215.

FAIRBOURN, M. L., F. RAUZI, AND H. R. GARDNER. 1972. Harvesting precipitation for a dependable, economical water supply. Journal of Soil and Water Conservation 27:23–26.

FINK, D. H., K. R. COOLEY, AND G. W. FRASIER. 1973. Wax-treated soils for harvesting water. Journal of Range Management 26:396–398.

FITCH, H. S., AND J. R. BENTLEY. 1949. Use of California annual-plant forage by range rodents. Ecology 30:306–321.

FLEISCHNER, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

FRASIER, G. W., K. R. COOLEY, AND J. R. GRIGGS. 1979. Performance evaluation of water harvesting catchments. Journal of Range Management 32:453–456.

FULBRIGHT, T. E., AND F. S. GUTHERY. 1996. Mechanical manipulation of plants. Pages 339–354 *in* P. R. Krausman, editor. Rangeland wildlife.

The Society for Range Management, Denver, Colorado, USA.
GALLIZIOLI, S. 1979. Effects of livestock grazing on wildlife. California-Nevada Wildlife Transactions 15:83–87.
GARTON, D. A. 1956*a*. Experimental big game watering device and detailed information on construction and costs. California Department of Fish and Game, Long Beach, USA.
———. 1956*b*. Experimental big game watering device and information on construction. California Department of Fish and Game, Long Beach, USA.
GATES, N. L., J. E. RICH, D. D. GODTEL, AND C. V. HULET. 1978. Development and evaluation of anti-coyote electric fencing. Journal of Range Management 31:151–153.
GLADING, B. 1947. Game watering devices for the arid southwest. Transactions of the North American Wildlife Conference 12:286–292.
GLASS, R. J. 1988. Habitat improvement costs on state-owned wildlife management areas in New York. U.S. Department of Agriculture, Forest Service, Research Paper NE-621.
GOGUEN, C. B., AND N. E. MATHEWS. 1998. Songbird community composition and nesting success in grazed and ungrazed pinyon-juniper woodlands. Journal of Wildlife Management 62:474–484.
GRANT, W. E., E. C. BIRNEY, N. R. FRENCH, AND D. M. SWIFT. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy 63:248–260.
GRAY, R. S. 1974. Lasting waters for bighorn. Transactions of the Desert Bighorn Council 18:25–27.
GUNN, J. 1990. Arizona's standard rainwater catchment. Pages 19–24 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.
GUTZWILLER, K. J., AND S. H. ANDERSON. 1986. Trees used simultaneously and sequentially by breeding cavity-nesting birds. Great Basin Naturalist 46:358–360.
HAILEY, T. L. 1979. A handbook on pronghorn antelope management in Texas. Texas Parks and Wildlife Department, Austin, USA.
HALL, F. C. 1985. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: management practices and options. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-189.
HALLORAN, A. F. 1949. Desert bighorn management. Transactions of the North American Wildlife Conference 14:527–537.
———, AND O. V. DEMING. 1956. Water development for desert bighorn sheep. U.S. Department of the Interior, Fish and Wildlife Service, Wildlife Management Service Leaflet 14.
———, AND ———. 1958. Water development for desert bighorn sheep. Journal of Wildlife Management 22:1–9.
HALLS, L. K., editor. 1984. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.
HAMILTON, C. L., AND H. G. JEPSON. 1940. Stock water developments: wells, springs, and ponds. U.S. Department of Agriculture, Farmer's Bulletin 1859.
HANLEY, T. A., AND J. J. ROGERS. 1989. Estimating carrying capacity with simultaneous nutritional constraints. U.S. Department of Agriculture, Forest Service, Research Note PNW-RN-485.
HAYWARD, B., E. J. HESKE, AND C. W. PAINTER. 1997. Effects of livestock grazing on small mammals at a desert cienega. Journal of Wildlife Management 61:123–129.
HEADY, H. F. 1975. Rangeland management. McGraw-Hill Book Co., New York, USA.
HENNY, C. J., L. J. BLUS, E. J. KOLBE, AND R. E. FITZNER. 1985. Organophosphate insecticide (Famphur) topically applied to cattle kills magpies and hawks. Journal of Wildlife Management 49:648–658.
HERBICIDE HANDBOOK COMMITTEE. 1994. Herbicide handbook of the Weed Science Society of America. Seventh edition. Weed Science Society of America, Champaign, Illinois, USA.
———. 1998. Supplement to the herbicide handbook, seventh edition. Weed Science Society of America, Champaign, Illinois, USA.
HILL, S. D., AND V. C. BLEICH. 1999. Monitoring wildlife water sources using low Earth orbiting satellites (LEOS). Wildlife Society Bulletin 27:25–27.
HOBBS, N. T., AND R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551–560.
———, AND D. M. SWIFT. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.
———, D. S. SCHIMEL, C. E. OWENSBY, AND D. S. OJIMA. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72:1374–1382.
———, D. L. BAKER, J. E. ELLIS, D. M. SWIFT, AND R. A. GREEN. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. Journal of Wildlife Management 46:12–21.
HOLECHEK, J. L. 1980. Livestock grazing impacts on rangeland ecosystems. Journal of Soil and Water Conservation 35:162–164.
———. 1981. Brush control impacts on rangeland wildlife. Journal of Soil and Water Conservation 36:265–269.
———. 1982. Managing rangelands for mule deer. Rangelands 4:25–28.
———, R. D. PIEPER, AND C. H. HERBEL. 1998. Range management: principles and practices. Third edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
HOOD, R. E., AND J. M. INGLIS. 1974. Behavioral responses of white-tailed deer to intensive ranching operations. Journal of Wildlife Management 38:488–498.
HOWARD, V. W., J. L. HOLECHEK, AND R. D. PIEPER. 1983. Roswell pronghorn study. New Mexico State University, Las Cruces, USA.
HOWARD, W. E., K. A. WAGNON, AND J. R. BENTLEY. 1959. Competition between ground squirrels and cattle for range forage. Journal of Range Management 12:110–115.
HUMPHREY, J. W., AND G. S. PATTERSON. 2000. Effects of late summer cattle grazing on the diversity of riparian pasture vegetation in an upland conifer forest. Journal of Applied Ecology 37:986–996.
JAIN, S., editor. 1976. Vernal pools: their ecology and conservation. Publication 9. Institute of Ecology, University of California, Davis, USA.
JENNINGS, M. R., AND M. P. HAYES. 1993. Decline of native ranids in the desert Southwest. Pages 183–211 *in* P. R. Brown and J. W. Wright, editors. Proceedings: herpetology of the North American deserts. Society of Southwestern Herpetologists, Special Publication Number 5.
JENSEN, S., AND W. S. PLATTS. 1987. Processes influencing riparian ecosystems. Proceedings of the Annual Meeting of the Society of Wetland Science 8:228–232.
JEPSON, R., R. G. TAYLOR, AND D. W. MCKENZIE. 1983. Rangeland fencing systems: state-of-the-art review. U.S. Department of Agriculture, Forest Service, Equipment Development Center, San Dimas, California, USA.
JOHNSON, M. K. 1982. Response of small mammals to livestock grazing in southcentral Idaho. Journal of Range Management 35:51–53.
JOHNSON, R. R., AND C. H. LOWE. 1985. On the development of riparian ecology. Pages 112–116 *in* R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, technical coordinators. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Department of Agriculture, Forest Service, General Technical Report RM-120.
———, P. S. BENNETT, AND L. T. HAIGHT. 1989. Southwestern woody riparian vegetation and succession: an evolutionary approach. Pages 135–139 *in* D. L. Abell, technical coordinator. Proceedings of the California riparian systems conference: protection, management, and restoration for the 1990's. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-110.
JOHNSON, T., AND R. A. W. JACOBS. 1986. Gallinaceous guzzlers. U.S. Department of the Army, Corps of Engineers, Wildlife Resource Management Manual, Section 5.4.1. Technical Report EL-86-8.
JONES, A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist 60:155–164.
JONES, K. B. 1988. Comparison of herpetofaunas of a natural and altered riparian ecosystem. Pages 222–227 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. U.S. Department of Agriculture, Forest Service, General Technical Report RM-166.
JULANDER, O., AND D.E. JEFFERY. 1964. Deer, elk, and cattle range relations on summer range in Utah. Transactions of the North American Wildlife and Natural Resources Conference 29:404–414.

———, and W. L. Robinette. 1950. Deer and cattle range relationships on Oak Creek Range in Utah. Journal of Forestry 48:410–415.

Karsky, R. 1988. Fences. U.S. Department of the Interior, Bureau of Land Management and U.S. Department of Agriculture, Forest Service, Technology and Development Program, Missoula, Montana, USA.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications...a review. Journal of Range Management 37:430–438.

Kazmaier, R. T., E. C. Hellgren, D. C. Ruthven III, and D. R. Synatzske. 2001. Effects of grazing on the demography and growth of the Texas tortoise. Conservation Biology 15:1091–1101.

Kerr, R. M. 1979. Mule deer habitat guides. U.S. Department of the Interior, Bureau of Land Management, Technical Note 336.

Kie, J. G. 1988. Annual grassland. Pages 118–119 *in* K. E. Mayer, and W. F. Laudenslayer, Jr., editors. A guide to the wildlife habitats of California. California Department of Forestry, Sacramento, USA.

———. 1991. Wildlife and livestock grazing alternatives in the Sierra Nevada. Transactions of the Western Section of The Wildlife Society 27:17–29.

———, and E. R. Loft. 1990. Using livestock to manage wildlife habitat: some examples from California annual grassland and wet meadow communities. Pages 7–24 *in* K. E. Severson, technical coordinator. Can livestock be used as a tool to enhance wildlife habitat? U.S. Department of Agriculture, Forest Service, General Technical Report RM-194.

———, V. C. Bleich, A. L. Medina, J. D. Yoakum, and J. W. Thomas. 1994. Managing rangelands for wildlife. Pages 663–688 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.

Kindschy, R. R., C. Sundstrom, and J. D. Yoakum. 1982. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon. Pronghorn. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-145.

Knight, D. H. 2001. Summary: aspen decline in the west? Pages 441–446 *in* W. D. Shepperd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, compilers. Sustaining aspen in western landscapes. U.S. Department of Agriculture, Forest Service, RMRS-P-18.

Knopf, F. L. 1988. Riparian wildlife habitats: more, worth less, and under invasion. Pages 20–22 *in* K. M. Mutz, D. J. Cooper, M. L. Scott, and L. K. Miller, technical coordinators. Restoration, creation and management of wetlands and riparian ecosystems in the American west. PIC Technology, Denver, Colorado, USA.

———, J. A. Sedgwick, and R. W. Cannon. 1988. Guild structure of a riparian avifauna relative to seasonal cattle grazing. Journal of Wildlife Management 52:280–290.

Koerth, B. H. 1996. Chemical manipulation of plants. Pages 321–337 *in* P. R. Krausman, editor. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Krausman, P. R., editor. 1996. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Krueger, W. C., M. A. Sanderson, J. B. Cropper, M. Miller-Goodman, C. E. Kelley, R. D. Pieper, P. L. Shaver, and M. L. Trlica. 2002. Environmental impacts of livestock on U.S. grazing lands. Issue Paper 22. Council for Agricultural Science and Technology, Ames, Iowa, USA.

Larsen, R. E., W. C. Krueger, M. R. George, M. R. Barrington, J. C. Buckhouse, and D. A. Johnson. 1998. Livestock influences on riparian zones and fish habitat: literature classification. Journal of Range Management 51:661–664.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. Journal of Range Management 44:427–433.

———. 1994. Implications of grazing vs. no grazing on today's rangelands. Pages 250–280 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the west. The Society for Range Management, Denver, Colorado, USA.

Leopold, A. S., T. Riney, R. McCain, and L. Tevis, Jr. 1951. The Jawbone deer herd. Game Bulletin 4. California Department of Fish and Game, Sacramento, USA.

Lesicka, L. M., and J. J. Hervert. 1995. Low maintenance water developments for arid environments: concepts, materials, and techniques. Pages 52–57 *in* D. P. Young, Jr., R. Vinzant, and M. D. Strickland, editors. Wildlife water development. Water for Wildlife Foundation, Lander, Wyoming, USA.

Lewis, M. D. 1973. Upland game guzzler evaluation: Lassen County. Federal Aid in Wildlife Restoration Job Progress Report, Project W-26-D-29-1. California Department of Fish and Game, Sacramento, USA.

Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. Journal of Wildlife Management 51:655–664.

Longhurst, W. M., R. E. Hafenfeld, and G. E. Connolly. 1982. Deer-livestock interrelationships in the western states. Pages 409–420 *in* J. M. Peek and P. D. Dalke, editors. Proceedings of the wildlife-livestock relationships symposium. University of Idaho, Moscow, USA.

———, E. O. Garton, H. F. Heady, and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. California-Nevada Wildlife Transactions 23:74–103.

———, M. B. Jones, R. R. Parks, L. W. Neubauer, and M. W. Cummings. 1962. Fences for controlling deer damage. Agricultural Experimental Station Circular 514. University of California, Davis, USA.

Loomis, J. B., E. R. Loft, D. R. Updike, and J. G. Kie. 1991. Cattle-deer interactions in the Sierra Nevada: a bioeconomic approach. Journal of Range Management 44:395–399.

Mackie, R. J. 1978. Impacts of livestock grazing on wild ungulates. Transactions of the North American Wildlife and Natural Resources Conference 43:462–476.

———. 1981. Interspecific relationships. Pages 487–501 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

Mapston, R. D., and R. S. ZoBell. 1972. Antelope passes: their value and use. U.S. Department of the Interior, Bureau of Land Management, Technical Note D-360.

Martinka, C. J. 1967. Mortality of northern Montana pronghorns in a severe winter. Journal of Wildlife Management 31:159–164.

Maser, C., J. W. Thomas, and R. G. Anderson. 1984. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: the relationship of terrestrial vertebrates to plant communities and structural conditions. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-172.

———, J. M. Geist, D. M. Concannon, R. Anderson, and B. Lovell. 1979. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon: geomorphic and edaphic habitats. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-99.

Megahan, W. F., and P. N. King. 1985. Identification of critical areas on forest lands for control of nonpoint sources of pollution. Environmental Management 9:7–18.

Menke, J. W., editor. 1983. Proceedings of the workshop on livestock and wildlife-fisheries relationships in the Great Basin. Special Publication 3301. University of California, Berkeley, USA.

Mensch, J. L. 1969. Desert bighorn (*Ovis canadensis nelsoni)* losses in a natural trap tank. California Fish and Game 55:237–238.

Messner, H. E., D. R. Dietz, and E. C. Garrett. 1973. A modification of the slanting deer fence. Journal of Range Management 26:233–235.

Miller, E. 1987. Effects of forest practices on relationships between riparian areas and aquatic ecosystems. Pages 40–47 *in* J. G. Dickson and O. E. Maughan, editors. Managing southern forests for wildlife and fish. U .S. Department of Agriculture, Forest Service, General Technical Report SO-65.

Moore, A. W., and E. H. Reid. 1951. The Dalles pocket gopher and its influence on forage production of Oregon mountain meadows. U.S. Department of Agriculture Circular 884.

Moore, W. H., and W. S. Terry. 1979. Short-duration grazing may improve wildlife habitat in southeastern pinelands. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 33:279–287.

Morris, J. E., and R. L. Elderkin. 1990. A heavy equipment tire guzzler. Pages 49–50 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

Myers, L. E., and G. W. Frasier. 1974. Asphalt-fiberglass for precipitation catchments. Journal of Range Management 27:12–15.

Myers, L. H. 1989. Grazing and riparian management in southwestern Montana. Pages 117–120 *in* R. E. Gresswell, B. A. Barton, and J. L. Kershner, technical coordinators. Practical approaches to riparian resource management: an educational workshop. U.S. Department of the Interior, Bureau of Land Management, Billings, Montana, USA.

Nass, R. D., and J. Theade. 1988. Electric fences for reducing sheep losses to predators. Journal of Range Management 41:251–252.

National Academy of Sciences. 1974. More water for arid lands: promising techniques and research opportunities. A report to the Advisory Committee on Technology Innovation, Board on Science and Technology for International Development. Commission on International Relations, Washington, D.C., USA.

Neill, W. M. 1990. Control of tamarisk at desert springs. Pages 121–126 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

Nelson, J. R., and D. G. Burnell. 1975. Elk-cattle competition in central Washington. Pages 78–83 *in* Range multiple use management. Cooperative Extension Service, Washington State University, Pullman, Oregon State University, Corvallis, and University of Idaho, Moscow, USA.

Niemi, G. J., and J. R. Probst. 1990. Wildlife and fire in the upper Midwest. Pages 32–47 *in* J. M. Sweeney, editor. Management of dynamic ecosystems. North Central Section, The Wildlife Society, West Lafayette, Indiana, USA.

Oakley, C. 1973. The effects of livestock fencing on antelope. Wyoming Wildlife 37(12):26–29.

Ohmart, R. D. 1996. Historical and present impacts of livestock grazing on fish and wildlife resources in western riparian habitats. Pages 245–279 *in* P. R. Krausman, editor. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Paige, C., and S. A. Ritter. 1999. Birds in a sagebrush sea: managing sagebrush habitats for bird communities. Partners in Flight Western Working Group, Boise, Idaho, USA.

Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145–156.

Parry, P. L. 1972. Development of permanent wildlife water supplies, Joshua Tree National Monument. Transactions of the Desert Bighorn Council 16:92–96.

Peek, J. M., and P. D. Dalke, editors. 1982. Proceedings of the wildlife-livestock relationships symposium. University of Idaho, Moscow, USA.

———, and P. R. Krausman. 1996. Grazing and mule deer. Pages 183–192 *in* P. R. Krausman, editor. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Pieper, R. D., and R. F. Beck. 1990. Range condition from an ecological perspective: modifications to recognize multiple use objectives. Journal of Range Management 43:550–552.

Platts, W. S. 1990. Managing fisheries and wildlife on rangelands grazed by livestock. White Horse Association, Smithfield, Utah, USA.

———, and R. L. Nelson. 1989. Characteristics of riparian plant communities and streambanks with respect to grazing in northeastern Utah. Pages 73–81 *in* R. E. Gresswell, B. A. Barton, and J. L. Kershner, technical coordinators. Practical approaches to riparian resource management: an educational workshop. U.S. Department of the Interior, Bureau of Land Management, Billings, Montana, USA.

———, and R. F. Raleigh. 1984. Impacts of grazing on wetlands and riparian habitat. Pages 1105–1117 *in* Developing strategies for rangeland management: a report. National Research Council and National Academy of Science, Westview Press, Boulder, Colorado, USA.

Rambo, J. L., and S. H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology 13:1047–1054.

Rauzi, F., M. L. Fairbourn, and L. Landers. 1973. Water harvesting efficiencies of four soil surface treatments. Journal of Range Management 26:399–403.

Reiner, R. J., and P. J. Urness. 1982. Effect of grazing horses managed as manipulators of big game winter range. Journal of Range Management 35:567–571.

Remington, R., W. E. Werner, K. R. Rautenstrauch, and P. R. Krausman. 1984. Desert mule deer use of a new permanent water source. Pages 92–94 *in* P. R. Krausman and N. S. Smith, editors. Deer in the Southwest: a symposium. Arizona Cooperative Wildlife Research Unit and the School of Renewable Natural Resources, University of Arizona, Tucson, USA.

Reynolds, T. D., and C. H. Trost. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. Journal of Range Management 33:122–125.

Rice, W. E. 1990. Soil cement application for wildlife developments and range developments. Pages 3–10 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

Riggs, R. A., S. C. Bunting, and S. E. Daniels. 1996. Prescribed fire. Pages 295–319 *in* P. R. Krausman, editor. Rangeland wildlife. The Society for Range Management, Denver, Colorado, USA.

Roberts, R. F. 1977. Big game guzzlers. Rangeman's Journal 4:80–82.

Robbins, C. T. 1973. The biological basis for the determination of carrying capacity. Dissertation. Cornell University, Ithaca, New York, USA.

Rodgers, K. J., P. F. Ffolliott, and D. R. Patton. 1978. Home range and movement of five mule deer in a semidesert grass-shrub community. U.S. Department of Agriculture, Forest Service, Research Note RM-355.

Rosenstock, S. S., W. B. Ballard, and J. C. deVos, Jr. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302–311.

———, J. J. Hervert, V. C. Bleich, and P. R. Krausman. 2001. Muddying the water with poor science: a reply to Broyles and Cutler. Wildlife Society Bulletin 29:734–738.

Russell, T. P. 1964. Antelope of New Mexico. Bulletin 12. New Mexico Department of Game and Fish, Santa Fe, USA.

Salwasser, H. 1980. Pronghorn antelope population and habitat management in northwestern Great Basin environments. Interstate Antelope Conference Guidelines, Fresno, California, USA.

———, C. Schonewald-Cox, and R. Baker. 1987. The role of interagency cooperation in managing for viable populations. Pages 159–173 *in* M. E. Soulé, editor. Viable populations for conservation. University of Cambridge Press, New York, USA.

Sampson, A. W., and H. E. Malmsten. 1926. Grazing periods and forage production on the national forests. U.S. Department of Agriculture, Bulletin 1405.

Sanchez, P. G. 1975. A tamarisk fact sheet. Transactions of the Desert Bighorn Council 19:12–14.

Sanders, S. D., and M. A. Flett. 1989. Montane riparian habitat and willow flycatchers: threats to a sensitive environment and species. Pages 262–266 *in* D. L. Abell, technical coordinator. Proceedings of the California riparian systems conference: protection, management, and restoration for the 1990's. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-110.

Schmidt, J. L., and D. L. Gilbert, editors. 1978. Big game of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Sedgwick, J. A., and F. L. Knopf. 1987. Breeding bird response to cattle grazing of a cottonwood bottomland. Journal of Wildlife Management 51:230–237.

Severson, K. E., technical coordinator. 1990. Can livestock be used as a tool to enhance wildlife habitat? U.S. Department of Agriculture, Forest Service, General Technical Report RM-194.

———, and C. E. Boldt. 1978. Cattle, wildlife and riparian habitats in the western Dakotas. Pages 91–102 *in* Regional rangeland symposium on management and use of northern plains rangeland. Dickinson State University, Dickinson, North Dakota, USA.

———, and A. L. Medina. 1983. Deer and elk habitat management in the southwest. Journal of Range Management Monograph 2.

Sivils, B. E., and J. H. Brock. 1981. Sand dams as a feasible water development for arid regions. Journal of Range Management 34:238–239.

Skovlin, J. M. 1984. Impacts of grazing on wetlands and riparian habi-

Comment Letter I9

tat: a review of our knowledge. Pages 1001–1103 *in* Developing strategies for rangeland management. National Research Council and National Academy of Science, Westview Press, Boulder, Colorado, USA.

SMITH, D. R., editor. 1975. Proceedings of the symposium on management of forest and range habitats for nongame birds. U.S. Department of Agriculture, Forest Service, General Technical Report WO-1.

SMITH, E. L. 1978. A critical evaluation of the range condition concept. Pages 226–267 *in* D. N. Hyder, editor. International Rangelands Congress. The Society for Range Management, Denver, Colorado, USA.

———. 1988. Successional concepts in relation to range condition assessment. Pages 113–133 *in* P. T. Tueller, editor. Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

SMITH, M. A., J. C. MALECHECK, AND K. O. FULGHAM. 1979. Forage selection by mule deer on winter range grazed by sheep in spring. Journal of Range Management 32:40–45.

SMITH, R. J. 1977. Conclusion. Pages 117–118 *in* J. E. Townsend and R. J. Smith, editors. Proceedings of a seminar on improving fish and wildlife benefits in range management. U.S. Department of the Interior, Fish and Wildlife Service, FSW/OBS-77/01.

SPILLETT, J. J., J. B. LOW, AND D. SILL. 1967. Livestock fences—How they influence pronghorn antelope movements. Bulletin 470. Utah Agriculture Experiment Station, Utah State University, Logan, USA.

STEDNICK, J. D. 1988. The influence of riparian/wetlands systems on surface water quality. Pages 17–19 *in* K. M. Mutz, D. J. Cooper, M. L. Scott, and L. K. Miller, technical coordinators. Restoration, creation and management of wetland and riparian ecosystems in the American West. PIC Technologies, Denver, Colorado, USA.

STEPHENSON, T. R., V. VAN BALLENBERGHE, AND J. M. PEEK. 1998. Response of moose forages to mechanical cutting on the Copper River Delta, Alaska. Alces 34:479–494.

STEVENSON, C. A. 1990. Identification and construction of slickrock water developments in southern Nevada by Nevada Department of Wildlife. Pages 25–35 *in* G. K. Tsukamoto and S. J. Stiver, editors. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

STODDART, L. A., A. D. SMITH, AND T. W. BOX. 1975. Range management. Third edition. McGraw-Hill Book Co., New York, USA.

STROMBERG, J. C., AND D. T. PATTEN. 1988. Total protection: one management option. Pages 61–62 *in* K. M. Mutz, D. J. Cooper, M. L. Scott, and L. K. Miller, technical coordinators. Restoration, creation and management of wetland and riparian ecosystems in the American West. PIC Technologies, Denver, Colorado, USA.

SVEJCAR, T. J. 1989. Animal performance and diet quality as influenced by burning in tallgrass prairie. Journal of Range Management 42:11–15.

SVEUM, C. M., W. D. EDGE, AND J. A. CRAWFORD. 1998. Nesting habitat selection by sage grouse in south-central Washington. Journal of Range Management 51:265–269.

SWANSON, F. J., S. V. GREGORY, J. R. SEDELL, AND A. G. CAMPBELL. 1982. Land-water interactions: the riparian zone. Pages 267–291 *in* R. L. Edmonds, editor. Analyses of coniferous forest ecosystems in the western United States. US/IBP Synthesis Series 14. Hutchinson Ross Publishing Company, Stroudsburg, Pennsylvania, USA.

SYKES, G. 1937. Sand tanks for water storage in desert regions. U.S. Department of Agriculture, Forest Service, Southwest Forest and Range Experiment Station, Research Note 9.

SZARO, R. C., S. C. BELFIT, J. K. AITKIN, AND J. N. RINNE. 1985. Impact of grazing on a riparian garter snake. Pages 359–363 *in* R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, technical coordinators. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Department of Agriculture, Forest Service, General Technical Report RM-120.

THOMAS, J. W., editor. 1979. Wildlife habitats in managed forests-The Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, Forest Service, Agriculture Handbook 553.

———, AND D. E. TOWEILL, editors. 1982. Elk of North America: ecology and management. First edition. Stackpole Books, Harrisburg, Pennsylvania, USA.

———, C. MASER, AND J. E. RODIEK. 1979*a*. Riparian zones. Pages 40–47 *in* J. W. Thomas, editor. Wildlife habitats in managed forests-The Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, Forest Service, Agriculture Handbook 553.

———, ———, AND ———. 1979*b*. Wildlife habitats in managed rangelands-The Great Basin of southeastern Oregon: riparian zones. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-80.

———, H. C. BLACK, JR., R. J. SCHERZINGER, AND R. J. PEDERSEN. 1979*c*. Deer and elk. Pages 104–127 *in* J. W. Thomas, editor. Wildlife habitats in managed forests-The Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, Forest Service, Agriculture Handbook 553.

THOMPSON, B. C. 1979. Evaluation of wire fences for coyote control. Journal of Range Management 32:457–461.

TOWNSEND, J. E., AND R. J. SMITH, editors. 1977. Proceedings of a seminar on improving fish and wildlife benefits in range management. U.S. Department of the Interior, Fish and Wildlife Service, FWS/OBS-77/01.

TSUKAMOTO, G. K., AND S. J. STIVER, editors. 1990. Proceedings, wildlife water development symposium. Nevada Chapter of The Wildlife Society, U.S. Department of the Interior, Bureau of Land Management, and Nevada Department of Wildlife, Reno, USA.

TURNER, G. T., R. M. HANSEN, V. H. REID, H. P. TIETJEN, AND A. L. WARD. 1973. Pocket gophers and Colorado mountain rangeland. Experimental Station Bulletin 554S. Colorado State University, Fort Collins, USA.

URNESS, P. J. 1976. Mule deer habitat changes resulting from livestock practices. Pages 21–35 *in* G. W. Workman and J. B. Low, editors. Mule deer decline in the west: a symposium. Utah State University, Logan, USA.

———. 1982. Livestock as tools for managing big game range in the Intermountain West. Pages 20–31 *in* J. M. Peek and P. D. Dalke, editors. Proceedings of the wildlife-livestock relationships symposium. University of Idaho, Moscow, USA.

———. 1990. Livestock as manipulators of mule deer winter habitats in northern Utah. Pages 25–40 *in* K. E. Severson, technical coordinator. Can livestock be used as a tool to enhance wildlife habitat? U.S. Department of Agriculture, Forest Service, General Technical Report RM-194.

U.S. DEPARTMENT OF AGRICULTURE. 2001. Sierra Nevada forest plan amendment: final Environmental Impact Statement and Record of Decision. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Vallejo, California, USA.

U.S. DEPARTMENT OF INTERIOR. 1964. Water development: range improvements in Nevada for wildlife, livestock, and human use. U.S. Department of the Interior, Bureau of Land Management, Reno, Nevada, USA.

———. 1966. Polyethylene liner for pit reservoir including trough and fencing. U.S. Department of the Interior, Bureau of Land Management, Technical Note P712C, Portland Service Center, Oregon, USA.

———. 1985. Fencing. U.S. Department of the Interior, Bureau of Land Management, Manual Handbook H-1741-1. Washington, D.C., USA.

———. 1992. Guidelines for domestic sheep management in bighorn sheep habitat. U.S. Department of the Interior, Bureau of Land Management, Instruction Memorandum 92–264.

———, AND CALIFORNIA DEPARTMENT OF FISH AND GAME. 2002. Recovery plan for the Sierra Nevada bighorn sheep, California. U.S. Department of the Interior, Fish and Wildlife Service, Portland, Oregon, USA.

U.S. GENERAL ACCOUNTING OFFICE. 1988. Public rangelands: some riparian areas restored, but widespread improvement will be slow: report to congressional questions. U.S. General Accounting Office, Resource and Community Economic Development Division, Report GAP/RCED-88–105.

VALENTINE, B. E., T. A. ROBERTS, S. P. BOLAND, AND A. P. WOODMAN. 1988. Livestock management and productivity of willow flycatchers in the central Sierra Nevada. Transactions of the Western Section of The Wildlife Society 24:105–114.

VALONE, T. J., M. MEYER, J. H. BROWN, AND R. M. CHEW. 2002. Timescale of perennial grass recovery in desertified arid grasslands

Comment Letter I9

following livestock removal. Conservation Biology 16:995–1002.

Van Soest, P. J. 1994. Nutritional ecology of the ruminant. Second edition. Cornell University Press, Ithaca, New York, USA.

Wagner, F. H. 1978. Livestock grazing and the livestock industry. Pages 121–145 *in* H. P. Brokaw, editor. Wildlife and America: contribution to an understanding of American wildlife and its conservation. Council on Environmental Quality. U.S. Government Printing Office, Washington, D.C., USA.

Wallmo, O. C., editor. 1981. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

Warner, R. E., and K. M. Hendrix. 1984. California riparian systems: ecology, conservation, and productive management. University of California Press, Berkeley, USA.

Wauer, R. H. 1977. Significance of Rio Grande riparian systems upon the avifauna. Pages 165–174 *in* R. R. Johnson and D. A. Jones, technical coordinators. Importance, preservation, and management of riparian habitat: a symposium. U.S. Department of Agriculture, Forest Service, General Technical Report RM-43.

Weaver, R. A. 1973. California's bighorn management plan. Transactions of the Desert Bighorn Council 17:22–42.

———, F. Vernoy, and B. Craig. 1959. Game water development on the desert. California Fish and Game 45:333–342.

Wehausen, J. D., V. C. Bleich, and R. A. Weaver. 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. Transactions of the Western Section of The Wildlife Society 23:65–74.

Welchert, W. T., and B. N. Freeman. 1973. 'Horizontal' wells. Journal of Range Management 26:253–256.

Werner, W. E. 1984. Bighorn sheep water development in southwestern Arizona. Transactions of the Desert Bighorn Council 28:12–13.

West, N. E., and T. P. Yorks. 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. Journal of Range Management 55:171–181.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1979. Interactions between mule deer and cattle on big sagebrush range in British Columbia. Journal of Range Management 32:299–304.

Wilson, L. O. 1977. Guidelines and recommendations for design and modification of livestock watering developments to facilitate safe use by wildlife. U.S. Department of the Interior, Bureau of Land Management, Technical Note 305.

Wood, J. E. 1969. Rodent populations and their impact on desert rangelands. Bulletin 555. Agricultural Experiment Station, New Mexico State University, Las Cruces, USA.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology—United States and southern Canada. John Wiley and Sons, New York, USA.

Yoakum, J. D. 1980. Habitat management guidelines for the American pronghorn antelope. U.S. Department of the Interior, Bureau of Land Management, Technical Note 347.

———, W. P. Dasmann, H. R. Sanderson, C. M. Nixon, and H. S. Crawford. 1980. Habitat improvement techniques. Pages 329–403 *in* S. D. Schemnitz, editor. Wildlife management techniques manual. Fourth edition. The Wildlife Society, Washington, D.C., USA.

Young, Jr., D. P., R. Vinzant, and M. D. Strickland, editors. 1995. Wildlife water development. Water for Wildlife Foundation, Lander, Wyoming, USA.

CHAPTER 17

Detecting Top-Down versus Bottom-Up Regulation of Ungulates by Large Carnivores: Implications for Conservation of Biodiversity

R. Terry Bowyer, David K. Person, and Becky M. Pierce

Models of predator–prey dynamics have a long and rich scientific history (Taylor 1984; Berryman 1992; Boyce 2000). Indeed, such models have underpinned our understanding of predator–prey systems and helped define how we view and implement conservation strategies for predators, prey, and the environments they inhabit (Ballard et al. 2001). Although predator–prey models are of considerable heuristic value (Hutchinson 1980), they also have played a key role in the applied ecology of large mammals. A knowledge of predator–prey systems underlies decisions about whether predator control may be necessary to meet societal goals (Gasaway et al. 1992), is used to formulate tactics for conservation of endangered prey (Sinclair et al. 1998), holds implications for understanding competition among large carnivores (Creel 2001), and has relevance for inbreeding depression and thereby time to extinction for prey (Hartt and Haefner 1995). Moreover, predator–prey dynamics may interact with habitat fragmentation to determine predator–prey equilibria and subsequent persistence of populations (Swihart et al. 2001), an outcome that makes implementation of conservation schemes based on single species risky (Prakash and de Roos 2002). Large carnivores also influence community structure of their prey (Henke and Bryant 1999). Predator–prey disequilibria affect interspecific behavior among large carnivores, as well as antipredator responses of their ungulate prey (Berger 1999; Brown et al. 1999; Berger et al. 2001a). Such disequilibria may result in trophic cascades that affect ecosystem structure and function (Bowyer et al. 1997; Kie et al. 2003 for reviews). Hence, the failure to consider predator–prey dynamics, in particular whether regulation of prey is primarily top-down or bottom-up, has ramifications for the conservation of biodiversity.

From their inception, predator–prey models have emphasized the role of predation in regulating prey, and discounted or ignored the effect of environmental carrying capacity (*K*—the number of prey at or near equilibrium with their food supply—McCullough 1979; Kie et al. 2003) on population dynamics of large herbivores and, thereby, on predator prey–relationships. Kie et al. (2003) provide a detailed discussion of the role of a variable climate and successional changes on *K*. The classic Lotka-Volterra equation for growth of a single species incorporates *K*, but that parameter is conspicuously absent from original equations describing predator–prey dynamics. Nonetheless, May (1974) demonstrated that inclusion of a resource-limitation term could have a stabilizing influence on predator–prey dynamics. Numerous advances in predator–prey theory have been made (Vucetich et al. 2002), but models depicting how such systems work are still largely predator driven. Only May (1974), Eberhardt (1998), and Person et al. (2001) have placed emphasis on *K* in models of predator–prey dynamics. Likewise, initial attempts at understanding the biology of predator–prey dynamics of large herbivores, and the carnivores that rely on them, concluded that resources would seldom be limiting for herbivores in terrestrial environments and that predation was consequently the most important factor constraining population growth of prey (Slobodkin et al. 1967). This "world is green" approach has been reconstituted in most predator–prey models proposed for large mammals and illustrates how our view of an ecosystem is constrained by the models we use to emulate its processes. Indeed, several authors still persist in the view that food seldom will be limiting for populations of large herbivores (Bergerud et al. 1983; Boertje et al. 1996), despite considerable evidence to the contrary (McCullough 1979; Kie et al. 2003 for reviews). Furthermore, similar thinking concerning the role of predation in regulating prey permeates modern approaches to predator–prey systems and many models forwarded to explain their dynamics (Boutin 1992; Ballard et al. 2001; Vucetich et al. 2002).

We maintain that controversy over whether population regulation of large mammals is top-down or bottom-up has its origins in the manner in which we model predator–prey dynamics, and that a predator-centric perspective has hindered our understanding of such systems. Resolving factors responsible for the dynamics of predator–prey systems is crucial to the management of large mammals and may hinge on how well we understand those processes. Although effective wildlife conservation may help mitigate risk of extermination for some species (Linnell et al. 2001b), large mammals, in general, and carnivores, in particular, historically have been at risk of extinction (Van Valkenburgh 1999)—they remain so today (Maehr 1997b; Woodroffe 2001). Our purpose is to provide a new framework in which to examine top-down and bottom-up regulation of populations of large herbivores. We contend that the need to understand population dynamics of these unique large mammals and interactions with carnivores that prey upon them is paramount for the effective conservation of biodiversity.

Conceptual Models of Predator–Prey Dynamics

Large mammalian herbivores are useful for studying top-down versus bottom-up regulation of populations. These animals are relatively large bodied, have comparatively long life spans, delay reproduction, have small litters, and exhibit high maternal investment in young. Ungulates generally exhibit life-history characteristics that are related to density dependence and, therefore, have a strong potential for population regulation at K (McCullough 1979; Fowler 1987; McCullough 1999; Kie et al. 2003). Likewise, these large herbivores are preyed upon by an impressive array of large mammalian carnivores (Mills 1989; Gasaway et al. 1992; Prins 1996; Smith-Flueck and Flueck 2001). The need to incorporate life-history information to produce realistic predator–prey models recently has been recognized by those studying insects (Dostalkova et al. 2002). We concur, and similarly argue that studies of organisms such as insect parasitoids and other arthropods with markedly differing life histories are unlikely to provide sufficient insights into predator–prey dynamics for large mammals so as to resolve issues related to top-down and bottom-up population regulation. We acknowledge, however, that implementing an experimental approach for these vagile, and sometimes difficult-to-study animals provides a daunting impediment to understanding complex predator–prey systems (McCullough 1979; Boutin 1992; Stewart et al. 2002; Kie et al. 2003).

Predator–prey dynamics for large mammals often have been examined from the perspective of four conceptual models: recurrent fluctuations, low-density

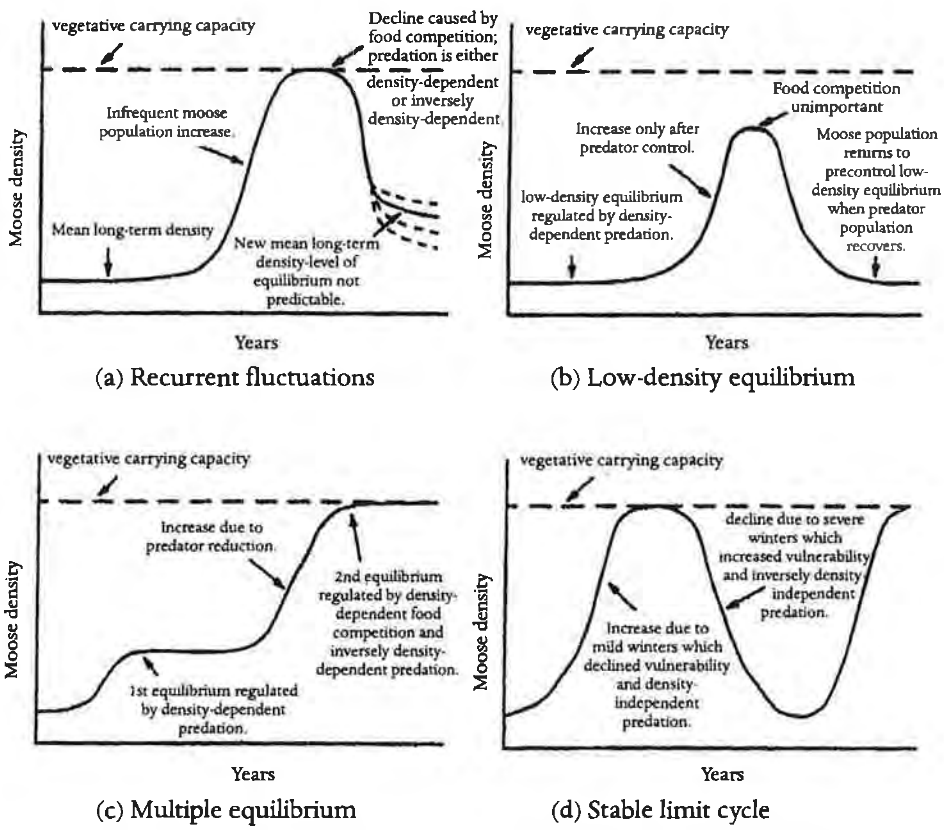

Figure 17.1
Four conceptional models for understanding population dynamics of ungulates and large mammalian carnivores (from Ballard et al. 2001, with permission—Copyright, The Wildlife Society).

equilibrium, multiple equilibria (predator pit), and the stable-limit cycle (Boutin 1992; Van Ballenberghe and Ballard 1994; Ballard et al. 2001; Fig. 17.1a–d). Although of considerable heuristic value, these conceptual models have had limited success in making empirically supported predictions concerning predator–prey dynamics (Boutin 1992 provides those predictions). This is a frustrating situation for those wishing to implement conservation and management initiatives for large mammals and their habitats based on these conceptual approaches.

A model of recurrent fluctuations (Fig. 17.1a) implies that an ungulate population fluctuates markedly in density but will not reach equilibrium. Although any perturbation can affect population numbers, such fluctuations are principally a result of severe weather, forage quantity and quality, and especially predation. Predation is inversely density dependent at high densities, and density dependent at low numbers of prey. Although prey may remain at low densities for extended periods of time, the long-term level of abundance cannot be predicted.

A low-density equilibrium (Fig. 17.1b) describes a system in which prey are held at low density by predation (i.e., density-dependent predation) for long periods. Should rates of predation lessen sufficiently (e.g., from predator control or a natural phenomenon), the prey population would rebound toward *K* but would never reach that level. Food limitation is unimportant under this model, and predation ultimately would reduce prey again to a low-density equilibrium.

A multiple-equilibria model (Fig. 17.1c) predicts regulation of prey by predators at low density, but allows for food limitation of the prey population at *K*. Prey populations are not thought to persist near *K*; however, multiple equilibria at various densities of prey below *K* are possible. One result of this model is a Ricker-like (McCullough 1979) predator pit in which predation results in a strong point of equilibrium at low density of prey. When released from predation pressure, prey density will increase until it has reached a higher-density equilibrium with predators. This scenario is often an underlying assumption and justification for predator control (Gasaway et al. 1992).

Stable-limit cycles (Fig. 17.1d) are thought to be the result of interactions among density-independent processes (e.g., severe weather), population density of prey in relation to *K*, and predation. Here predation is density independent during periods of increasing prey abundance, and inversely density independent during declines in prey. Those processes are hypothesized to generate cycles with regular amplitudes and durations of 30 to 40 years.

Failure to Consider Effects of *K*

Few of the four conceptional models (Fig. 17.1a–d) adequately consider effects of *K* on the dynamics of predator–prey relationships. Low-density equilibrium ignores *K*, recurrent fluctuations and stable-limit cycles predict only short-term periods where prey are near or at K, and multiple equilibria allow for an equilibrium near K, although even that situation is thought to be transitory. All models incorporate the concept of predation rate relative to prey density as a driving force. None allows for an overshoot of K and subsequent decline in K from overexploitation of forage—a likely outcome from population irruptions that may occur under low rates of predation or from the lack of other important sources of mortality (Leopold 1943; Klein 1968; Caughley 1970; McCullough 1979; Andersen and Linnell 2000). In addition, no model satisfactorily addresses effects of the approach or decline of the prey population to and from a potentially changing K and the subsequent influence of those changes on recruitment of prey on dynamics of predator–prey systems, except via kill rate. The assessment of kill rate can be misleading because all models assume that K is constant and mortality of prey additive, an unlikely set of circumstances.

The failure to more fully incorporate K into models of predator–prey relationships has further ramifications. A small change in K may precipitate a large change in prey numbers—a conclusion also reached by McCullough (1979). Such an outcome stems from the nonlinear density-dependent relation between annual recruitment and population density of prey with respect to K. The area under the curve representing maximum sustained yield (MSY) declines in a negative-exponential fashion as K is reduced (Fig. 17.2). Consequently, net annual recruitment of prey, which represents the portion of a prey population that can be removed by predators (and other sources of mortality) without causing a decline in the population, is reduced disproportionately to the decline in K. Indeed, Sutherland (1996) noted that lowering K will disproportionally alter demographic rates along a declining spectrum of prey densities. Those varying densities of prey and their effects on availability and distribution of food, as well as their inputs of urine and feces, are the mechanism whereby large herbivores bring about key changes in ecosystem structure and function (Molvar et al. 1993; Wallis de Vries 1995; McShea, this volume). Accordingly, whether predators exert top-down influences on prey, or fail to do so (i.e., limitation is bottom-up), has ramifications for the biodiversity of ecosystems.

Relying on these four conceptional models to understand predator–prey dynamics has other shortcomings. The time necessary to recognize which model likely was correct is decadal or longer. Important conservation issues related to habitat or conservation of predators or prey likely would be resolved (for good

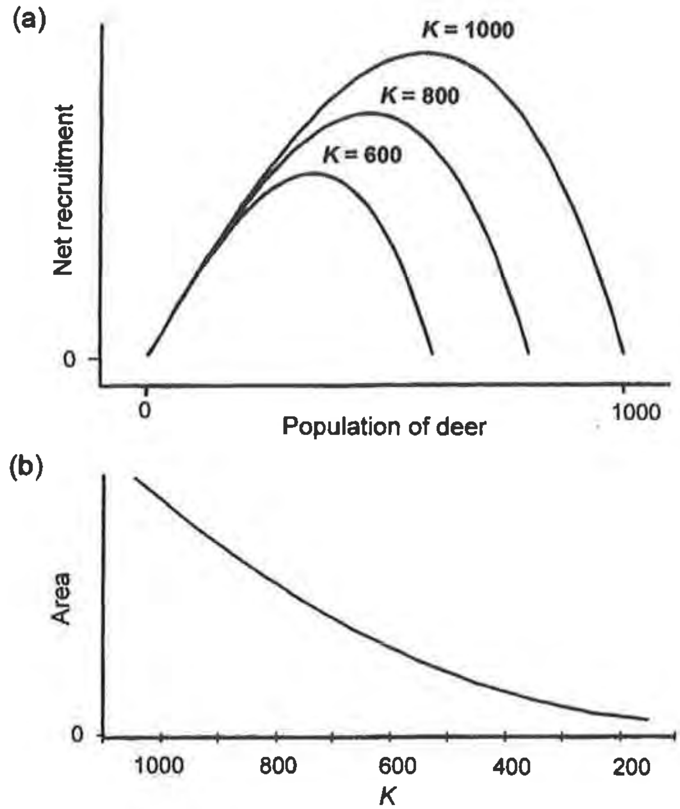

Figure 17.2
Hypothetical curves showing recruitment number of a large herbivore for varying levels of *K* (a), and relation between K and area under the recruitment curve as a function of *K* (b). As *K* is reduced, the area under the recruitment parabola declines in a nonlinear fashion.

or ill) long before an informed decision could be made. We argue that models that rely mostly on predation rate and fail to adequately consider *K*, or in some instances completely ignore this parameter, are ill suited to assess whether population regulation of prey is top-down or bottom-up. Indeed, the manner in which these models are conceptualized leads inexorably toward a conclusion of top-down regulation. For example, as *K* declines, stochastic events, such as severe winter weather (Sæther 1997; Solberg et al. 2001; Kie et al. 2003), or time lags in the numerical response of predators to changes in the density of their prey (O'Donoghue et al. 1998; Pierce et al. 1999; Keeling et al. 2000; Pierce et al. 2000a), may combine to limit number of prey to low levels without a concurrent reduction in predators. Under these circumstances, top-down control imposed by predation may appear to supersede effects of *K* on prey, an interpretation that could lead resource managers to undervalue the important role of habitat quality.

An example of how research might lead to potentially erroneous interpretations is provided by one study of wolves (*Canis lupus*) and black-tailed deer (*Odocoileus hemionus*) on Vancouver Island, Canada, which indicated that declines in populations of deer were the result of predation by wolves, and that changes in habitat because of logging had little effect on numbers of deer (Atkinson and Janz 1994; Hatter and Janz 1994). The authors suggested that numbers of deer declined in logged and unlogged landscapes and, thus, habitat change was not a factor influencing the decline of deer populations (Atkinson and Janz 1994; Hatter and Janz 1994). No information concerning relative densities of deer or *K* in logged and unlogged landscapes was provided. The authors further suggested that when numbers of deer were kept low by predation, deferring logging of winter habitat for deer was difficult to justify. In our view, studies such as these simply demonstrate that densities of ungulates are lower when exposed to predation by wolves than where wolves are absent. We hypothesize that the potential for populations of deer to rebound from low levels imposed by weather and predation is as dependent on *K* as it is on the reduction of predators. Indeed, using low densities of deer to justify reducing *K* for deer simply perpetuates a conceptual problem and risks a management catastrophe. We believe that failing to consider *K* of ungulate prey in dynamics of predators is an oversight that likely will result in misinterpretation of data and may hamper conservation efforts designed to assist predators and their prey or to maintain biodiversity.

Prey to Predator Ratios

Measures of the ratio of ungulate prey density (or their biomass) to predator density have been used widely to predict effects of predators on their ungulate prey (Keith 1983a; Fuller 1989; Gasaway et al. 1992; Person et al. 2001), thereby offering a potential mechanism to infer whether top-down or bottom-up processes were at work. One approach has been to use linear regression to predict density of predators from prey biomass (Keith 1983a; Fuller 1989; Gasaway et al. 1992; Messier 1995). The supposition is that density of predators is predicted by prey abundance, and this value represents an approximate carrying capacity or equilibrium density for predators (Gasaway et al. 1992). Accordingly, if predator densities are greater than predicted, or if prey–predator ratios are less than envisaged, then predators ostensibly would cause a decline in prey (i.e., regulation was top-down). An apparent time lag between numbers of mule deer (*Odocoileus hemionus*) and declining numbers of mountain lions (*Puma concolor*) indicates that interpretation of prey–predator ratios is difficult at best (Fig. 17.3). In that system, the mule deer population initially crashed during an extensive drought and only began recovering when the drought subsided—deer likely were tracking *K* (see Fig. 17.3). Mountain lion numbers initially remained high but ultimately declined with a substantial lag behind numbers of their principal prey (likely bottom-up forcing). Mule deer recovered much more slowly (well below their maximal intrinsic rate of increase) following the drought, even though the range and physical condition of deer had improved markedly (Pierce et al. 2000b; probably top-down limitation from mountain lion predation). The deer–mountain lion ratio in relation to number of mule deer during periods of deer recovery, however, is an exponentially increasing curve indicative of a prey population that had escaped effects of predation (bottom-up limitation). Differing conclusions concerning whether regulation is top-down or bottom-up are related to when predator–prey ratios are measured (Fig. 17.3). Even long-term data sets may not be sufficient to untangle potential biases in interpretation of prey–predator ratios.

Person et al. (2001) have cautioned that combining biomass from different species of prey is not advisable because this method obscures effects of variation in intrinsic rates of increase among prey species on predator–prey dynamics, including potential points of equilibria. Indeed, use of prey–predator ratios has been controversial (Theberge 1990; Messier 1994). Theberge (1990) further argued that changes in the functional response of predators to variation in prey density, prey-switching, and the nearness of the prey population to *K* would make interpretation of prey to predator ratios problematic. Moreover, predation rate per predator for a particular species of prey likely depends upon density of that prey, and the simultaneous density of alternative prey (Dale et al. 1994; Jędrzejewski et al. 2000).

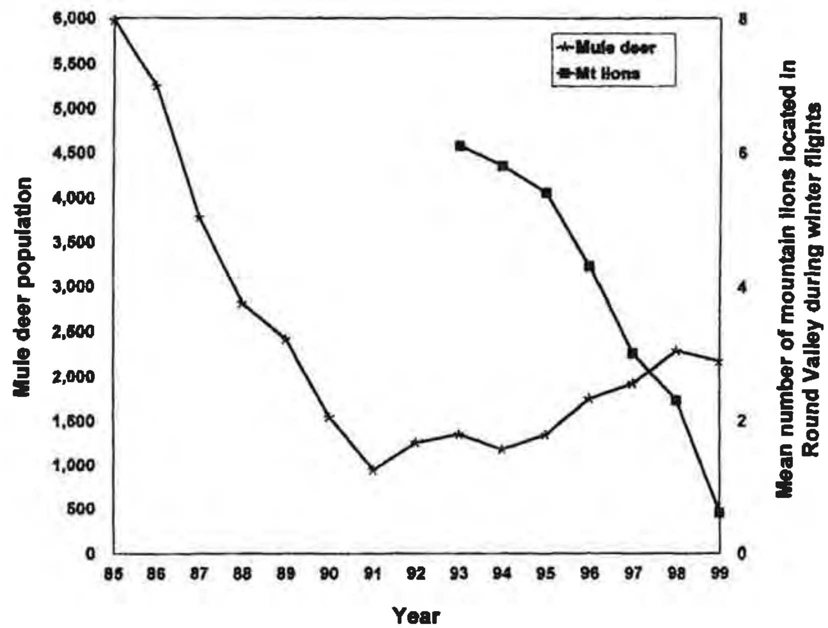

Figure 17.3
Numbers of mule deer and mountain lions in Round Valley, California, USA, during 1985–1999. A drought began in 1987 and ended in 1992. Note that numbers of prey to predators result in a ratio that increases exponentially from 1993 to 1999 (adapted from Pierce et al. 1999, 2000a).

Consequently, density-dependent changes in rate of killing by predators could require a reiterative interpretation of ungulate to predator ratios with changes in prey density for this method to offer meaningful insights into population regulation (Person et al. 2001)—a daunting task for those managing populations of either predators or their prey.

Kill Rates

Even the most sophisticated models (Vucetich et al. 2002) developed to explain predator–prey dynamics rely on the kill rate of predators in relation to either the abundance of prey (i.e., the functional response—Holling 1965) or the ratio of predator to prey. Although such modeling has become more elaborate over time, considerable debate exists over which model best describes predator–prey dynamics (Arditi and Ginzburg 1989; Ginzburg and Akçakaya 1992; Abrams 1994; Akçakaya et al. 1995; Abrams 1997). Many of these models are based on theoretical formulations, and much controversy has resulted from an absence of empirical data, especially for large mammals (Vucetich et al. 2002).

Vucetich et al. (2002) compared a variety of prey-dependent, ratio-dependent, and predator-dependent models against empirical data from wolves and moose (*Alces alces*) from 1971 to 2001 on Isle Royale, Michigan, USA. These authors concluded that, although both models may have value, they were overly simplistic —neither ratio-dependent nor prey-dependent models deserved primacy for understanding predator–prey relationships. We hypothesize that the relative poor fit ($R^2 \leq 0.36$) of the models examined by Vucetich et al. (2002) stems from the failure to include K in any model. Moreover, none of the models examined by these authors is tightly linked to the four conceptual models used to guide our understanding of predator–prey dynamics among large mammals (Fig. 17.1a–d).

Person et al. (2001) modeled density of wolves relative to moose by varying the population density of ungulates at which predation rate by wolves was halved (D), and the shape of the density-dependent growth curve for ungulates (θ). Those authors reported that, as the ratio of D to U (the prey population) became smaller, the influence of the functional response on the density of wolves decreased. Person et al. (2001) concluded that the functional response might have little effect on predator–prey systems of large mammals except at very low density with respect to K. Only at low density was there a discernable difference between simulations with D bounded by $[0, K/8]$ and simulations of $D = 0$ (which eliminated the functional response). Indeed, Marshal and Boutin (1999) cautioned that it was at such low densities, where reliable data were most difficult to obtain, that distinguishing between types of functional responses could be problematic because of low statistical power resulting from small sample size. Moreover, the effort and expense necessary to gather data for large mammals to estimate the type of functional response can be immense (Dale et al. 1994; Jędrzejewski et al. 2002). Studies by Marshal and Boutin (1999) and Person et al. (2001) draw into question the value of estimating the instantaneous kill rate of ungulates by large carnivores and, thereby, the worth of prey-dependent and predator-dependent models for un-

Comment Letter I9

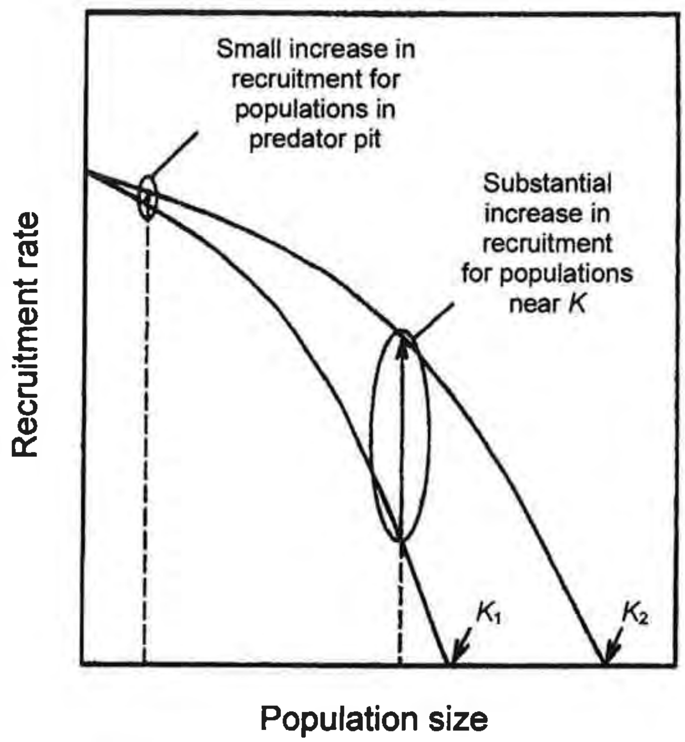

Figure 17.4
Variation in recruitment rate with increasing population size relative to long-term changes in carrying capacity (K) for an ungulate population. A substantial improvement in recruitment rate occurs only as the population increases from low to high density (from Kie et al. 2003, reprinted with the permission of Cambridge University Press).

derstanding predator–prey dynamics of large mammals and their subsequent effects on biodiversity.

Ratio-dependent models, likewise, have limitations for deciphering relationships between ungulates and the large carnivorous mammals that prey upon them. One prediction of these models is that an increase in K would result in an increase in both prey and predator. A simple population model for a large herbivore that includes K (McCullough 1979), however, indicates that an increase in K differentially affects recruitment rate relative to where the population is with respect to K. There is little increase in recruitment rate, therefore, for a population at low

Comment Letter I9

density because animals are not food limited and reproducing at near maximal rates (Fig. 17.4). The improvement in recruitment rate from enhancing *K* increases as the population moves toward the new carrying capacity (K_2) from its old one (K_1; see Fig. 17.4). This increase in recruitment rate from enhancing *K* results in differing prey availability to predators across a wide range of population densities with respect to *K*, which fits outcomes predicted by ratio-dependent models poorly. We note, however, it is at low density of prey where predator limitation (top-down forcing) has the greatest empirical support; these low densities of prey relative to *K* typically involve multiple-predator and multiple-prey systems (Gasaway et al. 1992; Bowyer et al. 1998; Hayes and Harestad 2000b).

A Prey-Based Approach for Understanding Top-Down and Bottom-Up Processes

If only bottom-up processes were involved in population regulation of ungulates, effects of large carnivores on prey numbers would be minimal, and conservation measures to benefit carnivores would have few consequences for biodiversity. Conversely, where these large predators alter the density of their prey relative to *K* (i.e., top-down forcing), the management of carnivores may have profound effects on biodiversity. We acknowledge that no system is regulated exclusively by either top-down or bottom-up processes and suggest that it is misleading to view such processes as a dichotomy. We also recognize that justifying the maintenance or restoration of large carnivores for the purpose of conserving biodiversity requires knowledge of their role in promoting ecosystem integrity. We caution, however, that effects of carnivores on their ungulate prey may change over time, and that predator-centric approaches, such as determining kill rates and prey to predator ratios, are poorly suited for determining whether forcing is primarily top-down or bottom-up.

We believe that an assessment of top-down versus bottom-up limitation of prey populations are most easily and accurately interpreted through simple models of prey population dynamics. Moreover, our approach does not require competing models that provide a yes-or-no answer to a process that is a continuum. Although questions concerning population regulation via predation or food often are framed as a dichotomy (populations of ungulates overshooting *K*, or being held at a low density by predation), a prey population might be regulated by top-down processes over one time period, and bottom-up effects during the next, a result suggested by May (1974). The most important consideration from a conservation perspective is to recognize what is regulating or limiting the population, and to take appropriate action relative to the conservation of predator, prey, or the biodiversity of their environment. Attempts to understand the intricate nature of predator–prey interactions are of considerable theoretical value but may hinder conservation efforts if they become the primary evaluative tool for making decisions concerning top-down and bottom-up processes and their effects on biodiversity.

We maintain that far too much reliance has been placed on the number of prey killed or the kill rate in interpreting predator–prey relationships. Although an adequately large kill of prey is necessary to invoke a predator-limited or regulated population, it is not sufficient to know that there is top-down regulation of prey. For instance, high mortality of young occurred in a mule deer population exposed to predation by coyotes (*Canis latrans*), in which both low reproductive rates of deer and poor range condition indicated the deer population was near *K* (Bowyer 1984, 1987, 1991). This outcome likely occurred because whether mortality of ungulate prey is additive or compensatory is related to proximity of the population to *K*. Mortality in prey populations becomes increasingly compensatory as the population grows from near MSY toward *K*, but it is largely additive at population densities below MSY (McCullough 1979; Kie et al. 2003; Fig. 17.5). Consequently, heavy losses of young in an ungulate population near *K* are not grounds for concern; those young would have died from other causes anyway (i.e., mortality was compensatory; Errington 1967). Simply documenting that predators are killing large numbers of prey is insufficient to infer top-down forcing and might lead to unnecessary control of predators.

We contend that life-history characteristics of ungulate prey (*sensu* Kie 1999; McCullough 1999; Keech et al. 2000; Kie et al. 2003) can be used to infer whether population limitation is top-down or bottom-up because of the strong density dependence exhibited by those large mammals (Table 17.1). Much of our knowledge concerning such processes comes from northern ecosystems. Nevertheless, our predictions are based on fundamental concepts of population

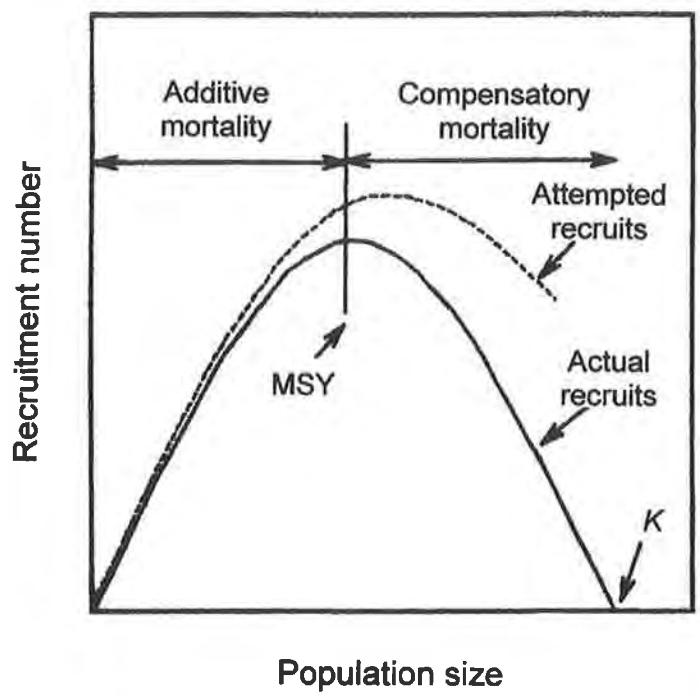

Figure 17.5
Changes in recruitment number and attempts to recruit young with increasing population size of an ungulate population. Females attempt to reproduce at a higher level than can be supported by the environment from densities ranging from maximum sustained yield (MSY) to carrying capacity (*K*), and that attempts to recruit young parallel the recruitment number below MSY because females are in good physical condition. Mortality tends to become increasingly compensatory from MSY to *K*, but is largely additive below MSY (from Kie et al. 2003, reprinted with the permission of Cambridge University Press; adapted from McCullough 1979).

ecology (Hutchinson 1980) and, consequently, should have wide applicability. Top-down processes would seldom result in ungulate populations near *K*, but rather in populations held at extremely low densities with respect to *K*. Consequently, measures of animal condition and reproduction in populations near *K* should be low, indicating bottom-up forcing. Conversely, top-down limitation implies that un-

Comment Letter I9

Table 17.1
Life-history characteristics of ungulates that reflect the relative differences in a population regulated by top-down versus bottom-up processes

Life-History Characteristic	Population Top-Down Regulated	Population Bottom-Up Regulated
Physical condition of adult females	Better	Poorer
Pregnancy rate of adult females	Higher	Lower
Pause in annual production by adult females	Less likely	More likely
Yearlings pregnant[a]	Usually	Seldom
Corpora lutea counts of adult females[a]	Higher	Lower
Litter size[a]	Higher	Lower
Age at first reproduction for females	Younger	Older
Weight of neonates	Heavier	Lighter
Mortality of young	Additive	Compensatory
Age at extensive tooth wear	Older	Younger
Diet quality	Higher	Lower

[a] Some species of ungulates may show limited variability in particular characteristics.

gulates would be held at a low density relative to *K*, and the physical condition and reproductive performance of individuals in such populations would be high (see Table 17.1). Likewise, dietary quality should vary with population density of ungulate prey relative to *K*, with intensified intraspecific competition near *K* resulting in a lower-quality diet than would be expected for populations held far below *K* by predation.

This approach has limitations but may offer the only data readily available to help determine if populations of ungulates are predator-limited, and allow biologists to respond with appropriate management in a timely manner (Kie et al. 2003). Obviously, factors other than predation can drive populations to low levels or cause them to oscillate near *K*. Difficulties in sorting among other potential causes of population change, however, are minimal compared with trying to determine which conceptual model of predator–prey dynamics is appropriate (Fig. 17.1a–d), or in trying to determine kill rate, especially at low densities where it is most likely to result in an equilibrium. Moreover, either indices of overgrazing and hedging of trees and shrubs (Caughley 1977; Riney 1982; Kie et al. 2003) or other forage-based estimates of *K* (Hobbs et al. 1982; Stewart et al. 2000) may be used to help calibrate where the prey population is with respect to *K*.

Future Directions for Predator–Prey Modeling

There is an obvious need to incorporate values of *K* in future models of predator–prey dynamics for large mammals. We can still engage in conservation efforts that require knowledge of whether limitation is top-down or bottom-up using the approach we have recommended (Table 17.1), but having realistic and predictive models ultimately would be of theoretical and applied value. There is also a clear necessity to manipulate populations of predators and prey to fully understand these systems (Boutin 1992). Such manipulations will be difficult to perform with populations of large mammals, but opportunities for adaptive management should be sought out with an eye to resolving existing issues concerning how these systems work, and specifically how predator–prey dynamics are linked to biodiversity.

Including more information related to the life-history characteristics of predators and prey is also likely to provide new insights into their dynamics (Gittleman 1993; McCullough 1999). For instance, populations of large polygynous ungulates sexually segregate for much of the year (Bowyer 1984; Bowyer et al. 1996; Bleich et al. 1997; Kie and Bowyer 1999; Barboza and Bowyer 2000). Consequently, the population density of adult females, rather than adult males, relative to *K* has the greatest effect on recruitment of young and thereby the dynamics of the population (McCullough 1979). Accordingly, a male ungulate killed by a predator will have a proportionally lower effect on recruitment of young into the ungulate population than would the death of a female. Because males of dimorphic ungulates are considerably larger than females (Weckerly 1998), the food they provide is likely to affect reproduction of predators more than that of smaller-bodied females or young. Both outcomes have potential to affect predator–prey dynamics, including top-down and bottom-up processes, in ways that are not considered in existing models. The manner in which the sexes of ungulates are distributed spatially upon the landscape and the effects of this pattern on predator–prey dynamics is a topic in dire need of additional research. Perhaps an initial approach would be to modify the classic Lotka-Volterra equations for resource competition (Tilman

1982) to represent different sexes rather than different species. In addition, Pierce et al. (2000b) documented that female mountain lions with young killed a disproportional number of young mule deer compared with other sex, age, and reproductive classes of lions. Such selectivity could also have effects on productivity of prey populations and, in consequence, predator–prey dynamics. Despite such potential improvements in theoretical modeling, we concur with Person et al. (2001) that limited resources for conducting research on predator–prey dynamics of large mammals should be concentrated on understanding the growth of prey populations with respect to habitat quality in relation to the predation behavior of carnivores. Indeed, few studies concerning the conservation of carnivores consider the habitat necessary to support adequate densities of associated prey, a point also raised by the National Research Council and its Committee on Management of Wolf and Bear Populations in Alaska (1997).

Linking Predator–Prey Dynamics to Ecosystem Processes and Biodiversity

Large carnivores affect prey other than via population regulation, including influencing degree of sociality, habitat use, foraging dynamics, and distribution of ungulates across the landscape (Berger 1991; Molvar and Bowyer 1994; Berger 1999; Kie 1999; Berger et al. 2001b; Bowyer et al. 2001; Mills, this volume). Likewise, species of available prey and their dispersion hold import for the social organization of predators (Mills 1989; Pierce et al. 2000a). Predators make for a rich environment that embodies a full array of natural behaviors in ungulates that are absent from depauperate ecosystems lacking these unique mammals—an element of biodiversity that is seldom considered.

Systems without large carnivores often experience trophic cascades in which ungulates have deleterious effects on vegetation and other animals (Hobbs 1996; Bowyer et al. 1997; Kie et al. 2003 for reviews). Changes in densities of large herbivores have the potential to drive nutrient cycling in terrestrial and aquatic systems (McNaughton 1984; Ruess and McNaughton 1987; Irons et al. 1991; Frank and McNaughton 1993; Molvar et al. 1993) and affect successional pathways of vegetation communities (Pastor et al. 1993; Wallis de Vries 1995), resulting in "ecological meltdowns" of some systems that markedly lower their biodiversity (Terborgh et al. 2001). Indeed, ecological cascades from foraging by ungulates on rodents (Keesing and Crawford 2001), birds (deCalesta 1994; McShea and Rappole 2000; Berger et al. 2001a), and insects (Suominen et al. 1999a; Souminen et al. 1999b) are well documented. It is axiomatic that top-down forcing of ungulate prey by carnivores, or regulation of ungulates by bottom-up processes, holds potential to affect the relation of the prey population to *K* and thereby ecosystem structure and function, and ultimately biodiversity. Consequently, predator–prey dynamics hold important consequences for the well-being and richness of ecological systems. Many challenges exist in conserving large carnivores (Miquelle et al. 1999; Ginsberg 2001) and, thus, the biodiversity of landscapes they inhabit. We believe that understanding the role of top-down and bottom-up regulation of prey is an essential step in this critical process.

Summary

We set forth predictions for determining whether populations of large herbivores are regulated primarily via top-down or bottom-up processes. We contend that existing models of predator–prey dynamics based on kill rates—including prey-dependent, ratio-dependent, and predator-dependent approaches—are not well suited for understanding top-down and bottom-up regulation of ungulates by their predators. These models make predictions that are not realistic, do not cope with carrying capacity (*K*) of ungulate prey, fail to consider that some mortality of prey may be compensatory, or do not explicitly deal with multiple-prey–multiple-predator systems. Similarly, the four conceptual models—recurrent fluctuations, low-density equilibrium, multiple equilibria (predator pit), and stable-limit cycle—are predator-centric and offer limited promise to explain population dynamics of large mammals. We have demonstrated that, except at very low density of prey relative to *K*, where kill rates are most difficult to measure, population density of prey with respect to *K* is most important in determining potential points of equilibria, and thereby whether regulation is strongest from above or below. Moreover, funding necessary to collect data sufficient to fit models that predict kill rates across seasons for a sufficient number of years are seldom available; conservation issues would be long resolved before the best model could be selected. We have constructed a conceptual framework to make predictions about whether populations of large herbivores are regulated by top-down or bottom-up processes, and propose criteria to assess whether predator control would be effective in releasing ungulate populations from low-density equilibria. Because of the critical role of large carnivores in influencing biodiversity, primarily through their effects on dynamics of ungulate populations and their subsequent influences on ecosystem processes, understanding the role of top-down and bottom-up regulation of prey is an essential step to conserving large carnivores and the biodiversity of landscapes they inhabit.

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Abstract:	Wildlife mortality caused by vehicles is a serious conservation and economic problem as collisions with large mammals are global, persuasive and increasing. This study reviewed the U.S. and European scientific literature pertinent to mitigating the effects of ungulate-vehicle collisions. The paper presents an analysis of ungulate movement and behavior in relation to roads for the purpose of developing general conclusions about locating high frequency collision areas, and documents some successes in reducing these collisions with fencing, modified fencing, and grade separation via crossing structures. Several case studies are also presented to illustrate animal detection driver warning systems, technology based deployments, applied to the problem of ungulate-vehicle collisions. The paper emphasizes the need for more sound statistical design in determining efficacy of treatments.
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INFLUENCES OF SEX AND WEATHER ON MIGRATION OF MULE DEER IN CALIFORNIA

Thomas E. Kucera[1]

ABSTRACT.—I examined differences by sex and influences of weather on timing and patterns of migration of Rocky Mountain mule deer (*Odocoileus h. hemionus*) in the eastern Sierra Nevada, California, during 1984–87. Deer initiated spring migration from the winter range at about the same time in all years and made extensive use of holding areas at intermediate elevations. Radio-telemetered deer showed strong fidelity to summer ranges over as many as four years. Fall weather produced different patterns of fall migration. Storms during October produced a pulsed migration, in which most animals migrated to the winter range during or soon after the storm; in a year without a storm, fall migration was gradual. Despite the influence of storms on the pattern of fall migration, the median date of fall migration by females did not vary over years; however, among males it was later in a year without fall storms.

Key words: migration, mule deer, Odocoileus hemionus, *sex differences, weather, radio telemetry, California.*

Seasonal migration is common among a wide variety of vertebrates (Baker 1978), including large terrestrial mammals (McCullough 1985, Fryxell and Sinclair 1988). Migration ultimately contributes to individual reproductive success (Baker 1978). Proximally, however, migration is related to the seasonal availability of resources (Sinclair 1983, Garrott et al. 1987). Migration is a common phenomenon among mule deer (*Odocoileus hemionus*) in the mountainous western United States, and various studies have described aspects of mule deer migration (Russell 1932, Leopold et al. 1951, Gruell and Papez 1963, McCullough 1964, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). However, questions remain as to the influence of proximate factors, especially weather, on the timing of migration. In addition, because studies of mule deer involving radio-telemetry rarely have included males (e.g., Garrott et al. 1987, Loft et al. 1989), little is known of differences between the sexes in migration patterns.

My objectives were (1) to describe the timing and pattern of seasonal migration of mule deer in the eastern Sierra Nevada, California; (2) to test the hypotheses that there were no differences by sex or year in the timing and pattern of migration and degree of summer-range site fidelity; and (3) to relate observed migration patterns to other aspects of the ecology of these animals.

STUDY AREA

The Sierra Nevada is a massive granite block tilted toward the west, extending for 600 km in a generally northwest-southeast direction (Storer and Usinger 1968). The west side of the mountain range slopes gradually for 75–100 km, from the foothills near sea level to the crest at 3000–4500 m. The eastern Sierra Nevada is more narrow and steep than the west side, with frequent elevational changes of 3000 m in <10 km.

A population of 3000–6000 Rocky Mountain mule deer (*Odocoileus h. hemionus*) winters at the base of the eastern escarpment of the Sierra Nevada in Round Valley, Inyo and Mono counties, California, about 15 km west of the town of Bishop (Fig. 1). An area of about 90 km^2 of Round Valley is used by mule deer as winter range, at elevations from about 1450 to 2100 m. Pine Creek forms the dividing line between what is termed the Sherwin Grade (SG) deer herd to the north and the Buttermilk (BM) herd to the south. These deer are hunted under bucks-only regulations, and posthunt adult sex ratios of 7–12 males:100 females occurred during this study (California Department of Fish and Game, Bishop, California).

As winter storms from the Pacific Ocean rise up the western slope of the Sierra Nevada, they deposit moisture, leaving a much more arid rain shadow on the east side. Precipitation in the

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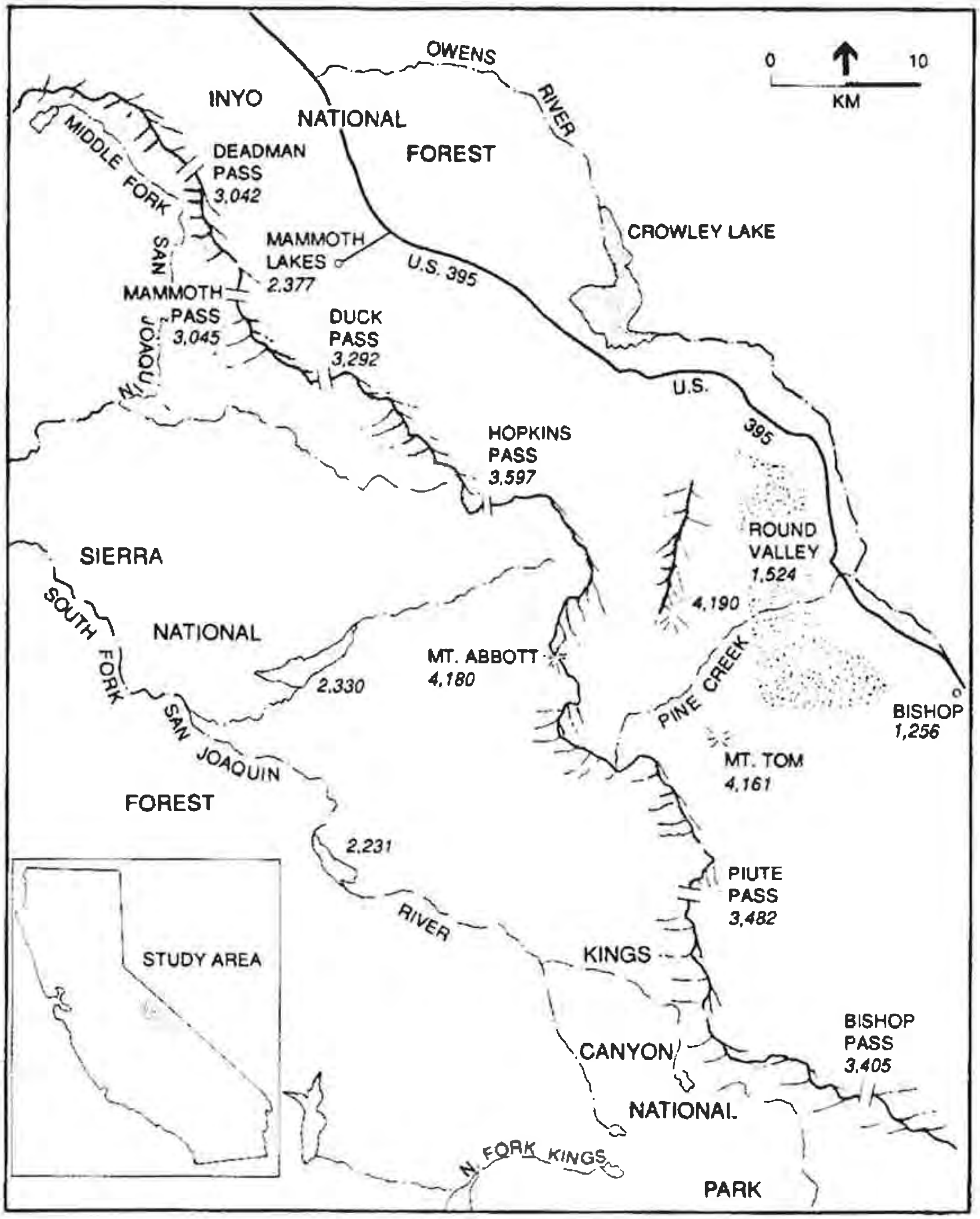

Fig. 1. Map of the study area showing the deer winter range as the shaded area in Round Valley; the crest of the Sierra Nevada is from northwest to southeast, with elevations (m) of selected peaks and major passes.

area ranges from an annual mean of 14.5 cm at the Bishop airport at 1240 m to 40.6 cm at 2860 m in Pine Creek Canyon (Vaughn 1983, National Oceanic and Atmospheric Administration 1987). Precipitation is strongly seasonal, with about 75% of the annual total occurring between November and March. Summers are hot, with daytime temperatures in July often >37 C. January is the coldest month, with an average temperature of 4 C and frequent nighttime lows of <−15 C. Potential evapotranspiration is 66.8 cm, or more than four times the mean precipitation.

Vegetation on the winter range is typical of the Great Basin Desert and conforms to the sagebrush belt of Storer and Usinger (1968). Shrubs are dominant, and blackbrush (*Coleogyne ramosissima*), rabbitbrush (*Chrysothamnus* spp.), big sagebrush (*Artemisia tridentata*), and antelope bitterbrush (*Purshia tridentata*) are most common. Deer summer ranges are on both sides of the Sierra crest, at elevations from about 2200 to >3600 m (Kucera 1988), and include the sagebrush, jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*P. murrayana*)–red fir (*Abies magnifica*), subalpine, and alpine belts (Storer and Usinger 1968).

Livestock use of deer winter range was light, consisting of 129 animal-unit-months of use by cattle, restricted to part of the SG range from 1 April to 15 October (U.S. Department of the Interior 1990). Use of deer summer areas by livestock (including horses, cattle, and sheep) varied from very heavy in more accessible locations on the east side of the mountain range to none at higher elevations and more remote areas.

METHODS

Fieldwork was conducted from January 1984 through May 1987. Deer were captured on the winter range January through March 1984 and January and February 1985 with a variety of methods including Clover traps (Clover 1956) baited with alfalfa, drive nets using a helicopter, and remotely triggered drop-nets; net guns fired from a helicopter and tranquilizer darts also were used to capture selected males. Deer captured in 1984 in Clover traps were chemically immobilized with Rompon (xylazine hydrochloride), the effects of which were reversed with yohimbine after handling (Jessup et al. 1985). Deer were captured also during May 1984 and 1985 with tranquilizer darts on a spring migration "holding area" (Bertram and Rempel 1977) about 50 km north of the winter range. This is an area where deer congregate for 2–6 weeks before continuing to areas occupied during the summer.

I fitted 8 males and 9 females from the BM winter range, 7 males and 10 females from the SG winter range, and 10 females captured on the spring holding area with radio collars (Telonics Inc., Mesa, Arizona). All deer were ≤2.5 years of age. I attempted to distribute capture efforts throughout accessible areas to minimize biases in the marked sample. I selected females for telemetry to include all age classes of adults; however, I selected males to receive radio collars on the basis of large size and relatively old age. I excluded smaller, younger males because of concerns arising from body growth: males do not approach maximal neck circumference until about 4 years of age (Anderson 1981), and this, combined with seasonal neck swelling during rut, could result in injury caused by radio-telemetry collars. Older males have achieved nearly maximum body growth; I allowed for seasonal neck swelling by attaching the nonexpandable collars with a circumference 20–25% larger than the animal's neck circumference after rut, measured midway between head and shoulders. I noticed no serious problems resulting from the use of radio collars on male deer in this study, although after a year or two, some fur appeared to be rubbed off the backs of the necks; a similar situation occurred with telemetered females. Collars on the males moved toward the head when the necks swelled during rut and hung loosely at other times.

While animals were on the winter range, I determined at least once per week, and usually more often, whether each radio-marked animal was on the BM or SG winter range by observing the direction of transmitter signals received from standard locations. These data were supplemented by additional radio locations and visual locations as observers moved through the winter ranges. During spring and fall migrations, and during summer, locations of telemetered deer were determined from a fixed-wing aircraft, from a vehicle, and from the ground. During the spring, locations were determined several times per week until the animals crossed the crest of the Sierra. Due to the remoteness of most summer ranges in roadless wilderness areas, frequency of locations of animals, determined from the air and the ground, on the west side of the Sierra Nevada was approximately twice per month. Of 42 deer that reached summer ranges, I located 38 from the ground.

Twenty-two deer were followed for more than one summer. Of these, 10 (45%; 1 male, 9 females) were located in two consecutive summers, 9 (41%; 3 males, 6 females) in three consecutive summers, and 3 (14%; 1 male, 2 females) in four consecutive summers. For these animals I expressed fidelity to summer range as the greatest linear map distance between mean locations in consecutive summers (1 July–7 September). During the fall, locations of animals were monitored from the east side of the Sierra crest at least several times per week, and frequently daily. I could thus determine, within several days and often within one day, when telemetered deer from the west side of the crest crossed to the east side.

I divided annual migration into three periods: (1) leaving winter range, defined as ascending to an elevation >2100 m; (2) crossing the Sierra Nevada crest in spring; and (3) crossing the crest in fall. The last two apply only to those animals (n = 34) that summered west of the crest. Because of logistic difficulties in locating animals on the west side of the crest, I did not attempt to determine precisely when animals crossing the crest reached their summer ranges. The steep eastern slope of the Sierra Nevada provided the opportunity to determine the presence or absence of a radio-marked animal on the east side with little error. In situations in which I could not determine an exact date of crossing, I estimated the date as the midpoint of the interval in which I did and did not receive a signal.

For analysis I determined frequencies of movement by week during an 8-week period of leaving the winter range beginning 1 April, a 7-week period of crossing the crest in spring beginning 15 May, and an 11-week period of crossing the crest in fall beginning 11 September. I used the Kolmogorov-Smirnov test with chi-square approximation (Siegel 1956) to test for sex differences in the timing of these components of migration. Steep mountains on the west side of Round Valley constrained movement off the winter range to northerly or southerly routes; I tested for sex differences in the direction (north or south) of migration from the winter range with the binomial test (Zar 1984:591). I expressed temporal patterns of fall migration as the percentage of radio-marked deer in an annual sample crossing the crest during any week. I tested for differences among years in the largest weekly percentage crossing the crest in any year with the Z-test (Zar 1984:396).

From April through June of 1985, 1986, and 1987, commencing as soon as snow conditions permitted, deer were counted from a vehicle along a standardized route of 11 km that passed through a major spring holding area located 1–8 km south of the town of Mammoth Lakes, approximately 50 km north of the winter range. These weekly surveys began 30 minutes before sunrise, and direction of travel was alternated on consecutive surveys.

Daily precipitation in the fall was measured at the U.S. Forest Service (USFS) weather station at the Mammoth Lakes Ranger Station, Inyo National Forest, Mammoth Lakes, California, at an elevation of about 2400 m. Winter snowfall totals were from the USFS weather station on Mammoth Mountain, at about 2940 m.

RESULTS

Spring Migration

From 1984 to 1986 the first radio-marked deer left the winter range during the first or second week of April in any year; in the same years the last radio-marked deer left during the second, third, and fourth weeks of May. For females the median departure date from the winter range was during the third, second, and third weeks of April 1984–86, respectively; for males, the median was during the second week of May and second and third weeks of April, respectively. The frequency differences by sex in weekly migration approached statistical significance (X^2 = 5.94, df = 2, .05 < P < .10).

Of the 17 telemetered deer from the BM range, 10 (3 of 8 males, 7 of 9 females) migrated north, through the SG range, to reach their summer range; 5 males and 2 females moved south. Of the 17 deer telemetered on the SG range, 15 (5 of 7 males, 10 of 10 females) migrated to the north; 2 males went south. Overall, more (P = .0003) females migrated north (n = 17) than south (n = 2). Analysis by herd showed a significant difference (P = .0001) in migration direction among SG females (n = 10); the difference among BM females (n = 9) approached statistical significance (P = .07). There were no significant differences among males in migration direction, either with all males combined (n = 15, P = .196), or by herd (BM: n = 8, P = .22; SG: n = 7, P = .16). Of the 10 females captured on the spring range, 4 wintered on the BM range, 5 wintered on the SG range, and 1 died before the fall migration.

Holding Areas

After leaving the winter range, telemetered deer moved to higher-elevation holding areas at

2200–2400 m on the east side of the Sierra Nevada. Hundreds of deer already were present on the first road surveys of the spring, and patterns of occurrence were similar in all years (Fig. 2). Largest numbers were counted in late April and early May; numbers then decreased through mid-June as deer moved to summer ranges. During early spring a portion of the wintering animals also foraged in irrigated meadows immediately adjacent to the winter range in Round Valley.

Diminution of deer counted on the holding area was reflected by an increase in deer crossing the crest to summer ranges. Of the radio-marked deer that summered west of the crest, the first crossed the crest during the third or fourth week of May in any year, and the last crossed during the third or fourth week of June. There were no sex differences in timing of spring crossing (X^2 = 3.50, df = 2, P > .10). The median for both sexes in all years was the first week of June.

The temporal uniformity over years in leaving the spring holding area for summer ranges occurred despite greatly different snow conditions. In the winters of 1983–84, 1984–85, and 1985–86, the USFS recorded total snowfalls of 671, 767, and 1021 cm, respectively, on Mammoth Mountain, geographically close and at an elevation similar to the passes that migrating deer crossed to reach summer ranges on the western slope. Despite these differences in snowfall and consequent snowpack at higher elevations, no differences in the timing of spring migration were evident. The snowfall of winter 1986–87 was only 246 cm, or less than one-quarter of that of the previous year. Although the sample size is small, the median week that three radio-marked males and two radio-marked females crossed the crest in the spring of 1987 was the same as the previous year, the first week of June. Thus, the amount of snow on the ground did not appear to influence the timing of migration over the Sierra crest in the spring.

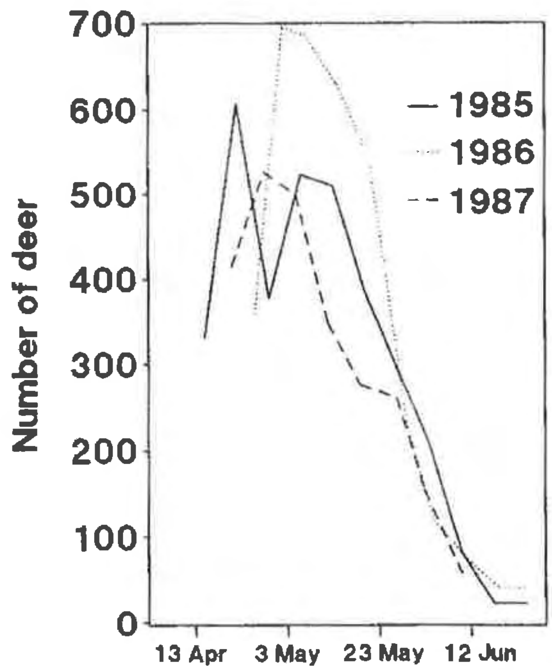

Fig. 2. Number of mule deer counted from a vehicle on standardized weekly surveys at dawn through a spring holding area near the town of Mammoth Lakes, Mono County, California, 1985–87. Surveys began in the spring when snow conditions made the roads passable.

Summer Range

Of the 32 deer captured on the winter range that reached summer ranges, 28 (87.5%) crossed the Sierra crest and summered on the west side. Summer range locations of these deer, plus those of deer captured on the spring range, extended from the headwaters of the Middle Fork of the San Joaquin River south throughout the upper San Joaquin River drainage above about 2134 m into the North and Middle forks of the Kings River (Kucera 1988). Two males and 4 females summered on the east side of the Sierra, from Mammoth Pass on the north to the North Fork of Bishop Creek on the south. Thus, an area nearly 100 × 25 km served as summer range for deer from the BM and SG herds.

Summer Range Fidelity

Distances between summer ranges of 22 deer located in consecutive years averaged 0.7 km (range = 0.2–4 km) for both males (n = 5) and females (n = 17). Only 1 deer, a female, was >1 km from a previous location in successive summers; she spent her second summer about 2.5 km from her first, and her third and fourth about 1.5 km farther away.

Fall Migration

In 1984, 1985, and 1986 the first radio-marked deer crossed to the east side during the first week of October and second and fourth weeks of September, respectively; all were females. The last crossed during the fourth week of October and second and fourth weeks

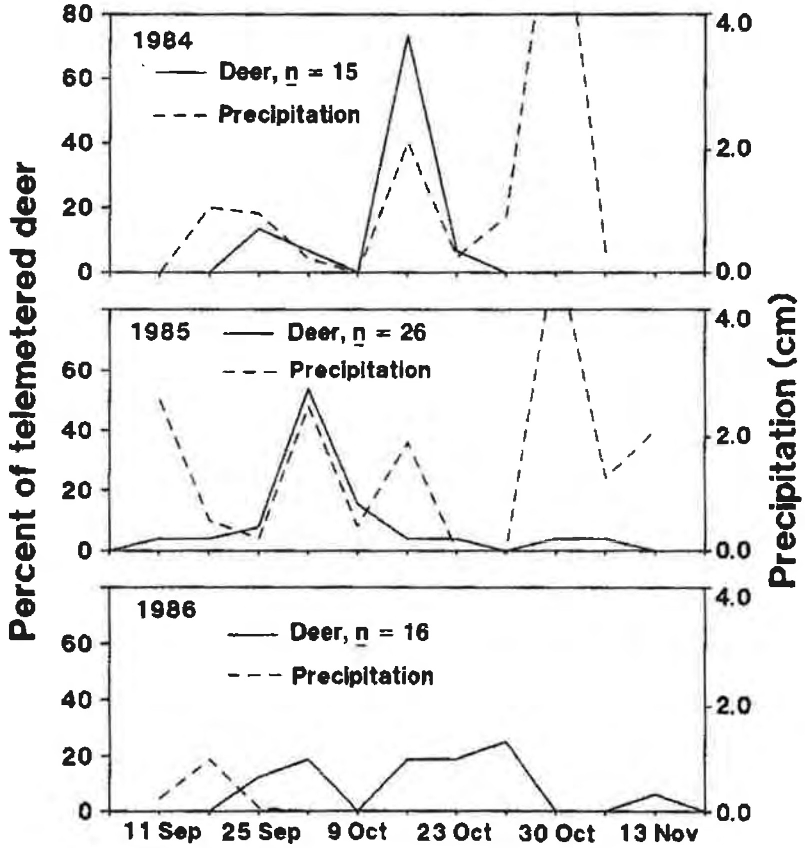

Fig. 3. Percentage of telemetered mule deer per week crossing the crest of the Sierra Nevada, Inyo and Mono counties, California, and weekly precipitation measured at the town of Mammoth Lakes, Mono County, in the fall of 1984–86.

of November; all were males. In 1984 and 1985 the median week of crossing the crest was the same for both sexes, the third and second weeks in October, respectively. In 1986 the median for females was the third week in October, but was two weeks later for males (X^2 = 18.72, df = 2, $P < .001$).

Length of time during which fall migration occurred also varied among years. In 1984, 11 of 15 (73%) and, in 1985, 14 of 26 (54%) telemetered deer, including both sexes, crossed the crest in a one-week period. These proportions were not different ($Z = 1.2$, $P > .11$). However, in 1986 no more than 4 of 16 (25%) radio-marked deer crossed the Sierra crest in any week. This proportion was smaller than those of the previous two years ($Z = 2.45$, $P < .007$), indicating that in 1986 there was no mass movement of deer in a short time period.

Differences among years both in timing and in pattern of fall migration were related to the presence or absence of major fall storms (Fig. 3). In 1984, 1.8 cm of precipitation in the form of about 20 cm of snow was recorded on 17 October at Mammoth Lakes; no doubt snow at the passes (400–1500 m higher) used by migrating deer was much deeper. This storm was accompanied by a rapid movement of radio-marked deer over the crest and to the winter range within a few days. Earlier storms, which resulted in virtually no snow at the recording station, did not trigger movement. In 1985, shortly after a storm on 7 October, there was another rapid movement of deer over the crest. The remaining deer appeared gradually on the east side of the crest through 13 November, when the last radioed animal, a male, migrated over the crest following a major winter storm. In both 1984 and 1985 I saw dozens to hundreds of deer migrating simultaneously with the telemetered animals, and many tracks and deep trails in the snow were evident. In 1986 there were no major fall storms. Migration was gradual and unpunctuated by any rapid, mass movements (Fig. 3). In all cases deer returned to the winter range (BM or SG) occupied in previous years.

DISCUSSION

In this study the timing of mule deer migration from the winter range did not differ among years. This occurred despite large differences in animal condition and vegetation growth measured on the winter range (Kucera 1988). One explanation may be that these deer had well-defined spring holding areas where they could predictably obtain nutritious forage, available even in years of heavy snowfall such as 1986, when hundreds of deer were on the holding area when counts began (Fig. 2).

Adult males may leave the winter range somewhat later than females, as reported from western Colorado (Wright and Swift 1942). Given the demands of pregnancy, females might be under greater nutritional stress than males, and if better forage conditions exist on spring ranges, females may tend to leave the winter range sooner to take advantage of them. Garrott et al. (1987) reported that spring migration of female mule deer in northwest Colorado varied between years by as much as one month, and they attributed these differences to the severity of winters and consequent energetic demands on deer. Bertram and Rempel (1977) reported that California mule deer (*O. h. californicus*) on the western slope of the Sierra Nevada varied the timing of their spring migration by two weeks, and attributed this to differences in plant phenology both on the winter range and along the migration route. Loft et al. (1989) also reported a similar relationship between initiation of spring migration and amount of snow and stage of plant growth in the western Sierra Nevada.

In my study most telemetered females migrated from the winter range to the north; males showed no significant selection for direction. I contend that this sex difference is a product of local geomorphology and land management patterns. Animals moving north had access to an extensive area of the west slope of the Sierra Nevada on national forest lands at elevations of 2200–2800 m. Animals moving south had access to summer range in King's Canyon National Park at higher and steeper, and thus more barren and less vegetated, elevations (Kucera 1988). The presence of more and better summer range to the north explains why most deer of both sexes would migrate to the north. However, those animals migrating to the north were in areas open to hunting both on their summer ranges and along the migration routes. That telemetered males showed no apparent selection for migration direction, whereas most females migrated to the north, probably resulted from the higher hunting mortality of males summering to the north, and the absence of hunting in the national park. Although as many males as females would be expected to migrate to the north, the higher mortality of adult males moving north could explain the apparent pattern of no directional preference. Because older males are disproportionately reproductively successful (Kucera 1978, Geist 1981, Clutton-Brock et al. 1982), the national park may act as a refuge for a large proportion of the most reproductively successful males.

Deer in this study made extensive use of holding areas in the spring (Fig. 2), which may be beneficial because of higher elevation, greater precipitation, and absence of winter feeding. Vegetation in these holding areas was largely sagebrush scrub (Munz and Keck 1959), a common vegetation type in the eastern Sierra Nevada. These areas are among the last large areas with vegetation suitable for deer present in the spring before the deer cross the Sierra crest. Large aggregations of deer on the holding areas may result from animals simply collecting in these areas for several weeks before ascending over the crest. Bertram and Rempel (1977) and Loft et al. (1989) described a similar pattern of use of spring ranges in the western Sierra Nevada and emphasized the importance of these holding areas in providing herbaceous forage. Further, Bertram and Rempel (1977) reported that spring holding areas typically occurred at the base of an abrupt elevation change, which was true in my study.

Timing of movement off the holding area and over the crest in spring did not differ among years or between sexes, suggesting that animal condition or vegetation did not greatly affect this stage of migration. The passes had snow in all years of study when deer crossed, but snow depths differed greatly. However, by spring snow was consolidated, enabling deer to walk over the surface.

In 1951 Jones (1954) found that BM deer began moving off the winter range about 1 April, and began crossing a nearby pass about 15 May.

Comment Letter I9

This agrees well with the present observations made more than three decades later. In the western Sierra Nevada, Russell (1932), Leopold et al. (1951), Bertram and Rempel (1977), and Loft et al. (1989) described spring migration as an "upward drift" of deer, controlled by the receding snowline and spring plant growth. My study showed a different pattern in the eastern Sierra Nevada. The upward movement of deer was blocked by the abrupt elevation change of the mountains. On the more gently sloping west side, deer can follow spring gradually up slope. On the abrupt east side, the need to cross high-elevation passes prevents such a pattern.

The strong fidelity to specific summer home ranges shown by individual deer in this study is characteristic of mule deer (Ashcraft 1961, Gruell and Papez 1963, Robinette 1966, Bertram and Rempel 1977, Garrott et al. 1987, Loft et al. 1989). With few exceptions, both males and females returned to the same summer home ranges, and winter ranges, for as many as four consecutive years.

The temporal pattern, pulsed or gradual, of the fall migration in the eastern Sierra Nevada is largely determined by weather, particularly snowstorms. In both years with significant snowfall in October, radioed deer moved rapidly and in a pulsed fashion from summer ranges to the winter range (Fig. 3). In a year without significant fall storms, movement was gradual, and males migrated significantly later than females. Previous studies discussed the relationship of snowstorms to fall migration (Russell 1932, Dixon 1934, Leopold et al. 1951, Richens 1967, Gilbert et al. 1970), although some cases were based on anecdotal evidence. Bertram and Rempel (1977) stated that deer on the west slope of the Sierra Nevada moved in anticipation of fall storms, but I found no evidence of this. Garrott et al. (1987) speculated that in northwest Colorado deer moved not because of snow, but to maximize the quality of their diets prior to winter. Differences in details of deer migration apparent between my study and studies in the western Sierra Nevada and in northwest Colorado indicate that deer migration can be influenced by local conditions.

Females may be constrained in their timing of fall migration by the nutritional and energetic demands of lactation and smaller body size, by the inability of fawns to cope with severe fall conditions, or both. Males do not have the same energetic, nutritional, or parental constraints. Additionally, as consequence of hunting regulations, those males that do migrate early are likely to be killed.

ACKNOWLEDGMENTS

Financial support was provided by Inyo and Mono counties, the Sacramento Safari Club, National Rifle Association, Mzuri Wildlife Foundation, Boone and Crockett Club, and Theodore Roosevelt Memorial Fund of the American Museum of Natural History. I thank the California Department of Fish and Game and U.S. Bureau of Land Management for their personnel, logistic, and administrative support. T. Blankinship, V. Koontz, D. R. McCullough, T. Russi, T. Taylor, R. D. Thomas, and others were instrumental in various parts of this work. I thank V. C. Bleich, R. T. Bowyer, and D. R. McCullough, and particularly an anonymous reviewer for their thoughtful reviews of the manuscript.

LITERATURE CITED

ANDERSON, A. E. 1981. Morphological and physical characteristics. Pages 27–97 *in* O. C. Wallmo, ed., Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

ASHCRAFT, G. C., Jr. 1961. Deer movements of the McCloud flats herd. California Fish and Game 47: 145–152.

BAKER, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier Publishers, New York.

BERTRAM, R. C., and R. D. REMPEL. 1977. Migration of the North Kings deer herd. California Fish and Game 63: 157–179.

CLOVER, M. R. 1956. Single-gate deer trap. California Fish and Game 42: 199–201.

CLUTTON-BROCK, T. H., F. E. GUINNESS, and S. D. ALBON. 1982. Red deer: ecology and behavior of two sexes. University of Chicago Press, Chicago.

DIXON, J. S. 1934. A study of the life history and food habits of mule deer in California. California Fish and Game 20: 181–282.

FRYXELL, J. M., and A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3: 237–241.

GARROTT, R. A., G. C. WHITE, R. M. BARTMANN, L. H. CARPENTER, and A. W. ALLDREDGE. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51: 634–643.

GEIST, V. 1981. Behavior: adaptive strategies in mule deer. Pages 157–223 *in* O. C. Wallmo, ed., Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln.

GILBERT, P. F., O. C. WALLMO, and R. B. GILL. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. Journal of Wildlife Management 34: 15–33.

Comment Letter I9

GRUELL, G. E., and N. J. PAPEZ. 1963. Movements of mule deer in northeastern Nevada. Journal of Wildlife Management 27: 414–422.

JESSUP, D. A., K. JONES, R. MOHR, and T. KUCERA. 1985. Yohimbine antagonism to xylazine in free-ranging mule deer and bighorn sheep. Journal of the American Veterinary Medical Association 187: 1251–1253.

JONES, F. L. 1954. The Inyo-Sierra deer herds. California Department of Fish and Game, Federal Aid Project W-41-R.

KUCERA, T. E. 1978. Social behavior and breeding system of the desert mule deer. Journal of Mammalogy 59: 463–476.

______. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Unpublished doctoral dissertation, University of California, Berkeley. 207 pp.

LEOPOLD, A. S., T. RINEY, R. MCCAIN, and L. TEVIS, JR. 1951. The Jawbone deer herd. California Department of Fish and Game, Game Bulletin Number 4.

LOFT, E. R., R. C. BERTRAM, and D. L. BOWMAN. 1989. Migration patterns of mule deer in the central Sierra Nevada. California Fish and Game 75: 11–19.

MCCULLOUGH, D. R. 1964. Relationship of weather to migratory movements of black-tailed deer. Ecology 45: 249–256.

______. 1985. Long range movements of large terrestrial mammals. Contributions in Marine Science 27: 444–465.

MUNZ, P. A., and D. D. KECK. 1959. A California flora. University of California Press, Berkeley.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1987. Local climatological data, annual summary with comparative data, Bishop, California. National Climatic Data Center, Asheville, North Carolina.

RICHENS, V. B. 1967. Characteristics of mule deer herds and their range in northeastern Utah. Journal of Wildlife Management 31: 551–666.

ROBINETTE, W. L. 1966. Mule deer home range and dispersal in Utah. Journal of Wildlife Management 30: 335–349.

RUSSELL, C. P. 1932. Seasonal migration of mule deer. Ecological Monographs 2: 1–46.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. International student edition. McGraw-Hill Kogakusha, Ltd., Tokyo, Japan.

SINCLAIR, A. R. E. 1983. The function of distance movements in vertebrates. Pages 240–258 *in* I. R. Swingland and P. J. Greenwood, eds., The ecology of animal movement. Clarendon Press, Oxford, England.

STORER, T. I., and R. L. USINGER. 1968. Sierra Nevada natural history. University of California Press, Berkeley.

U.S. DEPARTMENT OF THE INTERIOR. 1990. Bishop resource management plan and environmental impact statement. Bureau of Land Management, Bakersfield District, Bakersfield, California.

VAUGHN, D. E. 1983. Draft soil inventory of the Benton-Owens Valley area. U.S. Department of the Interior, Bureau of Land Management, Bakersfield District, Bakersfield, California.

WRIGHT, E., and L. W. SWIFT. 1942. Migration census of mule deer in the White River region of northwestern Colorado. Journal of Wildlife Management 6: 162–164.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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MIGRATION PATTERNS OF MULE DEER IN THE CENTRAL SIERRA NEVADA [1]

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Migration routes, holding areas, and winter ranges were identified for California and Rocky Mountain mule deer, *Odocoileus hemionus californicus* and, *O. h. hemionus*, respectively, inhabiting summer range in McCormick Creek Basin in the central Sierra Nevada, California. Radio-collared does migrated 27–51 km to winter ranges administered as 4 different herd units. Does migrating to the same winter range area also had high overlap in summer home ranges. In 1983, many does dropped their fawns on spring holding areas because the heavy snowpack precluded occupancy of summer ranges until July. Holding areas were used for a longer period of time during spring than during fall migrations. In the fall, deer generally traveled directly to the winter range upon leaving the summer range, but delayed upslope of specific winter home ranges during periods of mild weather. Habitat improvements to enhance forage and cover on spring and fall transitional ranges would be especially beneficial to deer following severe winters when deep snow prevents normal occupancy of summer range. Such habitat improvement projects would also reduce deer impacts on important winter range resources during the fall by offering desirable seral habitat. Large areas of contiguous habitat, in this case a state game refuge, provide winter range to deer with little disturbance from humans. Rocky Mountain mule deer wintering east of the Sierra Crest in Great Basin communities used valley bottoms and south facing mountain slopes as holding areas and winter ranges.

INTRODUCTION

Determining seasonal ranges used by deer is an important component of deer herd management. Knowledge gained from biotelemetry studies can aid resource managers by identifying areas which have the greatest potential return in deer herd productivity through habitat maintenance and improvement projects. Winter ranges, migration routes, holding areas and summer ranges can all be identified by monitoring radio-collared deer (Schneegas and Franklin 1972, Bertram and Rempel 1977, Loft, Menke and Burton 1984).

From 1982 to 1985, California mule deer, *Odocoileus hemionus californicus*, and Rocky Mountain mule deer, *O. h. hemionus*, inhabiting summer ranges in the McCormick Creek Basin (hereafter referred to as the Basin) of the Stanislaus National Forest were monitored to determine timing of migrations and routes taken between summer and winter ranges. Rocky Mountain mule deer winter on the east slope of the Sierra Nevada while California mule deer winter on the west slope. The objectives of this study were to identify migration routes, holding areas, and winter ranges of deer summering in the Basin. This

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State of California
Department of Fish and Game

Memorandum

Date: January 24, 2011

To: Tom Stephenson
Senior Environmental Scientist Supervisor
Inland Deserts Region

From: Jane McKeever
Associate Wildlife Biologist
Inland Deserts Region

Subject: Deer Survey Summary, Post-season – 2010

Post-season 2010 deer surveys in Region 6 encompassed Deer Zones X12, X9a (Round Valley and Casa Diablo), X9b, and D19. All surveys were conducted using a helicopter, except the Casa Diablo survey was a ground survey, and in Round Valley in addition to the helicopter survey there was also a ground survey. The X12 survey was conducted by Nevada Dept. of Wildlife; no Department of Fish and Game personnel participated on the survey. Results of all surveys are summarized in the three tables below. For comparison, separate composition ratios were calculated from the data collected by ground survey and helicopter survey in Round Valley. Confidence intervals (CI), at the 90% level, are in parentheses. Coefficient of variation (CV) for the ratio is in percentage. CI and CV calculated following methods of Hagen et al. 2008 and White et al. 1996, respectively.

Table 1. Deer Survey Summary. Ratios are per 100 does.

Deer Herd or Zone	Total Bucks	Total Does	Total Fawns	Total Uncl*	Total Deer	Buck:Doe Ratio Ratio (90% CI)	Buck:Doe Ratio % CV	Fawn:Doe Ratio Ratio (90% CI)	Fawn:Doe Ratio % CV
Zone X12 Total	282	1102	463	0	1847	26 (23, 29)	7	42 (38, 46)	6
Sherwin Grade	47	335	92	0	474	14 (11, 18)	16	28 (23, 33)	12
Buttermilk	87	405	100	0	592	22 (18, 26)	12	25 (21, 30)	11
Round Valley Total	134	740	192	0	1066	18 (16, 21)	9	26 (23, 30)	8
Casa Diablo	52	273	77	0	402	19 (15, 24)	15	28 (23, 35)	13
Zone X9a Total	186	1013	269	0	1468	18 (16, 21)	8	27 (24, 30)	7
Goodale, north	127	308	98	0	533	41 (35, 49)	11	32 (26, 38)	12
Goodale, south	88	180	49	0	317	49 (40, 60)	13	27 (21, 35)	16
Zone X9b Total	215	488	147	0	850	44 (39, 50)	8	30 (26, 35)	9
Zone D19 Total	33	76	40	27	176	43 (31, 61)	21	53 (38, 72)	20

Table 2. Results of Round Valley ground survey, combined with Casa Diablo ground survey for a Deer Zone X9a total.

Deer Herd or Zone	Total Bucks	Total Does	Total Fawns	Total Uncl*	Total Deer	Buck:Doe Ratio		Fawn:Doe Ratio	
						Ratio (90% CI)	Ratio % CV	Ratio (90% CI)	Ratio % CV
Sherwin Grade	19	118	33	0	170	16 (11, 24)	25	28 (20, 39)	20
Buttermilk	51	185	59	0	295	28 (21, 36)	16	32 (25, 41)	15
Round Valley Total	70	303	92	0	465	23 (19, 29)	13	30 (25, 37)	12
Casa Diablo	52	273	77	0	402	19 (15, 24)	15	28 (23, 35)	13
Zone X9a Total	122	576	169	0	867	21 (18, 25)	10	29 (25, 34)	9

Table 3. Survey Dates and Effort

Deer Herd or Zone	Survey Date	Total Deer Observed	Total Survey Hours	Deer Per Hour
Zone D19	10-11 December 2009	176	7	25
Round Valley (ground)	5 January 2011	465	5 observers x 1 day x 8 hrs = 40	12
Goodale	7 January 2011	850	5.3	160
Round Valley (helicopter)	8 January 2011	1066	1.2	888
Zone X12	13 Jan 2011 (approx)	1847	Not available	Not available
Casa Diablo (ground)	13 -14 January 2011	402	2 observers x 2 days x 8 hrs = 32	13

All pre-survey and post-survey databases and GIS-based files have been sent to Sacramento's Deer Program. If you have any questions or need additional information, please contact me at (760)751-1834.

Literature Cited

Hagen, C. A., and T. M. Loughin. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample size. J. Wildl. Manage. 72:1369-1375.

White, G. C, A. F. Reeve, F.G. Lindzey, and K.P. Burnham. 1996. Estimation of mule deer winter mortality from age ratios. J. Wildl. Manage. 60(1):37-44.

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Mr. T. Taylor
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Department of Fish and Game (WPB)
Mr. R. Mohr
Mr. D. Casady
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State of California
Department of Fish and Game

Memorandum

Date: April 14, 2011

To: Tom Stephenson
Senior Environmental Scientist Supervisor
Inland Deserts Region

From: Jane McKeever
Associate Wildlife Biologist
Inland Deserts Region

Subject: Deer Survey Summary, Spring 2011

Spring 2011 deer surveys encompassed Deer Zones X12, X9a, and X9b. Results of surveys are summarized in tables 1 and 2 below. Spring surveys were conducted by helicopter or ground and that is detailed in Table 1 also. Confidence intervals (CI), at the 90% level, are in parentheses. Coefficient of variation (CV) for the ratio is in percentage in brackets. CI and CV calculated following methods of Hagen et al. 2008 and White et al. 1996, respectively.

Table 1. Deer Survey Summary, Spring 2011. Fawn Ratio is fawns per 100 does, unless otherwise stated*.

Deer Herd	Survey Method	Adult Total	Fawn Total	Un-Class Total	Deer Total	Ratio Summary	
						Spring 2011 Fawn Ratio (CI) and [%CV]	Post-Season 2010 Fawn Ratio
West Walker	Helicopter	320	143	0	463	**45F:100A (38, 53) [10%]**	n/a
East Walker	Helicopter	162	74	7	243	**46F:100A (36, 57) [14%]**	n/a
Mono Lake	Helicopter	74	44	0	118	**59F:100A (44, 81) [19%]**	n/a
X12 Zone Total	Helicopter	556	261	7	824	**59 (52, 67) [8%]**	42 (38, 46)
Sherwin Grade	Ground	288	29	0	317	**11 (8, 16) [20%]**	28 (23, 33)
Buttermilk	Ground	471	71	0	542	**18 (15, 23) [13%]**	25 (21, 30)
Round Valley Total	Ground	759	100	0	859	**16 (13, 19) [11%]**	26 (23, 30)
Casa Diablo	Helicopter	617	192	0	809	**37 (32, 43) [8%]**	28 (23, 35)
X9a Zone Total	Helic/grnd	1376	292	0	1668	**25 (23, 28) [7%]**	27 (24, 30)
Northern Subherd	Ground	362	49	0	411	**19 (15, 25) [16%]**	32 (26, 38)
Southern Subherd	Ground	208	31	0	239	**22 (16, 31) [20%]**	27 (21, 35)
X9b Zone Total	Ground	570	80	0	650	**20 (17, 25) [12%]**	30 (26, 35)

* F = fawns and A = adults

Table 2. Survey Dates and Effort, Spring 2011

Deer Zone	Survey Date	Total Deer Observed	Total Survey Hours	Deer Per Hour*
Zone X12	25, 27 March 2011	824	7.2	114
Round Valley	17 March 2011	859	3 observers x 7 hrs = 21	41
Casa Diablo	28 March 2011	809	4.1	197
Zone X9b, Goodale	11 March – 7 April 2011	650	1 observer x 39 hrs = 39	17

*Rounded to whole number.

Helicopter surveys in Deer Zone X12 were conducted during windy weather, following a significant winter storm, and observers noticed deer bedded under cover and not willing to move. Therefore, it is presumed that many deer were missed during these two days of surveys.

Weather during the Casa Diablo March 28 helicopter survey was breezy but more favorable survey conditions. Notable is the fact that the survey resulted in the most deer ever recorded for a Casa Diablo spring deer survey. In addition, the only survey where more deer were observed was in fall 1988 when 940 deer were observed during a ground survey.

Goodale ground surveys were difficult this season due to a significant amount of deep snow cover, which resulted in access issues and the inability to get close enough to deer groups until early April in the southern portion of the zone.

All survey data and available files have been forwarded to the Deer Program of the Wildlife Branch. If you have any questions or need additional information, please contact me at (760)751-1834.

Literature Cited

Hagen, C. A., and T. M. Loughin. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample size. J. Wildl. Manage. 72:1369-1375.

White, G. C, A. F. Reeve, F.G. Lindzey, and K.P. Burnham. 1996. Estimation of mule deer winter mortality from age ratios. J. Wildl. Manage. 60(1):37-44.

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HABITAT SELECTION AND SURVIVAL OF MULE DEER: TRADEOFFS ASSOCIATED WITH MIGRATION

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We examined tradeoffs related to migration in a population of mule deer (*Odocoileus hemionus*) in southern California from 1989 to 1991. All male deer that we radiocollared were migratory, whereas females exhibited a mixed strategy with both migrant and resident individuals. Increased movements of deer were associated with decreased temperatures and increased weekly precipitation. No differences within seasons in the sizes of home ranges occurred for either migrant or resident deer. The size of home ranges of deer, however, was smaller in summer than in winter. Sizes of home ranges were associated positively with proximity to human development and to the amount of avoided (use was less than availability) habitat in the home range. Deer avoided human developments in all seasons. Further, males and resident females used areas farther from water in summer than expected by chance, whereas migratory females selected areas nearer to water. In summer, migratory females selected meadows, riparian habitats, and pine forests, whereas resident females avoided riparian habitats and used pine forests less than did migratory females. Migratory males used habitats in a way similar to migratory females, although they avoided meadows and riparian areas. Clear tradeoffs existed for deer in montane southern California about whether they migrated. Migratory females were farther from human disturbance and used habitats of high quality more often than did nonmigratory conspecifics. Nonetheless, deer were at increased risk of predation during migration and, in years of low precipitation (low snow), had higher rates of mortality than did resident deer. Thus, in areas with extremely variable precipitation and snow cover, a mixed strategy for migration can be maintained in populations of mule deer.

Key words: *Odocoileus hemionus*, mule deer, migration, habitat selection, home range, tradeoffs, survival, southern California

Patterns of migration have evolved to take advantage of spatial and temporal variation in the environment (French et al., 1989). Selection should favor those individuals that migrate, if by migrating, their reproductive success is enhanced (Baker, 1978). Because of environmental fluctuation and individual differences in costs of migration, several strategies related to migration can occur in the same species or in the same population (Fretwell, 1972). Indeed, mule deer (*Odocoileus hemionus*) are extremely variable throughout their distribution in whether they migrate. Many investigators have observed resident populations of deer (Bowyer, 1986; Eberhardt et al., 1984), migrant populations (Garrott et al., 1987; Gilbert et al., 1970; Zalunardo, 1965), or populations with both resident and migrant individuals (Brown, 1992; Kufeld et al., 1989; Loft et al., 1984; Pac et al., 1988).

The question of why some individuals in

a population migrate and others do not was examined by several authors. Theoretical models concerning whether individuals migrate have been built around optimization theory (Cohen, 1967) and the concept of evolutionarily stable strategies (Parker and Stuart, 1976); the currency of most models is reproductive success. Lifetime reproductive success is a function of both survivorship and birth rate (Caughley, 1977), and the adaptive significance of migration can best be understood by examining the selective forces acting on these life-history parameters (Dingle, 1980). Quality and availability of forage affect survivorship and birth rate, as does risk of predation; authors have implicated each as an ultimate factor affecting migration (Fryxell and Sinclair, 1988; Taylor and Taylor, 1977).

Although one defining characteristic of migration is a shift in use of habitat (Baker, 1978), this assessment is complicated by various sexes and ages of deer potentially selecting habitats differentially. Bowyer (1986) and Loft et al. (1987) noted that young had substantially different requirements of habitat, especially for concealment cover, than did adult deer. Moreover, Bowyer (1984), Scarbrough and Krausman (1988), and Bowyer et al. (1996) reported sexual differences in use of forages, habitats, or space by deer. Further, McCullough (1979) postulated that differential use of resources by sex accounted for the weak relationship observed between rate of recruitment of white-tailed deer (*O. virginianus*) and the number of male deer on the George Reserve, Michigan, whereas this inverse relationship was strong for adult females and recruited young.

Essential for understanding patterns of migration is the concept of home range. Although home range is one of the most commonly measured variables in animal ecology, most studies have concentrated on the measurement of size of home range rather than its biological basis (Bowers et al., 1990; Hundertmark, in press). Sizes of home ranges within local populations of mule deer are extremely variable; home ranges of 33 ha (Loft et al., 1984) and 9,300 ha (Eberhardt et al., 1984) were noted. Although composition of habitat (Riley and Dood, 1984), availability of water (Eberhardt et al., 1984), and interspecific competition (Loft et al., 1993) have been implicated, few studies have examined quantitatively the factors that affect size of home ranges in mule deer or other ungulates.

Descriptions of movements for many populations exist, but few authors have examined the tradeoffs involved in the migratory strategies of mule deer or other large herbivores. Populations of deer in the San Bernardino Mountains of southern California exhibit a mixed pattern of migration with both migrant and resident components (T. Paulek, in litt.). This afforded a unique opportunity to assess quantitatively the costs and benefits of migration.

We evaluated the causes and consequences of migration by a population of mule deer by quantifying the timing and extent of movements, examining the proximate factors associated with migration, quantifying the seasonal use of habitat by various classes of deer, and determining how migration was related to patterns of selection of habitat. We tested whether migratory mule deer benefited from decreased intraseasonal movements, increased use of habitats of high quality, and decreased predation compared with nonmigratory conspecifics.

Materials and Methods

Study area.—Our study was conducted in the San Bernardino Mountains, which compose part of the Transverse Ranges of coastal California. These mountains are oriented on an east-west axis and extend ca. 95 km from Cajon Pass on the west to Yucca Valley, in the Mojave Desert, on the east. The mountain range is bounded by the Mojave Desert on the north and by Banning Pass 40 km to the south. Most deer that we studied lived in the upper drainage of the Santa Ana River, a 32,000-ha area in the southwestern portion of that mountain range (centered at 34°10′34″N, 116°53′57″W; Fig. 1). This watershed was bounded on the north by Moon Ridge

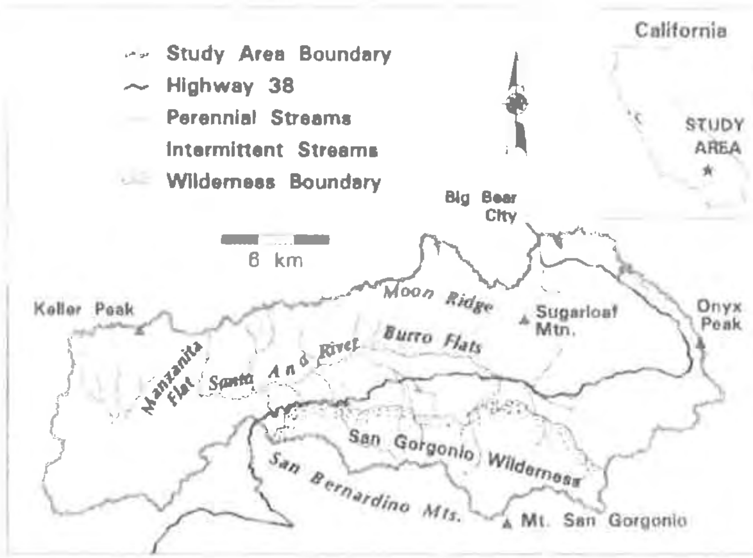

FIG. 1.—The study area in San Bernardino Co., California, depicting significant features of the landscape. Mule deer (*Odocoileus hemionus*) were captured and fitted with radiocollars on Manzanita Flat and Burro Flats.

and Big Bear City, and on the east and south by the crest of the San Bernardino Mountains. Tributaries of the Santa Ana River included Mill, Bear, Cienega, and Wildhorse creeks, and many other smaller streams. The River leaves the range of mountains near Redlands and flows westward across the coastal plain toward Los Angeles.

Slopes associated with the drainage of the Santa Ana River generally were steep and topographically diverse, which limited access of humans to some areas. Elevations ranged from 610 to 3,500 m at the summit of Mount San Gorgonio. Highway 38 paralleled the Santa Ana River for part of its length. Numerous dirt and paved roads also occurred in the study area, as did recreational campgrounds and ca. 200 special-use cabins managed by the United States Forest Service. Vehicular access to north-facing slopes south of Highway 38 was limited because this area was wilderness and lacked roads. Most of the lands within the watershed were administered by the San Bernardino National Forest, although some private holdings occurred along the lower Santa Ana River and in the community of Angelus Oaks.

The climate within the drainage of the Santa Ana River was typical of cismontane southern California. Annual temperatures range from >40°C at low elevations during summer to <−20°C on the highest peaks in winter. Rainfall occurred primarily during the cooler winter months. During late summer, thundershowers were common at higher elevations and temperatures were cooler. Above 1,500 m, winter precipitation occurred primarily as snow, however, on south-facing slopes, cover by snow was transitory. Annual precipitation was extremely variable but averaged >500 mm annually. During this investigation, 1989 and 1990 were dry years with 392 mm and 469 mm of precipitation, respectively, whereas, precipitation was average in 1991 (736 mm).

The study area encompassed a variety of types of vegetation typical of cismontane southern California (K. E. Mayer and W. F. Laudenslayer, in litt.). Foothills at lower elevations supported a coastal-scrub habitat composed primarily of *Eriogonum fasciculatum*, *Artemesia californica*, and *Salvia*. Above the coastal scrub was mixed-chaparral habitat typified by broad-leaved shrubs primarily of the genera *Arctostaphylos*, *Rhamnus*, *Ceanothus*, *Cercocarpus*, and *Quercus*. Pure stands of chamise chaparral dominated by *Adenostoma fasciculatum* also were present and integrated with mixed chaparral at moderate elevations (700–1,500 m). Stands of sagebrush (*Arte-*

mesia tridentata) existed at elevations >1,500 m. Nomenclature for plants was taken from Munz (1974).

Limited areas of montane riparian habitat and meadows occurred within the mesic areas of the drainage. Genera of plants typical of riparian habitat included *Salix*, *Populus*, *Quercus*, *Platanus*, *Rhus*, *Sambucus*, and *Alnus*. *Juncus* and *Carex* were abundant in meadows. Montane-hardwood habitat typically occurred on mountainous slopes and in valleys ≥1,500 m. Both deciduous and evergreen oaks (*Quercus*) dominated the overstory, whereas *Arctostaphylos*, *Ceanothus*, and *Cercocarpus* were abundant in the shrub layer. Various habitats of conifers also occurred in the area and were dominated by Jeffrey-ponderosa pine (*Pinus jeffreyi-P. ponderosa*), mixed pine, pinyon pine (*P. monophyla*), and juniper (*Juniperus occidentalis*).

Annual and perennial grasslands occurred throughout the drainage on south-facing slopes. These grasslands were dominated by *Agropyron*, *Bromus*, and *Sisymbrium*, and resulted from past fire and mechanical disturbance of habitat. Bare ground or talus slopes often occurred in areas with highly erosive soils and were commonly a result of past fires. Evidence of historical fires occurred throughout the study area. Most of the Santa Ana drainage east of the confluence of Bear Creek and the Santa Ana River (e.g., Manzanita Flat) burned in 1970 and again in 1980. Several small (<0.5 km^2), controlled burns were conducted east of Bear Creek since 1980. Excluding these controlled burns and small (<1 ha) wildfires, the remainder of the drainage has not burned in this century.

The study area was inhabited by several large, mammalian carnivores including bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*). Bowyer (1987) demonstrated that coyotes in southern California may be effective predators on adult deer, and these predators probably affected selection of habitat by deer (Bowyer, 1986; Hirth, 1977).

Several other species of ungulates occurred within the study area and these included bighorn sheep (*Ovis canadensis*), domestic cattle (*Bos taurus*), and feral asses (*Equus asinus*). The range of bighorn sheep (>100 animals) was centered on the crest of Mount San Gorgonio, although individuals were observed along the eastern end of the drainage of the Santa Ana River and north of Big Bear Lake. An allotment for livestock encompassed most south-facing slopes in the study area. Although cattle only were present in the area during summer and autumn of the 1st year of our study, the detrimental effects of past grazing by cattle were evident throughout the area. At least 80 feral asses occurred in the Big Bear watershed north of Moon Ridge. Although no apparent barriers prevented movements by feral asses, none of these equids was observed in the drainage of the Santa Ana River during this study. Quantitative estimates of size of populations for deer in the San Bernardino Mountains are lacking, but the herd was believed to be near its carrying capacity.

Sampling procedures and analyses.—In January 1989 and January 1990, we used a helicopter and drive nets (Beasom et al., 1980) to capture deer. At least eight people were stationed at three sites of capture where 30.5 by 2.4-m tangle nets were erected. We used a helicopter to drive deer into the nets. Personnel restrained deer with leather hobbles and blindfolds to prevent injury. Teams were trained to handle deer quickly and efficiently, and animals usually were restrained <10 min. We selected deer to fit with telemetric collars, which were equipped with sensors for mortality (6-h delay, Model 500, Telonics, Mesa, AZ). A total of 43 deer was captured (34 animals in 1989 and 9 in 1990) and 29 of these deer were fitted with radiocollars (22 adult females and seven adult males). Three deer with collars remained outside the study area for the duration of the study and were not considered in analyses.

All aspects of animal handling complied with methods adopted by the American Society of Mammalogists (Committee on Acceptable Field Methods, 1987) and were approved by an Animal Care and Use Committee at the University of Alaska Fairbanks. No deaths of deer occurred during capture, but one death may have resulted from factors relating to capture.

Using equipment and techniques described by Krausman et al. (1984) and a fixed-winged aircraft, we located deer with transmitters about every 10 days from 1 January 1989 to 27 November 1991. The flights for locating telemetered animals were between 0700 and 1800 h, Pacific Standard Time. When we determined the location of a deer, its geographic position was estimated using a LORAN-C navigation system. Deer with telemetric collars were relocated 1,521 times, of which 523 relocations were on winter range, 929 on summer range, and 69 between summer and winter ranges.

Because of inherent errors in data for locations of deer, we estimated the circular error associated with aerial telemetry and LORAN-C positioning. First, locations for LORAN-C were corrected for directional bias using the techniques of Patric et al. (1988). Second, we estimated the circular error by calculating the 90% confidence limits for the average distance of our estimates from actual locations of radiocollars placed at five specific locations. The circular error for aerial telemetry based upon 40 relocations was 177 m. Finally, we considered all habitat that occurred within a 177-m circle as an estimate of habitat used by a particular deer at that location.

A map of habitat was developed for the area from a LANDSAT-TM scene with cells of 25-m resolution. Using Terra Mar (Terra Mar. Inc., Garden Grove, CA) software, the drainage was classified into nine spectral classes that represented types of habitat. We verified the image using 1:9,200 color, aerial photographs and ground truthing. The final image was transferred to ARC/INFO (Environmental Systems Research Institute, Redlands, CA), the Geographic Information System (GIS) used in this study.

We generated a three-dimensional surface of terrain of the study area from 30-m resolution, 7.5′ digital models of elevation (United States Geological Survey) using the GRID module of ARC/INFO. This surface provided information on elevation, slope, and aspect, and was used to derive an index of diversity of terrain. Although many methods exist to assess diversity of terrain (e.g., Beasom et al., 1983; Bleich et al., 1997; Nellemann, 1991), these often are labor intensive or may not allow for adequate evaluation of the components of diversity of the terrain (i.e., variation in both slope and aspect). Therefore, we estimated the diversity of terrain for each location evaluated by calculating *SD* in slope and the mean angular deviation of aspect (Zar, 1984) in a circle of 177-m radius. Finally, an index to diversity of terrain was calculated as the product of these two deviations.

In addition to the map of habitat, model of terrain, and derived information, available geographic data on soils, history of fire, location of water, and human developments were digitized from 7.5′ quadrangle maps of the study area. Spatial information on human developments included the location of dirt and paved roads, special-use cabins, and campgrounds.

For each radiocollared animal, we entered into GIS a dataset of locations that was not significantly autocorrelated ($P \leq 0.05$). Autocorrelation was revealed by the multiresponse-sequence procedure (MRSP) of BLOSSOM statistical software (Slauson et al., 1991; Solow, 1989). If data within a season were significantly autocorrelated, locations were deleted from a dataset by a bootstrap procedure until sufficient autocorrelation was eliminated ($P > 0.05$). A total of 49 data points (3.2% of the dataset) was removed from analyses for selection of habitat, home range, and other analyses.

Degree of autocorrelation also was used as a means of identifying seasonal shifts in range by deer. Because serial autocorrelation is evaluated with MRSP by testing the null hypothesis of no difference between distance traveled between sequential locations and nonsequential ones, significant autocorrelation can occur if an animal moves either less or more between sequential locations than between nonsequential locations. Datasets for each animal were divided initially into seasons based on annual changes in temperature and precipitation; summer was defined as 15 April to 15 November, whereas the remainder of the year was considered winter. If large movements at the beginning or end of a season caused significant autocorrelation, those data points were removed and placed in the appropriate dataset. Locations that fell sequentially between seasonal sets of data were considered transitional points (i.e., migratory movements) between summer and winter ranges.

We generated circles with a radius of 177 m for each of 1,382 locations to estimate use of habitat by deer. The GIS included 30-m cells of habitat only if the center of the cell was inside the circle. Thus, a boundary of ±15 m existed around each circle where precise measurement of availability of habitat was not possible. Further, we used GIS to estimate distance from each telemetric location to location of water and human developments (i.e., Highway 38, dirt roads, cabins, and campgrounds). The distances to developments were used as indices to potential disturbance of deer by humans. Data on GIS were projected into similar geographic units for analyses, Universal Transverse Mercator meters (UTM—Snyder, 1984).

Statistical analyses.—Datasets that were not distributed normally were tested with appropriate nonparametric rank statistics. We used PC SAS (SAS Institute, Inc., 1988), BLOSSOM (Slauson et al., 1991), and CALHOME (Kie et. al., 1994) in our analyses.

We considered deer migratory if they exhibited directional movements and their seasonal home ranges did not overlap (McCullough, 1964; Schoen and Kirchhoff, 1985). For migratory deer, we determined mean dates of departure from summer and winter ranges by subdividing migration into intervals of 1 week and calculating a weighted mean and pooled variance for the date that deer were first observed outside their seasonal ranges. This method is an adaptation of a technique to estimate mean date of birth (Caughley, 1977).

The mean easting and northing, based on the UTM-coordinates of the locations for a deer in each season, were used as a measure of the center of activity (Hayne, 1949). Minimum distances to water (e.g., perennial streams, intermittent streams, or springs) and human developments from these centers of activity were determined using GIS, and entered into analyses of size of home ranges. Additionally, straight-line distance between seasonal centers of activity was an index to the distance traveled during migrations, although we recognized that straight-line distances underestimated the total distances moved by these animals (Bowyer, 1981). Fidelity to seasonal ranges for individual deer was tested by the multiresponse, randomized-block procedure of BLOSSOM (MRBP—Mielke, 1991; Slauson et al., 1991). We tested the null hypothesis that the distribution of locations for an individual in a particular season did not differ between years.

We calculated home ranges by season for non-autocorrelated datasets using a beta version of the program CALHOME (Kie et al., 1994). We reported the 95% minimum-convex polygons (MCP—Mohr, 1947) for comparison with other studies; a 95% polygon for home ranges also was estimated using the method for calculating the adaptive kernel (Worton, 1989). The beta version of CALHOME first estimated the parameter for optimum smoothing for the adaptive kernel (Kie et al., 1994; Worton, 1989). The program then calculated the results using 80, 100, and 120% of that optimum. CALHOME then reported the home ranges based on the adaptive kernel using the smoothing parameter that minimized the cross-validation scores from least squares (Worton, 1989).

To determine adequate sample size for estimating home ranges, we evaluated how size of home ranges varied with increasing sample sizes. Five individuals with the greatest number of locations and no significant shifts in home ranges between years were used in this analysis. We selected subsets of the locations for an individual that were combined by season for all years, and created incrementally larger subsamples until the maximum number of locations for an individual was attained. The maximum number of locations ranged from 23 to 27 for winter and from 47 to 53 for summer. We sampled each individual in this manner for five replicates of each sample size. The 95% home range based on the adaptive kernel was estimated for each subsample of each individual. We estimated the sample size necessary to compute home ranges using the nonlinear regression proceedure of SAS (PROC NONLIN): home-range size $= A(1 - e^{-bn})$, where A is the asymptote of the equation, e is the base of the natural log, n is sample size, and b is a constant. Based on these equations, we determined that estimated size of home range reached 90% of the asymptotic value for each individual at sample sizes of ca. 25 and 15 locations for summer and winter, respectively. To meet these criteria, we combined seasonal locations for individuals between all years where significant ($P \leq 0.05$) shifts in home range did not occur. Fifteen individuals lacked adequate sample size for estimation of size of seasonal home ranges and were eliminated from analyses. Mean ($\pm SD$) number of locations for estimating home ranges of the remaining deer was 40 ± 10.7 and 20 ± 4.6 for summer and winter, respectively.

We used Spearman-rank correlation (r_s) to examine relationships between movements of deer and climatic variables (Zar, 1984). A ranked analysis of variance (ANOVA—Conover and Iman, 1981; PROC GLM—SAS Institute, Inc., 1988) tested for differences in size of home ranges for various categories of sex and movement (i.e., migratory-nonmigratory) of telemetered deer. We used a Bonferroni correction for multiple comparisons (Rice, 1989). We used a Wilcoxon two-sample test to evaluate distances moved by deer within seasons. Additionally, we used stepwise regression analysis (α to enter =

0.15, α to remove = 0.20) to evaluate variables associated with size of home ranges (Zar, 1984); size of home range was $\log_{10}$ transformed for this analysis. Composition of home ranges for regression analysis was estimated from all habitats contained within a 177-m buffer of the 95% estimate for home ranges of deer.

The percentage of each of nine types of habitat contained within a circle with a radius of 177 m was used in analyses of habitat selection; these analyses relied primarily on one-way multivariate analysis of variance (MANOVA—Johnson and Wichern, 1988) to compare use of habitat by deer with habitat at random locations. This approach had the advantage of simultaneously comparing all components of habitat considered in analyses (Aebischer et al., 1993). Finally, selection of habitat (use was greater than availability) was estimated by subtracting percentage availability of a habitat from percentage of use of that habitat. We used this measure because it is intuitively simple; a positive value implies selection, whereas a negative one indicates avoidance (use was less than availability). We defined available habitat as all habitats occurring within the study area. Because the amount of available habitat at the level of the landscape did not differ between groups of animals or seasons, changes in use of habitat represent changes in selection of habitat for intergroup and interseason comparisons. Because we were interested in selection of habitat at the level of the population, we combined locations of deer for this analysis. We assumed that these noncorrelated samples of individuals on different days under differing environmental conditions represented independent samples (Hjeljord et al., 1990; Molvar and Bowyer, 1994). This procedure is conservative because it increases the variability of our dataset; however, it also increases sample sizes.

Survival of deer was estimated using the Kaplan-Meier, staggered-entry model (Pollock et al., 1989). Differences in survivorship were tested with a log-rank test (Pollock et al., 1989). We report means (± 1 *SD*) throughout our Results.

RESULTS

Movements and distribution.—All deer (one male, seven females) captured below 1,500 m in elevation at Manzanita Flat were migratory. These deer moved seasonally from mixed chaparral and chamise habitats at low elevation in the western end of the study area to mixed pine at high elevation in the San Gorgonio Wilderness and adjoining areas (Fig. 2). Distance traveled between winter and summer ranges was 12.6 ± 5.3 km and ranged from 8.6 to 19.8 km. Seventeen deer (5 males, 12 females) were captured on south-facing slopes above 1,500 m in elevation at Burro Flats in habitats dominated by live oak and chaparral. Three males migrated, but two died before their status could be determined. Of the 12 females, three migrated during each year of study, four migrated in some years, but not in others, and five were year-round residents of Burro Flats. Deer that migrated from Burro Flats moved up the canyon in summer to habitats at high elevation near Sugarloaf Mountain, Onyx Peak, and the San Gorgonio Wilderness. Distance moved for these deer was 8.1 ± 2.9 km (range = 4.4–11.3 km).

Departure from winter range occurred between the 1st week in March and 2nd week of May during 1989–1991, whereas departure from summer range occurred between the 1st week in October and 3rd week in January. Mean week of migration was relatively constant for the duration of the study (Table 1). No significant difference occurred among years for time of departure of deer from summer range ($F = 2.46$, $d.f. = 1, 22$, $P > 0.05$); however, time of departure from winter range differed among years ($F = 4.61$, $d.f. = 2, 30$, $P < 0.05$). Deer departed significantly earlier from winter range in 1989 than in 1990 or 1991 (Tukey's multiple-comparison test, $P < 0.05$). Timing of departure from winter range did not differ between 1990 and 1991 ($P > 0.05$).

Resident females moved less than did migratory females or migratory males ($Z = -2.24$, $d.f. = 1$, $P < 0.05$; $Z = 2.13$, $d.f. = 1$, $P < 0.05$, respectively) during spring (Fig. 3). Males moved more than did migratory and resident females in autumn ($Z = 2.47$, $d.f. = 1$, $P < 0.05$) during rut.

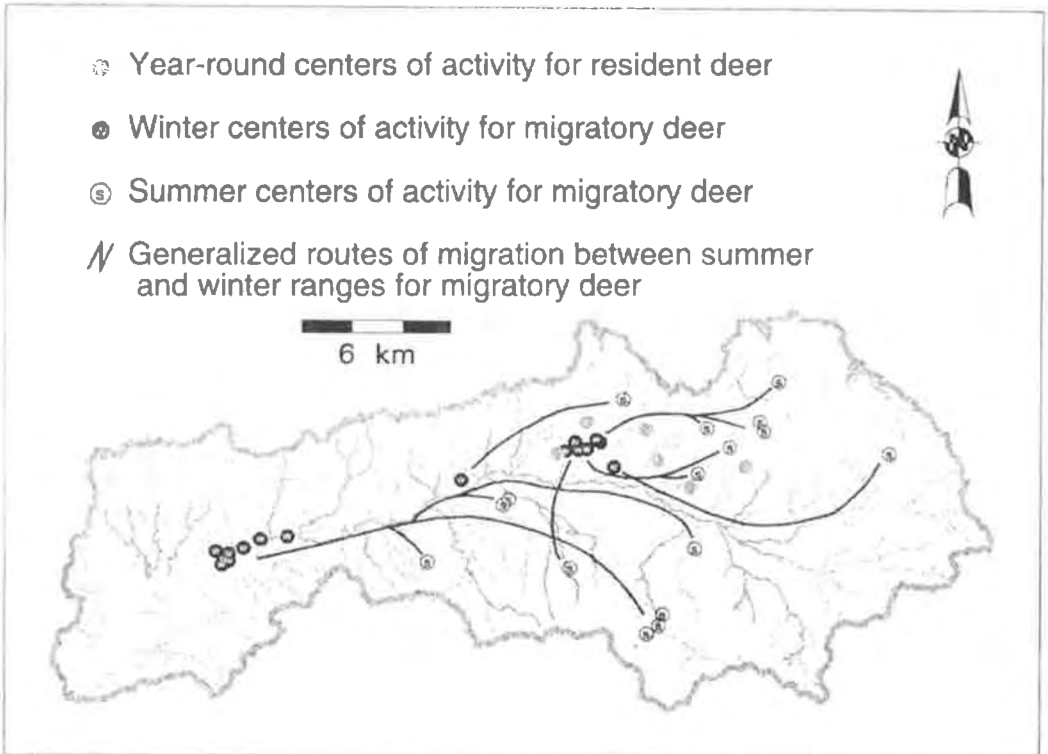

FIG. 2.—Seasonal distribution and generalized routes of migration of radiocollared mule deer (*Odocoileus hemionus*) in San Bernardino Co., California, 1989–1991.

Additionally, males moved more than did migratory females during winter ($Z = 2.09$, $d.f. = 1$, $P < 0.05$) and less than resident females during summer ($Z = -2.16$, $d.f. = 1$, $P < 0.05$). Differences in other comparisons were small (Fig. 3).

TABLE 1.—*Mean date of departure for spring and autumn migrations of mule deer* (Odocoileus hemionus) *in San Bernardino Co., California, 1989–1991*

Year	Departure from	Mean date ± *SD*	*n*
1989	Winter range	10 April ± 9.8 days	10
1989	Summer range	1 December ± 18.4 days	13
1990	Winter range	29 April ± 23.7 days	14
1990	Summer range	17 November ± 20.2 days	11
1991	Winter range	1 May ± 14.0 days	9

Deer exhibited seasonal differences in distance traveled between sequential locations from radiotelemetry for 1989–1991 (Kruskal-Wallis test: males, $\chi^2 = 17.47$, $d.f. = 3$, $P < 0.001$; migratory females, $\chi^2 = 12.09$, $d.f. = 3$, $P < 0.01$; resident females, $\chi^2 = 7.87$, $d.f. = 3$, $P < 0.05$). The greatest movements occurred in winter and spring when temperatures were coolest and precipitation was highest (Figs. 3, 4). We obtained negative correlations between movements of deer between sequential relocations and mean daily temperature ($r_s = -0.13$, $n = 1{,}336$, $P < 0.001$), whereas a positive correlation occurred between movement and total precipitation ($r_s = 0.11$, $n = 1{,}336$, $P < 0.001$).

Home ranges.—Radiotelemetered deer demonstrated high fidelity to home ranges during each season. Only 24% of 74 tests

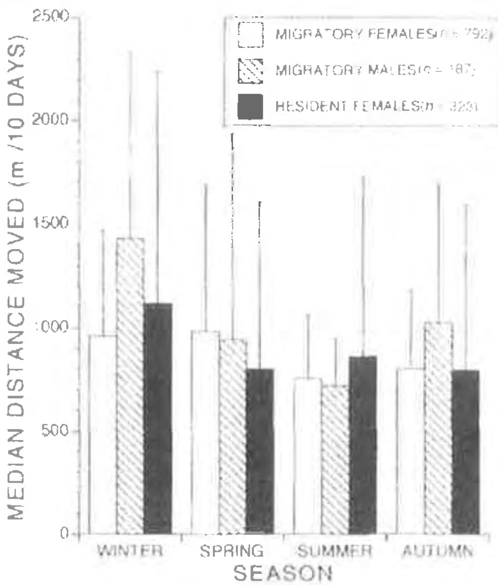

FIG. 3.—Median distance between consecutive telemetry locations by season for mule deer (*Odocoileus hemionus*) in San Bernardino Co., California, 1989–1991. Error bars indicate one-half the interquartile distance.

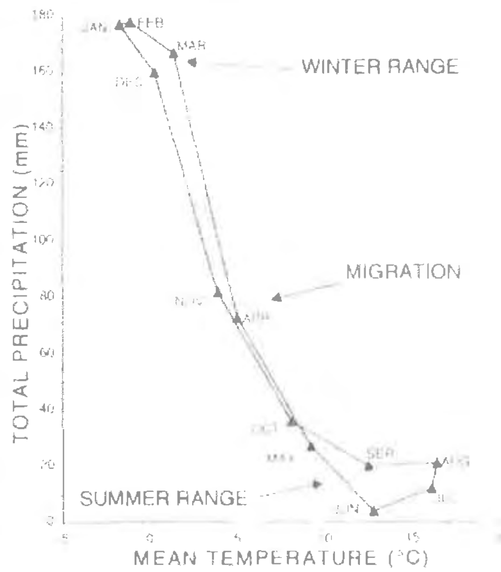

FIG. 4.—Climograph of mean monthly temperature and precipitation at Angelus Oaks, California (1,600 m elevation), 1989–1991.

for fidelity to home range showed significant changes in the position of home ranges of deer between years; every deer tracked >1 year had highly overlapping home ranges. Most annual changes in home ranges occurred for migratory deer; in only one instance did a resident deer have a significant shift in location of home ranges between years.

No difference ($P > 0.25$) occurred between either sex ($\chi^2 = 0.89$) or season ($\chi^2 = 0.76$) in the number of shifts in home ranges between years. One group of three female deer that had summer ranges near Sugarloaf Mountain accounted for nearly one-half of the shifts in locations of home ranges observed between years. This group did not migrate in winter 1989, migrated to Burro Flats in winter 1990, and delayed their movements to winter ranges on Burro Flats until March 1991, when snows in late winter forced them from their summer ranges at high elevation (>2,500 m). All other migratory deer had distinct winter and summer ranges in each year.

Home ranges of telemetered deer were extremely variable. The mean size of home range was 788.6 ± 691.8 ha as calculated by the adaptive kernel (minimum convex polygon = 443.9 ± 413.0 ha, $n = 33$). No significant difference in sizes of home ranges occurred between categories of deer, but home ranges were significantly smaller in summer than in winter (Table 2).

Two deer with summer ranges in the San Gorgonio Wilderness had significantly smaller home ranges (185 ha, $t = 6.73$, $df = 14$, $P < 0.001$, 304 ha, $t = 4.69$, $df = 14$, $P < 0.001$) than deer with home ranges elsewhere in the study area ($\bar{X} = 578.33 \pm 226.43$ ha, $n = 15$). Vegetative composition of the home range, distance from the center of activity to water, and distance to human developments explained substantial variation in the size of home ranges of deer in summer ($R^2_a = 0.81$, $df = 16$, $F = 9.59$, $P < 0.001$; $Y = 2.7633$ – 0.0002 distance to human development – 0.0177 percentage of sagebrush + 0.0401?

TABLE 2.—*Size of home ranges of mule deer* (Odocoileus hemionus) *associated with sex, season, and migratory status in San Bernardino Co., California, 1989–1991. Home ranges (in ha) of 95% are estimated with adaptive kernel and minimum convex polygon. F-values from MANOVA and significance levels presented were for tests of means above and below the respective statistic.*

		Adaptive kernel		Minimum convex-polygon	
Subset of the population	n	$\bar{X}$	SD	$\bar{X}$	SD
Summer					
Migratory males	3	392.3	196.7	257.3	43.8
		$F = 0.85$			
Migratory females	9	554.2	277.4	314.7	165.2
		$F = 0.11$			
Resident females	5	599.8	189.5	331.0	72.6
Winter					
Migratory males	3	396.0	108.3	230.3	108.3
		$F = 2.68$			
Migratory females	7	1,357.3	981.1	766.6	551.9
		$F = 0.37$			
Resident females	6	1,028.6	944.7	555.5	651.3
All deer					
Summer	17	539.1	240.0	309.4	126.0
		$F = 5.16$*			
Winter	16	1,053.8	902.1	586.9	551.9

* $P < 0.05$ after Bonferroni correction (Rice, 1989).

percentage of chamise − 0.00010 distance to water + 0.000710 percentage of bare ground). Partial regressions indicated that distance to human developments ($r^2 = 0.29$), percentage of chamise ($r^2 = 0.24$), and percentage of sagebrush ($r^2 = 0.15$) were most influential in affecting size of home range; other variables were less important ($r^2 < 0.09$). During winter, size of home ranges also was predicted well by habitat ($R_a^2 = 0.90$, $d.f. = 15$, $F = 35.4$, $P < 0.001$; $\hat{Y} = 2.0933 + 0.01889$ percentage of pine + 1.4191 percentage of meadow + 0.0172 percentage of bare ground). Partial regressions indicated meadow ($r^2 = 0.90$), bare ground ($r^2 = 0.80$), and pine ($r^2 = 0.53$) were all influential.

Use of habitat.—Deer distributed themselves differently than random with regard to distance from human developments (Fig. 5). In general, deer were farther than expected from potential human disturbance in summer and in winter. Moreover, we observed differences in how classes of deer distributed themselves with respect to potential disturbance. Migratory females were farther from human developments than were migratory males (summer, $KS_a = 3.39$, $P < 0.001$; winter, $KS_a = 1.72$, $P < 0.01$) and were observed farther from these disturbances than were resident females in summer ($KS_a = 4.59$, $P < 0.001$). Migratory males were farther from developments than were resident females in summer ($KS_a = 2.02$, $P < 0.001$). Male ($KS_a = 2.12$, $P < 0.001$) and female ($KS_a = 4.22$, $P < 0.001$) deer that were migratory were observed closer to human developments in winter than in summer, whereas resident females showed no trend ($P > 0.05$).

All deer differed from expected with regard to distance from water in both seasons (Fig. 5). Migratory females were observed closer than expected to water in summer and farther in winter. Resident females were distributed farther than the random distance from water in both seasons. Migratory males were farther from water in summer, whereas they were not significantly different from the expected distance in winter.

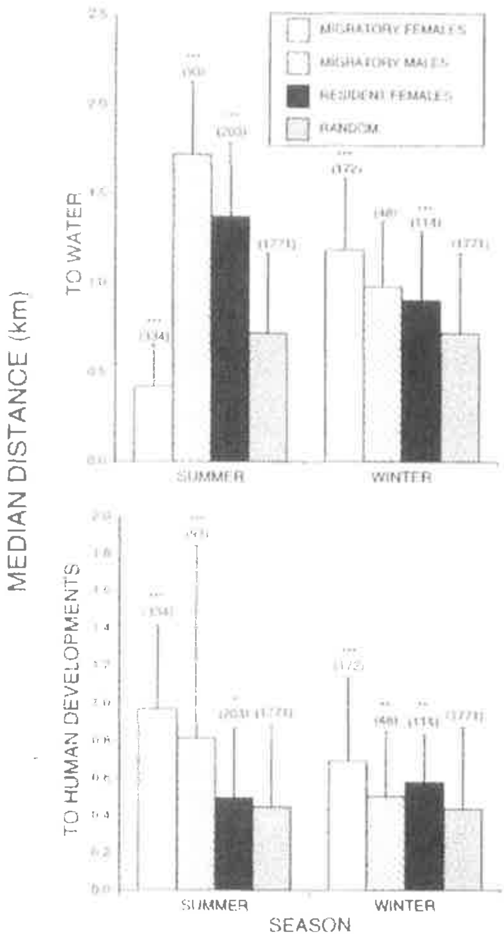

FIG. 5.—Median distance to water (above) and to developments of humans (below) for mule deer (*Odocoileus hemionus*) during summer and winter in San Bernardino Co., California, 1989–1991. Error bars indicate one-half the interquartile distance; sample sizes are above error bars. P values are from a Kolmogorov-Smirnov test against random locations: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Additionally, migratory females were observed closer to water than resident females ($KS_d = 2.12$, $P < 0.001$) or migratory males ($KS_d = 2.12$, $P < 0.001$) in summer; they occurred farther from water than did resident females ($KS_d = 2.12$, $P < 0.001$) or migratory males ($KS_d = 2.12$, $P < 0.001$) in winter. Finally, migratory males were observed farther from water than were resident females in summer, although we observed no difference between these two groups in winter ($P > 0.05$).

All deer differed from random in use of the available terrain. Generally, migratory deer occurred at higher elevations on more north-facing slopes during summer than in winter (Table 3). In contrast, resident deer remained year-round on steep, south-facing slopes. Further, male deer were observed at higher elevations during summer than were females.

For random sites, highly rugged areas as measured by changes in slope occurred at lower elevations (correlation between variation in slope and elevation, $r_s = -0.26$, $n = 1,771$, $P < 0.001$) and in areas of steeper slope (correlation between variation in slope and mean slope, $r_s = 0.21$, $n = 1,771$, $P < 0.001$), whereas areas of highly diverse terrain, as measured by changes in aspect, occurred at higher elevations (correlation between angular deviation in aspect and elevation, $r_s = 0.90$, $n = 1,771$, $P < 0.001$). Telemetered deer did not differ from expected regarding use of rugged terrain as measured solely by angular deviation (Table 4). Migratory females in both seasons and resident females in winter differed from expected in their use of rugged terrain; this difference represents selection or avoidance of areas of highly changing slope. Finally, migratory females occurred on the least-rugged slopes in summer and on the most-rugged terrain in winter.

Use of habitats by deer differed significantly between seasons (Figs. 6 and 7, Table 5), with migratory deer radically changing their patterns of use of habitat. Generally, migratory deer used habitats dominated by pine in summer and by oak and chaparral in winter. Additionally, migratory females used riparian habitat and meadows to a greater extent in summer than in winter. Use of habitat by resident females remained relatively constant throughout the year, although some seasonal changes occurred. Similar to migratory deer, resident females used more pine-dominated habitats in sum

TABLE 3.—*Mean (± SD) use of various characteristics of terrain by subsets of telemetered mule deer (*Odocoileus hemionus*) in San Bernardino Co., California, 1989–1991. Z-values from Wilcoxon two-sample test are given between categories of deer.*

		Characteristics of terrain		
Subset of population	*n*	Elevation (m)	Slope (degrees)	North-facing slopes (%)
Random	1,771	2,040.62 ± 586.11	20.88 ± 8.15	53.55 ± 37.3
Summer				
Migratory males	103	2,552.03 ± 228.36ab 7.36*	21.50 ± 5.96 5.74*	62.90 ± 38.66ab 2.51*
Migratory females	334	2,269.99 ± 359.64ab -1.55	17.69 ± 5.11ab 9.27*	76.34 ± 27.30ab -11.81*
Resident females	203	2,293.00 ± 204.79ab	22.75 ± 6.34a	38.42 ± 33.73ab
Winter				
Migratory males	64	1,754.33 ± 406.68a 6.87*	21.12 ± 6.50 −0.47	20.47 ± 28.06a -4.57*
Migratory females	172	1,308.33 ± 348.33a 12.66*	21.67 ± 6.79 1.65	35.12 ± 26.90a -5.45*
Resident females	114	2,119.79 ± 245.49	22.60 ± 6.64a	21.19 ± 29.43a

* $P < 0.05$, following Bonferroni correction (Rice, 1989).
[a] Denotes within-group means differed significantly ($P < 0.05$) from random distribution.
[b] Denotes within-group means differed significantly ($P < 0.05$) between seasons.

mer than in winter, interchanging use of pine forests with oak woodlands between seasons. Further, resident females used more grassland and sagebrush in winter than in summer. Differences in use of habitat between categories of deer occurred for nearly all comparisons of habitat (Table 5). Migratory females used significantly more pine and riparian habitats and less brush and grassland in summer than did migratory

TABLE 4.—*Mean (± SD) use of rugged terrain by subsets of telemetered mule deer (*Odocoileus hemionus*) in San Bernardino Co., California, 1989–1991. Ruggedness as measured by variation in slope, aspect, and a composite index is presented with F-values from a MANOVA comparing use of subsets of all measures of terrain.*

		Measures of ruggedness of terrain		
Subset of population	*n*	*SD* of slope	Angular deviation of aspect	Composite index of ruggedness
Random	1,771	44.7 ± 29.9	130.0 ± 16.7	5,834.0 ± 3,971.0
Summer				
Migratory males	103	42.4 ± 19.6 24.80***	131.8 ± 16.2 1.05	5,633.2 ± 2,910.2 24.55***
Migratory females	334	32.3 ± 16.8[ab] 12.36***	129.9 ± 13.5 2.61	4,221.0 ± 2,317.0[ab] 13.88***
Resident females	203	37.1 ± 17.6	132.1 ± 15.8	4,928.3 ± 2,566.0
Winter				
Migratory males	64	46.4 ± 29.7 19.74***	130.9 ± 16.3 0.53	6,024.4 ± 3,743.9 20.52***
Migratory females	172	74.3 ± 48.2[a] 82.69	132.2 ± 14.3 2.62	9,792.7 ± 6,500.1[a] 85.80***
Resident females	114	34.3 ± 16.2[a]	129.5 ± 15.4	4,462.8 ± 2,294.0[a]

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$
[a] Denotes within-group means differed significantly ($P < 0.05$) from random distribution
[b] Denotes within-group means differed significantly ($P < 0.05$) between seasons

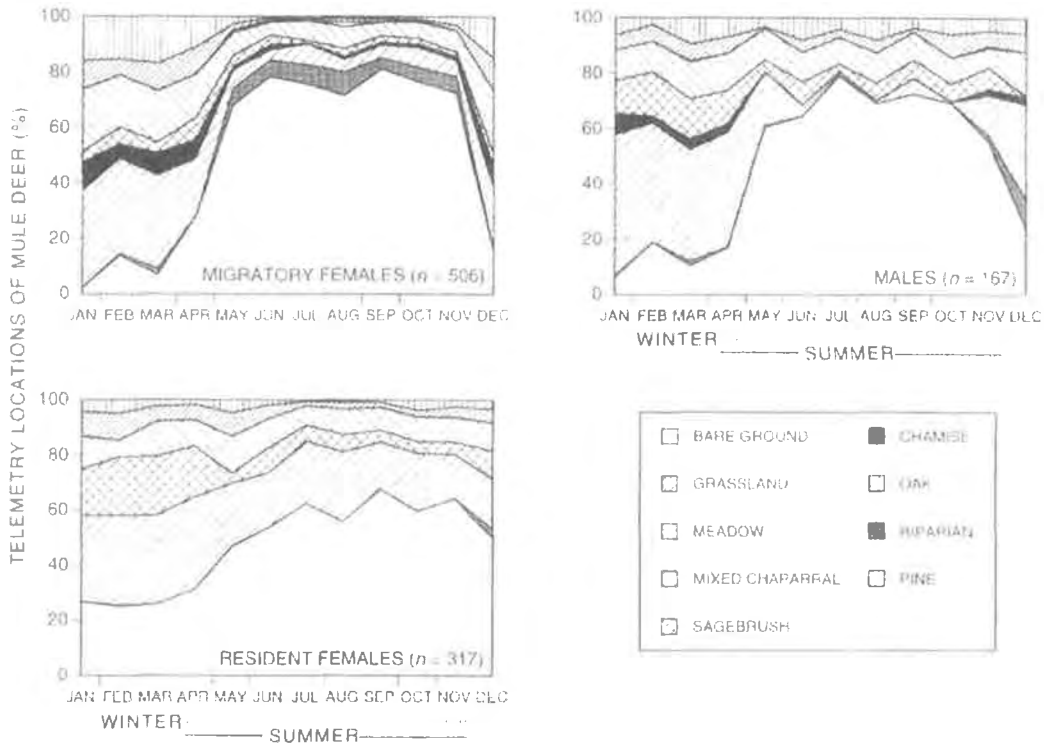

FIG. 6.—Percentage of telemetry locations related to habitats for mule deer (*Odocoileus hemionus*) in San Bernardino Co., California, 1989–1991.

males. Migratory females used more brush-dominated habitats and less tree-dominated ones than did migratory males in winter. Additionally, resident females selected significantly less pine and riparian habitat, and meadows and more oak and habitats dominated by brush than did migratory females in summer. Resident females used more sagebrush and pine and less chamise-chaparral than did migratory females in winter.

Significant differences occurred in the selection of type of habitat by adult deer (Fig. 7). During summer, resident females selected pine and oak, while avoiding riparian, chamise, mixed chaparral, meadows, grassland, and bare ground. Similarly, resident females selected oak forests and avoided riparian areas, chamise, chaparral, and bare ground in winter. Contrary to the summer patterns, resident females strongly selected sagebrush and avoided pine forests in winter.

In summer, migratory females selected pine forests, riparian areas, and meadows, while avoiding oak woodlands, chamise, sagebrush, mixed chaparral, grasslands, and bare ground. Migratory males also selected pine habitats and avoided oak woodlands and grasslands. Unlike migratory females, males avoided riparian areas while using meadows and bare ground in proportion to their availability (Fig. 7).

During winter, migratory females and males were similar in their selection of habitats. Both groups selected areas with oak woodlands and chamise, while avoiding pine forests. Migratory females selected mixed chaparral, grassland, and bare ground, whereas use of these habitats by males did not differ from their availability. Additionally, males selected sagebrush

Comment Letter I9

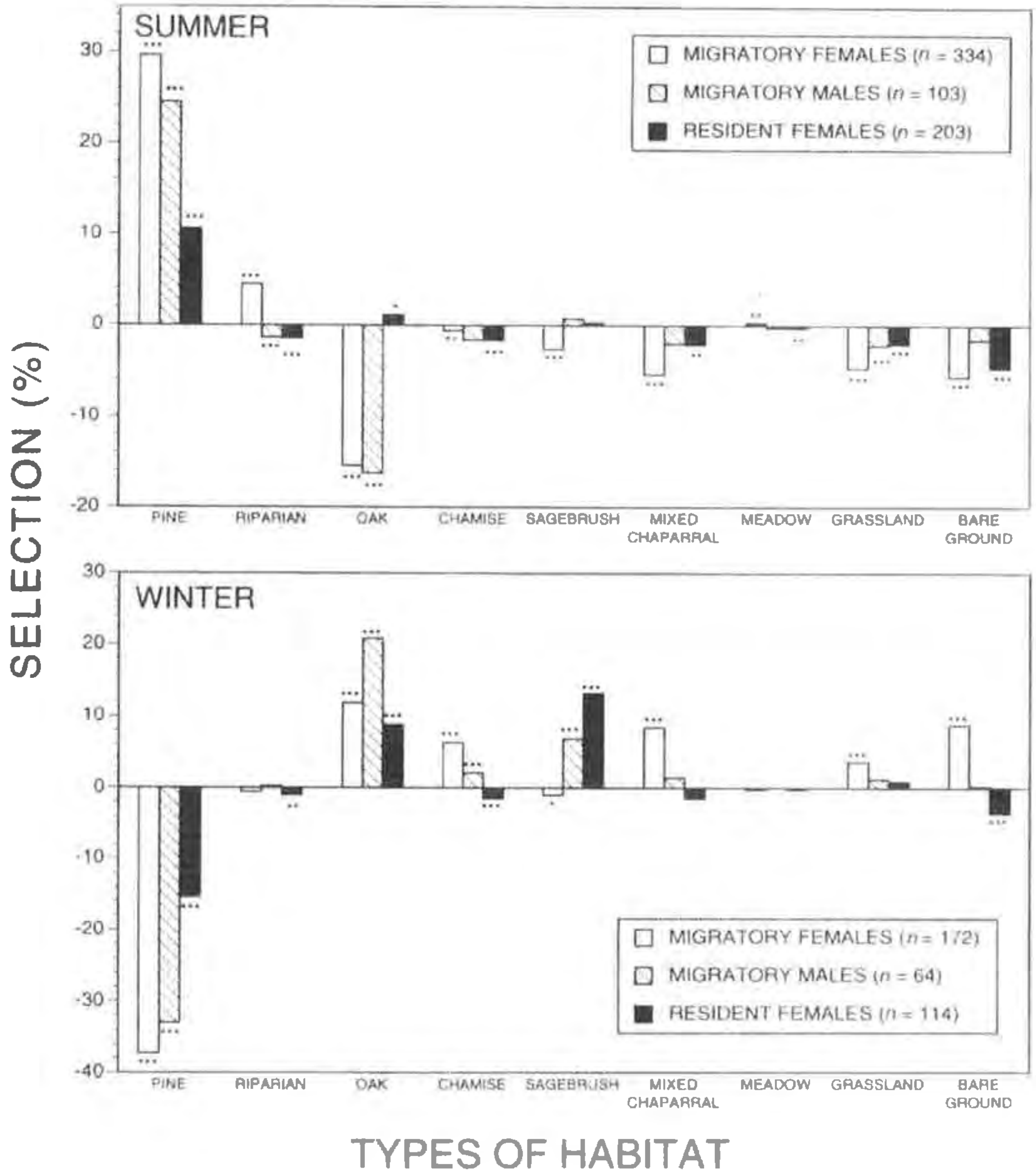

FIG. 7.—Selection (percentage used minus percentage available) by mule deer (*Odocoileus hemionus*) for habitats in San Bernardino Co., California, 1989–1991. *P*-values are from MANOVA; $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$.

habitats, and migratory females avoided those areas (Fig. 7).

Mortality.—Female deer showed marked differences in rates of survival between classes of migrating deer (Fig. 8). In years with low precipitation (1989–1990), survivorship was significantly lower in migratory deer than in resident deer. Conversely, in a year of normal precipitation (1991), resident females had higher rates of mortal

TABLE 5.—*Mean (± SD) percentage use of habitats by subsets of telemetered mule deer* (Odocoileus hemionus) *in San Bernardino Co., California, 1989–1991. F-values from a MANOVA comparing subset of all types of habitat*

		Type of habitat								
Subset of population	*n*	Pine	Oak	Riparian	Meadow	Chamise	Sagebrush	Mixed chaparral	Grasslands	Bare ground
Summer										
All deer	800	65.0 ± 30.0	8.7 ± 15.8	2.7 ± 8.1	0.3 ± 2.0	0.4 ± 2.5	5.3 ± 11.7	8.9 ± 10.5	3.0 ± 7.3	5.7 ± 12.82
Sex										
Migratory males	103	70.9 ± 22.3[a]	4.3 ± 11.6[a]	0.2 ± 0.7[a]	0.0 ± 0.0[a]	0.00 ± 0.00[a]	6.3 ± 12.1[a]	9.6 ± 7.6	3.6 ± 7.3[a]	5.3 ± 10.4
Migratory females	334	75.9 ± 23.7[a]	5.1 ± 9.8[a]	6.0 ± 11.7[a]	0.6 ± 2.7[a]	1.00 ± 3.75[a]	2.96 ± 10.2	6.2 ± 10.6[a]	1.1 ± 3.8[a]	1.2 ± 4.6[a]
F-value		7.61**	1.34	36.14***	9.65**	12.88***	23.49***	27.73***	23.32***	55.92***
Migratory status										
Resident females	203	56.9 ± 33.2[a]	21.6 ± 21.8[a]	0.1 ± 0.6	[illegible] 0.3	0.0 ± 0.0	5.82 ± 11.1[a]	9.5 ± 10.6	3.8 ± 10.5[a]	2.2 ± 6.7
Migratory females	334	75.9 ± 23.7	5.10 ± 9.8	6.0 ± 11.7	[illegible] 2.7	1.0 ± 3.8	2.96 ± 10.2	6.2 ± 10.6	1.1 ± 3.8	1.2 ± 4.6
F-value		63.73***	154.97***	73.97***	[illegible].55***	25.40***	28.88***	21.09***	29.84***	6.04*
Winter										
All deer	432	17.5 ± 25.0	30.6 ± 23.9	0.8 ± 4.1	0.2 ± 1.8	3.7 ± 7.2	13.5 ± 18.6	14.7 ± 13.5	8.5 ± 10.2	10.4 ± 15.6
Sex										
Migratory males	64	13.3 ± 19.4	41.4 ± 22.4	1.8 ± 7.3	0.3 ± 1.3	3.7 ± 7.2	12.4 ± 15.0	13.0 ± 11.2	7.0 ± 10.0	7.1 ± 11.1
Migratory females	172	9.1 ± 20.5	32.4 ± 23.0	1.0 ± 3.9	0.1 ± 0.1	7.8 ± 8.8	4.5 ± 11.3	20.0 ± 14.0	9.5 ± 8.7	15.7 ± 17.1
F-value		6.14	7.2**	0.70	0.74	20.71***	29.63***	11.68***	8.76**	17.24***
Migratory status										
Resident females	114	31.0 ± 30.6	29.4 ± 23.0	0.6 ± 3.3	0.1 ± 0.5	0.0 ± 0.0	18.8 ± 19.2	10.1 ± 14.0	6.7 ± 10.8	3.3 ± 9.9
Migratory females	172	9.1 ± 20.5	32.4 ± 23.0	1.0 ± 3.9	0.1 ± 0.04	7.8 ± 8.8	4.5 ± 11.3	20.0 ± 14.0	9.5 ± 8.7	15.7 ± 17.1
F-value		78.76***	3.16	2.48	0.25	172.31***	88.87***	42.41***	15.27***	79.02***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[a] Denotes within-group means differed significantly ($P < 0.05$) between seasons.

TABLE 5.—*Mean (± SD) percentage use of habitats by subsets of telemetered mule deer* (Odocoileus hemionus) *in San Bernardino Co., California, 1989–1991. F-values from a MANOVA comparing subset of all types of habitat.*

Subset of population	n	Pine	Oak	Riparian	Meadow	Chamise	Sagebrush	Mixed chaparral	Grasslands	Bare ground
		Type of habitat								
Summer										
All deer	800	65.0 ± 30.0	8.7 ± 15.8	2.7 ± 8.1	0.3 ± 2.0	0.4 ± 2.5	5.3 ± 11.7	8.9 ± 10.5	3.0 ± 7.3	5.7 ± 12.82
Sex										
Migratory males	103	70.9 ± 22.3[a]	4.3 ± 11.6[a]	0.2 ± 0.7[a]	0.0 ± 0.0[a]	0.00 ± 0.00[a]	6.3 ± 12.1[a]	9.6 ± 7.6	3.6 ± 7.3[a]	5.3 ± 10.4
Migratory females	334	75.9 ± 23.7[a]	5.1 ± 9.8[a]	6.0 ± 11.7[a]	0.6 ± 2.7[a]	1.00 ± 3.75[a]	2.96 ± 10.2	6.2 ± 10.6[a]	1.1 ± 3.8[a]	1.2 ± 4.6[a]
F-value		7.61**	1.34	36.14***	9.65**	12.88***	23.40***	27.73***	23.32***	55.92***
Migratory status										
Resident females	203	56.9 ± 33.2[a]	21.6 ± 21.8[a]	0.1 ± 0.6	0.1 ± 0.3	0.0 ± 0.0	5.82 ± 11.1[a]	9.5 ± 10.6	3.8 ± 10.5[a]	2.2 ± 6.7
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Sex										
Migratory males	64	13.3 ± 19.4	41.4 ± 22.4	1.8 ± 7.3	0.3 ± 1.3	3.7 ± 7.2	12.4 ± 15.0	13.0 ± 11.2	7.0 ± 10.0	7.1 ± 11.1
Migratory females	172	9.1 ± 20.5	32.4 ± 23.0	1.0 ± 3.9	0.1 ± 0.1	7.8 ± 8.8	4.5 ± 11.3	20.0 ± 14.0	9.5 ± 8.7	15.7 ± 17.1
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F value		78.76***	3.16	2.48	0.25	172.31***	88.87***	42.41***	15.27***	79.02***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Denotes within group means differed significantly ($P < 0.05$) between seasons.

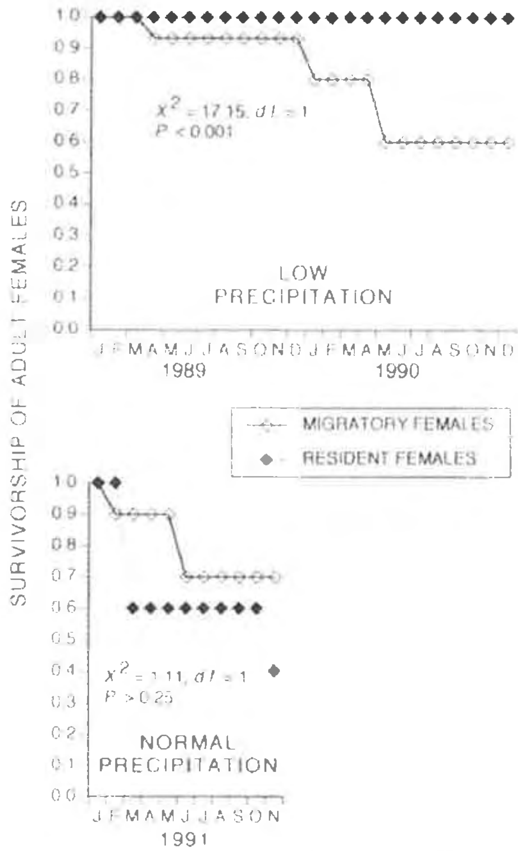

FIG. 8.—Survivorship of adult, female mule deer (*Odocoileus hemionus*) during years of low precipitation and normal precipitation in San Bernardino Co., California, 1989–1991. Number of telemetered females was six and 15 for resident and migratory deer, respectively.

ity than did migratory females, although this difference was not statistically significant (Fig. 8). The timing of mortalities also was different between the two groups. Deaths in migratory females occurred within 1 month of migration, whereas deaths for resident females were limited to winter. Annual survivorship in adult male deer was similar in low (0.83) and normal (0.90) years of precipitation.

DISCUSSION

Both migratory and nonmigratory deer inhabit the upper basin of the Santa Ana River. The existence of both patterns within a deer herd has been observed by others (Kufeld et al., 1989; Loft et al., 1984). Garrott et al. (1987) suggested that migration is obligatory for mule deer living in mountainous areas. Moreover, Gilbert et al. (1970) observed that depths of snow >46 cm preclude use of some ranges by deer. Our study area encompassed the highest elevations in southern California. Deer that occurred on north-facing slopes within the upper drainage of the Santa Ana River were migratory. Although Medin and Anderson (1979) suggested an elevational dividing line between summer and winter range of ca. 2,600 m for deer in Colorado, this pattern did not appear to exist on south-facing slopes in our study. Indeed, some deer were observed on south-facing slopes >3,000 m throughout winter. Deer were excluded largely from north-facing slopes >1,500 m, where accumulations of snow >4 m were observed.

Factors believed to affect the timing of migration include temperature, relative humidity, snowmelt, activity of insects, photoperiod, and maturing vegetation (Albon and Langvatn, 1992; Garrott et al., 1987; Leopold et al., 1951; McCullough, 1964; Russell, 1932; Van Ballenberghe, 1977). We observed that movements of deer were associated with low temperatures and high precipitation. Weather alone, however, is unlikely to affect when deer migrate. During the 1st year of study, migration to winter range occurred largely after major snowstorms, whereas in subsequent years, movements of deer were more gradual than we previously observed. Because the first deer to migrate in each year did so in October, before snow and low temperatures could force them from summer range, photoperiod and maturation of vegetation probably affected migration. Likewise, spring migration probably coincided with increasing temperatures, decreased precipitation, increased photoperiod, and low quality of vegetation on winter range. Effects of climate on quality and availability of forage is a likely explanation for the relationships between movements of deer and climatic variables.

Migratory and resident females used available range differently. In summer, migratory females used significantly more meadows and riparian habitat than did resident females. Although several studies have noted the importance of these habitats to deer (Bowyer, 1986; Loft et al., 1984), resident deer in our study avoided these habitats in all seasons. This pattern occurred because of the small amount of meadows and riparian habitats on south-facing slopes that resident deer inhabited. This pattern also resulted in resident deer occurring closer to potential human disturbance and farther from water than migratory females in summer. North-facing slopes that migratory females used had a greater proportion of available water and fewer human developments than south-facing slopes. Thus, deer migrated to locations that contained habitats of highest quality, which were only seasonally available.

Animals that are free to choose habitats and strategies of migration should maximize their reproductive success (Fretwell, 1972). If the frequency distribution of individuals that select each strategy stabilized in a deme, all individuals should experience equal reproductive success. Migratory populations of moose (*Alces alces*) selected habitats differently in winter than did nonmigratory ones (Histøl and Hjeljord, 1993). In our study, migratory deer selected a strategy that allowed them access to habitats of highest quality. Given this pattern, why do any deer remain resident on south-facing slopes in summer? This may occur because, during migration, an animal leaves an area with which it is familiar and moves through areas where it may be less knowledgeable regarding current distributions of escape terrain, hiding cover, and predators. Thus, when deer migrate, they may be at greater risk of predation. Indeed, O'Bryan and McCullough (1985) observed a higher rate of mortality in black-tailed deer that were recently translocated (0.85) compared with resident deer (0.28) in the area of translocation. In our study, four of seven deaths were due to predators that captured deer during short periods of migration. Conversely, predators often occur at greatest densities where prey is regularly available. Therefore, while deer move between winter and summer ranges, they may be at decreased risk of predation because predators are left behind (Baker, 1978). Nonetheless, migratory deer moved through the ranges of residents in our study on their way to and from summer range where predation occurred. Thus, predators have available prey year-round in ranges of residents, and predators likely occur on ranges used during migration. Consequently, deer probably are at increased risk of predation while migrating.

If migratory deer are at greater risk of predation than are resident deer, a tradeoff may exist in whether to migrate or stay. If deer migrate, they have access to habitats of high quality and may be able to produce more or healthier young, thereby increasing their reproductive success. Increased nutrition is a well-documented factor that affects reproductive performance in *Odocoileus* (McCullough, 1979). Nonetheless, migratory deer also may have an increased risk of predation, thereby reducing lifetime reproductive success.

Differences in survival between resident and migratory deer may not be the only factor affecting a mixed strategy for migration. Parker and Stuart (1976) argued that an optimal withdrawal point exists at which a resident individual should migrate. This point occurs when costs of remaining in a patch with resources are greater than gains associated with staying in that patch. Where suitability of resources declines with density of population within a patch, several withdrawal points or thresholds for migration can occur. The advantage of being a resident in a group of low density and waiting for others to leave might be countered by the possibility of being a member of a large group in a patch. For deer in the San Bernardino Mountains, density of the population on south-facing slopes likely declined during spring migration. Individuals that remained resident in those areas could be more selective and, thus, maintain a relatively high dietary plane in an area of low quality. What is unclear is whether the decreased density of the population and, thus, reduced competition was enough to compensate for differences in quality of habitat between north- and south-facing slopes. Nonetheless, this potential mechanism offers benefits related to nutrition to females that do not migrate.

Rates of survival and reproduction need not be similar in all years for a mixed strategy to be maintained in a population. Indeed, we observed higher rates of mortality in migratory deer than in resident deer for years with below-normal precipitation. In contrast, mortality was slightly higher for resident deer in the year of normal precipitation. Further, mortality in migratory females occurred exclusively around migration, whereas mortality in resident deer was limited to winter. Deep snow decreased access to forage for ungulates (Gilbert et al., 1970) and increased costs of locomotion (Fancy and White, 1987; Parker et al., 1984), both of which could contribute to increased rates of mortality (Klein and Olson, 1960; Robinette et al., 1952), or could affect subsequent maternal care of young (Langenau and Lerg, 1976; White and Luick, 1984). In areas of deep accumulations of snow, deer may be forced to migrate away from north slopes; however, where winter snows are transitory and depths of snow are extremely variable, some deer may remain on winter range. Thus, in montane southern California, where annual precipitation (and cover of snow) was extremely variable, some mule deer were facultative migrators. This hypothesis is supported by variation in timing of migration among years (Table 1) and by some females changing migratory strategies between years. Additionally, migratory behavior in this population of deer is unlikely to be fixed genetically. The shift of several females from migratory to resident status, and most males (all those collared) being migratory, but with ranges that overlapped both migratory and nonmigratory females during rut, indicate a degree of behavioral plasticity.

The mating season for mule deer in central California occurs from late October to January (Leopold et al., 1951), whereas mating occurs earlier in populations at more southerly latitudes and lower elevations (Bischoff, 1957; Bowyer, 1991). Rut peaks in mid-November for deer inhabiting the San Bernardino Mountains (J. Davis, pers. comm.). The estrous cycle in female mule deer lasts 22–28 days, however, they are only receptive to males from 24 to 36 h (Mackie et al., 1982). Thus, males must search actively for females over broad areas during that time. Male deer moved more between sequential locations than did females, which is not surprising. Increased movements and activity by male cervids have been observed during rut (Bowyer, 1981; Cederlund and Sand, 1994; Miquelle, 1990; Taber and Dasmann, 1958).

Although rut ends in December, males continued to move more than females during winter. Male cervids expend tremendous amounts of energy during rut while fighting with male competitors and searching for mates. During rut, these dominant males reduce the amount of forage they consume (Bowyer, 1981; Espmark, 1964; Miquelle, 1990; Taber and Dasmann, 1958). Thus, males enter winter with considerably less reserves of energy than they possessed before rut. Males often do not survive winter because of malnutrition or increased susceptibility to predation that results from a depleted condition (Klein, 1965). The increased movement of males as compared with females may be explained by increased movement related to foraging by males to compensate for the energy expended during rut. Likewise, overall increases in movements by deer during winter also may reflect reduced availability of forage of high quality. Thus, in an attempt to maintain nutrient intake, deer must spend more time foraging in winter. These arguments assume that increased movement by deer equates to increased foraging, an assumption not tested in our study.

Mule deer have high fidelity to seasonal home ranges (Gruell and Papez, 1963; Kufeld et al., 1989; Leopold et al., 1951). Indeed, deer in our study routinely returned to about the same home ranges. Only 25% of the home ranges of individuals differed between years. Most other studies have not used the techniques presented herein and meaningful comparisons cannot be made.

Home ranges of deer are extremely variable. Although home ranges reported in our study are large, they are by no means exceptional. Sizes of home ranges for mule deer that inhabit sagebrush habitat were as much as five times larger (Eberhardt et al., 1984) than those reported here. Even within our study, home ranges varied from 87 to 3,001 ha. This variability provided the opportunity to examine which factors were associated with size of home range in mule deer. According to models of optimal-foraging theory and bioenergetics, size of home range should be related inversely to maximum density of resources (Ford, 1983; McNab, 1963). As the amount of resources of high quality increases in a home range, the size of the home range should decrease. In this study, size of home range was not related to the amount of preferred (use was greater than availability) habitats in each home range. Rather, home ranges of deer were related positively to the amount of avoided (use was less than availability) habitats. If avoided habitats can be equated to resources of lower quality, size of home range is affected more by the amount of resources of poor quality than by the amount of resources of high quality. If preferred habitats were distributed widely into small patches, however, this might increase sizes of home ranges and result in more avoided habitats being included in larger home ranges.

The positive relationship between the abundance of avoided features and size of home ranges may explain why no differences were observed in size of home ranges among subsets of the population. Sexual differences in size of home ranges were observed by others; male deer had larger home ranges (Gompper and Gittleman, 1991; Pac et al., 1988). No such trend was observed in our study. Because migratory females used the resources of highest quality (i.e., meadows and riparian habitat) more than did resident females, optimal-foraging theory would predict that migratory females should have smaller home ranges than resident females. Although our data tended to support this hypothesis, we observed no statistically significant trend toward smaller home ranges in migratory females. The extreme variability in sizes of home ranges and the abundance of avoided features of the landscape and types of habitat throughout the study area may have contributed to rejection of predictions from optimal-foraging theory.

Human disturbance is a significant factor that affects deer in the drainage of the Santa Ana River. Indeed, all deer were observed farther than expected from human developments. Mule deer used areas near human development less than similar undisturbed sites (D. C. Cornett et al., in litt.; Rost and Bailey, 1979). Clearly, human disturbance reduced the value of habitat for mule deer. Although Bowyer (1984, 1986) noted that 77% of all mule deer observed were <500 m from water in summer, all male deer and resident female deer in our study were observed farther than expected from available water. One explanation for this discrepancy is the location of human developments in the study area. The Santa Ana River is paralleled by Highway 38 and several dirt roads for most of its length. Thus, by avoiding human disturbance, many deer occurred farther from water than expected. This interpretation is supported by the strong par-

Comment Letter I9

tial regression coefficient for distance to human developments and the weak one for distance to water in the model for home range for summer. Migratory females, however, by seasonally moving to areas farther from human developments, were able to exploit important resources with less chance for harassment by humans.

We observed significant differences in use of habitat between migratory and resident deer and between adult males and females. Patterns of spatial use by deer in our study suggest that mule deer primarily avoided negative features of the environment, and consequently, often avoided potentially valuable resources at the same time. Migration is a basic response to adversity (Taylor and Taylor, 1977). For deer in the drainage of the Santa Ana River, migration allows individuals to avoid human disturbance and guarantees access to habitats of high quality that are virtually absent from the ranges of resident deer. This likely translated into increased annual reproduction. Indeed, migration may have evolved because individuals opportunistically exploited areas of high quality. Nonetheless, a mixed strategy relative to migration in our study area was selected because deer were at increased risk of predation during migration. Migratory females had higher rates of mortality than did their resident counterparts during years of low precipitation, however, this relationship was reversed in years of normal precipitation. Such differences may be further exacerbated in years with deep snow. This tradeoff between lowered survival, but increased use of resources of higher quality by migratory deer as compared with residents, appears to be an important factor maintaining a mixed strategy for migration in this highly variable environment.

Acknowledgments

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Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, 74:1313–1325.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos, 65:502–513.

Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes & Meier Publishers, Inc., New York, 1012 pp.

Beasom S. L., W. Evans, and L. Temple. 1980. The drive net for capturing western big game. The Journal of Wildlife Management, 44:478–480.

Beasom, S. L., E. P. Wiggers, and J. R. Giardino. 1983. A technique for assessing land surface ruggedness. The Journal of Wildlife Management, 47:1163–1166.

Bischoff, A. I. 1957. The breeding season of some California deer herds. California Fish and Game, 43:91–96.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs, 134:1–50.

Bowers, M. A., D. N. Welch, and T. G. Carr. 1990. Home range size adjustments by the eastern chipmunk, *Tamias striatus*, in response to natural and manipulated water availability. Canadian Journal of Zoology, 68:2016–2020.

Bowyer, R. T. 1981. Activity, movement, and distribution of Roosevelt elk during rut. Journal of Mammalogy, 62:574–582.

———. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy, 65:410–417.

———. 1986. Habitat selection by southern mule deer. California Fish and Game, 72:153–169.

———. 1987. Coyote group size relative to predation on mule deer. Mammalia, 51:515–526.

———. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy, 72:138–145.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe.

Comment Letter I9

1996. Sexual segregation in black-tailed deer: effects of scale. The Journal of Wildlife Management, 70:10–17.

BROWN, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. The Journal of Wildlife Management, 56:246–253.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London, United Kingdom, 234 pp.

CEDERLUND, G., AND H. SAND. 1994. Home-range size in relation to age and sex in moose. Journal of Mammalogy, 75:1005–1012.

COHEN, D. 1967. Optimization of seasonal migratory behavior. The American Naturalist, 101:5–17.

COMMITTEE ON ACCEPTABLE FIELD METHODS IN MAMMALOGY. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. Journal of Mammalogy, 68 (supplement):1–18.

CONOVER, W. J., AND R. L. IMAN. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. The American Statistician, 35:124–130.

DINGLE, H. 1980. Ecology and evolution of migration. Pp. 1–101, *in* Animal migration, orientation, and navigation (S. A. Gauthreaux, Jr., ed.). Academic Press Inc., New York, 387 pp.

EBERHARDT, L. E., E. E. HANSON, AND L. L. CADWELL. 1984. Movement and activity patterns of mule deer in the sagebrush-steppe region. Journal of Mammalogy, 65:404–409.

ESPMARK, Y. 1964. Rutting behavior in reindeer (*Rangifer tarandus* L.). Animal Behaviour, 12:159–163.

FANCY, S. G., AND R. G. WHITE. 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology, 65:122–128.

FORD, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist, 23:315–326.

FRENCH, D. P., M. REED, J. CALAMBOKIDIS, AND J. C. CUBBAGE. 1989. A simulation model of seasonal migration and daily movements of the northern fur seal. Ecological Modelling, 48:193–219.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, 217 pp.

FRYXELL, J. M., AND A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution, 3:237–241.

GARROTT, R. A., G. C. WHITE, R. M. BARTMANN, L. H. CARPENTER, AND A. W. ALLDREDGE. 1987. Movements of female mule deer in Northwest Colorado. The Journal of Wildlife Management, 51:634–643.

GILBERT, P. F., O. C. WALLMO, AND R. B. GILL. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. The Journal of Wildlife Management, 34:15–23.

GOMPPER, M. E., AND J. L. GITTLEMAN. 1991. Home range scaling: intraspecific and comparative trends. Oecologia, 87:343–348.

GRUELL, G. E., AND N. J. PAPEZ. 1963. Movements of mule deer in northeastern Nevada. The Journal of Wildlife Management, 27:414–422.

HAYNE, D. W. 1949. Calculation of size of home range. Journal of Mammalogy, 30:1–18.

HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildlife Monographs, 53:1–55.

HISTØL, T., AND O. HJELJORD. 1993. Winter feeding strategies of migrating and nonmigrating moose. Canadian Journal of Zoology, 71:1421–1428.

HJELJORD, O., N. HOVIK, AND H. B. PEDERSEN. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Holarctic Ecology, 13:281–292.

HUNDERTMARK, K. J. In press. Home range, dispersal and migration. In The ecology and management of North American moose (A. W. Franzmann and C. C. Schwartz, eds.). Smithsonian Institution Press, Washington, D.C.

JOHNSON, R. A., AND D. W. WICHERN. 1988. Applied multivariate statistical analysis. Prentice Hall, Englewood Cliffs, New Jersey, 607 pp.

KIE, J. G., J. A. BALDWIN, AND C. J. EVENS. 1994. CALHOME: home range analysis program. United States Forest Service, Pacific Southwest Research Station, Fresno, California, 19 pp.

KLEIN, D. R. 1965. Ecology of deer range in Alaska. Ecological Monographs, 35:259–284.

KLEIN, D. R., AND S. T. OLSON. 1960. Natural mortality patterns of deer in Southeast Alaska. The Journal of Wildlife Management, 24:80–88.

KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1984. Radio tracking desert mule deer and bighorn sheep with light aircraft. Pp. 115–118, *in* Deer in the Southwest: a workshop (P. R. Krausman and N. Smith, eds.). School of Renewable Natural Resources, University of Arizona, Tucson, 131 pp.

KUFELD, R. C., D. C. BOWDEN, AND D. L. SCHRUPP. 1989. Distribution and movements of female mule deer in the Rocky Mountain foothills. The Journal of Wildlife Management, 53:871–877.

LANGENAU, E. E., JR., AND J. M. LERG. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. Applied Animal Ethology, 2:207–223.

LEOPOLD, A. S., T. RINEY, R. MCCAIN, AND L. TEVIS, JR. 1951. The jawbone deer herd. California Department of Fish and Game, Game Bulletin, 4:1–139.

LOFT, E. R., J. G. KIE, AND J. W. MENKE. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. California Fish and Game, 79:145–166.

LOFT, E. R., J. W. MENKE, AND T. S. BURTON. 1984. Seasonal movements and summer habitats of female black-tailed deer. The Journal of Wildlife Management, 48:1317–1325.

LOFT, E. R., J. W. MENKE, J. G. KIE, AND R. C. BERTRAM. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. The Journal of Wildlife Management, 51:655–664.

MACKIE, R. J., K. L. HAMLIN, AND D. F. PAC. 1982. Mule deer. Pp. 862–877, *in* Wild mammals of North America: biology, management, and economics (J. A. Chapman and G. A. Feldhamer, eds.). The Johns Hopkins University Press, Baltimore, Maryland, 1147 pp.

Comment Letter I9

McCullough, D. R. 1964. Relationship of weather to migratory movements of black-tailed deer. Ecology, 45:249–256.

———. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor, 271 pp.

McNab, B. K. 1963. Bioenergetics and determination of home range size. The American Naturalist, 97:133–140.

Medin, D. E., and A. E. Anderson. 1979. Modeling the dynamics of a Colorado mule deer population. Wildlife Monographs, 68:1–77.

Mielke, P. W. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. Earth-Science Reviews, 31:55–71.

Miquelle, D. G. 1990. Why don't bull moose eat during the rut? Behavioral Ecology and Sociobiology, 27:145–151.

Mohr, C. O. 1947. A table of equivalent populations of North American small mammals. The American Midland Naturalist, 37:223–249.

Molvar, E. M., and R. T. Bowyer. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. Journal of Mammalogy, 75:621–630.

Munz, P. A. 1974. A flora of southern California. University of California Press, Berkeley, 1086 pp.

Nellemann, C. 1991. Terreng som en viktig okologisk faktor. Faginfo, 23:219–226.

O'Bryan, M. K., and D. R. McCullough. 1985. Survival of black-tailed deer following relocation in California. The Journal of Wildlife Management, 49:115–119.

Pac, H. I., W. F. Kasworm, L. R. Irby, and R. J. Mackie. 1988. Ecology of mule deer, *Odocoileus hemionus*, along the east front of the Rocky Mountains, Montana. The Canadian Field-Naturalist, 102:227–236.

Parker, G. A., and R. A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. The American Naturalist, 110:1055–1076.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. The Journal of Wildlife Management, 48:474–488.

Patric E. F., T. P. Husband, C. G. McKiel, and W. M. Sullivan. 1988. Potential of LORAN-C for wildlife research along coastal landscapes. The Journal of Wildlife Management, 52:162–164.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. The Journal of Wildlife Management, 53:7–15.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution, 43:223–225.

Riley, S. J., and A. R. Dood. 1984. Summer movements, home range, habitat use, and behavior of mule deer fawns. The Journal of Wildlife Management, 48:1302–1310.

Robinette, W. L., O. Julander, J. S. Gashwiler and J. G. Smith. 1952. Winter mortality of mule deer in Utah in relation to range condition. The Journal of Wildlife Management, 16:289–299.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. The Journal of Wildlife Management, 43:634–641.

Russell, C. P. 1932. Seasonal migration of mule deer. Ecological Monographs, 2:1–41.

SAS Institute, Inc. 1988. SAS/STAT user's guide release 6.03 edition. SAS Institute, Inc., Cary, North Carolina, 1028 pp.

Scarbrough, D. L., and P. R. Krausman. 1988. Sexual segregation by desert mule deer. The Southwestern Naturalist, 33:157–165.

Schoen, J. W., and M. D. Kirchhoff. 1985. Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, Southeast Alaska. The Journal of Wildlife Management, 49:96–103.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. Users manual for BLOSSOM statistical software. United States Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, 61 pp.

Snyder, J. P. 1984. Map projections used by the U.S. Geological Survey. United States Government Printing Office, Washington, D.C., 313 pp.

Solow, A. R. 1989. A randomization test for independence of animal locations. Ecology, 70:1546–1549.

Taber, R. D., and R. F. Dasmann. 1958. The black-tailed deer of the chaparral: its life history and management in the North Coast Range of California. California Department of Fish and Game, Game Bulletin, 8:1–163.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration, and population mechanics. Nature, 265:415–421.

Van Ballenberghe, V. 1977. Migratory behavior of moose in southcentral Alaska. International Congress of Game Biologists, 13:103–109.

White, R. G., and J. R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. Symposia of the Zoological Society of London, 51:215–232.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology, 70:164–168.

Zalunardo, R. A. 1965. The seasonal distribution of a migratory mule deer herd. The Journal of Wildlife Management, 29:345–351.

Zar, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 718 pp.

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NUTRITIONAL ECOLOGY

Nutrition integrates environmental responses of ungulates

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Summary

1. Nutrition influences most aspects of animal ecology: juvenile growth rates and adult mass gain, body condition, probability of pregnancy, over-winter survival, timing of parturition, and neonatal birth mass and survival. We provide an overview among ungulates of the extent of these influences resulting from interactions among bioenergetics, foraging, and nutritional demands.

2. Body condition of an animal is the integrator of nutritional intake and demands, affecting both survival and reproduction. The deposition and mobilization of body fat and body protein vary with physiological requirements and environmental conditions as species use dietary income and body stores to integrate the profits of summer and the demands of winter. Results from our simulation model and uncertainty analysis of the influence of body mass and changes in body composition of *Rangifer* over winter indicate that percent body fat rather than body mass in early winter is most important in determining whether animals die, live without reproducing, or live and reproduce. Animal responses are also sensitive to rates of change in body protein. Depending on timing of calving and maternal reserves, seasonal habitats vary in their nutritional value for the production of offspring.

3. For free-ranging animals, life is a balance among numerous ecological factors, including nutritional requirements, nutritional resources to meet those demands, and intra- and inter-specific interactions. Predation effects on population demography may mask nutritional limitations of habitat. We suggest that over the long term of life histories, ungulates use seasonal strategies that minimize the maximum detriment, and that the basis for most strategies is nutritional.

Key-words: body condition, body fat, body protein, energetics, nutritional ecology

Introduction

Nutritional ecology is the science of relating an animal to its environment through nutritional interactions, whether those environments are natural ones or managed ones. Although the concept of nutrition is inherent in animal well-being, the implications of nutrition to management and conservation often are not realized. For free-ranging ungulates, nutritional interactions occur at the level of the individual, the population, and the ecosystem. Simplistically, individuals with access to high nutritional food resources often attain larger body sizes and better condition than individuals for which nutrition is inadequate, with subsequent influences on survival and reproduction. Wildlife populations with access to high-quality food often reach higher numbers than when limited by food. In contrast, severe nutritional limitation may provide selection pressure for the evolution of small size (Simard *et al.* 2008). At large ecosystem scales, population dynamics and feeding behaviour can stabilize or destabilize plant community structure (Hobbs 1996). In cases where ungulates limit the abundance and diversity of food supplies, there may be cascading effects that result in the reduction of other guilds or even the extirpation of other species including carnivores (Hazebroek *et al.* 1994; Focardi *et al.* 2000; Berger *et al.* 2001; Allombert *et al.* 2005; Côté 2005).

Considerable research efforts have been directed towards nutritional ecology of ungulates to define the relationships between the environment and the use of energy and nutrients by individuals and populations. Our nutritional knowledge base is broadest for cervids, such as arctic *Rangifer tarandus* (reindeer and caribou) and for north-temperate *Odocoileus* spp. (white-tailed deer, *O. virginianus*; mule deer, *O. hemionus hemionus*; black-tailed deer, *O. h. sitkensis*), *Cervus elaphus* (European red deer and North American elk), and *Alces alces*

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(moose). In addition to studies with specific nutritional emphasis, concepts of nutritional ecology are often embedded within studies of behavioural and population ecology, including long-term studies on red deer, roe deer (*Capreolus capreolus*), mountain goats (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*), chamois (*Rupicapra rupicapra*), and ibex (*Capra ibex*). In this review we present the strength of evidence for nutritional effects on survival and reproduction, and provide an overview of the interactions among bioenergetics, foraging, and nutrition in the field of ungulate ecology. We give examples from a variety of species, and place emphasis on *Rangifer* because that species is circumpolar, usually subjected to extreme seasonality, and likely to be most affected by large changes in climate.

Survival and reproduction depend on environmental constraints and the ability of animals to meet those demands with food and shelter. The need by management agencies and conservation biologists to define limiting factors for ungulate populations has led to numerous collaborations with physiological ecologists. Controlled mechanistic studies using captive or tamed animals at small scales define what animals are physically capable of doing, and thus provide insights for why free-ranging animals use their environments as they do. Field studies describe the strategies that animals use on different landscapes. Together, these two genres of study enable a better understanding of the physiological and behavioural adaptations of ungulates and the nutritional value of habitats.

We explore the following perspectives in our review and by providing a model for reproduction in *Rangifer*:

1. Nutrition is the basis for annual production of ungulates and other animals.
2. Nutrition has more than one currency (see Boggs 2009; Raubenheimer *et al.* 2009). Energy is a common currency for survival, but protein and other cellular components such as water and minerals may drive reproduction.
3. Environmental change alters the amount and quality of food in the time available for production.

Nutritional constraints: biological states and environmental limitations

ENERGY COSTS AND INTAKE

Nutritional constraints for free-ranging ungulates typically have been assumed to be energetic ones, largely because of environmental limitations induced by seasonally changing environments. Metabolic rates for the maintenance of body mass by northern ungulates are generally high compared to other ungulates (Hudson & Christopherson 1985; Hudson & Haigh 2002). In the arctic where food is abundant only over a very short season, higher metabolic rates enable tissue synthesis for growth and replenishment of body reserves during the short summer window (e.g., Lawler & White 2003). The lower energy requirements for maintenance by white-tailed deer in southern environments compared to more northern conspecifics serve as an adaptation to semi-arid environments with limited net primary productivity (Strickland *et al.* 2005). It is unknown whether seasonal cycles in basal metabolism, when corrected for previous intake, occur in all species (Mautz *et al.* 1992). When they do occur, it is unclear whether they are driven by photoperiod-induced appetite or by requirements for maintenance of different tissues and secretions because appetite and metabolic rate are linked to different hormones as well as influenced by the environment (Hudson & Haigh 2002).

Across species, lactation is the biological state when daily energy costs are highest for females. Energy requirements for female ungulates increase 65–215% during the first month post partum (Oftedal 1985; Robbins 1993). Before lactation, >90% of the energy requirements for gestating females occurs during the last trimester, and these costs are almost 50% higher for pregnant than non-pregnant animals (e.g., Pekins *et al.* 1998). Hence, highest energy costs for females occur from late winter to mid summer. For male ungulates, mass-specific seasonal energy requirements are typically highest during the autumn breeding period when animals are most active and when foraging is usually reduced, resulting in mass loss (e.g., bighorn sheep: Pelletier 2005; Himalayan tahr (*Hemitragus jemlahicus*): Forsyth *et al.* 2005; red deer: Yoccoz *et al.* 2002; *Rangifer*: Barboza *et al.* 2004). The consequences of reproductive effort were reviewed by Mysterud *et al.* (2004).

Variable and harsh weather augments seasonal energetic costs, with variable impacts depending on age structure of the population (Coulson *et al.* 2000) and potentially strong cohort effects (Fritz & Loison 2006). A weather-sensitivity hypothesis related to rain, strong wind, and low temperatures explained habitat segregation by male and female red deer (Conradt *et al.* 2000); the higher weather sensitivity of males due to higher energy losses relative to intake rates and the depletion of body reserves during the breeding season may make males more susceptible to the loss of forest cover. Rainfall during cool summer temperatures increased energy costs for black-tailed deer by 28% after 5 h in the rain (Parker 1989), and winter rainfall was a significant predictor of body condition in white-tailed deer (Garroway & Broders 2005). Although they are typically only small increases in metabolic cost, constant supplemental thermoregulatory expenditures can pose cumulative over-winter energetic drains, compounded with effects on daily foraging behaviours (e.g., feral goats (*Capra hircus*): Shi *et al.* 2003; kudus (*Tragelaphus strepsiceros*): Owen-Smith 2002). Managers have used lower and upper limits of thermoneutrality to define the importance of vegetative cover as thermal cover from heat and cold. Of note, the long-time prescriptions for retaining forested stands as thermal cover from temperature and wind for elk populations are now being revisited in light of the contrasting benefits of solar heat gain by wintering animals in non-cover areas (Cook *et al.* 1998). Increased energetic demands associated with cold temperatures, wind and deep snow are the long-standing impetus for the management of deer yards as shelter.

In regions with snowfall, snow depths directly influence the choice of traditional wintering areas, where energy costs are usually lower and food availability is higher (e.g., Sabine *et al.* 2002). Energetic costs of movement increase exponentially depending on sinking depth of the animal, doubling at 60% of brisket height (Hudson & Haigh 2002) and reaching three to eight times the cost of locomotion without snow depending on snow density for both cervids (Parker *et al.* 1984; Fancy & White 1987) and bovids (Dailey & Hobbs 1989). Snow depth is the primary influence on body condition of wintering white-tailed deer (Garroway & Broders 2005) and plays a significant role in energy balance of Alaskan black-tailed deer (Parker *et al.* 1999). Delayed snowmelt increases winter mortality of deer and bighorn sheep (Dumont *et al.* 2000; Jacobson *et al.* 2004) if body reserves are depleted long before new plant growth resumes. Following winters with deep snows, caribou give birth to smaller calves (Adams 2005). Consequently, the cumulative energetic effects of snow over consecutive winters can negatively influence population demography (e.g., Patterson & Power 2002).

Metabolic demands necessitate dietary consequences. For many ungulates characterized by sexual dimorphism, absolute metabolic costs are higher for larger males and relative (per kg) energy costs differ between sexes depending on season, resulting in intra-specific dietary differences (reviewed by Pérez-Barbería *et al.* 2008). Barboza & Bowyer (2000, 2001) proposed a gastrocentric hypothesis for cervids that explains seasonal differences in diet selection and habitat segregation among reproductive females, non-reproductive females, and males. Because reproductive females have higher nutritional demands during gestation and lactation, the requirements for higher dietary minima favour segregation from non-reproductive females and males in late winter and summer, but not during autumn. Reproductive females also increase feeding times in both winter and summer compared to non-reproductive animals. Males, with larger ruminal capacity and longer retention of forages, can subsist on the lowest quality diets. This nutritional basis for segregation of the sexes indicates that differences in foraging behaviour may be a consequence of different metabolic demands rather than social constraints or competitive exclusion.

In environments with prominent seasonal changes, food resources are commonly limited during dormant seasons. Dietary quantity and quality are highly variable, with significant declines in digestible nutrients during the winter or dry season. Consequently, highest intakes of digestible nutrients by herbivores occur in summer or rainy seasons. Seasonal patterns of intake generally coincide with seasonal patterns of reproduction and maintenance (Owen-Smith 2002). Ungulates are able to discriminate between feeding patches on the basis of quantity and quality of food, which has major implications for time budgets and nutritional status (Langvatn & Hanley 1993). Metabolic and nutritional requirements may preclude animals from feeding in areas with low forage abundance or low nutritive value (Cook 2002).

The mechanics of how animals forage for nutritional gain over different temporal and spatial scales, and the physiological and physical factors that influence intake rates have been defined by numerous reductionist studies. Across species, maximum short-term intake rates scale with body mass and correspond with scaling of metabolic rates (Shipley *et al.* 1994). Rates of food intake in relation to food abundance (the functional response of an animal to its nutritional environment) vary directly with bite size and indirectly with fibrousness of the food; they depend further on digestive constraints, gut morphology, and interactions with plant chemistry (Shipley *et al.* 1999; see also Torregrossa & Dearing 2009). Food availability is the main constraint on daily intake at low food abundance, whereas digestive processing capacity limits intake at high food abundance when food quality is low or metabolic demands are very high (Owen-Smith 2002). At high food abundance and high quality, surplus energy intake beyond immediate metabolic needs may be stored. At intermediate food abundance, animals adjust intakes in relation to nutritional values. Food abundance from the animal's perspective includes only available foods that it will consume, and which subsequently support metabolism, growth, and reproduction.

Ungulates use physiological and behavioural mechanisms to accommodate seasonal variation in both their nutritional requirements and the nutritional value of habitats. Presumably to conserve energy, cervids in north-temperate regions reduce intake rates voluntarily in winter (corresponding with natural declines in food availability), even when provided with *ad libitum* access to foods (e.g., black-tailed deer: Parker *et al.* 1993; white-tailed deer: Taillon *et al.* 2006; elk: Hudson & Haigh 2002; moose: Schwartz & Renecker 1998; *Rangifer*: Barboza & Parker 2008). Interestingly, white-tailed deer on low-quality diets reduced food intake less than deer on higher quality food, potentially to compensate for the lower nutrient content of the diet (Taillon *et al.* 2006). Dietary breadth was constrained for white-tailed deer by low forage quality as well as by mobility in snow (Dumont *et al.* 2005). For black-tailed deer, the processing of lower quality food in coastal environments in winter resulted in more time spent ruminating and fewer foraging bouts; deer did not increase time spent foraging to compensate for decreasing dietary quality, perhaps to avoid the high energy costs of movement in snow (Parker *et al.* 1999). They also reduced dietary breadth with decreasing nutritional value of available forages. In contrast, during the adverse dry season in tropical savanna, kudus spent more time active and increased both foraging time and dietary breadth to compensate for declines in forage quality (Owen-Smith 1994). Resource heterogeneity, duration of the dormant season, and the rate of decline in forage quality all affect the seasonal cycle of intake (Illius 2006). Because of interactions between the abundance and value of food resources, the quantity, quality and composition of the diet also vary with changes in population density (Nicholson *et al.* 2006).

Ultimately, nutrient intake, which depends on bite size and the digestible nutrient content of those bites, in relation to nutritional requirements, provides a critical link between food resources and animal performance (Parker *et al.* 1996). Bite sizes taken during foraging are a small-scale process that can have large consequences. The nutritional influence of numerous bites compounds over a foraging bout, a day, and a season to affect growth, survival, and reproduction (reviewed by Shipley 2007). Even small differences in food value can have large influences on animal performance through multiplier effects (White 1983). More than 75% of diet selection by red deer could be attributed to maximizing energy intake during winter and spring (van Wieren 1996), and daily rates of energy intake explained selection of feeding patches (Wilmshurst & Fryxell 1995). As a consequence of snow in winter and the increased demands of lactation in summer, availability of digestible energy was the greatest nutritional limiting factor for black-tailed deer in Alaska (Parker *et al.* 1999). Similarly, white-tailed deer in Quebec consistently preferred diets that were highest in digestible energy content in winter (Berteaux *et al.* 1998), presumably reflecting physiological needs. Energy intake during summer strongly affects body mass gain, including deposition of both body fat and body protein (Allaye Chan-McLeod *et al.* 1994). Energy balance on a year-round basis is generally more sensitive to variations in energy intake than in energy costs (Fancy 1986; Hobbs 1989), and consequently, intake rates drive what is possible in terms of body mass and condition of the animal. Yet animals probably have less control over maximum energy intake, which is largely dependent on plant growth, than their energy expenditures for activity.

PROTEIN DEMANDS

Nutritional constraints for ungulates may be more than just energetic constraints. In addition to short-term elemental or chemical needs that influence movements and distribution of ungulates (Ayotte *et al.* 2006, 2008), there is increasing evidence that protein constraints may be an important nutritional challenge. Protein requirements are typically highest during body growth, which usually coincides with highest forage protein. Neonatal growth of red deer depends on milk protein, and protein to fat ratios in milk are highly correlated with birth mass (Landete-Castillejos *et al.* 2001, 2003). Lactating caribou allocate mostly surplus protein not used for the replacement of maternal protein to milk production (Allaye Chan-McLeod *et al.* 1994, 1999). Male reindeer that lose 23% of body protein during the breeding period and incur potentially more protein losses over winter must rely on spring and summer forage to replenish these protein stores (Barboza *et al.* 2004). Short-term protein intake rates in summer influence the selection of food patches (Langvatn & Hanley 1993).

Similar to energy demands, high-protein demands also can occur when the nutrient content of food resources is low. Protein requirements increase during foetal growth, particularly in late winter when 80% of foetal mass is deposited (Robbins & Robbins 1979; Robbins 1993) and forage protein is lowest of the year. During lactation, protein requirements may increase 110–130% in *Rangifer* (Barboza & Parker 2008), with high early-lactation requirements often occurring before the new growth of plants in spring. For reindeer and caribou that consume large quantities of low-protein lichens during a long winter followed by lactation demands, protein balance can be negative for 7 months of the year (Gerhart *et al.* 1996). Lichens, with their low protein content, are relatively high in digestible energy content, and the ratio of digestible energy to protein is much higher in lichens than in forage species consumed by other cervids during winter (Parker *et al.* 2005). To minimize excretory nitrogen losses and spare the use of body protein, *Rangifer* employs mechanisms such as urea recycling and oxidizing nitrogen from dietary protein (Barboza & Parker 2006, 2008). The extent to which protein is a limiting factor (possibly in addition to energy) has not been researched in detail for many northern wintering ungulates. Northern populations of moose consume winter forages that are near the limits of adequate protein content to support maintenance or reproductive requirements (D.E. Spalinger, unpublished; Schwartz & Renecker 1998). There is also some evidence from sapling fertilization experiments suggesting that white-tailed deer discern differences in protein content of individual plants and increase foraging rates on browse species with highest protein content during winter (Tripler *et al.* 2002).

Animal condition: mass, body fat, body protein

Body condition of an animal is the integrator of its location-specific energy and protein demands and its food intake, and the potential driver of demographic variation. Male ungulates are typically in best condition in autumn before the breeding season and in worst condition in late winter. By comparison, timing of highest and lowest body condition is delayed for reproductive females. Females are typically in best condition at the onset of winter when their nutritional demands are lowest and in worst condition 2–3 weeks after parturition in spring. Body size and condition, as indicators of habitat and weather (Hobbs 1989), have direct consequences to reproduction and population dynamics. The probability of conceiving and carrying a foetus to term is determined primarily by summer conditions and autumn body mass (e.g., caribou: Cameron *et al.* 1993; Gerhart *et al.* 1996; Cook *et al.* 2004a). Timing of parturition, birth mass, and early survival of offspring are closely linked to winter and spring nutrition (e.g., reindeer: Skoogland 1989; Dall's sheep (*O. dalli*): Rachlow & Bowyer 1991; bison (*Bison bison*): Berger 1992; moose: Keech *et al.* 2000; elk: Cook 2002). Physiological indicators reflecting changes in condition, food intake, and stress were reviewed by Parker (2003).

BODY MASS

Nutritional resources available in summer and autumn are used by juveniles to increase the likelihood of attaining a body mass that enables them to survive winter. Because of their smaller size, limited body reserves, and relatively higher metabolic demands, juveniles are most susceptible to harsh conditions. Juvenile survival, which determines recruitment, is commonly the key factor in the dynamics of their populations (Gaillard *et al.* 1998, 2000; Coulson *et al.* 2001). Elk calves with access to higher nutritional levels reach larger body sizes; and the larger the body mass at the beginning of winter, the more days they survive (Cook *et al.* 2004a). Body mass at the beginning of winter was also the best predictor of over-winter survival by white-tailed deer fawns (Taillon *et al.*

Comment Letter I9

2006). In areas with winter supplemental feeding programs to reduce loss of body mass, higher dietary intake may increase nutritional status by reducing endogenous tissue catabolism (Tarr & Pekins 2002; Page & Underwood 2006); and the heat increment from additional feeding may compensate for much of the energetic costs of thermoregulation associated with winter severity (Jensen *et al.* 1999). Pettorelli *et al.* (2003) suggested that the presence of key preferred plant species in maternal home ranges shapes winter body mass of roe deer fawns; others also have noted the overwhelming importance of habitat quality in determining body mass of juveniles (Côté & Festa-Bianchet 2001; Ericssen *et al.* 2002; Kjellander *et al.* 2006). Juvenile size, whether influenced by variation in environmental conditions or density-induced nutritional limitations, also affects age at first reproduction (e.g., Solberg & Saether 1994; Gaillard *et al.* 2000) and subsequent adult body mass (e.g., Pettorelli *et al.* 2002). Given that compensatory growth is rare (e.g., Feder *et al.* 2008, but see Toïgo *et al.* 2006), animals that are born small or have restricted early growth rates often remain compromised as smaller adults that are likely to produce fewer offspring over their lifetimes (Gaillard *et al.* 2003).

Regain of the body mass lost during winter is critical for adults, which typically mobilize body reserves because of reduced forage resources. Losses in body mass for northern ungulates over winter commonly range from 15–30%, with highest absolute and proportional losses incurred by the largest animals (Parker *et al.* 1993; Allaye Chan-McLeod *et al.* 1999; Hudson & Haigh 2002; Festa-Bianchet & Côté 2008). The timing for when mass regain occurs has important implications for critical habitats. Female caribou lose body mass for approximately 3 weeks following calving because of the high costs of lactation (Parker *et al.* 1990). They subsequently put on significant body mass during the summer period, emphasizing the importance of good summer habitats to regain body condition before winter. This strategy contrasts with another Arctic ungulate, the muskox (*Ovibos moschatus*), which after calving maintains that body mass (without losing additional mass) through the summer, and then relies on autumn habitats to regain mass and condition (Parker *et al.* 1990). The nutritional contribution of summer versus autumn habitats, therefore, may differ among species even within similar regions. Heavier females are more likely to reproduce and to produce offspring earlier than lighter females (e.g., Cameron *et al.* 1993; Gerhart *et al.* 1997; Adams & Dale 1998; Festa-Bianchet *et al.* 1998). There also may be nutritional consequences of adult body sizes to sex of the offspring. Reindeer mothers with high body mass in autumn are more likely to produce male calves the following spring (Holand *et al.* 2006); male calves, which are usually heavier at birth, require greater maternal investment.

BODY FAT

Body fat is the major energy reserve of the body. The year-round body fat cycle for ungulates in northern environments where energy costs exceed forage energy in winter was aptly described by Mautz (1978). Carry-over or temporally lagged effects of previous nutritional deprivation may ultimately affect pregnancy rates if animals are unable to replenish reserves following severe winters or successive years of producing young (Fig. 1). Garroway & Broders (2007) noted that the winter severity of one year *before* gestation (not the winter during which gestation took place) reduced the probability of producing a foetus. This suggests an adaptive ability to divert energy away from reproduction as a consequence of environmental constraints. Others have posed a 'selfish cow' explanation (Russell *et al.* 1993, 2005) in which mature females conserve maternal condition for self maintenance and future reproduction at the expense of allocating already depleted resources to potentially smaller offspring that have low chances of survival (Clutton-Brock *et al.* 1989). Similarly, if producing and supporting a neonate drains maternal body stores excessively, the next pregnancy may be compromised (Cameron 1994; Gerhart *et al.* 1997; Cook 2002; Hudson & Haigh 2002) (Fig. 1). Not reproducing every year may better ensure survival and higher lifetime reproduction (Festa-Bianchet & Côté 2008).

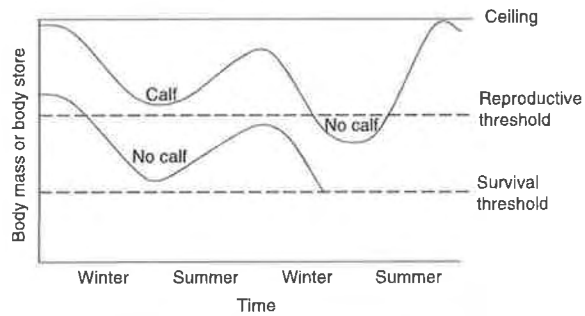

Fig. 1. Conceptual model of the seasonal relationships and lag effects among body mass or body stores, thresholds for survival and reproduction, and calf production by ungulates.

Autumn body fat levels depend largely on summer-autumn nutrition. Even with high energetic costs of lactation during summer causing body fat levels of females to be 50% less than non-lactating animals, lactating females can accrue as much fat by mid-autumn as non-lactating animals, assuming adequate summer forage quality (e.g., Cook *et al.* 2004a). Failure to breed is a function of low body fat levels in elk (Cook *et al.* 2004a, 2004b), caribou (Gerhart *et al.* 1996; Gustine *et al.* 2007), and moose (Heard *et al.* 1997). Body fat thresholds indicating sufficient condition for pregnancy have been proposed for elk (>5%, Cook *et al.* 2004a) and caribou (6–7·8%, Crête *et al.* 1993; Ouellet *et al.* 1997). Elk females with the most body fat breed at earlier dates in autumn (Cook *et al.* 2004a). Higher fat levels in moose increase the likelihood of pregnancy, twinning, and larger calves (Heard *et al.* 1997; Testa & Adams 1998; Keech *et al.* 2000). From an adaptive standpoint, young of the year accumulate larger fat reserves in areas with severe winter conditions, particularly in northern environments (Lesage *et al.* 2001; Kjellander *et al.* 2006). The maximum fat reserve accumulated in autumn by fawns, when coupled with the forage energy available during winter, may set the northern limits of white-tailed deer range in North America (Lesage *et al.* 2001). Juvenile mountain goats living in harsh mountain environments may accumulate energy reserves at the expense of body growth (Festa-Bianchet & Côté 2008).

Winter and spring body fat levels buffer the effects of declining food supplies when energetic demands can not be met by foraging alone (Parker *et al.* 1999). With low fat levels, there may be increased incidence of embryonic mortality in some species (caribou: Russell *et al.* 1998), although there is strong selection to maintain pregnancy at almost any cost in other species (elk: Cook *et al.* 2002). Differences in body condition thresholds for aborting the foetus may reflect the likelihood of recovering condition during gestation; long winters limit recovery of body condition lost in early winter and favour a greater incidence of abortion in caribou. Under adverse conditions females in poor condition may extend gestation length to potentially match calving date with maximum plant production (red deer: Garcia *et al.* 2006). The interaction between nutritional condition and available food resources also may influence timing of movements to spring ranges. Winter feeding programs that increase nutritional status can induce behavioural effects of postponed migration by prolonging nutrient availability of natural forages (mule deer: Peterson & Messmer 2007).

BODY PROTEIN

More recently, some studies have addressed the role of protein in body condition (DelGiudice *et al.* 2001). To meet energy demands, mobilization of body protein may be necessary to supplement mobilization of body fat by malnourished animals. Rates of protein depletion are usually less than fat depletion (Parker *et al.* 1993; Barboza & Parker 2006), but tissue wasting may increase significantly when fat stores are depleted. Reindeer are in negative protein balance in winter when >46% of excreted urea-nitrogen originates from body tissue (Barboza & Parker 2006). To meet protein demands, dietary protein usually is used before body protein, but intake of very low-protein foods may necessitate the use of additional body protein, and possibly impact foetal growth and neonatal mass. In *Rangifer*, calf mass at birth is correlated with maternal protein reserves (Allaye Chan 1991). Those reserves are mobilized during pregnancy and early lactation (Barboza & Parker 2008), and the replacement of maternal protein reserves in summer becomes critical for future foetal investment.

Barboza & Parker (2008) provided evidence that the resilience of *Rangife*r populations to changing environments may be influenced by their ability to alter timing and allocation of body protein to reproduction. Both caribou and reindeer rely on body protein for most of foetal growth and for calf growth during the first month of lactation. On one end of a continuum for body capital and dietary income, reindeer with large fat reserves and relatively sedentary behaviour are able to spare the use of body protein to meet energetic demands during winter. Because they calve approximately one month earlier than caribou, they must rely on body stores (capital) that were put down in the autumn to produce a calf. On the other end of this continuum, caribou that migrate and calve later in spring closer to spring green-up can use more income from the diet at calving grounds that have predictable timing of plant growth for calf production. Hence, depending on the timing of calving, autumn habitats versus spring habitats vary in their nutritional value for the production of offspring. Across species, Moen *et al.* (2006) posited that most large herbivores in arctic and alpine areas are closer to the capital breeder end of the continuum. Body reserves in capital breeders serve as insurance against unforeseen conditions during winter and early spring (Fauchald *et al.* 2004). Capital breeders such as bighorn sheep and Soay sheep (*O. aries*) provide initial post-natal care from body reserves and are less affected by temporal mismatches between vegetation green-up and birth date (Durant *et al.* 2005). Roe deer are the ultimate income breeder, which does not accumulate body reserves or change condition substantively throughout the year and which times birthing to match a less variable spring green-up (Andersen *et al.* 2000).

Energy versus protein: influence on animal response

Researchers have tended to concentrate on energy costs, available forage energy, and body fat more than protein demands, forage protein intake, and body protein, but the two nutritional currencies are clearly linked in defining the role of nutrition in population dynamics. High-energy high-protein diets of spring and summer allow ungulates to regain mass and condition, replenishing the endogenous reserves that are necessary for over-winter survival and foetal growth (Fig. 1). These diets also support the high energetic costs of lactation and the protein demands for neonatal growth. Under poor nutritional conditions, foetal growth and milk production may be impaired (Oftedal 1985). Winter diets, even with low digestible energy and/or protein content, reduce the extent of mobilization of body reserves, allowing animals to survive winter deficits. Experimental approaches using matched diets indicate that cervids may be able to discriminate between dietary energy and protein (Berteaux *et al.* 1998). Consequently, selection that assumes some nutritional wisdom would be expected to vary with biological state and a constantly changing environment. Seasonal losses and gains in body condition are probably less variable than intakes and diet, and more representative of an animal's physiological needs.

Changes in body fat and body protein enable different animal responses. Over winter, the mobilization of fat and protein stores acquired primarily in summer determines whether animals (i) die, (ii) live without reproducing, or (iii) live and reproduce. We posed the question: does body mass, fat, or protein have the greatest influence on animal response? Population trends result as a consequence of variation around condition and rates of change in condition. To assess the relative importance of that variation, we developed a simulation

Table 1. Parameters (mean ± SD) used in the simulation model and uncertainty analysis of the importance of peak body mass, and changes in body fat and protein reserves during winter by *Rangifer* to animal responses at the end of winter. Rates of change in body fat and protein differed between reproductive and non-reproductive caribou and reindeer

	*Rangifer**		Percent contribution to animal response†	
Parameter	Caribou	Reindeer	Caribou	Reindeer
Body mass (kg)	109·8 ± 12·0	119·7 ± 16·2	0·05	1·0
Body fat (%)	16 ± 8	20 ± 9	61·8	39·3
Body protein (%)	18 ± 2	17 ± 2	16·0	9·2
Change in body fat (g $kg^{-0.75}$ day^{-1})			4·5	23·0
Pregnant	−0·22 ± 0·37	−1·69 ± 1·45		
Not pregnant	0·00 ± 0·95	0·49 ± 0·87		
Change in body protein (g $kg^{-0.75}$ day^{-1})			17·7	27·5
Pregnant	−0·83 ± 0·54	−1·66 ± 0·79		
Not pregnant	−0·51 ± 1·94	0·09 ± 1·10		
Died (%)‡	22·2 ± 1·4	72·6 ± 1·4		
Lived without calf (%)‡	9·4 ± 0·8	6·8 ± 0·8		
Lived with calf (%)‡	68·3 ± 1·5	20·6 ± 1·4		

*Data are from Barboza & Parker (2008).
†Based on results of uncertainty analyses using the contribution of the relative partial sum of the squares in regressions predicting animal response.
‡Animal response as predicted by the simulation model (see text).

model using peak body mass and associated body composition, and the changes in mass and condition of adult females over winter. The rates of change are a quantification of how animals integrate their energy losses and nutritional gains.

For this exercise, we used data for *Rangifer*, a species that is documented to be limited by energy or protein constraints, or both (data from Barboza & Parker 2008). We generated normal distributions (based on means and SD) for initial body mass, percent body fat and protein, and rates of change in body fat and protein per unit metabolic mass to adjust for allometric differences in demand (Table 1). For each run of the model, we randomly sampled from these five distributions using 1000 simulations to predict animal response. Feasible ratios of body fat to body protein were set between 0·123 and 2·058 for a plausible animal (data from Barboza & Parker 2008). We assumed a minimum of 6% body fat for reproduction (Ouellet *et al.* 1997). We used the following criteria for animal response at the end of a 23-week period in winter (from peak body mass to parturition): (i) Animals died if either final body fat was <3% or final body protein was <65% of initial body protein. Minimum possible fat content was 3% based on the composition of young *Rangife*r (Gerhart *et al.* 1996). The labile protein store was 35% of peak body protein based on the seasonal gain of body protein in adult females (Barboza & Parker 2006). (ii) Animals lived if body fat was ≥3% and final body protein was ≥65% of initial body protein. (iii) Animals reproduced if the protein ≥65% of initial body protein was >0·67 kg protein, as estimated from Gerhart *et al.* (1996) for a minimum-sized viable *Rangifer* calf weighing 3·9 kg (Skoogland 1989; Adams 2005). For both caribou and reindeer, we ran the model 25 times (1000 simulations each) and then summarized the resulting outcomes (Table 1). Given these parameters and their inherent variation, the model predicted higher incidence of successful reproduction and lower mortality by caribou than reindeer. The capital strategy of reindeer relies on using stores of both fat and protein for both survival and reproduction. Conversely, the income strategy of caribou is associated with low rates of fat and protein loss from stores of body fat and protein that are similar to reindeer. Severe winters increase the rates of fat and protein loss and therefore increase the likelihood of death or reproductive failure in both caribou and reindeer. Changes in food intake, however, could partially compensate for high rates of energy and protein loss. The model responses are driven by variation around the parameters, and may not reflect conditions experienced within a particular herd of free-ranging *Rangifer* or the ability of the animal to vary food intake. In the model, high mortality of reindeer reflects the importance of restoring body tissue from diet for capital breeders with high rates of protein and fat loss.

We then evaluated the effects of the input parameters (Table 1) on the predicted animal response. These uncertainty analyses assessed the relative influence of initial body mass and composition, and the changes in body fat and protein on the three animal responses across the range of variation of all input parameters (Latin hypercube design, Swartzman & Kaluzny 1987). For each analysis we considered each of the five input parameters to be uniformly distributed between the mean ± 2 SD. We divided each distribution into 1000 equal intervals, and for each of 1000 iterations, we randomly sampled each parameter without replacement. The input values for each parameter and predicted responses were saved. After ranking the parameters, we regressed the dependent variable (animal response) against the independently selected ranked parameters. To remove the potential effects of the other parameters in the regression, we calculated the relative partial sum of squares (RPSS, SAS Institute Inc. 2005) (Bartell *et al.* 1986; Swartzman & Kaluzny 1987), and then calculated the percent contribution of each parameter (its RPSS) as a percentage of the sum of the RPSS. Parameters with high contributions to the total RPSS are those that had a relatively higher contribution to modelled animal response.

Peak body mass explained little variation in the modelled responses over winter for adult female caribou or reindeer. Rather, percent body fat had the greatest influence as a single parameter in determining whether animals died, lived without reproducing, or lived and reproduced at the end of the 23-week period (Table 1). In caribou, animal response was also sensitive to percent body protein and to rates of protein change. In reindeer, the rates of change in protein and fat together explained more variation in animal response than percent body fat. These results underscore the importance of fat and fat dynamics, which have been well studied and incorporated in specific models of energy balance (e.g., Hudson & White 1985; Hobbs 1989; Russell *et al.* 1993; Moen *et al.* 1998; Parker *et al.* 1999; Russell *et al.* 2005). However, the results also indicate that protein may contribute substantively to animal response. Interestingly, when we ran simulations that increased the mean rates of both protein and fat loss of caribou to those of reindeer, there was greater sensitivity to protein loss (28·2% vs. 17·7 % and less sensitivity to initial fat content (39·9% vs. 61·8%). Protein stores therefore become more important as winter severity increases for animals such as caribou that use smaller body stores of fat and rely more on dietary income for reproduction. Increasing the range of body fat content in caribou to that of reindeer reduced the sensitivity to the rate of protein loss, as body fat spares body protein. For juvenile animals without extensive body fat and protein reserves, body mass associated with body size directs survival (e.g., Toïgo *et al.* 2006).

Minimizing the maximum detriment to free-ranging ungulates

For free-ranging ungulates, life is a balance among numerous ecological factors that include nutritional requirements, availability of nutrients to meet those needs, and intra- and inter-specific interactions. Constraints to resource gain in a habitat may be digestive, metabolic, thermal, or the risk of mortality (Owen-Smith 2002). Animals may select forages defended by toxic plant chemicals if the nutrient content outweighs the negative effects (McArthur *et al.* 1993). Animals may alter foraging patterns to avoid thermal costs or forage during heat and cold stress if the nutrient gains from food resources outweigh the costs (Dussault *et al.* 2004; Maloney *et al.* 2005; Hay *et al.* 2008). Animals may forego the best foraging opportunities to avoid predation risk, particularly when it is associated with reproduction (e.g., Festa-Bianchet 1988; Poole *et al.* 2007). Field biologists strive to define *what* and *when* is most critical to sustain populations. We suggest that over the long term of life histories, animal strategies tend to minimize the maximum detriment to fitness, and that the underlying foundation of the detriment is nutritional.

In winter, the maximum detriment to the individual and the population would be to have low body stores that reduce adult survival or foetal development. Consequently, animal strategies should minimize energy costs and the loss of protein stores. Numerous studies have shown that ungulates reduce activity in winter (and corresponding increased energetic costs in snow and in very cold temperatures) when food quantity and quality are limited (e.g., Cook 2002; van Oort *et al.* 2007) and daily food intake can decline by 70% compared to summer (Parker *et al.* 1999). Under extreme conditions, animals partition the use of reserves down to the minimum by eating and resting, with minimal other activity. This reduced mobilization of fat reserves to meet energetic demands also spares the use of body protein. In spring, the maximum detriment would be unsuccessful calving or failed parturition. Predation pressure is usually biased towards juveniles in most ungulate populations (Linnell *et al.* 1995; Fritz & Loison 2006). Consequently, animals should avoid predation risk in areas where large carnivores are present and maximize intake of high-quality forage (digestible energy and protein). Caribou, for example, commonly avoid areas of high vegetation biomass if those areas are associated with high predation risk, and may use topography to increase segregation from predators (Barten *et al.* 2001; Griffith *et al.* 2002). Parturient caribou forage selectively though in areas of relatively high vegetation quality to meet the nutritional requirements of lactation (Gustine *et al.* 2006). In summer, the maximum detriment would be mass and condition regains by adults that are insufficient for breeding and growth rates of calves that are too low for over-winter survival. Animals must maximize intake to avoid compromising these gains. For black-tailed deer, intake rates in summer compared to winter were four times higher for digestible energy and 10 times higher for digestible protein (Parker *et al.* 1999). Adult females had intake rates per kilogram that were twice as high as males at the end of summer following high lactation demands. Red deer and reindeer in Scandinavia use a diversity of altitudes and aspects to continually access high-quality (protein and energy) forage, resulting in larger autumn body mass (Albon &Langvatn 1992; Mysterud *et al.* 2001), and minimizing the potential consequence of lower mass regains during summer. By following snowmelt patterns to higher altitudes, animals access high-quality emerging shoots 'in spring conditions as long as possible during the summer' (Moen *et al.* 2006). Similarly, Stone's sheep (*O. dalli stonei*) track a phenological gradient of high forage protein by moving up in elevation as the growing season progresses (Walker *et al.* 2006). In autumn, the maximum detriment would be if breeding was not successful or if body reserves were not sufficient for over-winter survival. Animals should continue to maximize intake where possible, and begin to decrease energy costs. Females often allocate more time than males to foraging during the breeding season, but males increase their foraging times significantly post-breeding (Bunnell & Gillingham 1985) even though they may not always recover the body mass they lost during breeding before winter (Barboza *et al.* 2004). Given these seasonal strategies, animals should select for high nutritional value in spring, summer, and autumn before the dormant season. From an applied perspective, habitats should be managed or conserved to provide the widest window of nutrient gain between spring and autumn for both genders.

Free-ranging ungulates typically show flexibility or plasticity within seasonal strategy. At large spatial and temporal scales, there is often more than one way for animals to use the landscape and get to the same endpoint of having sufficient body condition to survive and reproduce. Rettie & Messier (2000) proposed that the factors with the greatest potential to limit individual fitness are those that influence large-scale selection. They also noted that there may be a hierarchy of limiting factors. As an example, woodland caribou (*R. t. caribou*) selected calving areas that tended to be at higher elevations and steeper than the landscape around them, have relatively low risk of predation by wolves (*Canis lupus*) compared to the areas around them, and have relatively low vegetation biomass (Gustine *et al.* 2006). The calving sites that caribou chose within the general calving areas had lower risk of grizzly bear (*Ursus arctos*) predation and relatively high vegetation quality despite low biomass. Caribou subsequently moved to summering areas with higher vegetation quantity, thereby maximizing nutrient intake. From Rettie & Messier's perspective, predation affecting large-scale selection may be the proximate factor most limiting individual fitness, as observed for numerous woodland caribou populations (e.g., Chowns & Gates 2004). Within hierarchical selection, nutritional attributes defined the choice of calving sites and summer habitats. From the strategy of minimizing the maximum detriment, both factors (nutrition and predation) are significant. Similarly, barren ground caribou (*R. t. granti*) move to calving grounds on the Arctic Coastal Plain of Alaska in response to predictable green-up of high-quality vegetation and reduced predation risk; and move away from calving grounds to summering areas with higher forage biomass (Griffith *et al.* 2002).

Nutrition matters to population health even if predation is a limiting factor (e.g., Brown & Mallory 2007; Brown *et al.* 2007). Poor nutrition contributes to the high rate of predator-caused mortality for juveniles (Mech 2007). Maternal nutrition during winter may also predispose neonates to early death if body condition or foetal development is compromised (Roffe 1993). Furthermore, predation on neonates may result in increased body condition of adult females. Females that are relieved of the energetic constraints of lactation can regain mass quickly to conceive the next fall (Allaye Chan-McLeod *et al.* 1999). Predator removal may benefit short-term recruitment, but higher gestational and lactational demands on adult females can ultimately result in lower pregnancy rates and recruitment for the population if the nutritional value of habitats is lacking.

Conclusion and perspectives

Food and nutrient availability are the ultimate causes of the reproductive cycle of ungulates (Pekins *et al.* 1998), but there are complex interactions between internal physiological regulators and the external environment (Schwartz & Renecker 1998). The cycle is both restricted and adaptive, with dates of conception and parturition in synchrony with cycles of body reserves and the onset of spring green-up. Late winter and early spring may be a critical time in the bioenergetics of ungulates when body stores are depleted and when nutritional demands increase for gestation and lactation. Although bottlenecks to individual survival and population growth are associated with the dormant season for many large herbivores and there has been emphasis placed on the importance of resources used then (Illius 2006), those resources are *not* necessarily the key factor determining population size. Nutrient availability in summer drives replenishment of body reserves and subsequent reproductive success (Fig. 1). Because reserves are not deposited without limit, of course food resources in winter are also important. Our model describing differences in the reproductive strategies of two *Rangifer* subspecies synthesizes the interactions between body fat representing the profits of summer and rates of body protein and fat loss reflecting winter severity. Some researchers have reported that digestible energy in summer regulates populations because of its influence on condition and probability of reproduction (elk: Cook *et al.* 2004a); others have shown that protein constrains reproduction (*Rangifer*: Barboza & Parker 2008). Differences in energy and nutrient demands between reproductive and non-reproductive animals lead to differences in the timing of deposition and mobilization of body tissues (Allaye Chan-McLeod *et al.* 1999). Hence, nutrient partitioning and allocation strategies vary among ungulates given different physiological demands and environmental conditions, including habitat, topography, weather and predation.

As environmental conditions change, survival and reproduction will depend on whether habitats can meet animal demands. Climatic fluctuations influence demography through direct effects of snow depth and hardness, and energetic demands on winter survival and foetal development (Post & Stenseth 1998, 1999; Forchhammer *et al.* 2001; Patterson & Power 2002; Moen *et al.* 2006) and through indirect effects of increased vulnerability to predation in deep snow (Post & Stenseth 1998, 1999; DelGiudice *et al.* 2002). Climatic changes to precipitation regimes may alter the timing of both spring and fall movements (Sabine *et al.* 2002) and the onset of spring green-up (Pettorelli *et al.* 2005), which subsequently affect maternal condition and juvenile growth rates. Inter-annual variation in plant phenology caused by climatic variability particularly in northern, arctic, alpine, and mountainous environments may induce variation in the timing of parturition (Post *et al.* 2003), number of calves born (Post & Forchhammer 2008), and growth and survival of juveniles (Weladji & Holand 2003; Pettorelli *et al.* 2007). To forecast the effects of long-term climate or anthropogenic changes on timing, duration, and abundance of resources (Durant *et al.* 2005) and the responses of ungulates to those changes, it is important to understand how different species use dietary income and body stores to integrate the profits of summer and the demands of winter.

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References

Adams, L.G. (2005) Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. *Journal of Mammalogy*, **86**, 506–513.

Adams, L.G. & Dale, B.W. (1998) Reproductive performance of female Alaskan caribou. *Journal of Wildlife Management*, **62**, 1184–1195.

Albon, S.D. & Langvatn, R. (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, **65**, 502–513.

Allaye Chan, A.C. (1991) *Physiological and ecological determinants of nutrient partitioning in caribou and reindeer*. PhD thesis, University of Alaska, Fairbanks.

Allaye Chan-McLeod, A.C., White, R.G. & Holleman, D.F. (1994) Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. *Canadian Journal of Zoology*, **72**, 938–947.

Allaye Chan-McLeod, A.C., White, R.G. & Russell, D.E. (1999) Comparative body composition strategies of breeding and nonbreeding female caribou. *Canadian Journal of Zoology*, **77**, 1901–1907.

Allombert, S., Gaston, A.J. & Martin, J.-L. (2005) A natural experiment on the impact of overabundant deer on songbird populations. *Biological Conservation*, **126**, 1–13.

Andersen, R., Gaillard, J.-M., Linnell, J.D.C. & Duncan, P. (2000) Factors affecting maternal care in an income breeder, the European roe deer. *Journal of Animal Ecology*, **69**, 672–682.

Ayotte, J.B., Parker, K.L. & Gillingham, M.P. (2008) Use of natural licks by four ungulate species in north-central British Columbia. *Journal of Mammalogy*, **89**, 1041–1050.

Ayotte, J.B., Parker, K.L., Arocena, J.M. & Gillingham, M.P. (2006) Chemical composition of lick soils: functions of soil ingestion by four ungulate species. *Journal of Mammalogy*, **87**, 878–888.

Barboza, P.S. & Bowyer, R.T. (2000) Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy*, **81**, 473–489.

Barboza, P.S. & Bowyer, R.T. (2001) Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces*, **37**, 275–292.

Barboza, P.S. & Parker, K.L. (2006) Body protein stores and isotopic indicators of N balance in female reindeer (*Rangifer tarandus*) during winter. *Physiological and Biochemical Zoology*, **79**, 628–644.

Barboza, P.S. & Parker, K.L. (2008) Allocating protein to reproduction in arctic reindeer and caribou. *Physiological and Biochemical Zoology*, **81**, 835–855.

Barboza, P.S., Hartbauer, D.W., Hauer, W.E. & Blake, J.E. (2004) Polygynous mating impairs body condition and homeostasis in male reindeer (*Rangifer tarandus tarandus*). *Journal of Comparative Physiology B*, **174**, 309–317.

Bartell, S.M., Breck, J.E., Gardner, R.H. & Brenkert, A.L. (1986) Individual parameter perturbation and error analysis of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 160–168.

Barten, N.L., Bowyer, R.T. & Jenkins, K.J. (2001) Habitat use by female caribou: tradeoffs associated with parturition. *Journal of Wildlife Management*, **65**, 77–92.

Berger, J. (1992) Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology*, **73**, 323–329.

Berger, J., Stacey, P.B., Bellis, L. & Johnson, M.P. (2001) A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications*, **11**, 947–960.

Berteaux, D., Crête, M., Huot, J., Maltais, J. & Ouellet, J.-P. (1998) Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*, **115**, 84–92.

Boggs, C. (2009) Understanding insect life histories and senescence through a resource allocation lens. *Functional Ecology*, **23**, 27–37.

Brown, G. & Mallory, F. (2007) *A Review of Ungulate Nutrition and the Role of Top-Down and Bottom-Up Forces in Woodland Caribou Population Dynamics*. National Council for Air and Stream Improvement, Inc. Technical Bulletin 934, Research Triangle Park, North Carolina.

Brown, G.S., Landriault, L., Sleep, D.J.H. & Mallory, F.F. (2007) Comment arising from a paper by Wittmer *et al.*: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. *Oecologia*, **154**, 485–492.

Bunnell, F.L. & Gillingham, M.P. (1985) Foraging behaviour: dynamics of dining out. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 53–79. CRC Press, Inc., Boca Raton.

Cameron, R.D. (1994) Reproductive pauses by female caribou. *Journal of Mammalogy*, **75**, 10–13.

Cameron, R.D., Smith, W.T., Fancy, S.G., Gerhart, K.L. & White, R.G. (1993) Calving success of female caribou in relation to body weight. *Canadian Journal of Zoology*, **71**, 480–486.

Chowns, T. & Gates, C.C. (2004) *Ecological Interactions among Caribou, Moose, and Wolves: Literature Review*. National Council for Air and Stream Improvement, Inc. Technical Bulletin 893, Research Triangle Park, North Carolina.

Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. (1989) Fitness costs of gestation and lactation in wild mammals. *Nature*, **337**, 260–262.

Conradt, L., Clutton-Brock, T.H. & Guinness, F.E. (2000) Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour*, **59**, 1049–1060.

Cook, J.C. (2002) Nutrition and food. *North American Elk: Ecology and Management* (eds D.E. Toweill & J.W. Thomas), pp. 259–349. Smithsonian Institution Press, Washington.

Cook, R.C., Cook, J.G., Garrott, R.A., Irwin, L.L. & Monfort, S.L. (2002) Effects of diet and body condition on fecal progestagen excretion in elk. *Journal of Wildlife Diseases*, **38**, 558–565.

Cook, J.G., Irwin, L.L., Bryant, L.D., Riggs, R.A. & Thomas, J.W. (1998) Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. *Wildlife Monographs*, **141**, 1–61.

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. & Irwin, L.L. (2004a) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.

Cook, R.C., Cook, J.G. & Mech, L.D. (2004b) Nutritional condition of northern Yellowstone elk. *Journal of Mammalogy*, **85**, 714–722.

Côté, S.D. (2005) Extirpation of a large black bear population by introduced white-tailed deer. *Conservation Biology*, **19**, 1668–1671.

Côté, S.D. & Festa-Bianchet, M. (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia*, **127**, 230–238.

Coulson, T., Milner-Gulland, E.J. & Clutton-Brock, T.H. (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society of London B*, **1454**, 1771–1779.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.

Crête, M., Huot, J., Nault, R. & Patenaude, R. (1993) Reproduction, growth, and body composition of Rivière George caribou in captivity. *Arctic*, **46**, 189–196.

Dailey, T.V. & Hobbs, N.T. (1989) Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology*, **67**, 2368–2375.

DelGiudice, G.D., Moen, R.A., Singer, F.J. & Riggs, M.R. (2001) Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. *Wildlife Monographs*, **147**, 1–60.

DelGiudice, G.D., Riggs, M.R., Joly, P. & Pan, W. (2002) Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management*, **66**, 698–717.

Dumont, A., Crête, M., Ouellet, J.-P., Huot, J. & Lamoureux, J. (2000) Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. *Canadian Journal of Zoology*, **78**, 764–776.

Dumont, A., Ouellet, J.-P., Crête, M. & Huot, J. (2005) Winter foraging strategy of white-tailed deer at the northern limit of its range. *Ecoscience*, **12**, 476–484.

Durant, J.M., Hjermann, D.Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. & Stenseth, N.C. (2005). Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters*, **8**, 952–958.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L. & Larochelle, J. (2004) Behavioural responses of moose to thermal condition in the boreal forest. *Ecoscience*, **11**, 321–328.

Ericsson, G., Ball, J.P. & Danell, K. (2002) Body mass of moose calves along an altitudinal gradient. *Journal of Wildlife Management*, **66**, 91–97.

Fancy, S.G. (1986) *Daily energy budgets of caribou: a simulation approach*. PhD thesis, University of Alaska, Fairbanks.

Fancy, S.G. & White, R.G. (1987) Energy expexpenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*, **65**, 122–128.

Fauchald, P., Tveraa, T., Henaug, C. & Yoccoz, N. (2004) Adaptive regulation of body reserves in reindeer, *Rangifer tarandus*: a feeding experiment. *Oikos*, **107**, 583–591.

Feder, C., Martin, J.G.A., Festa-Bianchet, M., Bérubé, C. & Jorgenson, J. (2008) Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia*, **156**, 773–781.

Festa-Bianchet, M. (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**, 580–586.

Festa-Bianchet, M. & Côté, S.D. (2008) *Mountain Goats: Ecology, Behavior, and Conservation of an Alpine Ungulate*. Island Press, Washington, DC.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J.T. (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist*, **152**, 367–379.

Focardi, S., Capizzi, D. & Monetti, D. (2000) Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. *Journal of Zoology*, **250**, 329–334.

Forchhammer, M.C., Clutton-Brock, T.H., Lindström, J. & Albon, S.D. (2001) Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology*, **70**, 721–729.

Forsyth, D.M., Duncan, R.P., Tustin, K.G. & Gaillard, J.M. (2005) A substantial energetic cost to male reproduction in a sexually dimorphic ungulate. *Ecology*, **86**, 2154–2163.

Fritz, H. & Loison, A. (2006) Large herbivores across biomes. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergström, P. Duncan & J. Pastor), pp. 19–49. Cambridge University Press, Cambridge.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gaillard, J.-M., Loison, A., Toigo, C., Delmore, D. & Van Laere, G. (2003) Cohort effects and deer population dynamics. *Ecoscience*, **10**, 412–420.

Garcia, A.J., Landete-Castillejos, T., Carrion, D., Gaspar-Lopez, E. & Gallego, L. (2006) Compensatory extension of gestation length with advance of conception in red deer (*Cervus elaphus*). *Journal of Experimental Biology*, **305A**, 55–61.

Garroway, C.J. & Broders, H.G. (2005) The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, **83**, 1246–1256.

Garroway, C.J. & Broders, H.G. (2007) Adjustment of reproductive investment and offspring sex ratio in white-tailed deer (*Odocoileus virginianus*) in relation to winter severity. *Journal of Mammalogy*, **88**, 1305–1311.

Gerhart, K.L., White, R.G., Cameron, R.D. & Russell, D.E. (1996) Body composition and nutrient reserves of Arctic caribou. *Canadian Journal of Zoology*, **74**, 136–146.

Gerhart, K.L., Russell, D.E., van de Wetering, D., White, R.G. & Cameron, R.D. (1997) Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. *Journal of Zoology London*, **242**, 17–30.

Griffith, B., Douglas, D.C., Walsh, N.E., Young, D.D., McCabe, T.R., Russell, D.E., White, R.G., Cameron, R.D. & Whitten, K.R. (2002) The Porcupine caribou herd. *Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries*, pp. 8–37. U.S. Geological Survey, Biological Resources Division, Biological Science Report 2002-0001, Anchorage, Alaska.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P. & Heard, D.C. (2006) Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, **165**, 1–32.

Gustine, D.D., Parker, K.L. & Heard, D.C. (2007) Using ultrasound measurements of rump fat to assess nutritional condition of woodland caribou in northern British Columbia, Canada. *Rangifer*, **17**, 249–256.

Hay, C.T., Cross, P.C. & Funston, P.J. (2008) Trade-offs of predation and foraging explain sexual segregation in African buffalo. *Journal of Animal Ecology*, **77**, 850–858.

Hazebroek, E., Groot Bruiderink, G.W.T.A. & Van Biezen, J.B. (1994) Changes in the occurrence of small mammals following exclusion of red deer, roe deer, and wild boar. *Lutra*, **38**, 50–59.

Heard, D., Barry, S., Watts, G. & Child, K. (1997) Fertility of female moose (*Alces alces*) in relation to age and body condition. *Alces*, **33**, 165–176.

Hobbs, N.T. (1989) Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs*, **101**, 1–39.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *Journal of Wildlife Management*, **60**, 695–713.

Holand, Ø., Mysterud, A., Røed, K.H., Coulson, T., Gjøstein, H., Weladji, R.B. & Nieminen, M. (2006) Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society: Biological Sciences Series B*, **273**, 293–299.

Hudson, R.J. & Christopherson, R.J. (1985) Maintenance metabolism. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 122–137. CRC Press, Inc., Boca Raton.

Hudson, R.J. & White, R.G. (1985) Computer simulation of energy budgets. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 261–290. CRC Press, Inc., Boca Raton.

Hudson, R.J. & Haigh, J.C. (2002) Physical and physiological adaptations. *North American Elk: Ecology and Management* (eds D.E. Toweill & J.W. Thomas), pp. 199–257. Smithsonian Institution Press, Washington, DC.

Illius, A. (2006) Linking functional responses and foraging behavior to population dynamics. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergström, P. Duncan & J. Pastor), pp. 71–96. Cambridge University Press, Cambridge.

Jacobson, A.R., Provenzale, A., von Hardenberg, A., Bassano, B. & Festa-Bianchet, M. (2004) Climate forcing and density-dependence in a mountain ungulate population. *Ecology*, **85**, 1598–1610.

Jensen, P.G., Pekins, P.J. & Holter, J.B. (1999) Compensatory effect of the heat increment of feeding on thermoregulation costs of white-tailed deer fawns in winter. *Canadian Journal of Zoology*, **77**, 1474–1485.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W. & Stephenson, T.R. (2000) Life history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management*, **64**, 450–462.

Kjellander, P., Gaillard, J.-M. & Hewison, A.J.M. (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia*, **146**, 521–530.

Landete-Castillejos, T., Garcia, A.J. & Gallego, L. (2001) Calf growth in captive Iberian red deer (*Cervus elaphus hispanicus*): effects of birth date and hind milk production and composition. *Journal of Animal Science*, **79**, 1085–1092.

Landete-Castillejos, T., Garcia, A.J., Gomez, J.A., Molina, A. & Gallego, L. (2003) Subspecies and body size allometry affect milk production and composition, and calf growth in red deer: comparison of *Cervus elaphus hispanicus* and *Cervus elaphus scoticus*. *Physiological and Biochemical Zoology*, **76**, 594–602.

Langvatn, R. & Hanley, T.A. (1993) Feeding-patch choice by red deer in relation to foraging efficiency: an experiment. *Oecologia*, **95**, 164–170.

Lawler, J.P. & White, R.G. (2003). Temporal responses in energy expenditure and respiratory quotient following feeding in muskox: influence of season on energy costs of eating and standing and an endogenous heat increment. *Canadian Journal of Zoology*, **81**, 1524–1538.

Lesage, L., Crête, M., Huot, J. & Ouellet, J.-P. (2001) Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia*, **126**, 30–41.

Linnell, J.D.C., Aanes, R. & Andersen, R. (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology*, **1**, 209–223.

Maloney, S.K., Moss, G., Cartmell, T. & Mitchell, D. (2005) Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *Journal of Comparative Physiology A*, **191**, 1055–1064.

Mautz, W.W., Kantner, J. & Pekins, P.J. (1992) Seasonal metabolic rhythms of captive female white-tailed deer: a re-examination. *Journal of Wildlife Management*, **56**, 656–661.

Mautz, W.W. (1978) Sledding on a bushy hillside: the fat cycle in deer. *Wildlife Society Bulletin*, **6**, 88–90.

McArthur, C., Robbins, C.T., Hagerman, A.E. & Hanley, T.A. (1993) Diet selection by a ruminant generalist browser in relation to plant chemistry. *Canadian Journal of Zoology*, **71**, 2236–2243.

Mech, L.D. (2007) Femur-marrow fat of white-tailed deer fawns killed by wolves. *Journal of Wildlife Management*, **71**, 920–923.

Moen, J., Andersen, R. & Illius, A. (2006) Living in a seasonal environment. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergström, P. Duncan & J. Pastor), pp. 50–70. Cambridge University Press, Cambridge.

Moen, R., Cohen, Y. & Pastor, J. (1998) Linking moose population and plant growth models with a moose energetics model. *Ecosystems*, **1**, 52–63.

Mysterud, A., Langvatn, R., Yoccoz, N.G. & Stenseth, N.C. (2001) Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology*, **70**, 915–923.

Mysterud, A., Langvatn, R. & Stenseth, N.C. (2004) Patterns of reproductive effort in male ungulates. *Journal of Zoology, London*, **264**, 209–215.

Nicholson, M.C., Bowyer, R.T. & Kie, J.G. (2006) Forage selection by mule deer: does niche breadth increase with population density? *Journal of Zoology*, **269**, 39–49.

Oftedal, O.T. (1985) Pregnancy and lactation. *Bioenergetics of Wild Herbivores* (eds R.J. Hudson & R.G. White), pp. 216–238. CRC Press, Inc., Boca Raton.

Ouellet, J.P., Heard, D.C., Boutin, S. & Mulders, R. (1997) A comparison of body condition and reproduction of caribou on two predator-free arctic islands. *Canadian Journal of Zoology*, **75**, 11–17.
Owen-Smith, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, **75**, 1050–1062.
Owen-Smith, N. (2002) *Adaptive Herbivore Ecology*. Cambridge University Press, Cambridge.
Page, B.D. & Underwood, H.B. (2006) Comparing protein and energy status of winter-fed winter-tailed deer. *Wildlife Society Bulletin*, **34**, 716–724.
Parker, K.L. (1989) Effects of heat, cold, and rain on black-tailed deer. *Canadian Journal of Zoology*, **66**, 2475–2483.
Parker, K.L. (2003) Advances in the nutritional ecology of cervids at different scales. *Ecoscience*, **10**, 395–411.
Parker, K.L., Robbins, C.T. & Hanley, T.A. (1984) Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management*, **48**, 474–488.
Parker, K.L., White, R.G., Gillingham, M.P. & Holleman, D.F. (1990) Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Canadian Journal of Zoology*, **68**, 106–114.
Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. (1993) Seasonal patterns in body weight, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. *Canadian Journal of Zoology*, **71**, 1397–1404.
Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. (1996) Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. *Canadian Journal of Zoology*, **74**, 442–450.
Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. (1999) Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildlife Monographs*, **143**, 1–48.
Parker, K.L., Barboza, P.S. & Stephenson, T.R. (2005) Protein conservation of female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *Journal of Mammalogy*, **86**, 610–622.
Patterson, B.R. & Power, V.A. (2002) Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia*, **13**, 62–71.
Pekins, P.J., Smith, K.S. & Mautz, W.W. (1998) The energy costs of gestation in white-tailed deer. *Canadian Journal of Zoology*, **76**, 1091–1097.
Pelletier, F. (2005) Foraging time of rutting bighorn rams varies with individual behavior, not mating tactic. *Behavioural Ecology*, **16**, 280–285.
Pérez-Barbería, F.J., Pérez-Fernández, E., Robertson, E. & Alvarez-Enríquez, B. (2008) Does the Jarman-Bell principle at intra-specific level explain sexual segregation in polygynous ungulates? Sex differences in forage digestibility in Soay sheep. *Oecologia*, **157**, 21–30.
Peterson, C. & Messmer, T.A. (2007) Effects of winter-feeding on mule deer in northern Utah. *Journal of Wildlife Management*, **71**, 1440–1445.
Pettorelli, N., Gaillard, J.-M., Duncan, P., Kjellander, P., Liberg, O., Delorme, D., Maillard, D. & Van Laere, G. (2002) Variations in adult body mass in roe deer: the effects of population density at birth and habitat quality. *Proceedings of the Royal Society of London B Biological Sciences*, **269**, 747–754.
Pettorelli, N., Dray, S., Gaillard, J.-M., Chessel, D., Duncan, P., Illius, A., Guillon, N., Klein, F. & Van Laere, G. (2003) Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia*, **137**, 363–369.
Pettorelli, N., Weladji, R.B., Holand, Ø., Mysterud, A., Breie, H. & Stenseth, N.C. (2005) The relative role of winter conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biology Letters*, **1**, 24–26.
Pettorelli, N., Pelletier, F., von Hardenberg, A., Festa-Bianchet, M. & Côté, S.D. (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology*, **88**, 381–390.
Poole, K.G., Serrouya, R. & Stuart-Smith, K. 2007. Moose calving strategies in interior montane ecosystems. *Journal of Mammalogy*, **88**, 139–150.
Post, E. & Forchhammer, M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society of London B*, **363**, 2369–2375.
Post, E. & Stenseth, N.C. (1998) Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology*, **67**, 537–543.
Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322–1339.
Post, E., Bøving, P.S., Pedersen, C. & MacArthur, M.A. (2003) Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology*, **81**, 1709–1714.
Rachlow, J.L. & Bowyer, R.T. (1991) Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy*, **72**, 487–492.
Raubenheimer, D., Simpson, S.J. & Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, **23**, 4–16.
Rettie, W.J. & Messier, M. (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.
Robbins, C.T. (1993). *Wildlife Feeding and Nutrition*. 2nd edn. Academic Press, San Diego.
Robbins, C.T. & Robbins, B.L. (1979) Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *American Naturalist*, **114**, 101–116.
Roffe, T.J. (1993) Perinatal mortality in caribou from the Porcupine herd, Alaska. *Journal of Wildlife Diseases*, **29**, 295–303.
Russell, D.E., Martell, A.M. & Nixon, W.A.C. (1993) Range ecology of the Porcupine caribou herd in Canada. *Rangifer*, **13**, 1–168.
Russell, D.E., Gerhart, K.L., White, R.G. & van de Wetering, D. (1998) Detection of early pregnancy in caribou: evidence for embryonic mortality. *Journal of Wildlife Management*, **62**, 1066–1975.
Russell, D.E., White, R.G. & Daniel, C.J. (2005) *Energetics of the Porcupine Caribou Herd: a Computer Simulation Model*. Canadian Wildlife Service, Technical Report Series no. 431, Ottawa.
Sabine, D.L., Morrison, S.F., Whitlaw, H.A., Ballard, W.B., Forbes, G.J. & Bowman, J. (2002) Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *Journal of Wildlife Management*, **66**, 718–728.
SAS Institute Inc. (2005) *SAS Version 9·1·3*. Cary, North Carolina.
Schwartz, C.C. & Renecker, L.A. (1998) Nutrition and energetics. *Ecology and Management of North American Moose* (eds A.W. Franzmann & C.C. Schwartz), pp. 441–478. Smithsonian Institution Press, Washington, DC.
Shi, J.B., Dunbar, R.I.M., Buckland, D. & Miller, D. (2003) Daytime activity budgets of feral goats (*Capra hircus*) on the Isle of Rhum: influence of season, age, and sex. *Canadian Journal of Zoology*, **81**, 803–815.
Shipley, L.A. (2007) The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, **116**, 1964–1974.
Shipley, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T. & Wunder, B.A. (1994). The scaling of intake rate in mammalian herbivores. *American Naturalist*, **143**, 1055–1082.
Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T. & Spalinger, D.E. (1999) Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. *Oikos*, **84**, 55–68.
Simard, M.A., Côté, S.D., Weladji, R.B. & Huot, J. (2008) Feedback effects of chronic browsing on life-history traits of a large herbivore. *Journal of Animal Ecology*, **77**, 678–686.
Skoogland, T. (1989) Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology*, **29** (suppl.), 1–74.
Solberg, E.J. & Saether, B.E. (1994) Male traits as life-history variables: annual variation in body mass and antler size in moose (*Alces alces*). *Journal of Mammalogy*, **75**, 1069–1079.
Strickland, B.K., Hewitt, D.G., DeYoung, C.A. & Bingham, R.L. (2005) Digestible energy requirements for maintenance of body mass of white-tailed deer in southern Texas. *Journal of Mammalogy*, **86**, 56–60.
Swartzman, G.L. & Kaluzny, S.P. (1987) *Ecological Simulation Primer*. Macmillan, New York.
Taillon, J., Sauvé, D.G. & Côté, S.D. (2006) The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. *Journal of Wildlife Management*, **70**, 1445–1454.
Tarr, M.D. & Pekins, P.J. (2002) Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, U.S.A. *Canadian Journal of Zoology*, **80**, 6–15.
Testa, J.W. & Adams, G.P. (1998) Body condition and adjustments to reproductive effort in female moose (*Alces alces*). *Journal of Mammalogy*, **79**, 1345–1354.
Toïgo, C., Gaillard, J.-M., Van Laere, G., Hewison, M. & Moerellet, N. (2006) How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography*, **29**, 301–308.
Torregrossa, A.-M. & M. Denise Dearing, A. (2009) Nutritional toxicology of mammals: regulated intake of plant secondary compounds. *Functional Ecology*, **23**, 48–56.
Tripler, C.E., Canham, C.D., Inouye, R.S. & Schnurr, J.L. (2002) Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. *Oecologia*, **133**, 517–524.
van Oort, B.E.H., Tyler, N.J.C., Gerkema, M.P., Folkow, L. & Stokkan, K.A. (2007) Where clocks are redundant: weak circadian mechanisms in reindeer living under polar conditions. *Naturwissenschaften*, **94**, 183–94.

Comment Letter I9

van Wieren, S.E. (1996) Do large herbivores select a diet that maximizes short-term energy intake rate? *Forest Ecology and Management*, **88**, 149–156.
Walker, A.B.D., Parker, K.L. & Gillingham, M.P. (2006) Behaviour, habitat associations and intrasexual differences of female Stone's sheep. *Canadian Journal of Zoology*, **84**, 1187–1201.
Weladji, R.B. & Holand, Ø. (2003) Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia*, **136**, 317–323.
White, R.G. (1983) Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos*, **40**, 377–384.
Wilmshurst, J.F. & Fryxell, J.M. (1995) Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's (1993) results. *Oecologia*, **104**, 297–300.
Yoccoz, N.G., Mysterud, A., Langvatn, R. & Stenseth, N.C. (2002) Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society of London B*, **269**, 1523–1528.

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Comment Letter I9

Cheatgrass

James A. Young, Raymond A. Evans, Richard E. Eckert, Jr., and Burgess L. Kay

Editor's Note: The authorship of the paper represents 120 years of collective research on cheatgrass. The readers may also wish to read "The Case for Cheatgrass" by James G. DeFlon *Rangelands* 8(1):14-17 1986, and "Piemeisel Exclosures" by M. Hironoka *Rangelands* 8(5):221-223 1986.

This article is dedicated to Raymond Evans and Richard Eckert, Jr.

Range managers might well ask, "Will the real cheatgrass stand up and be recognized?" Cheatgrass is a major forage species in the Intermountain area. This introduced annual grass is also a major range weed and its herbage provides the fuel that triggers many of the disastrous wildfires that occur on sagebrush rangelands. Competition from cheatgrass for moisture is the major factor limiting the establishment of perennial forage species, forbs, grasses, or shrubs on most big sagebrush rangelands. Cheatgrass is the classic example of a plant species that is difficult to live with, but would cause disruptions in forage bases if the range livestock industry was forced to live without it. Cheatgrass has become a center of discussion in ecological theory and a growing political issue.

Origin and Distribution of Cheatgrass

The origins of cheatgrass are obscure. Apparently, the species evolved in southwestern Asia in the same area where sheep, goats, and cattle were first domesticated. Cheatgrass has followed in the shadow of man and his flocks to some of the world's more remote rangelands.

Cheatgrass is widely distributed in the United States occurring in all areas except for the coastal southeast. In the Pacific northwest, cheatgrass is a serious weed in fields of grass grown for seed production. In the Palouse wheat country of eastern Washington and northern Idaho, cheatgrass is a pest in fields of winter wheat. A population density of 10 cheatgrass plants per square feet will give an average 27% reduction in wheat yield. Cheatgrass continues to be a problem in winter wheat areas through Montana down the western Great Plains to Oklahoma. On semiarid rangelands, cheatgrass reaches its greatest development on degraded big sagebrush/bunchgrass ranges in the Intermountain area between the Sierra-Cascade and Rocky Mountains. Despite the abundance of alien grasses on the annual ranges, cheatgrass is relatively rare on the California ranges with Mediterranean climates.

With its wide distribution, cheatgrass has been labeled with a variety of common names. In local areas ranchers may refer to the annual as bronco grass or six-weeks grass. The Weed Science Society of America adopted the common name of downy brome for *Bromus tectorum* to distinguish it from cheat *(Bromus secalinus)*.

Cheatgrass was probably introduced into the United States independently several times. It was first reported in the far western United States near the end of the 19th century. The trained botanists David Griffith and P.B. Kennedy failed to report cheatgrass in northern Nevada during the course of extensive field surveys at the turn of the century. The first report of the annual grass in Elko County, Nev., occurred in 1906. Once introduced to the sagebrush rangelands, cheatgrass spread in the biological vacuum created by excessive grazing and reduction of the native herbaceous vegetation after 1870.

Cheatgrass spread rapidly through the sagebrush ranges. Following World War I, the country had fallen into an agricultural depression, and numerous dryland homesteads along the Snake River plains of Idaho were abandoned. Often the sandy-loam textured surface soils were subjected to wind erosion before being colonized by the alien weed, Russian thistle. Gradually the Russian thistle gave way to tumble mustard or tansy mustard, and finally the fields were covered with cheatgrass. Disturbance by spring grazing or even rodent activity was sufficient to perpetuate this successional continuum with cheatgrass always coming out on top. R.L. Piemeisel was assigned to do something about the problem of abandoned cropland, not as a range manager, but as an entomologist interested in eliminating the broadleaf species in these successional communities because they were alternate hosts for leafhoppers. In a series of papers, Piemeisel enumerated the stages in succession that led to cheatgrass dominance and suggested that plant succession on millions of acres of sagebrush rangelands was irrevocably changed. Piemeisel speculated that wholesale accelerated erosion would have occurred over vast areas if the alien weeds had not been available to colonize abandoned farm lands during the 1930's.

Adaptation of Cheatgrass

Cheatgrass is an adaptable species. In areas like the Palouse of the Pacific Northwest, seeds (caryopses) of cheatgrass germinate in the fall with the first effective rain. Grant Harris of Washington State University had shown how roots from fall-germinated plants of cheatgrass continued to elongate during the winter while the aerial portion of the plant remained a prostrate rosette. The developed root system provided a competitive advantage to cheatgrass seedlings in the spring when temperatures are adequate for shoot growth. In the more arid portions of the Great Basin, cheatgrass germinates in the fall about once every five years. Usually by the time effective moisture is received, it is too cold for germination. In this more arid environment germination occurs in the early spring and cheatgrass must complete its life cycle before soil moisture is exhausted.

During the 1940's Joseph Robertson in Nevada formulated the concept that cheatgrass-dominated communities in the sagebrush/grasslands were closed to the establishment of seedlings of perennial grass because of competition from this annual grass. Detailed laboratory and field studies by R.A. Evans and R.E. Eckert, Jr., in Nevada and Grant Harris and associates in the Pacific Northwest confirmed that available soil moisture was the limiting seedling establishment factor in these cheatgrass-dominated sites. As few as four

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Re: Comments on Public Draft Joint Environmental Impact Statement and Environmental Impact Report for Casa Diablo IV Geothermal Development Project

To whom it may concern,

Per request by Pamela Epstein of Adams, Broadwell, Joseph & Cardozo, I have reviewed the Public Draft Joint Environmental Impact Statement and Environmental Impact Report ("Draft EIS/R") for the Casa Diablo IV Geothermal Development Project ("CD-IV Project" or "Project"), proposed by ORNI 50 LLC, a wholly-owned subsidiary of Ormat Nevada, Inc. ("Applicant"). The CD-IV Project would consist of constructing, operating, maintaining, and decommissioning a 33-Megawatt ("MW") net binary geothermal power generating facility and related infrastructure near Mammoth Lakes in Mono County, CA in the vicinity of the existing Mammoth Pacific L.P. geothermal complex located near the town of Mammoth Lakes in Mono County, California. The CD-IV Project would construct a new 33 net MW binary power plant, consisting of two Ormat Energy Converters ("OECs"); develop an expanded geothermal well field of up to 16 geothermal resource wells, construct pipelines to bring the geothermal brine to the power plant and pipelines to take the cooled brine to injection wells, and install an electric transmission line to interconnect to a Southern California Edison substation.[1]

The Draft EIS/R for the CD-IV Project has been prepared in accordance with the National Environmental Policy Act, as amended ("NEPA"); the Federal Land Policy and Management Act; and the California Environmental Quality Act ("CEQA). The lead federal agency is the United States Department of the Interior, Bureau of Land Management ("BLM"), with the Department of Agriculture, Forest Service ("USFS") as a cooperating federal agency; the Great Basin Unified Air Pollution Control District ("GBUAPCD") is the lead agency under the California Environmental Quality Act ("CEQA").[2]

My review of the Draft EIS/R focuses on the CD-IV Project's potential impacts related to air quality and hazardous materials.

I. The Draft EIS/R Fails to Adequately Analyze and Mitigate Construction-Related Emissions

The Draft EIS/R finds that operation of diesel equipment during Project construction would result in emissions of nitrogen oxides ("NOx") in excess of the applicable CEQA significance threshold for maximum daily emissions, indicating that Project construction could cause or contribute to an exceedance of the state 1-hour or 8-hour ambient air quality standard for ozone.[3,4] The Draft EIS/R finds that implementation of Mitigation Measure AQ-1 would reduce NOx emissions associated with mobile off-road equipment; however, total mitigated maximum daily emissions would still exceed the applicable CEQA significance threshold and therefore construction-related NOx emissions are considered to result in significant and unavoidable impacts on air quality, both individually.[5] The Draft EIR finds that construction-related emissions of reactive organic gases ("ROG") and particulate matter

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[1] Draft EIS/R, p. ES-2.

[2] United States Department of the Interior, Bureau of Land Management, and United States Department of Agriculture Forest Service, and Great Basin Unified Air Pollution Control District, Public Draft Joint Environmental Impact Statement and Environmental Impact Report for the Casa Diablo IV Geothermal Development Project, November 2012, DOI Control #: DES 12-21, Publication Index #: BLM/CA-ES-2013-002+1793, State Clearinghouse No. 2011041008.

[3] Draft EIS/R, p. 4.2-14.

[4] Nitrogen oxides (as well as reactive organic gases) are ozone precursors.

[5] Draft EIS/R, p. 4.2-14.

equal to or smaller than 10 micrometers ("PM10") and 2.5 micrometers ("PM2.5") would be below the applicable CEQA thresholds for maximum daily emissions and are therefore considered to be less than significant.[6] As discussed in the comments below, the Draft EIS/R may have underestimated construction-related emissions of all pollutants and fails to require adequate mitigation for the significant NOx emissions. I9-156

I.A Maximum Daily Combustion Exhaust Emissions from Drill Rigs during Well Construction Are Not Adequately Supported and May Be Underestimated

Maximum daily emissions from combustion exhaust during construction are primarily related to well drilling activities, mostly from the diesel-powered engines on drill rigs.[7] These emissions are unsupported and may be underestimated. I9-157

Horsepower and Hours of Operation

The Draft EIS/R estimates maximum daily emissions from drill rig engines assuming that three 1,354 brake horsepower ("bhp") drill rigs (Units #1-3) each operate 10 hours per day and one 197-bhp drill rig (Unit #4) operates 2 hours per day.[8] These assumptions appear to conflict with information provided elsewhere in the Draft EIS/R, which indicates that based on actual fuel use data during recent well drillings obtained from Ormat, it is assumed that well development would require two large drill rigs each including approximately four engines with a combined engine rating of over 4,250 bhp per drill rig and operating a combined total of 16 hours per drill rig.[9] The Draft EIS/R should be revised to provide consistent information, and, if indicated, emission calculations should be revised to reflect actual equipment usage. I9-158

Registration with California Air Resources Board's Portable Equipment Registration Program

Further, the Draft EIS/R calculates worst-case emissions from drill rigs assuming that the engines would meet U.S. Environmental Protection Agency ("USEPA") and California Air Resources Board ("CARB") Tier 2 emission standards for diesel-powered off-road engines: I9-159

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[6] *Ibid*.

[7] Draft EIS/R, p. 4.2-9.

[8] Draft EIS/R, Appx. C, p. C-7.

[9] Draft EIS/R, p. 4.2-2.

> Because the drill rigs would be registered with CARB's Statewide Portable Equipment Registration Program, it is expected that the drill rig engines would meet USEPA and CARB Tier 2 standards for off-road engines. Therefore, the Tier 2 grams/brake horsepower-hour (g/bhp-hr) emission standards obtained from CARB and SCAQMD for ROG, NOx, CO, and PM10 were used as worst case emission rates for the drill rigs.[10]

However, CARB's Statewide Portable Equipment Registration Program ("PERP"), is a voluntary program that allows owners or operators of portable engines and certain other types of equipment to register their units in order to operate their equipment throughout California without having to obtain individual permits from local air districts. Registration does not guarantee that drill rig engines used for Project construction would comply with Tier 2 emission standards; the drill rig engines could have been registered with PERP before December 31, 2009 and their registration renewed in which case the engines only have to comply with Tier 1 emissions standards, which are considerably higher.[11,12] Thus, absent a specific mitigation measure requiring that drill rig engines used for Project well drilling would comply with USEPA/CARB Tier 2 standards, there is no guarantee that they in fact would, and, thus, emissions from drill rigs may be underestimated.

The Draft EIS/R should be revised to adequately discuss, support, and, if necessary, revise its emission estimates for drill rigs.

I9-159 cont.

I.B Additional Feasible Mitigation for NOx Emissions from Drill Rigs Exists and Should Be Required

NEPA requires the evaluation of all feasible mitigation measures which would avoid and or lessen a significant impact. Similarly, CEQA requires implementation of all feasible mitigation measures to reduce significant impacts. Here, the Draft EIS/R states that no further feasible NOx emission control technology is feasible for the drill rigs because the engines would comply with USEPA/CARB Tier 2 emission standards for off-road equipment. As discussed above, the assumption that drill rig engines would comply with Tier 2 standards is not supported. Further, the Draft EIS/R fails to discuss why compliance Tier 3 or the current Tier 4 standards is not considered feasible

I9-160

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[10] *Ibid.*

[11] *See* CARB, Statewide Portable Equipment Registration Program (PERP); http://www.arb.ca.gov/portable/portable.htm; and Off-Road Compression-Ignition (Diesel) Engine Tiers; http://www.arb.ca.gov/portable/perp/tiers_1-21-10.pdf.

[12] Tier 0 engines are no longer eligible for registration with PERP; *see* California Air Resources Board, PERP 2011 Regulation Changes; http://www.arb.ca.gov/portable/perp/perpchanges.pdf.

mitigation. Further, retrofitting existing equipment with a selective catalytic reduction system ("SCR") may be a feasible option for older equipment. Retrofit of SCR systems on drill rig engines has been found feasible and is offered by several manufacturers[13,14] and has been successfully implemented elsewhere. For example, Shell Exploration & Production Co. has equipped some of its natural gas drill rigs operating in Wyoming with SCR systems.[15] The manufacturer states that because of the modular design of the system, it is easy to transport and reassemble at a new drilling location with minimal effort.[16] The BLM considered retrofitting drill rigs with SCR systems as a potential mitigation measure, *e.g.*, to reduce NOx emissions for the Casper Resource Management Plan.[17]

I9-160 cont.

The Draft EIR should be revised to provide an adequate discussion of all feasible mitigation to reduce the significant construction-related NOx emissions to the maximum extent feasible and require more stringent mitigation measures such as engine certification to higher than Tier 2 and/or retrofit of drill rig engines with SCR systems.

I.C Mitigation Measure AQ-1 for NOx Emissions from Off-road Mobile Equipment Should Be Amended to Strengthen Its Language

The Draft EIS/R requires implementation of Mitigation Measure AQ-1 to reduce NOx emissions from off-road mobile equipment:

> ORNI 50, LLC shall develop and implement a plan that demonstrates that the mobile off-road equipment (more than 50 horsepower) to be used in the Proposed Action (*i.e.*, owned, leased, and subcontractor vehicles) would achieve a Project wide fleet-average 20 percent NOx reduction compared to the most recent CARB fleet average. The plan shall be approved by GBUAPCD prior to the commencement of construction activities. Acceptable options for reducing emissions include the use of late model

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[13] *For example*, Johnson Matthey, Inc., Case No. 801: Controlling NOx from Gas Drilling Rig Engines with Johnson Matthey's Urea SCR System, 2008; http://www.jmsec.com/Library/Fact-Sheets/801-Shell_Gas_Drill_Rig.pdf.

[14] *For example*, Miratech http://www.miratechcorp.com/site/miratech/section/21;

[15] Dawn M. Geske, Wyoming Becomes Home to Cleaner Drilling, *Diesel Progress*, North American Edition, November 2008; http://jmsec.com/Library/Articles/DPNA920-2.pdf.

[16] *Ibid*.

[17] BLM, Proposed Resource Management Plan and Final Environmental Impact Statement for the Casper Field Office Planning Area, June 2007, Appendix L, Air Quality Mitigation Matrix; http://www.blm.gov/wy/st/en/programs/Planning/rmps/casper/feis_prmp.html.

engines, low-emission diesel products, alternative fuels, engine retrofit technology, after-treatment products, and/or other options as they become available.[18]

This mitigation measure is feasible and, in similar form, is routinely required by other agencies. However, I suggest amending Mitigation Measure AQ-1 as follows to strengthen its language:

- The CARB's *Fleet Average Calculators*[19] can be used to identify an equipment fleet that achieves this reduction.
- The Project representative shall submit to the GBUAPCD a comprehensive inventory of all off-road construction equipment, equal to or greater than 50 horsepower, that will be used an aggregate of 40 or more hours during any portion of the construction project. The inventory shall include the horsepower rating, engine model year, and projected hours of use for each piece of equipment. The inventory shall be updated and submitted monthly throughout the duration of the project, except that an inventory shall not be required for any 30-day period in which no construction activity occurs. At least 48 hours prior to the use of subject heavy-duty off-road equipment, the project representative shall provide the GBUAPCD with the anticipated construction timeline including start date, and name and phone number of the project manager and on-site foreman.

I9-161

II. Hydrogen Sulfide Emissions from Well Drilling May Result in Significant Odor Impacts and/or Unhealthful Concentrations in Ambient Air

The Draft EIS/R recognizes that releases of hydrogen sulfide ("H_2S") could occur during well drilling and construction yet it does not provide a quantitative analysis of potential H_2S releases during construction of the CD-IV Project's wells, instead stating that "given the temporary nature of construction activities and the lack of long-term emissions, health risks are assessed qualitatively."[20] The Draft EIS/R provides the following discussion of potential public health risks and odor during construction of the CD-IV Project:

I9-162

> During well cleanout and flow testing, geothermal fluids would likely be pumped into large open containers. H_2S may temporarily be released from the geothermal fluid for several hours during these activities. The local H_2S emissions during these activities could exceed the GBUAPCD H_2S emissions standard of 2.5 kg/hr/source and could

[18] Draft EIS/R, p. 4.2-20.

[19] CARB, Fleet Average Calculators; http://www.arb.ca.gov/msprog/ordiesel/documents/documents.htm.

[20] Draft EIS/R, p. 4.2-4.

> produce an objectionable "rotten egg" odor in the immediate vicinity of each well. However, these concentrations would not be expected to pose a health hazard and would not reach far beyond the vicinity of the well under normal conditions. Potential H_2S emissions resulting from these activities would be temporary at each well development site and would occur for a relatively short period of several hours.[21]

This terse discussion is not adequate to assess potential public health risks and odor impacts that could occur due to H_2S emissions from construction of the Project's wells and its conclusions are unsupported.

I9-162 cont.

Health Effects of Hydrogen Sulfide

Hydrogen sulfide, which has the characteristic odor of rotten eggs, is an irritant and can be poisonous at high concentrations. Health effects range from nose, throat and lung irritation, digestive upset and loss of appetite, headache, and dizziness to sudden collapse, unconsciousness, and death depending on its concentrations. The U.S. Department of Health and Human Services summarizes health effects of exposure to H_2S as follows:

> Exposure to low concentrations of hydrogen sulfide may cause irritation to the eyes, nose, or throat. It may also cause difficulty in breathing for some asthmatics. Brief exposures to high concentrations of hydrogen sulfide (greater than 500 ppm) can cause a loss of consciousness. In most cases, the person appears to regain consciousness without any other effects. However, in some individuals, there may be permanent or long-term effects such as headaches, poor attention span, poor memory, and poor motor function. … Deaths due to breathing in large amounts of hydrogen sulfide have been reported in a variety of different work settings, including sewers, animal processing plants, waste dumps, sludge plants, oil and gas well drilling sites, and tanks and cesspools.[22]

The Draft EIS/R fails to provide any discussion of odor thresholds or potential health effects at various levels of exposure to H_2S. In parts per million ("ppm"), these can be approximated as follows:

I9-163

0.001–0.13 ppm	odor threshold (highly variable)
1–5 ppm	moderately offensive odor, possibly with nausea, or headaches with prolonged exposure
20–50 ppm	nose, throat and lung irritation, digestive upset and loss of appetite, sense of

[21] Draft EIS/R, p. 4.2-10.

[22] U.S. Department of Health and Human Services, Agency for Toxic Substances and Disease Registry, *Toxicological Profile for Hydrogen Sulfide*, July 2006, p. 4; http://www.atsdr.cdc.gov/toxprofiles/tp114.pdf

	smell starts to become "fatigued," odor cannot be relied upon as a warning of exposure
100–200 ppm	severe nose, throat and lung irritation, ability to smell odor completely disappears
250–500 ppm	potentially fatal build-up of fluid in the lungs (pulmonary edema) in the absence of central nervous system effects (headache, nausea, dizziness), especially if exposure is prolonged
500 ppm	severe lung irritation, excitement, headache, dizziness, staggering, sudden collapse ("knockdown"), unconsciousness and death within 4-8 hours, loss of memory for period of exposure
500–1000 ppm	respiratory paralysis, irregular heartbeat, collapse, and death; it is important to note that the symptoms of pulmonary edema, such as chest pain and shortness of breath, can be delayed for up to 48 hours after exposure.[23]

I9-163 cont.

To put these numbers in perspective, 1 ppm H_2S equals 1.5 milligrams per cubic meter ("mg/m³") or 1,500 micrograms per cubic meter ("µg/m³") in air. In comparison, the Draft EIS/R states that well cleanout and testing could result in H_2S releases in excess of 2.5 kilograms (2,500,000 milligrams or 2,500,000,000 micrograms) per hour.[24] When hydrogen sulfide is released as a gas, it remains in the atmosphere for an average of 18 hours.[25] Thus, large quantities of H_2S could accumulate in the vicinity of and disperse from the well site and present an odor nuisance as well as a public health hazard to nearby receptors. Because exposure to H_2S can result in both acute and chronic health effects, the cited "temporary" nature of construction activities is no excuse for an adequate assessment, especially given the potential of cumulative impacts from other planned (*e.g.*, Mammoth Pacific I Replacement Project) and existing geothermal developments in the area.

Proximity and Potential Exposure of Public to Hydrogen Sulfide Releases

As shown in the inset map (excerpted from the Draft EIS/R) below, several recreational areas are within a mile of the proposed Project geothermal well locations: the New Shady Rest Campground, the Pine Glen Campground and the Shady Rest Park; the latter is located within less than 0.5 miles of six new well sites (Nos. 15-25, 25-25, 34-25, 52-25, 50-25, and 38-25 and three existing well sites (Nos. 14-25, 12-25,

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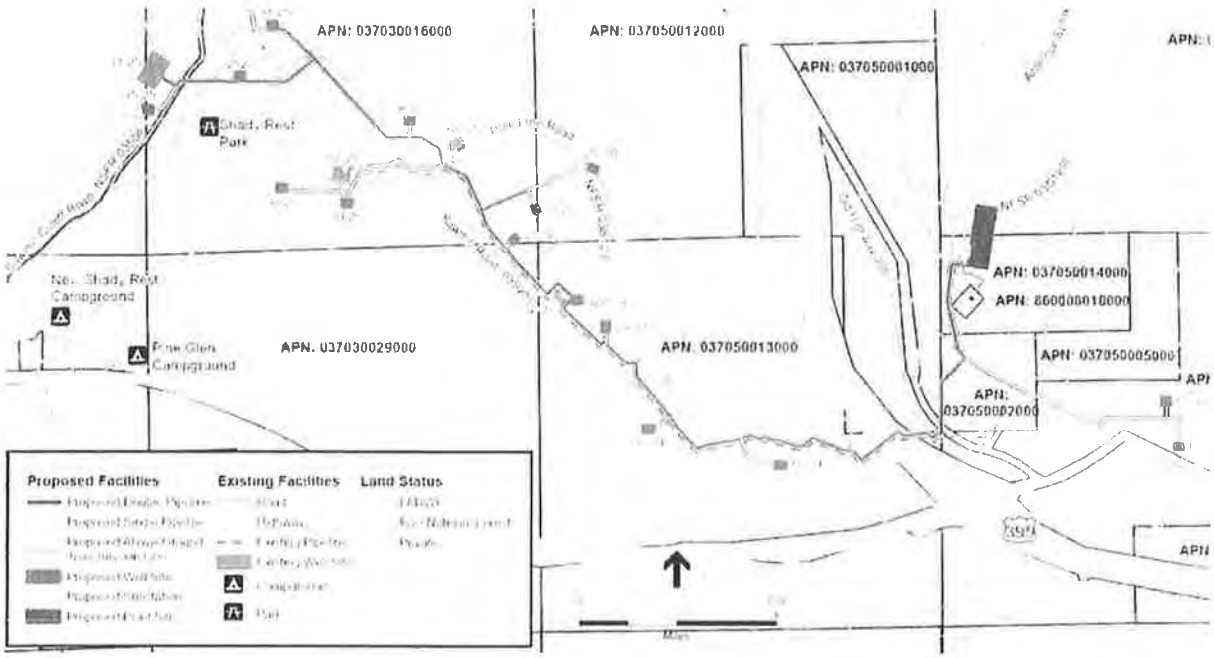
[23] Organisation for Economic Co-operation and Development, WGCA Steering Group of Analysis of H_2S Incidents, *Analysis of H_2S- Incidents in Geothermal and Other Industries*, Preliminary Analysis of Data, p. 7; http://www.vinnueftirlit.is/vinnueftirlit/upload/files/skyrslur/oecd_analysis_of_h2s-incidents.pdf.

[24] Draft EIS/R, p. 4.2-10.

[25] *Toxicological Profile for Hydrogen Sulfide*, p. 2.

and 57-25). Publicly accessible trails and roads traverse the area where geothermal wells and pipelines are proposed or already exist.



According to the Draft EIS/R, drilling and development of the up to 16 Project wells would occur for about six months per year over the two-year construction period with a total of two wells being constructed simultaneously. These activities would occur during non-winter months, *i.e.*, June through November[26], and would, thus, coincide with the period when the nearby recreational areas likely have the highest occupancy rates and the public would use trails and roads in proximity to the wells and pipelines. The public could be exposed to elevated concentrations of H_2S released during well cleanout and testing as well as a result of spills, pipeline ruptures or uncontrolled releases from the wells ("well blowouts")[27], a well-recognized risk for the geothermal industry.[28]

As summarized above, the odor threshold for H_2S in air is very low (less than one ppm) and subtle to distinct physiological effects can be detected at just slightly higher concentrations ($\leq$ 50 ppm). Serious health effects occur over concentrations of **I9-164**

[26] Draft EIS/R, p. 2-35.

[27] Draft EIS/R, pp. 4.2-10 and 4.4-8.

[28] *See, e.g., Analysis of H_2S- Incidents in Geothermal and Other Industries.*

only 50 ppm. Because hydrogen sulfide is heavier than air and because children are shorter than adults, children may be exposed to more hydrogen sulfide than adults could be exposed to higher health risks.[29]

Based on the proximity of the public to the areas of geothermal development and the potential for elevated concentrations of H_2S during well cleanout and testing and potential well blowouts or pipeline failures, the potential odor impacts and health risks from the Project, particularly considering the cumulative exposure and impacts from the existing and permitted geothermal plants, wells, and pipeline network, should be carefully evaluated. I9-164 cont.

Since the Applicant already operates a number of existing geothermal wells, pipelines and power plants in the vicinity, information about potential H_2S releases and concentrations that may occur during well testing and venting should be readily available. Based on this information and a dispersion model for the spread of gaseous sulfur compounds, the Draft EIS/R should be revised to model maximum potential H_2S concentrations, adequately evaluate the potential health and odor impact on the public including an assessment of potential odor and health impacts for the residence at Chance Ranch[30], and determine whether there is a potential that H_2S concentrations in ambient air would exceed the state 1-hour state ambient air quality standard of 42 $\mu g/m^3$. If indicated by the results of this assessment, the Draft EIS/R should require as a mitigation measure that trails and recreation areas are closed to the public during well drilling and development in order to avoid exposure to unhealthful concentrations of H_2S in the air. I9-165

III. The Draft EIS/R's Analysis of Reactive Organic Gas Emissions from the Project's Motive Fluid System Is Deficient

According to the Draft EIS/R, Project operation and maintenance would result in emissions of more than 400 lb/day of ROG, by far in excess of the applicable CEQA threshold of 75 lb/day. These ROG emissions are almost exclusively related to fugitive emissions of the motive fluid, n-pentane, at the binary power plant.[31] Reactive organic gases are ozone precursors for which the area has been designated as being in non-attainment with the state 1-hour and 8-hour ozone standards.[32]

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[29] *Toxicological Profile for Hydrogen Sulfide*, p. 5.

[30] *See* Draft EIS/R, p. 3.2-5.

[31] Draft EIS/R, Table 4.2-4, p. 4.2-12.

[32] Draft EIS/R, p. 4.2-6.

III.A Emission Estimates Are Not Adequately Supported

The Draft EIS/R presents an estimate of 410.0 lb/day and 74.8 ton/year ROG for fugitive n-pentane emissions from the Project.[33] The Draft EIS/R does not provide any calculations to arrive at this estimate but instead refers to a document that is not provided, specifically, the Applicant's 2010 *Application for Geothermal Drilling, Commercial Use, Site License, and Construction Permit, Plan of Development (POD), Plan of Operation and Plan of Utilization (POU)*.[34]

Review of application materials obtained by your office from the GBUAPCD[35] shows that the Draft EIS/R's estimates of ROG emissions are unsupported. According to a letter from Ormat to the GBUAPCD, emission estimates for fugitive n-pentane emissions from "OEC operational losses (fill, drain, tube leaks) are based on "engineering estimates using motive fluid inventory at similar facilities." Review of the application materials and accompanying calculations show that the Applicant did not provide a motive fluid inventory to the GBUAPCD either but instead simply presents an estimate for operational losses from two OECs "Based on Ormat O&M experience" for a "Typical 36 MW Air Cooled Ormat Binary Power Plant".[36] Based on information from CEQA documents for the Applicant's Mammoth Pacific I Replacement Project, it appears that the Applicant relies on emissions of 92 lb/day or 1.73 kilograms per hour per OEC.[37] There, the information was provided for a "Typical 16 MW Air-Cooled OEC," also without any further documentation. As such, the emission estimates are not adequately supported. While the Applicant may have carefully evaluated potential emissions and provided engineering estimates based on best engineering judgment, mere hearsay without adequate documentation and evidence in the record which leaves the reviewer with the only option to accept the presented emissions at face value, is not adequate for purposes of CEQA or NEPA review. I9-166

Further, neither maximum daily nor total annual emissions of n-pentane are proposed to be monitored in any way and, thus, no verification of the Applicant- I9-167

[33] Draft EIS/R, Tables 4.2-4 and 4.2-5, p. 4.2-12.

[34] *See* Footnotes b to Draft EIS/R, Tables 4.2-4 and 4.2-5, p. 4.2-12, and Reference Section, p. 10-25.

[35] Letter from Ron Leiken, Ormat Nevada, to Duane Ono, Deputy Air Pollution Control Officer, GBUAPCD, Re: Application for Authority to Construct for the CD-4, ORNI 50, LLC, Geothermal Power Plant Development Project, May 24, 2012.

[36] *Ibid*, Attachment "Typical 36MW Air Cooled Ormat Binary Power Plant, Emission calc" dated May 1, 2012.

[37] County of Mono, Mammoth Pacific I Replacement Project, Final Environmental Impact Report, California Clearinghouse Number 2011022020, September 2012, Response to Comment 9D-04, p. 39.

supplied values would ever occur. This undermines the very intent of the CEQA and NEPA review process to adequately disclose air pollutant emissions and associated impacts on air quality in the first place. Further, because binary geothermal plants are a relatively new technology, care should be taken to establish appropriate emission rates in order to avoid perpetuating unsupported and potentially erroneous assumptions during the environmental review for similar projects in the future. I9-167 cont.

To verify the Applicant's emission estimates, the Draft EIS/R should be revised to provide purchase inventory records for other similar facilities and accompanying emission calculations or, alternatively, require that an annual n-pentane purchase inventory be submitted to the GBUAPCD and compared to the emission estimates presented in the Draft EIS/R and application to the GBUAPCD. I9-168

III.B The Draft EIS/R Fails to Require Best Available Control Technology for Operational Emissions of Reactive Organic Gases

The estimated ROG emissions from operation of the Project are almost exclusively related to fugitive emissions of the motive fluid, n-pentane, at the binary power plant. The Draft EIS/R claims that because the Project "is proposed to include state of the art equipment and best available technology that would limit fugitive ROG (*i.e.*, n-pentane) emissions, *no additional feasible mitigation measures are available* to further substantially reduce fugitive ROG emissions, and the CD-IV Project would result in a significant and unavoidable impact related to long-term fugitive emissions of n-pentane."[38] The statement that no additional feasible mitigation measures are available is incorrect. I9-169

The Applicant's Best Available Control Technology ("BACT") analysis, submitted to the GBUAPCD with the Application for an Authority to Construct ("ATC") for the Project[39], proposes implementation of the following concepts and technologies:

- Reducing the number of valves, flanges, and other connections compared to the first generation plants such as G-1, G-2, and G-3.
- Installation of vapor recovery devices estimated to return at least 99% of the motive fluid back to the system.

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[38] Draft EIS/R, p. 4.2-11, *emphasis* added.

[39] Letter from Ron Leiken, Ormat Nevada, to Duane Ono, Deputy Air Pollution Control Officer, GBUAPCD, Re: Application for Authority to Construct for the CD-4, ORNI 50, LLC, Geothermal Power Plant Development Project, May 24, 2012.

- Use of a maintenance vapor recovery unit during OEC unit maintenance activities to capture motive fluid that could otherwise be released.
- Lower pressure of motive fluid system compared to motive fluid used at older existing plants, thus, less potential for fugitive leaks/emissions.
- Placement of pentane-specific vapor sensors and flame detectors at strategic locations around the around the turbine, motive fluid pumps, and motive fluid storage tank and connection to power plant computer control system to quickly alert plant operators to any potentially hazardous situations, which would help to keep a check on significant leaks.
- Leak checks, inspections, monitoring, and leak logging.

Leakless Technology for Motive Fluid System

An additional technology available to reduce fugitive emissions of n-pentane from equipment leaks is the use of leakless technology for the Project's motive fluid system. Pipes, valves, pumps and other equipment are commonly connected using flanges that are welded or screwed. Here, it appears that the Applicant proposes to use screwed, or threaded, flanges.[40] Threaded flanges leak, no matter how carefully executed; welded connections on the other hand do not (unless defective) and, thus, eliminate 100% of the emissions. Thus, reducing the number of valves, flanges and connectors, while undoubtedly effective, as proposed, is only the first step in reducing fugitive equipment leaks. Instead, BACT for the Project's motive fluid system is the use of leakless equipment components, a technology that is routinely required for construction of new or modification of existing refineries and chemical facilities and equally feasible here. The Draft EIS/EIR should be revised to require the use of leakless components for all equipment components that could result in fugitive leaks of the motive fluid n-pentane. Further Project Design Measure AQ-3 should be revised to specifically refer to "BACT as required by GBUAPCD Rule 209-A, Section D (for new stationary sources of emissions which would result in a net increase in emissions of 250 or more lb/day of any air pollutant or precursor except for CO and particulate matter)" instead of "best available equipment and design" for which no legal definition exists. I9-170

[40] *Ibid*, Attachment "Typical 36MW Air Cooled Ormat Binary Power Plant, Emission calc" dated May 1, 2012: "Flanges, Connetors [sic], Screwed."

Vapor Recovery Unit Control Efficiency

The Applicant proposes a 99% control efficiency as BACT for the vapor recovery devices. Yet, the Draft EIR states that "other facilities similar to what is proposed for the CD-IV Project have demonstrated better than 99.6 percent efficiency in controlling and recovering n-pentane emissions *during normal operations*."[41] Thus, it appears that BACT, as demonstrated in practice, is 99.6% rather than 99% control efficiency. The Draft EIR (and the ATC Application to the GBUAPCD) should provide a top-down analysis of control efficiency for vapor recovery devices and revise the BACT determination accordingly. I9-171

Leak Detection and Repair Program

The Applicant's proposed BACT measures for equipment leaks include the "placement of pentane-specific vapor sensors at strategic locations" as well as "leak checks, inspections, monitoring, and leak logging." While the proposed measures may prevent help prevent significant leaks, they are not adequate to address smaller and slow leaks and do not constitute BACT for the Project. The USEPA has developed leak detection and repair ("LDAR") regulations for petroleum refineries and chemical manufacturing facilities. Implementation of an LDAR program is equally feasible for the Project's motive fluid system. LDAR incorporates the elements of the proposed inspection program but goes further. For example it requires quantification of fugitive ROG leaks with a portable analyzer (per USEPA Reference Method 21). The Draft EIR should be revised to require as a mitigation measure the use of LDAR following USEPA's *Best Practices Guide*[42]. I9-172

IV. The Draft EIS/R Fails to Provide an Off-Site Consequence Analysis for Transportation of the Flammable Motive Fluid n-Pentane to the Site

The motive fluid that would be used at the CD-IV Project, n-pentane, is a highly flammable liquid at standard temperature and pressure which is typically transported and stored under pressure.[43] The Draft EIS/R recognizes that the use of n-pentane requires a risk management plan ("RMP") due to the potential risk of explosion and fire and acknowledges that transportation of n-pentane "could indirectly result in an I9-173

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[41] Draft EIS/R, p. 4.2-12, *emphasis* added.

[42] USEPA, Leak Detection and Repair Compliance Assistance Guidance, A Best Practices Guide; http://www.epa.gov/compliance/resources/publications/assistance/ldarguide.pdf.

[43] Draft EIS/R, p. 4.13-6.

incremental increase in the potential for accidents"[44] but fails to provide an off-site consequence analysis for transportation of the hazardous substance to the site as required by the Chemical Accident Prevention Provisions under USEPA's RMP rule (Section 112(r) of the federal Clean Air Act).[45] Instead, the Draft EIS/R only states that Applicant "would update its existing RMP and incorporate the CD-IV facility into its Process Safety Program Safety Management Program".[46] This approach improperly defers an analysis into the future that should be part of the CEQA/NEPA review process for the Project and is therefore not permissible. I9-173 cont.

The Draft EIS/R should be revised to provide an off-site consequence analysis for the flammable motive fluid n-pentane using USEPA's RMP*Comp model as required by the USEPA's RMP to satisfy the requirements of CEQA and disclose all potential impacts to the public. This analysis should include potential cumulative risks from other planned and existing geothermal facilities in the vicinity.

V. Recommendation

I recommend that the lead agencies prepare a revised Draft EIS/R for review and comment by the public that addresses the above discussed issues. I9-174

Please feel free to call me at (415) 492-2131 or e-mail at petra.pless@gmail.com if you have any questions.

With best regards,

Petra Pless, D.Env.

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[44] Draft EIS/R, p. 4.13-7.

[45] U.S. Environmental Protection Agency, Risk Management Plan (RMP) Rule; http://epa.gov/emergencies/content/rmp/index.htm.

[46] Draft EIS/R, p. 4.13-7.

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Dr. Pless has over 15 years of experience in environmental engineering and science conducting and managing interdisciplinary environmental research projects and preparing and reviewing environmental permits and other documents for U.S. and European stakeholder groups. This broad-based experience includes air quality and air pollution control; water quality, water supply, and water pollution control; biology; public health and safety; and noise studies. National Environmental Policy Act ("NEPA"), California Environmental Quality Act ("CEQA"), and Clean Air Act ("CAA") review; industrial ecology and risk assessment; and use of a wide range of environmental software.

EDUCATION

Doctorate in Environmental Science and Engineering (D.Env.), University of California, Los Angeles, 2001

M.S. Biology (with focus on botany/ecology/limnology), Technical University of Munich, Germany, 1991

PROFESSIONAL HISTORY

Environmental consultant 2006–present

Leson & Associates (previously Leson Environmental Consulting), Kensington, CA, Environmental Scientist/Project Manager, 1997–2005

University of California Los Angeles, Graduate Research Assistant/Teaching Assistant, 1994–1996

ECON Research and Development, Environmental Scientist, Ingelheim, Germany, 1992–1993

Biocontrol, Environmental Projects Manager, Ingelheim, Germany, 1991–1992

REPRESENTATIVE EXPERIENCE

Air Quality and Pollution Control

Projects include CEQA/NEPA review; attainment and non-attainment new source review ("NSR"), prevention of significant deterioration ("PSD") and Title V permitting; control technology analyses (BACT, LAER, RACT, BARCT, MACT); technology evaluations and cost-effectiveness analyses; criteria and toxic pollutant emission inventories; emission offsets; ambient and source monitoring; analysis of emissions estimates and ambient air pollutant concentration modeling. Some typical projects include:

- Critically reviewed and prepared technical comments on the air quality, biology, noise, water quality, and public health and safety sections of CEQA/NEPA documents for numerous commercial, residential, and industrial projects (*e.g.*, power plants, airports, residential developments, retail developments, hospitals, refineries, slaughterhouses, quarries, and mines).
- Critically reviewed and prepared technical comments on the air quality and public health sections of the Los Angeles Airport Master Plan (Draft, Supplement, and Final Environmental Impact Statement/Environmental Impact Report) for the City of El Segundo. Provided technical comments on the Draft and Final General Conformity Determination for the preferred alternative submitted to the Federal Aviation Administration.
- For several California refineries, evaluated compliance of fired sources with Bay Area Air Quality Management District ("BAAQMD") Rule 9-10. This required evaluation and review of hundreds of source tests to determine if refinery-wide emission caps and compliance monitoring provisions were being met.
- Critically reviewed and prepared technical comments on Draft Title V permits for several refineries and other industrial facilities in California.
- Reviewed state-wide average emissions, state-of-the-art control devices, and emissions standards for construction equipment and developed recommendations for mitigation measures for numerous large construction projects.
- Researched sustainable building concepts and alternative energy and determined their feasibility for residential and commercial developments, *e.g.*, regional shopping malls and hospitals.
- Evaluated the public health impacts of locating big-box retail developments in densely populated areas in California and Hawaii. Monitored and evaluated impacts of diesel exhaust emissions and noise on surrounding residential communities.
- In conjunction with the permitting of several residential and commercial developments, conducted studies to determine baseline concentrations of diesel exhaust particulate matter using an aethalometer.
- For an Indiana steel mill, evaluated technology to control NOx and CO emissions from fired sources, including electric arc furnaces and reheat furnaces, to establish BACT. This required a comprehensive review of U.S. and European operating experience. The lowest emission levels were being achieved by steel mills using selective catalytic reduction ("SCR") and selective non-catalytic reduction ("SNCR") in Sweden and The Netherlands.
- For a California petroleum coke calciner, evaluated technology to control NOx, CO, VOCs, and PM10 emissions from the kiln and pyroscrubbers to establish BACT and LAER. This required a review of state and federal clearinghouses, working with regulatory agencies and pollution control vendors, and obtaining and reviewing permits and emissions data from other similar facilities. The best-controlled facilities were located in the South Coast Air Quality Management District ("SCAQMD").
- For a Kentucky coal-fired power plant, identified the lowest NOx levels that had been permitted and demonstrated in practice to establish BACT. Reviewed operating experience of European, Japanese, and U.S. facilities and evaluated continuous emission monitoring data.

The lowest NOx levels had been permitted and achieved in Denmark and in the U.S. in Texas and New York.

- In support of efforts to lower the CO BACT level for power plant emissions, evaluated the contribution of CO emissions to tropospheric ozone formation and co-authored report on same.
- Critically reviewed and prepared technical comments on applications for certification ("AFCs") for numerous natural-gas fired and geothermal power plants in California permitted by the California Energy Commission ("CEC"). The comments addressed construction and operational emissions inventories and dispersion modeling, BACT determinations for combustion turbine generators, etc.
- Critically reviewed and prepared technical comments on draft PSD permits for several natural gas-fired power plants in California, Indiana, and Oregon. The comments addressed emission inventories, BACT, case-by-case MACT, compliance monitoring, cost-effectiveness analyses, and enforceability of permit limits.
- For a California refinery, evaluated technology to control NOx and CO emissions from CO Boilers to establish RACT/BARCT to comply with BAAQMD Rule 9-10. This required a review of BACT/RACT/LAER clearinghouses, working with regulatory agencies across the U.S., and reviewing federal and state regulations and State Implementation Plans ("SIPs"). The lowest levels were required in a SCAQMD rule and in the Texas SIP.
- In support of several federal lawsuits filed under the Clean Air Act, prepared cost-effectiveness analyses for SCR and oxidation catalysts for simple cycle gas turbines and evaluated opacity data.
- Critically reviewed draft permits for several ethanol plants in California, Indiana, and Ohio and prepared technical comments.
- Provided comprehensive environmental and regulatory services for an industrial laundry chain. Facilitated permit process with the SCAQMD. Developed test protocol for VOC emissions, conducted field tests, and used mass balance methods to estimate emissions. Reduced disposal costs for solvent-containing waste streams by identifying alternative disposal options. Performed health risk screening for air toxics emissions. Provided permitting support with SCAQMD. Renegotiated sewer surcharges with wastewater treatment plant. Identified new customers for shop-towel recycling services.
- Designed computer model to predict performance of biological air pollution control (biofilters) as part of a collaborative technology assessment project, co-funded by several major chemical manufacturers. Experience using a wide range of environmental software, including air dispersion models, air emission modeling software, database programs, and geographic information systems ("GIS").

Water Quality and Pollution Control

Experience in water quality and pollution control, including surface water and ground water quality and supply studies, evaluating water and wastewater treatment technologies, and identifying, evaluating and implementing pollution controls. Some typical projects include:

- For a homeowner's association, reviewed a California Coastal Commission staff report on the replacement of 12,000 linear feet of wooden bulkhead with PVC sheet pile armor. Researched and evaluated impact of proposed project on lagoon water quality, including sediment resuspension, potential leaching of additives and sealants, and long-term stability. Summarized results in technical report.
- For a 500-MW combined-cycle power plant, prepared a study to evaluate the impact of proposed groundwater pumping on local water quality and supply, including a nearby stream, springs, and a spring-fed waterfall. The study was docketed with the CEC and summarized in a journal article.
- Evaluated impacts of on-shore oil drilling activities on large-scale coastal erosion in Nigeria.
- For a 500-MW combined-cycle power plant, identified and evaluated methods to reduce water use and water quality impacts. These included the use of zero-liquid-discharge systems and alternative cooling technologies, including dry and parallel wet-dry cooling. Prepared cost analyses and evaluated impact of options on water resources. This work led to a settlement in which parallel wet dry cooling and a crystallizer were selected, replacing 100 percent groundwater pumping and wastewater disposal to evaporation ponds.

Applied Ecology, Industrial Ecology and Risk Assessment

Experience in applied ecology, industrial ecology and risk assessment, including human and ecological risk assessments, life cycle assessment, evaluation and licensing of new chemicals, and fate and transport studies of contaminants. Experienced in botanical, phytoplankton, and intertidal species identification and water chemistry analyses. Some typical projects include:

- For the California Coastal Conservancy, San Francisco Estuary Institute, Invasive Spartina Project, evaluated the potential use of a new aquatic pesticide for eradication of non-native, invasive cordgrass (*Spartina spp.*) species in the San Francisco Estuary with respect to water quality, biological resources, and human health and safety. Assisted staff in preparing an amendment to the Final EIR.
- Evaluated likelihood that measured organochlorine pesticide concentrations at a U.S. naval air station are residuals from past applications of these pesticides consistent with manufacturers' recommendations. Retained as expert witness in lawsuit.
- Prepared human health risk assessments of air pollutant emissions from several industrial and commercial establishments, including power plants, refineries, and commercial laundries.
- Managed and conducted studies to license new pesticides. This work included the evaluation of the adequacy and identification of deficiencies in existing physical/chemical and health effects data sets, initiating and supervising studies to fill data gaps, conducting environmental fate and transport studies, and QA/QC compliance at subcontractor laboratories. Prepared licensing applications and coordinated the registration process with German licensing

agencies. This work led to regulatory approval of several pesticide applications in less than six months.

- Designed and implemented database on physical/chemical properties, environmental fate, and health impacts of pesticides for a major European pesticide manufacturer.
- Designed and managed toxicological study on potential interference of delta-9-tetrahydro-cannabinol in food products with U.S. employee drug testing; co-authored peer-reviewed publication.
- Critically reviewed and prepared technical comments on AFCs for several natural-gas fired and geothermal power plants and transmission lines in California permitted by the CEC. The comments addressed avian collisions and electrocution, construction and operational noise impacts on wildlife, risks from brine ponds, and impacts on endangered species.
- For a 180-MW geothermal power plant, evaluated the impacts of plant construction and operation on the fragile desert ecosystem in the Salton Sea area. This work included baseline noise monitoring and assessing the impact of noise, brine handling and disposal, and air emissions on local biota, public health, and welfare.
- Designed research protocols for a coastal ecological inventory; developed sampling methodologies, coordinated field sampling, determined species abundance and distribution in intertidal zone, and analyzed data.
- Designed and conducted limnological study on effects of physical/chemical parameters on phytoplankton succession; performed water chemistry analyses and identified phytoplankton species; co-authored two journal articles on results.
- Conducted technical, ecological, and economic assessments of product lines from agricultural fiber crops for European equipment manufacturer; co-authored proprietary client reports.
- Developed life cycle assessment methodology for industrial products, including agricultural fiber crops and mineral fibers; analyzed technical feasibility and markets for thermal insulation materials from plant fibers and conducted comparative life cycle assessments.
- Conducted and organized underwater surveying and mapping of plant species in several lakes and rivers in Sweden and Germany as ecological indicators for the health of limnological ecosystems.

PRO BONO ACTIVITIES

Founding member of "SecondAid," a non-profit organization providing tsunami relief for the recovery of small family businesses in Sri Lanka. (www.secondaid.org)

PROFESSIONAL AFFILIATIONS

Association of Environmental Professionals

SELECTED PUBLICATIONS

Leson G. and Pless P., Hemp seeds and hemp oil, in: Grotenhermen F. and Russo E. (eds.), *Cannabis* und Cannabinoids, Pharmacology, Toxicology, and Therapeutic Potential, The Haworth Integrative Healing Press, New York, 2002.

Leson G., Pless P., Grotenhermen F., Kalant H., and ElSohly M., Evaluating the impact of hemp food consumption on workplace drug tests, Journal of Analytical Toxicology, Vol. 25, No. 11/12, pp. 1-8, 2001.

Leson G. and Pless P., Assessing the impact of THC uptake from hemp oil cosmetics on workplace drug testing, Report to the Agricultural Research and Development Initiative ("ARDI"), Morris, MB, 2001.

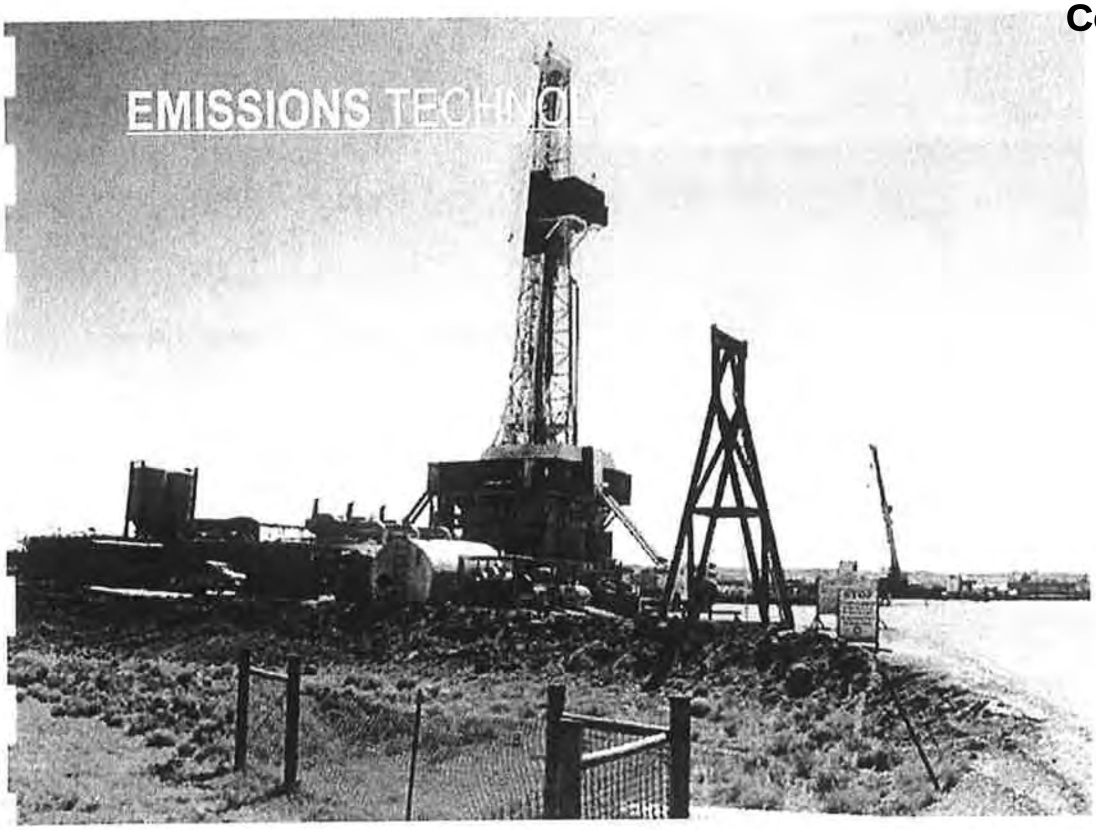
Pless P., Technical and environmental assessment of thermal insulation materials from fiber crops, doctoral dissertation in Environmental Science and Engineering, University of California, Los Angeles, 2001.

Center for Waste Reduction Technologies in the American Institute of Chemical Engineers, Collaborative Biofilter Project, Technical Report, co-author with Leson G. of sections 'Compound Database,' 'Design Manual,' and 'Literature Database,' 1998.

Hantke B., Domany I., Fleischer P., Koch M., Pless P., Wiendl M., and Melzer M., Depth profiles of the kinetics of phosphatase activity in hardwater lakes of different trophic level, Arch. Hydrobiologia, vol. 135, pp. 451–471, 1996.

Hantke B., Fleischer P., Domany I., Koch M., Pless P., Wiendl M., and Melzer M., P-release from DOP by phosphatase activity in comparison to P-excretion by zooplankton: studies in hardwater lakes of different trophic level, Hydrobiologia, vol. 317, pp. 151–162, 1996.

Pless P., Untersuchungen zur Phytoplanktonentwicklung im Herrensee (investigations on phytoplankton succession in an oligotrophic hardwater lake), Masters Thesis in biology with focus on botany/ecology/limnology, Technical University of Munich, Germany, 1991.



Shell Exploration & Production Co. has begun equipping its natural gas drilling rigs operating in Wyoming with Johnson Matthey's selective catalytic reduction (SCR) systems as part of an initiative to reduce NO_x in the region. Three urea SCR systems are installed per drill rig, one on each of the three Caterpillar diesel engine-powered generators used to power the drills.

WYOMING BECOMES HOME TO CLEANER DRILLING

Shell retrofits drilling rigs with Johnson Matthey advanced SCR systems to reduce NO_X in Pinedale Anticline

BY DAWN M. GESKE

The Pinedale Anticline in Wyoming is one of the largest natural gas fields in the U.S. The area sits adjacent to the Wind River Mountains in the southeastern portion of the state with a picturesque view of the mountain range and abundant wildlife. As part of an effort to conserve the region, Shell Exploration & Production Co. has taken the initiative in cooperation with the State of Wyoming and the U.S. Bureau of Land Management (BLM) to retrofit its natural gas drilling rigs with selective catalytic reduction (SCR) systems.

"Our challenge in Pinedale is balancing drilling for natural gas with protecting the environment," said Jim Sewell, environmental engineer at Shell Exploration & Production Co. "One of the most important things we have to do is protect visibility. NO_X emissions can impact visibility as the chemistry forms in the atmosphere. Our challenge was to reduce our NO_X emissions levels."

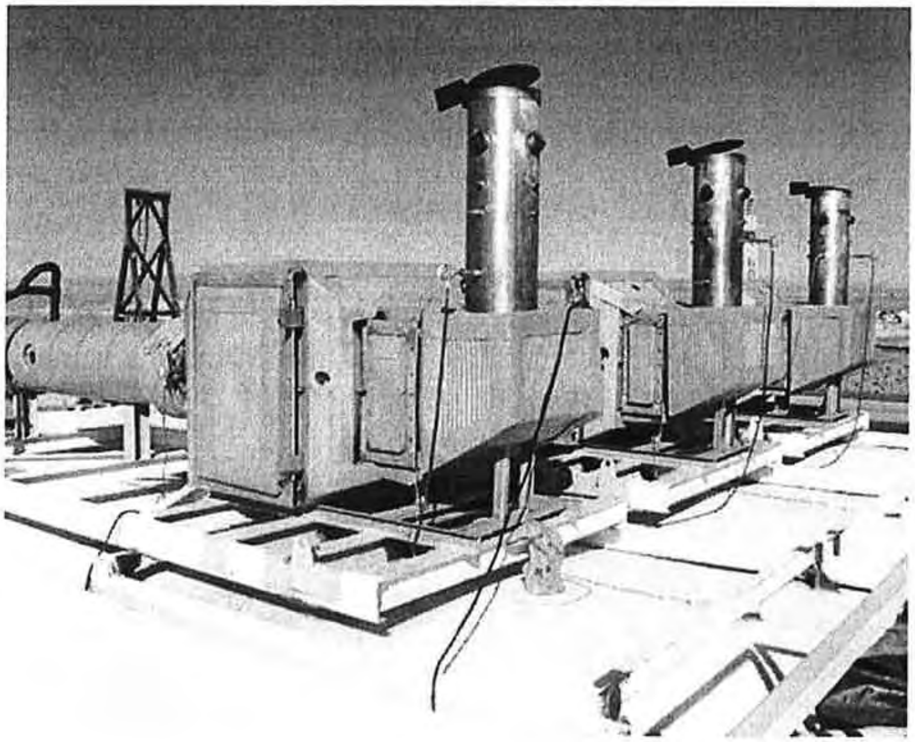
Shell, in collaboration with Wyoming and the BLM — the U.S. governmental body that oversees the management and conservation of public land — developed a Record of Decision (ROD) laying out the terms of operation in the area. Shell is developing the Pinedale region, drilling 80 to 90 new wells per year with a fleet of eight drilling rigs as well as producing wells at a rate of 500 million cu.ft. of natural gas per day.

Under the ROD, Shell is required to reduce NO_X emissions, which led it to partner with Johnson Matthey in March for a test installation of three urea SCR systems. The units were equipped on three Caterpillar diesel engine-powered generators used to power a drill rig. Following the test phase, Shell elected to outfit the rest of its drilling fleet with the SCR system for a total of 21 systems — three per rig.

"From Shell's standpoint this is a leading-edge application of technology to achieve the goals required to protect the environment," said Sewell. "Johnson Matthey has, in our opinion, risen to the occasion to work with us and make this technology work. I'm confident that the other seven rigs that we outfit with the technology will be successful."

Each drill rig is powered by three Caterpillar diesel-powered generators. The generators are equipped with Cat 3512BDITA diesel engines rated 1476

Comment Letter I9



Johnson Matthey's SCR system is placed on top of the generator enclosure on a skid outfitted with a Johnson Matthey catalyst, a catalyst housing, a mixing duct and the Johnson Matthey urea injection lance/nozzle. The top portion of the control cabinet houses all of the electronics for the injection system while the lower portion holds the mechanical components of the system such as the pumps and valves used to provide the correct, load-specific urea dosing rate.

hp and located 50 to 100 ft. from the rigs. The three generators work in conjunction with each other, running nonstop at varying loads — making it difficult to control NO_X levels, which vary along with the load.

The Johnson Matthey system was specifically designed for the drilling application and its demanding requirements, said Mike Baran, senior sales engineer for Johnson Matthey's Stationary Source Emissions Control Group (SSEC). "The temperature, weather and wild load swings really made it a difficult application for an SCR system. They run these (generators) at widely fluctuating loads. Since NO_X levels fluctuate along with the load cycling, we had to do some special things in catalyst design to ensure that the SCRs were going to work correctly.

"We had to vary the amounts and types of catalysts that were installed," Baran said.

The SCR system is placed on top of the generator enclosure on a skid equipped with a Johnson Matthey catalyst, a catalyst housing, a mixing duct and the Johnson Matthey urea injection lance/nozzle. "Our system sits right on top of the enclosure and bolts into place on the skid," said Baran. "Urea lines are connected to our SCR control cabinet, penetrated through the enclosure, and then attached to our injection nozzle."

The top portion of the control cabinet houses all of the electronics for the injection system while the lower portion holds the mechanical components of the system such as the pumps and valves used to provide the correct, load-specific urea dosing rate.

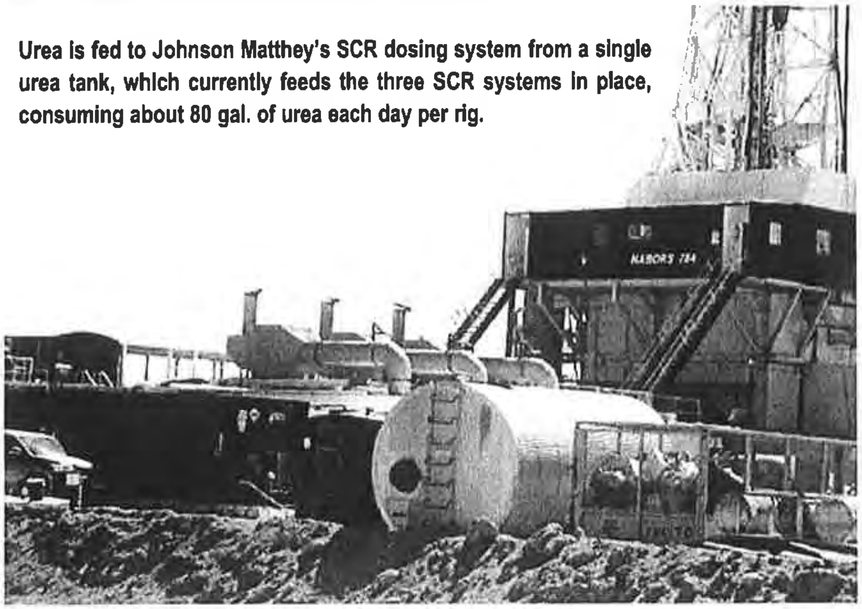
Each SCR system has a touch-screen control panel that provides monitoring capability, showing various temperature measurements, the urea injection rate, the system's status and any system alarms.

Urea is fed to the SCR dosing system from a single urea tank, which will feed all three SCR systems on a rig. With the three SCR systems currently in place, Sewell said about 80 gal. of urea is consumed each day per rig.

While one of the challenges in fitting the generators with the SCR system was the fluctuating load patterns, the region's extreme winter temperatures posed another. "A run-of-the-mill SCR system can't really address that," said Baran. "Typically the exhaust temperature must be at 600°F or greater for an SCR system to work properly. We designed this system to work as low as 500°F while still maintaining capability at higher exhaust temperatures. That was important to Shell because substantial engine runtime is at lower loads and in a temperature range that might be problematic for a conventional SCR system."

The SCR system was designed to reduce NO_X by greater than 90%, and limit the amount of ammonia slip to a maximum of 10 ppm at the SCR system outlet. "Controlling NO_X is fairly straightforward with respect to SCR systems," said Baran. "An unsophisticated system can inject urea through the system at a very high rate and get a lot of NO_X reduction, but this setup will end up emitting excessive ammonia to the environment. A proper SCR system needs to be designed to simultaneously control NO_X and meet low ammonia slip numbers." According to Johnson Matthey, the SCR systems averaged ammonia emissions of 2 to 3 ppm, much less than the 10 ppm requirement.

Natural gas exploration and develop-



Urea is fed to Johnson Matthey's SCR dosing system from a single urea tank, which currently feeds the three SCR systems in place, consuming about 80 gal. of urea each day per rig.

ment in the area is mobile with rigs moving to different locations in the field to drill new wells. Based on this, Shell required a system that could be maneuvered along with the drill rigs and assembled/disassembled quickly. "They needed to move the equipment with the rig so these are quick-disconnect systems," said Baran. "They can pull them off the rig, move the engine and enclosure, drop the system back on top, and bolt them on and go."

As part of the agreement with Shell, Johnson Matthey will provide engineering, project management, installation and service support of the systems. Shell will perform maintenance checks on the units. "There's very little maintenance," said Baran. "They basically check the urea filter from time to time to make sure it is not clogged, inspect the catalyst to see if it's covered with particulate, which can be lightly vacuumed, and inspect the injection nozzle for any urea buildup."

A rolling schedule will be used for the installation of the remaining SCR systems. Nine new units are slated for completion at the end of 2008, fitting half of the drill rig fleet. The balance is expected to be installed in the first quarter of 2009. **dp**

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Contents

Summary

A preliminary search for available data on incidents involving Hydrogen Sulphide (H_2S) incidents in industry generally and in particular the geothermal industry was carried out. The search was directed at publicly accessible information sources and specialised databases. In particular databases which document chemical accidents were considered, concentrating on the accidental release of H_2S.

General data on occupational exposure to H_2S (accidental or long-term low level) were not collected and analysed to any large extent, these data are kept in national accident or medical databanks by OSH and health care agencies. Therefore, a comprehensive search into occupational incidents, neither geothermal nor other, could be performed at his stage.

From the incidents considered the following general observations can be made.

- In those incidents in which toxic effects due to H_2S were experienced there appears to have been a lack of adequate knowledge of the hazards. That is a lack of knowledge that a H_2S release could occur and the potential consequences of H_2S exposure.
- Due to the lack of awareness relating to the occurrence of H_2S, there was, in many cases, a lack of adequate preparedness to deal with the release of toxic gas.
- The lack of suitable gas alarms and personal protective equipment led, in a number of cases, to fatal H_2S exposure.
- H_2S is a life threatening hazard in the geothermal industry and a number of other industrial activities as indicated by the data shown here.
- Some industries (chemical processing, petroleum refining and petrochemical), whilst having H_2S-incidents, do not appear to suffer fatal consequences to the same degree as perhaps the geothermal and waste treatment industries. Here is an opportunity to learn lessons relating to good practice across industry sectors.

- In particular an apparently disproportionate involvement of contractor employees in H_2S incidents, carrying out repair, maintenance and cleaning activities is of particular concern.
- Data on geothermal incidents which are readily available were few, however there are indications that more detailed information may be obtainable within the major geothermal nations
- Many occupational exposures to H_2S either go unrecorded or escape a systematic documentation and data collection. Generally it can be said that occupational accidents with fatalities are systematically recorded, however access to this data is limited.

1 Introduction

Within the Chemical Accidents 2009 – 2012 Work Programme Iceland proposed the project on the analysis of H_2S-incidents and offered to take the lead. H_2S is very toxic, quickly reactive, and causes serious accidents. Geothermal wells are a source of H_2S that pose specific problems. It is proposed to collect data and analyse incidents and accidents caused by hydrogen sulphide in industry with a focus on geothermal facilities.

The proposed project originates from discussions on geothermal stations work environment at AOSH in Iceland. Such a project will be relevant to many member countries, where geothermal energy is used. However, there are many other situations in which H_2S is an issue.

The objective of the proposed project is to collect data and undertake an analysis to better understand H_2S accidents in the geothermal industry as well as other industries involving H_2S.

The data collected will be used to determine counter-measures to H_2S hazards. Those will be applicable to geothermal power plants and to some other industrial facilities. The accessibility of data could limit the analysis of accidents' causes. Geothermal areas are of varying types when comes to H_2S.

Problems with the data and the accessing of data are discussed. Conclusions that can be drawn from this preliminary study are given in a general manner at the end of the report and outlines of possible further study are also discussed.

At the 18th Working Group on Chemical Accidents Meeting a steering group was formed and it was agreed to collect and review accident data / statistics from the geothermal industry as well as from other relevant (industrial) sectors such as the petro-chemical industry.

2 H_2S -occupational hazards

Hydrogen sulphide (H_2S) is a very toxic gas at normal temperatures. It poses a very serious inhalation hazard. Effects at various exposure levels are believed to be as follows [4].

0.001-0.13 ppm	odour threshold (highly variable)
1-5 ppm	moderately offensive odour, possibly with nausea, or headaches with prolonged exposure;
20-50 ppm	nose, throat and lung irritation, digestive upset and loss of appetite, sense of smell starts to become "fatigued", odour cannot be relied upon as a warning of exposure;
100 -200 ppm	severe nose, throat and lung irritation, ability to smell odour completely disappears;
250-500 ppm	potentially fatal build-up of fluid in the lungs (pulmonary oedema) in the absence of central nervous system effects (headache, nausea, dizziness), especially if exposure is prolonged;
500 ppm	severe lung irritation, excitement, headache, dizziness, staggering, sudden collapse ("knockdown"), unconsciousness and death within 4-8 hours, loss of memory for period of exposure;
500-1000 ppm	respiratory paralysis, irregular heart beat, collapse, and death. It is important to note that the symptoms of pulmonary oedema, such as chest pain and shortness of breath, can be delayed for up to 48 hours after exposure.

Prolonged exposure (for several hours or days) to concentrations as low as 50-100 ppm can lead to rhinal inflammation, cough, hoarseness, and shortness of breath. Prolonged exposure to higher concentrations can produce bronchitis, pneumonia and a potentially fatal build-up of fluid in the lungs (pulmonary oedema).

The interim AEGL-values are:

Hydrogen sulphide 7783-06-4 (Interim)

ppm 9/10/02					
	10 min	30 min	60 min	4 hr	8 hr
AEGL 1	0.75	0.60	0.51	0.36	0.33
AEGL 2	41	32	27	20	17
AEGL 3	76	59	50	37	31

3 H_2S environments in industry

Hydrogen sulphide is encountered in many workplaces. These include:

- chemical and related industries where the gas itself is used,
- industries handling sulphides or other sulphuric substances, or where it occurs as an intermediate or as a waste product.
- the oil & gas industry and other types of raw-material extraction and handling where it is part of the original raw material. This includes geothermal fluid extraction and processing.
- workplaces where fermentation and other anaerobic decomposition of organic material, organic or inorganic sulphur containing material occur, such as in biomass processing, farm work and waste handling and processing. This is caused by groups of so called sulphate-reducing bacteria that reduce sulphur compounds, including sulphite, thiosulphate or elemental sulphur, to sulphide

Following are examples of industries where H_2S hazard occurs:

- -Oil and gas:

Crude oil refineries (primarily sour crude oil), crude oil processing/handling plants and transmissions/pipelines, sour natural gas processing/handling plants/stations storages and transmissions/pipelines

- Animal fat and oil processing
- Asphalt storage
- Blast furnaces
- Breweries and fermentation processes
- Chemicals and related production processes, various:
  Carbon disulphide, dyes, thiophene, sulphur, bromide-bromine, soap, phosphate purification, hydrochloric acid purification, cellophane, rubber, plastics, soap, silk, rayon, photoengraving, synthetic fibers, polysulphide caulking, artificial flavour, refrigerants, glues, textile printing, etc
- Clean-up activities of organic/sulphur containing slurry/sludge, various
- Coal gasification plants
- Coke ovens
- Copper ore sulphidising and metallurgy, gold ore, lead ore, lead removal, barium carbonate and barium salt production, pyrite burning etc.
- Farms and livestock operations
- Fertilizer production
- Fishing vessel holds, fat fish processing

- Geothermal plants and utilities
- Landfills of municipal/farm/organic waste
- Metal processing, various:
- Pulp and paper production
- Sewage treatment plants
- Slaughterhouses and rendering plants
- Sugar production
- Sulphur and hydrogen sulphide production
- Tanneries
- Waste treatment operations

There are numerous case reports of deaths, especially in the oil and gas extraction industry [25], sewage maintenance, and on farms. Most fatalities have occurred in relatively confined spaces (e.g. sewers, sludge tanks, cesspools, or H_2S collecting in depressions on open land or in buildings) [7]. In many cases, multiple deaths have occurred at a single site. Rescuers, attempting to save an unconscious co-worker, have entered a confined area without respiratory protection or safety lines. They, in turn, have been overcome by H_2S. Workers who survive a serious short-term H_2S exposure may recover completely or may experience long-term effects. [4, 1, 2, 3, 7, 32].

4 Geothermal industry and H_2S

4.1 Widespread and growing geothermal utilisation

Many countries have utilised geothermal energy for decades and some for centuries. These are mainly in the tectonic rift zones where the continental plates either collide or diverge. There the heat from the Earth's interior is closest to the surface and cracks and porous rock allows water to seep down into the hot crust and steam and hot water to seep upwards. Geothermal heat can also be found in other locations where the temperature increase with depth may be slower and porosity for water less than in the rift zones but in some instances the heat is worthwhile drilling for. Even hot deep rock is being used to heat water and return to surface [17]. The following table lists countries that utilise geothermal energy (see also IGA lists [29] of both total geothermal energy and geothermal electric energy production).

Table of geothermal utilisation by country, GWh/year (year 2000) [28].

Rank	Countries	Amount
1	China	8,724
2	United States	5,640
3	Iceland	5,603
4	Turkey	4,377
5	New Zealand	1,967
6	Georgia	1,752
7	Russia	1,703
8	Japan	1,621
9	France	1,360
10	Sweden	1,147
11	Mexico	1,089
12	Italy	1,048
13	Romania	797
14	Hungary	785
15	India	699
16	Switzerland	663
17	Serbia and Montenegro	660
18	Slovakia	588
19	Israel	476
20	Bulgaria	455
21	Austria	447
22	Algeria	441
23	Germany	436
24	Jordan	428
25	Canada	284

26	Slovenia	196
27	Lithuania	166
28	Croatia	154
29	Macedonia, The Former Yugoslav Republic of	142
30	Finland	134
31	Argentina	125
32	Greece	107
33	Australia	82
34	Poland	76
35	Colombia	74
36	Tunisia	48
37	Czech Republic	36
= 38	Belgium	30
= 38	Guatemala	30
40	Denmark	21
41	Netherlands	16
42	Peru	14
43	Indonesia	12
44	Portugal	10
45	Norway	9
46	Philippines	7
= 47	United Kingdom	6
= 47	Nepal	6
49	Honduras	5
= 50	Thailand	4
= 50	Venezuela	4
52	Kenya	3
53	Chile	2
	Total	44,709

Part of the geothermal calories that are tapped as steam from the high temperature areas is used for electricity generation, in particularly USA, Philippines, Mexico, Indonesia, Italy, Japan, New Zeeland and Iceland. There are 24 countries who have installed geothermal electric capacity. The total world-wide geothermal electricity production capacity was 9.7 GW in 2007 and is projected to grow to nearly 11 GW in 2010 [30].

4.2 Hazards from H_2S and other geothermal gasses

In Icelandic "hveralykt" means the smell of geysers, the rotten-egg smell of hydrogen sulphide usually associated with hot springs. Geologists distinguish between high-temperature and low-temperature fields. The high-temperature fluid, steam with boiling water droplets torn up in varying amounts brings up more gases but their concentration varies from one place to the other and even in time. The low temperature areas give geothermal water which contains dissolved gasses such as N_2, and smaller amounts of CO_2 and H_2S. The geothermal steam from the high-temperature areas, of which 0.5-1 w% can be gas, contains a different blend of gasses such as CO_2, H_2S, H_2 and CH_4 in varying concentrations. The CO_2 is usually in the largest concentration followed by H_2S and hydrogen (when molar concentration is considered). As an example, one 200 MW electric geothermal plant in Iceland uses geothermal steam of which around 0.5 w % is gas, of that about 80-85 w% is CO_2 and about 15 w % is H_2S. This plant produces nearly 10,000 tons annually of H_2S. The gasses are left as the steam condenses. Any container, closed or semi-closed space in a geothermal plant where pressure drops or cooling of the geothermal steam occurs can contain or even accumulate H_2S gas. It is heavier than air and settles in low lying areas. H_2S is a good scavenger of oxygen in aqueous solution and consumes oxygen dissolved in the geothermal water. Consumption of oxygen by H_2S in the gas phase, when it mixes with atmospheric oxygen, is less well known but given the right environment and sufficient time, H_2S will react with oxygen and deplete it in stagnant air bodies. If the oxygen content goes (from 21%) below 10% in the working environment, inhaling a breath can cause nearly immediate unconsciousness, a similar effect to what happens when the H_2S content reaches a few hundred ppm. This means that plant equipment to handle geothermal fluids as well as the plant working environment can be hazardous to workers as experience from Iceland and other countries show. Sudden and even unpredictable presence of H_2S, as well as the other asphyxiating non-poisonous geothermal gasses, causes incidents and the oxygen scavenging effect of H_2S plus the oxygen thinning effect of the other gasses can make spaces dangerously low in oxygen. This complicates analysis of the chemical cause of incidents.

To sum up the special properties of geothermal steam that makes it hazardous:

- Geothermal gasses remain in the steam processing and turbine system, after the steam has condensed, until vented out
- Seemingly harmless leaks of steam from piping or equipment inside buildings, into confined or semi-confined spaces, can generate large volumes of gas
- Accumulation of gas in low lying, poorly ventilated spaces

- Knock-down effect of H_2S: Inducing unconsciousness in seconds without warning
- H_2S is an oxygen scavenger and, given the right conditions, consumes oxygen in stagnant air.

Icelandic firms and institutions working internationally in the geothermal business have encountered stories of many H_2S incidents and near-misses. There is a lack of written and organised data on these incidents many of whom have occurred at the stage of development or start-up, some in rather remote areas, some in developing countries. An example can be the following verbal account from a senior researcher in the Icelandic Energy Authority:

> In a geothermal plant in Kenya a photographer went into a manhole to photograph the inside of a flash tank to record corrosion on its walls. He was knocked down whereupon a person went into the tank to save him and was also knocked unconscious whereupon the third person tried to save the two and was also knocked down. All died and it appears H_2S was the main cause of death.

5 Data search

A preliminary search for information on H_2S incidents was carried out using readily accessible databases and other information sources without special inquiries or requests. Following are some excerpts and abstracts of pertinent data encountered in the search.

5.1 International medical abstracts on H_2S -poisoning.

From Ovid Medliner database:

- Hydrogen sulphide poisoning: Clarification of some controversial issues.

Hydrogen sulphide is a toxic gas about which much has been written. We discuss here several issues we believe would benefit from further clarification. Conclusions: We conclude that: 1) Certain neurotoxic effects of exposure are probably due to a direct toxic effect on the brain, while others are almost certainly a result of hypoxia secondary to H_2S -induced respiratory insufficiency; 2) pulmonary oedema is a common consequence of poisoning and there is suggestive evidence of hyperactive airway responses in some individuals following brief H_2S -induced unconsciousness (knockdown); 3) criteria for acceptable community levels are very different than those governing occupational standards; 4) urinary thiosulphate determinations can be useful for monitoring occupational exposure; and 5) determination of sulphide ion concentrations in blood or major organs can be useful in corroborating a diagnosis of fatal H_2S toxicity, but there are many pitfalls in collecting, storing, and analyzing tissue and fluid samples [10].

- A review of 152 cases of acute poisoning of hydrogen sulphide.

Clinical data of 152 cases of acute poisoning of hydrogen sulphide were analysed. Of these cases 5 were diagnosed as irritant reaction, 10 mild poisoning, 56 moderate, and 81 severe. Eight of the 152 cases died, with a fatality rate of 5.3%. 137 cases (90%) lost consciousness temporarily. The degree of disturbance of consciousness provided important basis for determining diagnostic grade. Recommendations for treatment were mainly comprehensive, supportive measures as well as first aid. Certain neuropsychic sequelae were found in some of the 95 cases followed up for 1 to 10 years[13].

5.2 France, ARIA database.

The search term "hydrogène sulfuré" generates a report of 108 incidents from the ARIA database, which covers incidents from France and also other countries. The database is maintained by BARPI [27]. A selection of some of the more recent incidents is summarised in English in Annex 1.

The ARIA database contains a range of incidents from smaller (sub-Seveso) to larger industrial events which are also reported in the EU MARS database. ARIA also contains a number of incidents from outside France. All reports are in French, a few "special cases" are also provided in English.

The fatal accidents are commonly in various waste handling and processing (including waste water and sewage treatment) followed by petroleum extraction and processing. A number of incidents occurred within inhabited areas, leading to effects within the local population

5.3 Germany. ZEMA-database and other sources

In Annex 2 there is a table of incidents recorded in Germany from 1969-2007

Eleven incidents are registered by the ZEMA [21] database which is the German federal database for recording reportable major accidents under the Major Accident Ordinance (Störfall-Verordnung). The most serious incident, i.e. those involving loss of life, injuries to persons, large scale contamination of the environment or substantial damage to property are then reported to the EU MARS database.

Five of the incidents listed have been reported in the media and were either amaller scale incidents or outside the scope of the Major Accident Ordinance

Five incidents are documented in the UBA publication Handbuch Störfälle (out of print) which records a large number of incidents of various types, details are often lacking and the original sources for the entries were very often press reports and not official investigations [22].

Of the 21 incidents above, over ½ are in chemical industry and somewhat less than ½ is in waste treatment or recycling activities. The more recently notified accidents are mostly in the chemical and oil & gas industry but waste treatment and recycling suffer more fatal accidents. As previously noted, temporary personnel in particularly maintenance, clean-up and loading/unloading are those who are most often seriously affected by H_2S-incidents. Production shut-down and start-ups are the most hazardous phases of plant operation as demonstrated in the list, half of the accidents are during construction, start-ups/shut down or maintenance and only about a third during normal process runs. In normal operation corrosion often plays a major part in the release of H_2S. In the recent fatal accidents, the known pattern of double/multiple fatality is demonstrated when helping hands to the first victim become victims as well

5.4 UK. Incidents of exposure in industry, 1990-2003.

HSE compiled a list of 35 on-shore H_2S -incidents between 1990 and 2003. Of those, nearly a half were apparently caused by some form of biological decomposition in a variety of environments where organic matter was present; from various waste, sludge, slurries, sumps and manure. Also acidification of sulphide containing residues in clean-up operations caused H_2S-releases. About a half of the listed incidents involve confined and semi-confined spaces. The other half of the incidents in the list were mostly in the handling of chemicals, from leaking H_2S equipment in chemical and related industries and in chemicals production. A few were in metallurgy and in labs. This half of the incidents did not as a rule involve confined spaces. Oil & gas industry incidents off-shore are not in the list. Six of the incidents (17%) are said to have been fatal and, alarmingly, two of them (33%) double, both by biologically generated H_2S; in a distillery effluent tank and in a slurry storage at a farm. Many of the incidents were serious and lead to unconsciousness. The brief accounts of these incidents show again how often it is difficult to make a distinction between asphyxiation and poisoning, let alone quantify a combined effect of both H_2S-poisoning and oxygen deficiency. The list states in some instances that asphyxia was the cause of illness. See Appendix 2 [19].

5.5 EU. The MARS database

The MARS-database of the EU is maintained by the Major Accident Hazards Bureau at the JRC and contains now about 600 accidents and near misses in establishments that come under the Seveso Directives, i.e. those that handle large amounts of dangerous substances. It is for the EU similar to what ZEMA is for Germany and would include accidents counted for there also. Accounts date back to 1982.

As an example of an on-line search in the database, it gives 39 major accidents where hydrogen sulphide releases led to human injuries between the years 1985 and 2008. Of the 39, 7 (18%) were fatal. The accidents were mainly in larger process plants of chemicals, oil, metallurgy and waste processing [31]. MARS is also the reporting database for the OECD Chemical Accidents programme. In this case the reports by non-EU countries is on a voluntary basis.

5.6 USA. Institutions. Workplace deaths by H_2S

CSB (The Chemical Safety Board) investigates chemical incidents in the US [8]. OSHA keeps also records of chemical incidents in industries. For a period of one decade (´84-´94) there were an average of 8 fatalities per year from H_2S-poisoning whereof nearly a quarter were co-workers rushing to help the first victim, a familiar pattern of H_2S fatal accidents generally.

-Occupationally related hydrogen sulphide deaths in the United States from 1984 to 1994

Alice Hamilton described fatal work injuries from acute hydrogen sulphide poisonings in 1925 in her book *Industrial Poisons in the United States.* There is no unique code for H_2S poisoning in the *International Classification of Diseases, 9th Revision*; therefore, these deaths cannot be identified easily from vital records. We reviewed US Occupational Safety and Health Administration (OSHA) investigation records for the period 1984 to 1994 for mention of hazardous substance 1480 (hydrogen sulphide). There were 80 fatalities from hydrogen sulphide in 57 incidents, with 19 fatalities and 36 injuries among coworkers attempting to rescue fallen workers. Only 17% of the deaths were at workplaces covered by collective bargaining agreements. OSHA issued citations for violation of respiratory protection and confined space standards in 60% of the fatalities. The use of hydrogen sulphide detection equipment, air-supplied respirators, and confined space safety training would have prevented most of the fatalities [23].

5.7 Canada. Oil & gas workers. Environmental releases.

-Oil and gas workers exposed to H_2S in Alberta

In their 1997 study, Hessel et al. submitted a questionnaire about health effects from hydrogen sulphide exposure to 175 oil and gas workers in Alberta, Canada, a known region for sour gas wells associated with the oil and gas industries. Of the 175 workers, on third reported having been exposed to H_2S, and 14 workers (8%) experienced knockdown, a term for the loss of consciousness due to inhaling high concentrations of hydrogen sulphide. The workers who had experienced knockdown exhibited the respiratory symptoms of shortness of breath, wheezing while hurrying or walking up hill, and random wheezing attacks. The investigators found no “measurable pulmonary health effects as a result of exposure to H_2S that were intense enough to cause symptoms but not intense enough to cause unconsciousness [24, 25].

- Environmental release occurrences in Canada 2000-2009

Records that cover nearly a decade, from 2000 to 23.6 2009, show 117 release incidents. Most of them are in petroleum or gas, waste water treatment plants and pulp and paper industries. In the oil and gas sectors, gas well blowouts are the most common cause. The Lodgepole incident in Alberta 1982 is perhaps the most significant and well documented in the literature. Since then, Alberta Energy Conservation Board has done risk research on modelling sour gas releases. Of the listed causes of releases equipment failure, likely often because of lack of maintenance, seems to be the most frequent single cause in cases where the cause is known. No quantifications of damages or fatalities are included in the list but most of them could apparently have been hazardous and caused H_2S poisoning [18].

5.8 *Japan. The RISCAD-database.*

The RISCAD database registers chemical incident in Japan. The number of serious accidents in the chemical industry decreased although accidents still happen with e.g. H_2S during non-operating condition in process plants [33].

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-Trends in chemical hazards in Japan

In the past, the chemical industry in Japan has been the cause of a number of major industrial accidents. Subsequent to each accident, specific lessons have been learned. These lessons learned have been implemented in terms of safety education of the employees and/or safety measures of the equipment and facilities resulting in a rapid decrease of corresponding accident frequencies. In this paper, we summarized both recent and past major accidents caused by chemical substances in fixed installations in Japan. Case studies show that runaway reactions are among the main causes of major accident occurrences in the chemical process industry in Japan. A recent fatal poisoning accident caused by H_2S gas generated during maintenance work again highlights the necessity of adequate safety management in a chemical factory. Therefore, even if hazard evaluation of chemical substances and chemical processes is necessary to prevent runaway reactions, human error is also an important factor contributing to reaction hazards [26] (se also: Wakakura, M. (1997) Human factor in chemical accidents, J. Safety Eng. High Press. Gas. Safety Inst. Japan, 34, 846).

5.9 *Iceland. Data of incidents in geothermal industry.*

-General discussion of H_2S-hazards in geothermal plants

Records of accidents with gas poisoning in the geothermal industry are remarkably scarce in Iceland. One of the problems of finding H_2S poisoning incidents in older accounts in Icelandic records is that they are often unrecognisable from confined space accidents.

People in the geothermal industry have nevertheless many stories to tell of incidents with H_2S where luckily no lasting effects were observed. The geothermal springs have been utilised for heating for a long time although distant heating by piping started in 1906. Drill holes have so called hole-cellars built around them where workers often encountered H_2S that accumulated there, originating in the steam that leaked from the piping. Today, the drill hole cellars are shallower and have a ventilation system that ensures constant draft up from the cellar floor. The geothermal steam condenses and disappears or becomes a small drying pool on the floor but H_2S stays and accumulates in the cellars or building with deficient ventilation as it is heavier than air. Experience has taught people in the industry to be aware of this property of H_2S. Caution, including gas masks and alarm sensors, is exerted in buildings and confined spaces as well as outdoor areas in the geo-electric power plants nowadays. The short term exposure limit is 15 ppm but the alarms are often set on 10 ppm, the 8-hour limit.

Most fearsome is the special property of the gas to induce immediate loss of consciousness at one breath at concentration of several hundred ppm. Those exposed have in most instances regained consciousness within minutes with seemingly no lasting health effects. Some accounts indicate that sheer luck has prevented a fatality. Often contractor personnel have been most prone to accidents, as familiar in the chemical industry.

In the last decades, new geothermal plants that primarily produce electricity in steam turbines has increased the H_2S problem as these plants are fed high-temperature geothermal steam with relatively high H_2S-contents compared to the regional heating systems in the low-temperature (hot water) areas. When the steam condenses, the H_2S-laden gas is left in the steam system where it is usually vented off to special stacks together with the other gasses and exhaust steam that is released to the atmosphere. There are plants, at least in the US, that clean the H_2S from the exhaust gas by oxidation processes in a similar fashion to what the gas and oil refineries do by e.g. the Claus process. The loss into buildings of this H_2S-laden gas from the turbine piping system, before venting, can cause poisoning incidents, e.g. when starting up or closing down turbines, switching well feeds or on maintenance holds. Most unrecorded incidents are of short time exposures where people have been able to leave the exposure area without external help.

-Recent recorded H_2S-incidents in geothermal plants in Iceland

-In September, 2007, turbines in a new electric power plant were being started and restarted during a plant start-up program. Pressure built up after start in the condensate collectors and relive valves opened and the H_2S-laden gas (which was left in the condensers when the steam condensed after turn-off) escaped into the machine hall where operators and contractor personnel was working. The turbine hall had to be closed on occasions and smoke divers with SCBA brought in to close the valves. On an occasion, three workers were seriously affected. One of them narrowly escaped to a walkway from the hall, there he lost consciousness but regained it quickly. The others had milder poisoning symptoms. Medical examination indicated no lasting health effect and the men returned to work the day after. After these incidents, the faulty valves were replaced, escape routes were redesigned and air fed respirators installed in critical places [16].

-In December 2008, a worker standing outside the plant building was exposed to H_2S from an up-wind gas venting chimney. He was taken ill with reddened eyes and face and by midday developed nausea and subsequently vomited blood on the way to the hospital. He recovered fully in a short time. The cause was judged by doctors to be H_2S. It was possibly in rather low concentration [16].

-Recent H_2S -related fatal accident in a geothermal plant in Iceland

-In august, 2008, two workers died in a new geothermal electric plant in Iceland. They entered a steam evaporator tank immediately after they had cut a manhole on its side. Doctors' report said the case was of lack of oxygen but implicated other gasses, among them H_2S, as a contributing cause. A chemical engineering evaluation of the gas that entered the tank originally, and the formation of the deadly atmosphere inside the tank, indicated that H_2S had probably consumed a substantial part of the atmospheric oxygen from the air that was vented into the evaporator after turn-off several weeks before the accident. This was a case of confined or semi-confined space with stagnant air and H_2S together with other geothermal gasses in equipment that had been put on hold for modification. Entry through the manhole had been banned. The deaths occurred very suddenly just inside the manhole [16].

5.10 International medical abstracts on geothermal H_2S - poisoning.

From Ovid Medliner:

-A fatal case of hydrogen sulphide poisoning in a geothermal power plant.

An adult man entered an oil separator room to remove waste oil from a vacuum pump in a geothermal power plant. He suddenly collapsed and died soon after. Since hydrogen sulphide gas was detected in the atmosphere at the scene of the accident, poisoning by this gas was suspected and toxicological analysis of sulphide and thiosulphate in blood, brain, lung, femoral muscle was made using the extractive alkylation technique combined with gas chromatography/mass spectrometry (GC/MS). The concentrations of sulphide in these tissues were similar to those previously reported for fatal cases of hydrogen sulphide gas. The concentration of thiosulphate in the blood was at least 48 times higher than the level in control samples. Based on these results, the cause of death was attributed to hydrogen sulphide gas poisoning [9].

-Health hazards from volcanic gases: A systematic literature review.

Millions of people are potentially exposed to volcanic gases worldwide, and exposures may differ from those in anthropogenic air pollution. A systematic literature review found few primary studies relating to health hazards of volcanic gases. SO_2 and acid aerosols from eruptions and degassing events were associated with respiratory morbidity and mortality but not childhood asthma prevalence or lung function decrements. Accumulations of H_2S and CO_2 from volcanic and geothermal sources have caused fatalities from asphyxiation. Chronic exposure to H_2S in geothermal areas was associated with increases in nervous system and respiratory diseases. Some impacts were on a large scale, affecting several countries (e.g., Laki fissure eruption in Iceland in 1783-4). No studies on health effects of volcanic releases of halogen gases or metal vapors were located. More high quality collaborative studies involving volcanologists and epidemiologists are recommended. [11]

-Investigation of health effects of hydrogen sulphide from a geothermal source.

Little is known about health effects from chronic exposure to hydrogen sulphide (H_2S). The city of Rotorua, New Zealand, is exposed to H_2S by virtue of its location over a geothermal field. In this study, the authors classified areas within Rotorua as high-, medium, or low-H_2S exposure areas. Using 1993-1996 morbidity data, standardized incidence ratios were calculated for neurological, respiratory, and cardiovascular effects. Poisson regression analysis was used to confirm results. Results showed exposure-response trends, particularly for nervous system diseases, but also for respiratory and cardiovascular diseases. Data on confounders were limited to age, ethnicity, and gender. The H_2S exposure assessment had limitations. Assumptions were that recent exposure represented long-term exposure and that an individual's entire exposure was received at home. The results of this study strengthen the suggestion that there are chronic health effects from H_2S exposure. Further investigation is warranted [12].

-Hydrogen sulphide poisonings in hot-spring reservoir cleaning: Two case reports.

The potential hazards to maintenance personnel cleaning hot-spring reservoirs are reported following two severe and unusual episodes of acute hydrogen sulphide poisoning involving seven workers. In the first episode, five victims lost consciousness immediately after climbing down a manhole to the bottom of a reservoir disregarding a strong odour of rotten eggs. One of them died immediately. Of the four who lived, three developed hemorrhagic keratoconjunctivitis and aspiration pneumonia, but no sequelae were observed 2 years later. In the second episode, two workers had been cleaning the reservoir for about 2 hours when one collapsed and his companion went to seek help. Both died of acute respiratory distress syndrome due to pulmonary oedema within 12 hours. Since hot-spring bathing is a popular recreation in Taiwan, other accidents of hydrogen sulphide poisoning may have occurred but have not been reported. Such clinical information is helpful to enable regulators to initiate proper precautions to safeguard those workers involved [14].

-The health hazards of volcanoes and geothermal areas

Volcanoes and their eruptions can result in a wide range of health impacts, arguably more varied than in any other kind of natural disaster. At least 500 million people worldwide live within potential exposure range of a volcano that has been active within recorded history. Many volcanic and geothermal regions are densely populated and several are close to major cities, threatening local populations. Volcanic activity can also affect areas hundreds or thousands of kilometres away, as a result of airborne dispersion of gases and ash, or even on a hemispheric to global scale due to impacts on climate. Healthcare workers and physicians responding to the needs of volcanic risk management might therefore find themselves involved in scenarios as varied as disaster planning, epidemiological surveillance, treating the injured, or advising on the health hazards associated with long range transport of volcanic emissions [15].

6 Data sources

The search for data described in this report is intended for preliminary analysis of H_2S-poisoning incidents with focus on the geothermal industry. Information was sought from specialised databases, especially those who register accidents at larger establishments with dangerous substances, a medical database as well as publicly accessible information sources and a few national data. The data collection was not intended as a complete assembly of records on H_2S-poisoning incidents. Request for information on incidents from authorities or agencies in OECD-member countries was deemed to be premature and too time consuming given the limited scope and time frame of this preliminary analysis. Therefore, analysis of data from national OSH-bodies is not included.

Following are our comments to the search, information sources and obtained data:

1. Besides information sources that are accessible to the general public, we have identified the following specialised pertinent data sources on H_2S-incidents in industry: MARS in the EU, records at the CSB and OSHA in the USA, ZEMA in Germany, ARIA in France, RISCAD in Japan, HSE records in the UK. Also Ovid medical database where research papers on medical aspects of H_2S poisoning in industry are registered.

2. Accidents in the main chemical, oil & gas as well as many other advanced or larger industries are well documented in developed countries in databases such as those mentioned above and some of the data are relatively accessible there. Information on off-shore oil & gas incidents were as a rule not included in the scanned data.

3. Systematic scanning of databases on occupational injuries of H_2S was not performed although some information from a few countries is included. These databases were inaccessible and evidently also deficient in some instances. It is probably still more difficult to gain exact information on smaller workplaces as well as from less industrially developed countries.

4. Literature references of H_2S-incidents in the geothermal industry are scarce and inaccessible and authors of this report found rather few publicly accessible sources that specifically mention geothermal source of the H_2S in cases of H_2S-poisoning in occupational environments. Exemptions were a few pertinent references in medical science journals. Information, such as national accident accounts or statistics from the main geothermal countries turned out to be rather unavailable. There are also apparently cases where accounts are non-existent and/or incidents not registered in accessible databases. Specific enquiries to OSH institutions in the geothermal countries would possibly reveal if there are data on the geothermal industry which could provide patterns and statistics about poisoning incidents in this industry.

7 Preliminary analysis of obtained data

1. From the incidents considered general conclusions may be drawn.

- In those incidents in which toxic effects due to H_2S were experienced there appears to have been a lack of adequate knowledge of the hazards. That is a lack of knowledge that a H_2S release could occur and the potential consequences of H_2S exposure.
- Due to the lack of awareness relating to the occurrence of H_2S, there was, in many cases, a lack of adequate preparedness to deal with the release of toxic gas. There could be a lack in awareness in some industries that there is no warning by the odour of hydrogen sulphide, as the ability to smell hydrogen sulphide disappears if a hazardous concentration is reached. The lack of suitable gas alarms and personal protective equipment led, in a number of cases, to fatal H_2S exposure. Filter gas masks are potentially perilous in many of these circumstances of high H_2S-concerntration as they can become saturated quickly and provide false security. Air-fed respirators are necessary in the geothermal industry and works need instruction in their use. A personal gas sensor with alarm is also a necessary piece of personal protection equipment (PPE).
- H_2S is a life threatening hazard in the geothermal industry and a number of other industrial activities as indicated by the data shown here.
- Some industries (chemical processing, petroleum refining and petrochemical), whilst having H_2S-incidents, do not appear to suffer fatal consequences to the same degree as perhaps the geothermal and waste treatment industries. Here is an opportunity to learn lessons relating to good practice across industry sectors.

2. H_2S remains a serious occupational hazard in many workplaces as demonstrated recently by 80 workplace fatalities reported during one decade in the US alone, as well as other data.
3. Accidents involving fatalities or serious injuries seem mostly to occur at non-standard operating, intermittent conditions such as start-ups, production halts

for modifications, repair and maintenance and clean-ups or at loading and unloading.

4. Contractors in installation, maintenance and clean-up operations seem to be in most danger by H_2S-hazards. It is most likely that contractors are more often affected whilst carrying out these activities because cleaning and maintenance operations are regularly contracted out to specialised companies.
5. Many of the fatal incidents seem to be associated with confined or semi-confined spaces.
6. Part of the data (e.g. US study) indicates that personnel of smaller companies are more prone to the H_2S-hazards although the place of incident may be a large workplace.
7. Biologicaly generated H_2S from organic material, including many types of waste, seems to be the cause of disproportionately many H_2S fatalities as compared to the chemical and related process industries.
8. The larger chemical industry, petroleum refining and other developed industries, have apparently a relatively good control of the H_2S occupational hazards although serious incidents do occur, as shown by the major accidents databases (e.g. MARS and ZEMA). The hazard can also affect their neighbourhood due to large quantities besides the contractors or temporary engaged personnel on site.
9. The borderline between asphyxia and H_2S-poisoning seems sometimes to be blurred in the accounts of incidents. Medical examinations as well as on-site investigations do not always reveal what the real causes of injury/death were only that H_2S was found to be present at the scene. Asphyxiating non-poisonous gasses with small amounts of H_2S can work together to impair consciousness
10. Many incidents probably go unrecorded. This could particularly be a problem where the gas appears as an unexpected product of waste or other organic material decomposition and in incidents involving unplanned reactions outside chemical plants, such as acidification of sulphides in waste and residues.
11. Analysis of data on the geothermal industry.

From the small number of accounts it is clear that H_2S is a very serious and life-threatening hazard to people in the geothermal industry and quite many fatalities have occurred considering the modest size of that industry worldwide. The data acquired reveal the same quality of the gas as evident in other industries; workers taken by surprise and the knock-down effect leaves them helpless and too often their first helpers also. The data also indicate that more education and personal gas alarm sensors would have averted the incidents. Data also reveal that not only the high-temperature geothermal steam, which contains H_2S in larger quantities, is hazardous but also the lower temperature geothermal liquid (hot water) used for heating and baths, which usually contains less amount of H_2S. Further analysis of data would have to be made on incident data from the national occupational safety and health authorities in the countries that use geothermal energy in order to give an industry specific pattern of causes and statistics.

8 General Conclusions for Chemical Accident Prevention, Preparedness and Response as they relate to Hydrogen Sulphide

From this analysis of data on incidents involving H_2S releases it is clear that key Guiding Principles [35] as highlighted in the "Golden Rules" need to be applied to the industries concerned. It is absolutely vital that the industry identifies and understands the hazards and their associated risks as they apply to the activities being carried out. This means, with particular consideration of H_2S that:

- The industries concerned must be aware of where H_2S may be found (generated), how it may be released (also unintentionally) and what the impact of such releases may be.
- The industries need to consider specific characteristics associated with the very toxic gas Hydrogen Sulphide. This means not only the toxic, and dispersive aspects, but also the corrosive attack which may be associated with moist H_2S atmospheres and the related potential for loss of containment.

- The industries need to develop their safety culture, striving for a "zero" or at least minimal release tolerance. Incidents should be reported and investigated and appropriate measures to prevent their repetition adopted and shared within the industrial communities.
- Appropriate planning and training to deal with emergencies needs to be carried out. This includes thorough training relating to the rescue of collapsed employees, who may have been exposed to a toxic atmosphere.
- The Authorities which oversee, regulate and inspect the industries concerned need to be aware of the risks within these industries which are due to the potential release of Hydrogen Sulphide. They need to ensure that the industries address these risks and that appropriate communication and co-operation amongst stakeholders takes place
- Emergency responders should be aware of those industries in their locality for which a release of Hydrogen Sulphide is a potential risk. Appropriate response plans, training and measures to communicate with the local community should be put in place. In particular because of the obnoxious odour at very low concentrations, which may lead to widespread concern in the community.
- Regulations and recommendations on occupational safety for entering confined spaces have to be communicated to and respected by all industries.

9 Outline of further study

A- This preliminary study did not establish the real extent of H_2S-incidents in the geothermal industry or some of the other industries of interest. In order to quantify the injurious impact H_2S has had, a more detailed data search would be needed. Lessons from such a search could improve understanding of the specific causes of incidents in certain industries but to what extent is difficult to say at this stage, considering the fact that for example the geothermal industry is relatively small and new.

B- The incidents seem often to stem from lack of experience and knowledge, both by the workplace management and also by the competent authorities that oversee the activities. In order to improve the situation, collected experiences and lessons learned from incidents in these specific industries could be a base for developing guidelines, recommendations or information booklets to be targeted at the operators of these workplaces and possibly the overseeing agencies also.

C- This study indicates that well established methods of prevention and preparedness (Chapter 8), such as education, training and protective equipment, would have averted the majority of the injurious incidents we found accounts of. Definition of potential future work or redefinition of the project should take this into account.

D- In case further studies are undertaken, the main issue seems to be why relatively many accidents happen in certain industries and if there are unique conditions in these industries, as for example the geothermal industry, which further studies could shed light on.

E- To better map the present condition in the geothermal industry, it would be necessary to gain cooperation with institutions in the countries that utilise geothermal energy.

In case further analysis is undertaken, it would have to involve a more detailed review of, besides the data sources scanned in this report, data assembled by means of inquiries or otherwise, particularly data on occupational injuries generally, from many countries, of what human toll H_2S takes in industry. These data collections should already be in place in many countries although they are not easily accessible but could be gained access to by further search and direct approach to pertinent institutions, particularly national ones who could have information on incidents hidden away in their own institutional files or buried in statistics. This seems valid for not least the information on incidents in the geothermal industries. A way would be to send inquiries to national authorities, for example in the main geothermal countries′ OSH administrations. There are 53 nations that use geothermal energy but only 24 that use the more H_2S-laden steam from high temperature fields. Information on the other exposed branches, such as biological decomposition and certain contractor activities, could also be gained access to by direct inquiries to government agencies. There are also associations and other non-government bodies that could have information worth looking at. Science journals abstracts should also be explored better.

In case a further study is done, a preliminarily outline could be as follows:

a- Definition and selection of specific exposed industries, in particularly new, emerging or expanding sectors, such as:

1- Geothermal industry
2- Waste processing/recycling industry
3- Selected sectors of bio-technology industry
4- Selected industries outside the main chemical and oil & gas sectors
5- Contractors in process industry installation, repair, maintenance and industrial clean-up and a few other services

b- A questionnaire could be sent to appropriate branches of government and particularly OSH and health institutions, to furnish national data or provide a country report on H_2S-related accidents.

c- Processing of data to deduct conclusions and patterns as to causes, common features, statistics and general lessons from the accidents in order to evaluate actions of prevention and preparedness to the hazards of H_2S.

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References

1. The Nordic Expert Group for Criteria Documentation of Health Risks from Chemicals and The Dutch Expert Committee on Occupational Standards. 127. Hydrogen sulphide. Kristin Svendsen. Nordic Council of Ministers. NIWL, Stockholm.2001
   http://www.inchem.org/documents/kemi/kemi/ah2001_14.pdf

2. International Volcanic Health Hazard Network
   http://www.dur.ac.uk/claire.horwell/ivhhn/guidelines/gas/h2s.html

3. Concise International Chemical Assessment Document 53. Hydrogen Sulfide: Human Health Aspects. First draft prepared by Dr C.-H. Selene J. Chou. World Health Organization. Geneva, 2003
   http://www.inchem.org/documents/cicads/cicads/cicad53.htm

4. Chemical Profile Hydrogen Sulfide. CCOHS
   http://www.intox.org/databank/documents/Chemical/hydrosul/cie313.htm

5. Managing hydrogen sulphide detection offshore. HSE.
   http://www.hse.gov.uk/offshore/infosheets/is6-2009.htm

6. Bowyer, J. Residence Time for Hydrogen Sulfide in the Atmosphere Litterature Search Results. Feb 6, 2003
   http://daq.state.nc.us/toxics/studies/H2S/H2S_Ambient_Air.pdf

7. Toxicological Profile for Hydrogen Sulfide. NTIS 1999.
   http://www.atsdr.cdc.gov/toxprofiles/tp114.pdf

8. U.S. Chemical Safety and Hazard Investigation Board.
   Investigation Report January 2003.: Hydrogen Sulfide Poisoning. Georgia-Pacific, Naheola Mill, Pennington, Alabama, January 16,2002. Report No. 2002-01-I-AL.
   http://www.chemsafety.gov/assets/document/GP_Report.pdf

9. Kage S. Ito S. Kishida T. Kudo K. Ikeda N. A fatal case of hydrogen sulfide poisoning in a geothermal power plant. Journal of Forensic Sciences. 43(4):908-10, 1998 Jul. [Case Reports. Journal Article] UI: 9670519

10. Milby TH. Baselt RC. Hydrogen sulfide poisoning: Clarification of some controversial issues. American Journal of Industrial Medicine. 35(2):192-5, 1999 Feb.

11. Hansell A. Oppenheimer C. Health hazards from volcanic gases: a systematic literature review. Archives of Environmental Health. 59(12):628-39, 2004 Dec.

12. Bates MN. Garrett N. Shoemack P. Investigation of health effects of hydrogen sulfide from a geothermal source. Archives of Environmental Health. 57(5):405-11, 2002 Sep-Oct. [Journal Article. Research Support, Non-U.S. Gov't] UI: 12641180

13. Wang DX. Chung-Hua Yu Fang i Hsueh Tsa Chih. [A review of 152 cases of acute poisoning of hydrogen sulfide]. [Chinese] [Chinese Journal of Preventive Medicine]. 23(6):330-2, 1989 Nov. [Clinical Trial. English Abstract. Journal Article. Multicenter Study] UI: 2697541

14. Deng JF. Chang SC. Hydrogen sulfide poisonings in hot-spring reservoir cleaning: two case reports. American Journal of Industrial Medicine. 11(4):447-51, 1987.

15. A L Hansell, C J Horwell and C Oppenheimer . The health hazards of volcanoes and geothermal areas. Occupational and Environmental Medicine 2006;63:149-156; doi:10.1136/oem.2005.022459. UK

16. Chemical accident reports (Efnaóhöpp H-files) Hellisheidarvirkjun 17.9.2007, 20.8.2008, 10.12.2008, Icelandic. Administration of Occupational Safety and Health, Iceland.

17. List of countries of participants 1979-2008. United Nations University. Geothermal Program. 2009. Iceland

http://www.os.is/page/jhs_fellows_intro

18 Hydrogen Sulphide Spills 2000-23.6.2009. Environmental Emergencies Division, Environment Canada, 2009.

19 UK on-shore hydrogen sulphide incidents 1990-2003. HSE, England. 19/09/05.

20 McGavran, P. Literature Review of the Health Effects Associated with the Inhalation of Hydrogen Sulfide. Idaho Department of Environmental Quality, Boise, Idaho June 19, 2001
http://www.deq.state.id.us/air/prog_issues/pollutants/H2S_lit_review.pdf

21 ZEMA database. BAM and Umweltbundesamt.Germany
http://www.infosis.bam.de/

22 Kier, B. Müller, G.: Handbuch der Störfälle: Dokumentation über Störfälle In Chemieanlagen. UBA-FB-83-023 (German Environmental ministry)

23 Fuller, Douglas C. MD, MPH; Suruda, Anthony J. MD, MPH. Occupationally Related Hydrogen Sulfide Deaths in the United States From 1984 to 1994 Journal of Occupational and Environmental Medicine: September 2000 - Volume 42 - Issue 9 - pp 939-942.

24 Hessel, Patrick A., PhD. et al.. "Lung Health in Relation to Hydrogen Sulfide Exposure in Oil and Gas Workers in Alberta, Canada." *American Journal of Industrial Medicine*. 31:554-557. 1997.

25 Skrtic, L. Hydrogen Sulfide, Oil and Gas, and People's Health, May 2006 Energy and Resources Group. University of California, Berkeley. http://erg.berkeley.edu/people/Lana%20Skrtic%20-%20Masters%20Paper%20H2S%20and%20Health.pdf

26 Wakakura, M., Iiduka, Y. Trends in chemical hazards in Japan. Elsevier Science Ltd. (Available online 21 December 1998). http://www.sciencedirect.com/science

27 ARIA database. French Ministry of the Environment. BARPI. France. http://www.aria.developpement-durable.gouv.fr/

28 Nation Master, World Statistics. http://www.nationmaster.com/graph/ene_geo_pow_use-energy-geothermal-power-use

29 International Geothermal Association

http://www.geothermal-energy.org/index.php

30 Bertani, R. World Geothermal Generation in 2007. Enel – International Division – Renewable Energy Business Development. Rome.

http://geoheat.oit.edu/bulletin/bull28-3/art3.pdf

31 MARS Database, Joint Research Centre, Major Accidents Hazard Bureau,

http://mahb-srv.jrc.it/

32 The ABCs of Hydrogen Sulphide in Geothermal Bores. Occupational Safety & Health Service. New Zealand. http://www.osh.dol.govt.nz/order/catalogue/pdf/hydrogensulphide.pdf

33 RISCAD database. National Institute of Advanced Industrial Science and Technology. Japan. http://www.aist.go.jp/index_en.html

34 Fendler, R. H_2S-incidents in Germany. Prepared for the OECD WGCA Steering Group of Analysis of H_2S-incidents.Umweltbundesamt III 2.3-P, Dessau-Roßlau, Germany. 26.08.09.

35 OECD Guiding Principles for Chemical Accident Prevention, Preparedness and Response (2nd Edition), Paris, 2003

Annex 1: Selection of incidents involving the release of hydrogen sulphide in the ARIA database

www.aria.ecologie.gouv.fr

The search term “hydrogène sulfuré” generates a report of 108 incidents from the ARIA database, which covers incidents from France and also other countries. The database is maintained by BARPI.

A selection of these incidents is provided in the following table

ARIA-No.	Date	Industry	Description
35905	02/09/2008	Petroleum Refining	BELGIUM - ANTWERP The plant at which the incident occurred is a refinery in Antwerp. It produces fuels like propane, butane. LPG, benzene, kerosene and gas oil, and chemical products like hexane, heptane, benzene, toluene and others. The capacity of the refinery is 13.5 million tons a year. The plant is situated at the eastern riverbank of the river Schelde to the north of Antwerp about 6 kilometres south of the border between Belgium and The Netherlands. Electrical power is supplied tot the refinery by two 36 kV power lines. The morning of September the second, maintenance work was planned by the company that supplies the electrical power to the refinery. The two power lines had proved to be fragile and it was planned to replace the connections in both power lines. To that order one of the power lines was shut of at 11.56 am. A plan to do this had been communicated beforehand, and it was tested that the remaining power supply would have enough capacity to transmit the necessary electrical power. At 11.57, whilst maintenance work was being carried out at one of the two the electrical power supply lines, the remaining second supply line failed, thus rendering the refinery

ARIA-No.	Date	Industry	Description
			without electrical power supply. At 11.57, start of the execution of the emergency plan, implying emergency shut down of the refinery, evacuating all not necessary personnel and retaining only the emergency staff and starting of the emergency power supply to restart the central operating desk. At 12.00, product stream is led to torch, leading to large flame and release of soot (carbon black) to the atmosphere. At the same time opening of several safety valves emitting several kinds of hydrocarbons to the atmosphere among which Benzene. Also H_2S (hydrogen sulphide) is emitted. At 12.14, the Antwerp environmental services are by fax informed of the incident with an emergency shut down. No assistance was deemed necessary by the operator or the environmental services. At 12.30, assistance of emergency services is requested by neighbouring companies because of large soot deposits on their sites and respiratory problem of some of their personnel. At 12.41, arrival of the emergency services at the site. They are informed of the incident. At 13.00, the crisis staff of the ministry of the interior of the state of Belgium is informed about the incident. At 17.15, the supply of electrical power is restarted, and preparations are started to restart the refinery. In the first minutes of the incident a safety valve opened and released 70 kilograms of hydrogen sulphide (approximately 40 m3 of pure H_2S gas). The safety valve is situated at a height of about 40 meters. After the release a cloud of H_2S formed, which migrated, with a speed of 45 kilometres/hour in north-north-eastern direction. Later analysis revealed that at ground level the concentration of H_2S reached about 0.6 ppm whilst in the centre of the cloud the concentration was in excess of 10 ppm. After ca. 5 minutes the cloud reached inhabited areas to the north of the refinery, causing acute illness, nausea, respiratory problems and a general feeling of unwell being. In the course of the next 70 minutes the cloud travelled about 50 kilometres over Belgium

ARIA-No.	Date	Industry	Description
			and parts of The Netherlands, affecting several hundreds of people. Fifty-seven people needed medical care, but nobody was seriously injured.
35850	06/02/2009	Petroleum Refining	FRANCE - 76 - GONFREVILLE-L'ORCHER A release of carbon monoxide (CO) and hydrogen sulphide (H_2S) wass produced in a refinery during maintenance operations on a tank. 3 employees were injured and transported to hospital. Concentrations of 80 ppm CO and 20 ppm H_2S in the vessel and 0 ppm CO and 4 ppm of H_2S on the platform outside the tank were measured.
35703	05/01/2009	Petroleum Refining	FRANCE - 13 - CHATEAUNEUF-LES-MARTIGUES An employee was found unconscious at about 11:15 in the visbreaking unit of a refinery. He was transported to the hospital, but died in the night. The suspected cause is poisoning by inhalation of hydrogen sulphide (H_2S) as beforehand the victim carried out an activity on equipment that may contain H_2S. An autopsy has been performed and a judicial inquiry is to be conducted.
35293	16/10/2008	Manufacture of basic organic chemicals	FRANCE - 64 - LACQ Leakage of hydrogen sulphide (H_2S) from a transport pipe (DN 50, pressure 5 bar) was detected at around 4 pm by an employee at a bridge in a chemical plant. Upon receipt of the alert, the operator decompress the pipe actuates the automatic sectioning valves and alerted the emergency services. Fire fighters used fire hoses to disperse the hydrogen sulphide fumes, and established a security perimeter and subsequently carried out concentration measurements. The concentrations measured were 300 ppm to the right of the leak, and 50 ppm at 20m. No casualties or environmental impact occurred. External corrosion by changing atmospheres following the stagnation of rain water is the cause of the event. The corrosion area is about 20 cm after the pipeline exits the soil, and was not protected by a coal tar coating.
34786	24/06/2008		FRANCE - 92 - Villeneuve-la-Garenne

ARIA-No.	Date	Industry	Description
			In the afternoon, hydrogen sulphide (H_2S) leaked from the sewage pipes into a building of 66 Apartments, severe intoxication girl 13 years (coma), who was hospitalized for several hours. The 200 inhabitants of the building were evacuated for the night. Evacuees can return home the next day at 18 h. The police carry out an investigation and samples were taken The accident could be an accident or malicious. It was finally concluded by the investigators that it was probably the result of a spill of incompatible chemicals into the sewers.
34316	15/11/2007	Extraction of crude petroleum	FRANCE - 64 - Burosse-Mendousse Two employees were injured by a product of hydrogen sulphide (H_2S) during operations on a pigging station of a 10" pipeline. After checking for the absence of a toxic atmosphere, the operators proceeded to isolate, purge and then open the station. After closing the latter, one of the employees suddenly collapsed and lost consciousness. Having brought him to safety and ensured his resuscitation, the decided to continue the work to close the station. He also collapsed and lost consciousness. The first person who had remained on site, to helped him in turn. They then left the scene, raise the alarm and then proceeded to the medical centre near by. Investigations were conducted to determine the origin of the toxic gases.
34177	01/11/2007	Treatment and disposal of hazardous waste	UNITED STATES - SUPERIOR In a landfill, 4 employees died of asphyxiation by hydrogen sulphide gas, when they were repairing a pump in a sewer.
32802	05/09/2006	Petroleum Refining	FRANCE - 76 - GONFREVILLE-L'ORCHER Around 9:30 am, an emission of carbon monoxide (CO) and hydrogen sulphide (H_2S) occurred which required the evacuation of 980 people on site of a unit being built at one of the entrances to the refinery. Fire fighters from the refinery carried out measurements and detected H_2S levels up to 7 ppm. Eight people contacted the hospital, 7 of them were hospitalized and kept for 24 h observation. Traces of CO were detected in their blood but the symptoms were due to H_2S. No installation of this new unit was likely to emit H_2S, the operator identified the unit CR4/FCC

ARIA-No.	Date	Industry	Description
			(catalytic cracking unit) as leading to the emission of H_2S. During the initial phase of the FCC, CO is generated during the 30 min during which the load through the catalyst at a temperature below 700 ° C. Similarly, the H_2S from the smoke from the furnace receiving waters of the stripping unit, is discharged directly to the atmosphere. The amount of H_2S released is estimated at 225 kg. Restart following 5 days of stoppage generated CO and H_2S discharged directly to stack during exceptional weather conditions (low wind). No anomaly in the start-up process was identified and the consequences of this event are allocated to the combination of weather conditions and continued massive human presence near the stack. To reduce the likelihood of renewal of this event, the weather will be taken into account before any restart of the FCC to ensure good conditions for dispersion of smoke.
32429	07/08/2006	Extraction of crude petroleum	FRANCE - 64 - LACQ The emergency plan is triggered at 22:15 following the warning gas detectors following the loss of containment of a network line entry of bleed desulphurization units. The network is isolated and unpacked. The failure of the line comes from an external corrosion under insulation at the level of support. The fluid released (approximately 500 l) corresponds to condensate of hydrocarbons containing hydrogen sulphide, the substance of which was collected.
32205	06/06/2006	Extraction of crude petroleum	UNITED STATES - ALLENTOWN In an extraction of crude oil, 2 employees of subcontractors were poisoned, 1 fatally, by hydrogen sulphide, during standard maintenance on the valve of a tank. The extraction wells had previously been stopped for intervention. An investigation is conducted to determine the exact causes of the accident. On the site, hydrogen sulphide, a byproduct from extraction of crude oil, is fed back to a depth of 4 500 m underground.
31863	12/06/2006	Other cleaning activities	FRANCE - 78 - POISSY During the flushing of a settling tank of sewage works to Poissy, 3 sewer workers, aged 22 to 44 years, dies, another is seriously injured as a result of a release of hydrogen sulphide (H_2S).

ARIA-No.	Date	Industry	Description
			Twice a year, 4 employees of sanitation firm clean the settling tank for the neighbourhood "La Collegiate." The operation was to pump the contents of the settling tank of 30 m and 5 m deep in to trucks to remove sludge and other wastes. Preventive work started at 9:30 am to guarantee a good flow of wastewater into the sewers. Around 10 am, 3 workers were overcome by toxic fumes, probably as they reached a pocket of H_2S, occurring as the result of the decomposition of organic matter. The fourth worker, who was a little further back, was seriously affected and transported to hospital. Once the alarm was given by a passer-by, almost fifty fire fighters with twenty vehicles attended the scene, joined by 4 ambulance teams. Two investigations were conducted; one judicial and the other by the labour inspectorate to check whether all protocols to be implemented for this type of activity have been complied with.
29906	27/05/2005	Collection and Wastewater Treatment	FRANCE - 78 - HOUDAN Eleven children of a group of 53, ages 8 to 11 years are affected by stomach pains and nausea, following the visit of a sewage treatment plant in the morning. They were taken to hospital for examination. Measures of toxicity at the site of the WWTP are positive for hydrogen sulphide (H_2S).

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Annex 2: Selection of incidents involving the release of hydrogen sulphide in Germany from the ZEMA Database and other sources

Source	Date	Industry	Description
ZEMA 2007-11-21 Fire in an oil gasification plant of a refinery	21/11/2007	Distillation, refining and processing of mineral oil and products	GERMANY - NORDRHEIN WESTFALEN In an oil gasification plant sulphur containing cracker residues are converted to synthesis gas (H_2 + CO) in the presence of steam and oxygen at a temperature of 1,300 °C and pressure of 30 bars. The gasification takes place in three reactors which are connected to a common flare stack for start-up and shut-down operations. - On 21st November 2007 two of the three reactors were out of operation due to repair work on the exhaust gas line. In preparation for the start-up operations they were heated up, but still separated from the flare system. - Due to a leakage of "false air" a sulphur-iron fire occurred in the flare stack. Natural gas, which is to support the ignition flame, ignited on the flare stack (probably due to the sulphur-iron fire) and an explosion occurred. A short while later a second, but weaker explosion occurred with flames emanating from the manhole of the flare. The flare stack has a dished end for the collection of condensates; this has a drain pipe with a valve connected on the outside of the stack. - Following the explosion of the flare the dished end was blown into the base of the flare construction and the drainage pipe was found next to the base. The flare was now open towards the base and the sulphur-iron fire was further supported. The causes were given as two possibilities: 1. a leak on an imperfect weld of the dished end (poor weld quality and corrosion) led to the ingress of air into the flare system. 2. During the start-up and the operation of the vacuum system a valve which was either open or not gas-tight allowed air to be sucked into the flare system.

Source	Date	Industry	Description
			The investigation came to the conclusion that within the flare system sulphur-iron compounds had accumulated which can auto-ignite in contact with air. No injuries were reported and amounts of H_2S released are not given.
ZEMA 2007-06-18 Release of Hydrogen Sulphide from the Conversion Unit of a Refinery	18/06/2007	Distillation, refining and processing of mineral oil and products	GERMANY - NORDRHEIN WESTFALEN Hydrogen sulphide is removed from the refinery gas in an absorptions column by using ADIP (Di-isopropanolamine). The cleaned gas is passed onto the heating gas system of the refinery and the loaded ADIP is regenerated. The Hydrogen sulphide which is won in the regeneration process is converted to sulphur in the Claus unit. - At the time of the incident the level-low trip of the column was activated. Normally following this a regulator valve would be closed and the level in the column would rise. However, the regulator value was blocked in the "open" position by metal pieces (internal to the column). Thus the column level fell to null, the loaded ADIP was completely directed to the regenerator and a Hydrogen Sulphide break through via the ADIP-Generation to the Claus unit occurred. Not only the Claus unit, but also the catalytic thermal combustion unit were overloaded and the H_2S gas was released with almost no conversion to Sulphur dioxide through the 175m chimney of the conversion unit. In total 1,275 kg H_2S were released. No injuries were recorded, however a strong odorous nuisance for more than an hour occurred.
ZEMA 0525 (2005-12-29) Release of Hydrogen Sulphide at an hazardous waste treatment installation BARPI, ARIA Report No.: 32574	29/12/2005	Waste - chemical-physical treatment and handling plant	GERMANY – BADEN-WÜRTEMBERG On 29th December 2005 an accident took place in a hazardous waste treatment facility in which an employee was killed and six others (two employees, two members of the emergency services, and two employees of contact companies) suffered injuries and required hospital treatment. The cause, based on current knowledge, was the release of hydrogen sulphide (H_2S) from the tank vent of the vacuum truck whilst liquid wastes were being pumped from steel drums into the vacuum-truck. A fork-lift truck driver who happened to be in the immediate vicinity was found dead near by; the cause of death being the toxic effects of hydrogen sulphide. Five of those

Source	Date	Industry	Description
			treated in hospital were also suffering from the health effects of hydrogen sulphide The fire-brigade could not identify any hazardous gas concentration on arrival at the scene. The fire-brigade then left the site. To secure the scene for the police investigation, the police ordered that the contents of the suction hose should be drawn into the vacuum-truck. The vacuum pump was restarted and once again hazardous sub-stances were released from the tank vent. This process led to the collapse of the vacuum-truck driver. As a result the police ordered that the operation should cease and the fire-brigade and an emergency doctor were called to the scene. The immediate cause of the production of toxic gas was the combining of liquid wastes which on mixing react together releasing H_2S. An organo-sulphur (thio) compound was mixed with an organic, acidic compound leading to an unexpected liberation of hydrogen sulphide The indications are that the organisational measures which had been taken were not adequate to prevent this event. The operator was not able to demonstrate that adequate measures for the identification, assessment and documentation of the hazards of the individual containers of hazardous waste received. The hazardous wastes which were received in drums and brought together in a vacuum-truck were to be transported from the waste treatment facility to another location because they could not be treated on site. The operator was not able to demonstrate that adequate measures were in place to regulate how the drums should be pumped into the vacuum-truck (order, ruling out of any hazardous chemical reactions). There were no adequate measures for the safe discharge of gases vented from the vacuum-truck.
ZEMA 0430 (2004-12-14) Release of Hydrogen Sulphide	14/12/2004	Chemicals Production, Mineral oil	GERMANY – SACHSEN-ANHALT The failure of the pump on an exhaust gas scrubber led to the release of Hydrogen Sulphide. The plant went automatically into a safe mode. The

Source	Date	Industry	Description
from an evaporation plant.		refining and processing of mineral oil products	cause of the failure was a short circuit in the motor of the pump. Two employees suffered effects from the release. As a precautionary measure for the future the personnel is to be provided with gas detection and warning equipment.
ZEMA 0414 (2004-05-18) Release of Hydrogen sulphide and Sulphur dioxide from a Carbon Disulphide Plant	18/05/2004	Chemicals Production, Mineral oil refining and processing of mineral oil products	GERMANY - NORDRHEIN WESTFALEN Following a shut down of several weeks duration the Carbon Disulphide plant was restarted. In doing so the reactor furnace, the Claus unit and the exhaust gas combustion unit were started up one after the other. The exhaust gas combustion unit showed an irregular operation caused by an excess natural gas feed into the reaction furnace due to a defective Methane measurement. As a result the Natural gas could not be completely reacted in the reaction furnace and the excess gas reached the exhaust gas system and the combustion unit. - Until the exhaust gas combustion could be stabilized unreacted amounts of H_2S and SO_2 were emitted via the 150m high stack. The process upset lasted for about 50 minutes. Estimates give the emitted amount of H_2S as between 40 kg (best case) and 120 kg (worst case). - Near to a school there were complaints of health effects (nausea, headaches and vomiting) 47 persons received medical treatment. 19 persons were taken to hospital for observation as a precautionary measure. Two of these were kept in overnight.
ZEMA 9925 (1999-07-17) Release by a crude oil tank	17/07/1999	Storage of mineral oil or liquid mineral oil products or methanol (capacity 50000 tonnes or more)	GERMANY – BADEN-WÜRTTEMBERG A tank was filled with crude oil. During a control an employee smelled the oil and discovered that the floating roof was covered with crude. The filling of the tank was stopped and the fire fighters covered the crude on the roof with foam.
ZEMA 9901 (1999-01-25) Release of Hydrogen Sulphide from a multi-purpose chemical	25/01/1999	Installation for the industrial production of	GERMANY – BADEN-WÜRTTEMBERG Wash water from a reactor was transferred to a multi-purpose collection tank

Source	Date	Industry	Description
production		substances by chemical reactions	by nitrogen pressure. The automatic pumping of the waste water to the waste water treatment could not take place as the tank was full and the valve closed. This led to an overfilling of the multi-purpose collection tank and the escape of waste water into the exhaust gas system leading to the exhaust gas treatment. Another container into which ca. 4,000 kg Phosphorous Pentasuphide had been charged was also connected to the same exhaust gas system. Water was thus able to enter this container so that the Phosphorous Pentasulphide and water were able to react, generating Hydrogen Sulphide. Due to the sudden increase in pressure a seal partially failed releasing Hydrogen Sulphide into the room in which the plant was housed. The H_2S-alarm was triggered automatically. Through the mechanical ventilation system and through doors and windows, the Hydrogen Sulphide was able to escape into the neighbourhood were it was rapidly dispersed. However the smell was clearly noticeable in the nearby residential area. There were no injuries or fatalities recorded.
ZEMA 9403 (1994-02-13 Explosion of Hydrogen and Gasoil causing a fire	13/02/1994	Distillation, refining and processing of mineral oil and products	GERMANY – BRANDENBURG During the heating up process in a heat exchanger for gas products a leak occurred which ignited ca. 1,200 kg of flammable gases, 100 kg Hydrogen and 10 kg H_2S were released. No injuries were recorded, however approximately 0.5 Mill. EUR damage to the installation was reported. The cause of the accident was suggested as material failure
ZEMA 9310 (1993-03-24) Fire of highly flammable and flammable liquids	24/03/1993	Distillation, refining and processing of mineral oil and products	GERMANY – NORDRHEIN WESTFALEN Hydrocarbons were release by the burst of a pipe and were ignited due to a temperature of 350 - 370 °C. An emergency shut off was made and the system depressurised to the flare. The burst was caused by corrosion by hydrogen sulphide containing water.
ZEMA 9302 (1993-02-02) Release of H_2S-containing	02/02/1993	Distillation, refining and	GERMANY – NORDRHEIN WESTFALEN

Source	Date	Industry	Description
flammable gases		processing of mineral oil and products	During repair work in a hydrocracker, on a pipe under pressure, (hot tapping) the gas tight casing was damaged leading to the releasing of ca 14.5 t Hydrocarbons. The released hydrocarbons contained 1,380 kg H_2S. Three employees of a contractor were injured, one of which died. The cause of the damage to the gas tight casing was the incorrect feed indicator on the drilling machine which was used.
http://www.n24.de http://www.gsb-mbh.de	04/08/2008	Waste - chemical-physical treatment and handling plant	GERMANY – BAYERN Maintenance works in the pump building caused a release of H_2S at the chemical and physical hazardous waste treatment plant of the GSB at München-Fröttmaning. The release occurred when the plant manager drained a pipe to install a new valve. The plant manager, four employees and three police officers were injured. The plant, operating since 1990, is located next to a new constructed football stadium.
http://www.mz-web.de	20/03/2008	waste landfill	GERMANY – SACHSEN-ANHALT Authorities inspected the former clay pit of the Sporkenbach Ziegelei GmbH at Möckern and analysed the releases to air. They found H_2S and HCN in the releases and assume that these releases are caused by the illegal dumping of waste. The operator declared that there are no release of H_2S and HCN according to own analyses.
http://.www.abendblatt.de	27/11/2006	Distillation, refining and processing of mineral oil and products	GERMANY – HAMBURG A H_2S release at a lubricant oil refinery injured 46 employees. The CEO said, the release may be caused by the failure of a valve.
http://www.westline.de	04/10/2006	hazardous waste, landfill	GERMANY – NORDRHEIN WESTFALEN An employee of a cleaning company entered a leachate tank of a hazardous waste landfill wearing protective gear including a respirator mask. The connection from the air supply hose to the mask broke. The employee

Source	Date	Industry	Description
			collapsed in the tank. The company owner at the manhole regarded this and entered the tank without protective gear. Both died.
http://www.webserver-nrw.de	10/11/2005	Waste water treatment	GERMANY – NORDRHEIN WESTFALEN Two of the clarifiers of the waste water treatment plant at (51766) Bickenbach released H_2S. The operator introduced iron salts in the clarifiers to precipitate the sulphide.
http://www.sicherheitserziehung-nrw.de/uploads/media/Unfall_in_der_Biogasanlage2005.pdf http://www.landenergietechnik.de/PDF/Unfall%20Zeven.pdf BARPI, ARIA Report No. 31000	08/11/2005	Waste treatment, biogas4.4-1	On the 5th of November 2005, after collecting the Heparin by a pharmaceutical company in the Netherlands and adding bisulphite, the remaining material was transported by truck to a fermentation facility in Germany. The truck arrived too late and had to wait for unloading overnight in front of the facility. On site the normal unloading procedure was not followed due to the failure of the unloading equipment. The reception pit was open because the hoist used to close the heavy metal doors was defective. In this pit there were some acidic remains present from earlier loads. While unloading the material (pH 8,5, >60°C) a large quantity of hydrogen sulphide (H_2S) was emitted. Due to the H_2S emission an operator was poisoned. Another operator, the truck driver and some other people who were present also suffered the toxic effects of H_2S. The outcome was 4 fatalities and one seriously ill in hospital. Members of the rescue team which had been involved in the reanimation and who had not worn protective equipment suffered later from skin irritation, headache and nausea. It is assumed that this was caused by release of hydrogen sulphide from the clothing of the persons rescued. Therefore all clothing worn and material used inside the reception building was enclosed for decontamination.
Release of toxic gas (69003) Handbuch Störfälle (UBA, Germany)	25/04/1969	Distillation, refining and processing of mineral oil and	GERMANY – NORTHRHEIN WESTFALEN Release of H_2S from a flaring unit during maintenance.

Source	Date	Industry	Description
		products plant	
Release of toxic gas (76001) Handbuch Störfälle (UBA, Germany)	24/02/1976	Automotive industry – production of car parts	GERMANY – HESSEN Release of H_2S from a tank during maintenance work
Release of toxic gas (78019) Handbuch Störfälle (UBA, Germany)	07/09./1976	Waste water treatment, sewage pipe	GERMANY – BADEN-WÜRTTEMBERG Release of H_2S during construction work
Release of toxic gas (79002) Handbuch Störfälle (UBA, Germany)	06/01/1979	Installation for the industrial production of substances by chemical reactions	GERMANY – BAVARIA
Release of toxic substances (79015) Handbuch Störfälle (UBA, Germany)	08/06/1979	Coking plant	GERMANY – NORTHRHEIN WESTFALEN Release of H_2S from the waste water treatment

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Annex 3: UK on-shore hydrogen sulphide incidents 1990 -2003

Exposure

Date	Description
9006	Double fatality in a distillery biological effluent treatment plant. The fatalities occurred in an underground sump tank.
9007	Gassing incident involving slurry mixing. A young farmer was overcome and 17 cattle died.
9009	Two men overcome in fish storage silo.
9101	The pathologist's report on a tanker driver, who was found dead in a sitting position underneath a sludge tanker, was that he died of asphyxia.
9101	As part of the operation of clearing blocked drains, four men pumped nearly empty one deep chamber. One man then climbed down into it and collapsed. Three would-be rescuers successively climbed down and collapsed. The first three men died and the fourth recovered after a long illness. Analysis indicated that hydrochloric acid was put into two of the chambers. This and the disturbance of the sludges produced large quantities of hydrogen sulphide gas.
9108	Two construction workers collapsed underground
9209	Visit made to determine cause of failure of valve on a 1 cubic metre hydrogen sulphide drum. The gland locking nut had failed. The valve spindle had seized in the nylon packing. In my opinion the nut was on the point of failure and when an operator tried to open the valve during the drum filling process the nut fractured and he inadvertently unscrewed the gland nut which allowed the spindle to be blown out. The operator was wearing protective clothing and no persons were injured.
9308	Three sullage lighter workers were affected by hydrogen sulphide which was generated in-situ in the cargo wastes from Naval vessels, probably by sulphate-reducing bacteria. The hazard had not been recognised at Portsmouth though it has elsewhere. Aeration of the cargo produced hydrogen sulphide concentrations up to 450 ppm.
9411	Visit to investigate collapse of worker in confined space at Whittlesea STW.
9412	A pipe manifold situated on top of a high pressure gas storage vessel failed. Hydrogen sulphide gas was released. The failure occurred in a pipe branch T-piece.
9504	Two of three persons had been overcome on 13 April 1995 while working with in a port wing tank of a barge undergoing repair. The wing-tank was a confined space. On the day of the visit the air within the tank was fit to breathe. However a sample of sludge from the bottom of the tank emitted hydrogen sulphide gas when acidified.
9504	An operative in a metal processing factory was overcome by H_2S fumes when he removed the plastic lid from a drum containing freshly milled material. The actual exposure is not known but is likely to have been in excess of 200ppm.
9604	Opened manlid of 7 tonne vessel. Exposed to H_2S and mercaptan fumes.
9608	H_2S exposure in newly upgraded press house when lifted lids to inspect sludge cake.
9610	IP cleaning tanning drum. Overcome by H_2S fumes from reaction of sodium sulphide and cleaning agent.

Date	Description
9611	Leakage from H_2S 550kg cylinder.
07/01/97	Leak from 500 kg cylinder of hydrogen sulphide. Cylinder removed and connected to scrubber. Vented and purged with nitrogen. Smell persisted for 27 hours as leak could not be stopped during purging/venting process. 8 ppb at site boundary FOCUS
9707	Release of vapours, 5ppm H_2S from refinery header unit.
9708	Fitter fell down supernatant liquid well when overcome by H_2S fumes. Broke leg. Trying to clear blockage in a submersible pump and entered the tank without ppe.
9709	Maintenance technician testing pressure sensors. Did not follow procedures. Did not close valve when purging with nitrogen. H_2S in autoclave released.
9711	Failure of PTW. Attempting to clear product line from reactor. Opened wrong line. Fumes including H_2S released. RPE not suitable for H_2S.
98/02	IP cleaning out tanning effluent sump. Overcome by H_2S fumes from sludge.
9804	Accidental mixture of chemicals resulted in H_2S fumes. IPs affected during clean up operations.
9804	DP asphyxiated in tanning effluent sump at NCT Leather Ltd. DP entered to clear block age. High levels of H_2S
11/09/98	IP cleaning out reactor. Opened the manhole and was overcome by fumes. Smell suggested H_2S.
9904	Escaped from tunnel when detected 10ppm H_2S.
09/04/99	Sour gas (natural gas with 1000ppm H_2S) released from amine tank. Scrubber could not cope.
20/03/00	Man entered slurry tank at pig farm and was overcome by fumes including 500 ppm H_2S.
4/00	Repairing aluminum rudder to allow connection of anodes. Drilled holes when explosion occurred. Believed hydrogen sulphide had accumulated inside rudder.
06/07/00	IP in school laboratory knocked over bottle of ammonium sulphide. Ammonia and H_2S fumes.
26/07/00	10 workers complained of illness after working in pumped out water course. High levels of H_2S in sludge.
23/03/01	IP overcome by fumes when sampling from tank. Gas generated by mixing acid and sulphides
July 2001	Fatality DP overcome by hydrogen sulphide fumes leaking from a tank. Health and Safety at Work March 2003
06/03/02	Cylinder venting released H_2S at oil service company.
27/01/03	Farmer and worker trying to rescue young cow from slurry storage system. Overcome by H_2S fumes. 2 fatalities.

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References

Toxicology of substances in relation to major hazards – hydrogen sulphide
HSE

SSHSCC/45/F Hydrogen sulphide (HSE website)

Fire safety in the paper and board industry section on hydrogen sulphide
HSE

OECD WGCA Preliminary data analysis Geothermal H_2S-incidents, Sept. 2009

AIS26 managing confined spaces on farms - Slurry storage systems
HSE

Detection of hydrogen sulphide 1997 HSE Offshore Safety Division

Prevention and detection of hydrogen sulphide releases 1995 HSE Offshore Safety Division

EH64 D124 Hydrogen sulphide

Hydrogen sulphide HSC ACTS 2000

Internet References

Safety Newsletter Shell Global Solutions August 2002
Multiple Fatalities – H2S released from molecular sieves after contact with water

97 victims as a result of hydrogen sulphide venting in Volgograd April 2003

NIOSH
International Chemical Safety Cards – hydrogen sulphide

Workplace health and safety – hydrogen sulphide July 1998
Alberta Human resource and development

Air Liquide Safety data sheet Hydrogen Sulphide July 2002

Miscellaneous references

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IChemE Loss prevention Bulletin 155 2000

Comment Letter I9

Leak Detection and Repair

A Best Practices Guide

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY

United States
Environmental Protection Agency
Office of Compliance
Office of Enforcement and Compliance Assurance
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Disclaimer

Contents

Tables

Appendices

1.0 Purpose

In general, EPA has found significant widespread noncompliance with Leak Detection and Repair (LDAR) regulations and more specifically, noncompliance with Method 21 requirements. In 1999, EPA estimated that, as a result of this noncompliance, an additional 40,000 tons of VOCs are emitted annually from valves at petroleum refineries alone.

This document is intended for use by regulated entities as well as compliance inspectors to identify some of the problems identified with LDAR programs focusing in on Method 21 requirements and describe the practices that can be used to increase the effectiveness of an LDAR program. Specifically, this document explains:

- The importance of regulating equipment leaks;
- The major elements of an LDAR program;
- Typical mistakes made when monitoring to detect leaks;
- Problems that occur from improper management of an LDAR program; and
- A set of best practices that can be used to implement effective an LDAR program.

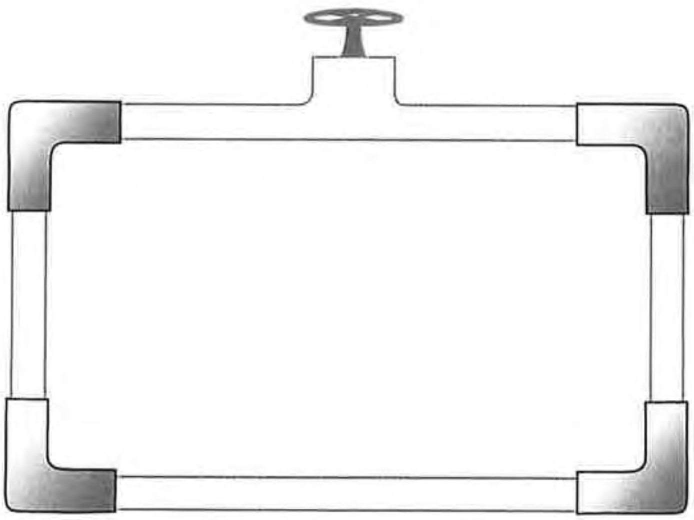
Some of the elements of a model LDAR program, as described in Section 7.0, are required by current Federal regulations. Other model LDAR program elements help ensure continuous compliance although they may not be mandated from a regulatory standpoint. Furthermore, State or local requirements may be more stringent than some elements of the model LDAR program, such as with leak definitions. Prior to developing a written LDAR program plan, all applicable regulations should be reviewed to determine and ensure compliance with the most stringent requirements.

2.0 Why Regulate Equipment Leaks?

EPA has determined that leaking equipment, such as valves, pumps, and connectors, are the largest source of emissions of volatile organic compounds (VOCs) and volatile hazardous air pollutants (VHAPs) from petroleum refineries and chemical manufacturing facilities. The Agency has estimated that approximately 70,367 tons per year of VOCs and 9,357 tons per year of HAPs have been emitted from equipment leaks. Emissions from equipment leaks exceed emissions from storage vessels, wastewater, transfer operations, or process vents.

VOCs contribute to the formation of ground-level ozone. Ozone is a major component of smog, and causes or aggravates respiratory disease, particularly in children, asthmatics, and healthy adults who participate in moderate exercise. Many areas of the United States, particularly those areas where refineries and chemical facilities are located, do not meet the National Ambient Air Quality Standard (NAAQS) for ozone. Ozone can be transported in the atmosphere and contribute to nonattainment in downwind areas.

Some species of VOCs are also classified as VHAPs. Some known or suspected effects of exposure to VHAPs include cancer, reproductive effects, and birth defects. The highest concentrations of VHAPs tend to be closest to the emission source, where the highest public exposure levels are also often detected. Some common VHAPs emitted from refineries and chemical plants include acetaldehyde, benzene, formaldehyde, methylene chloride, naphthalene, toluene, and xylene.



3.0 Sources, Causes And Control Of Equipment Leaks

A typical refinery or chemical plant can emit 600-700 tons per year of VOCs from leaking equipment, such as valves, connectors, pumps, sampling connections, compressors, pressure-relief devices, and open-ended lines.

Table 3.1 shows the primary sources of emissions from components subject to equipment leak regulations. In a typical facility, most of the emissions are from valves and connectors because these are the most prevalent components and can number in the thousands (Table 3.2). The major cause of emissions from valves and connectors is seal or gasket failure due to normal wear or improper maintenance.

Previous EPA studies have estimated that valves and connectors account for more than 90% of emissions from leaking equipment with valves being the most significant source (Table 3.3). Newer information suggests that open-ended lines and sampling connections may account for as much as 5-10% of total VOC emissions from equipment leaks.

3.1 How are emissions from equipment leaks reduced?

Facilities can control emissions from equipment leaks by implementing a leak detection and repair (LDAR) program or by modifying/replacing leaking equipment with "leakless" components. Most equipment leak regulations allow a combination of both control methods.

- Leaks from open-ended lines, compressors, and sampling connections are usually fixed by modifying the equipment or component. Emissions from pumps and valves can also be reduced through the use of "leakless" valves and "sealless" pumps. Common leakless valves include bellows valves and diaphragm valves, and common sealless pumps are diaphragm pumps, canned motor pumps, and magnetic drive pumps. Leaks from pumps can also be reduced by using dual seals with or without barrier fluid.

- Leakless valves and sealless pumps are effective at minimizing or eliminating leaks, but their use may be limited by materials of construction considerations and process operating conditions. Installing leakless and sealless equipment components may be a wise choice for replacing individual, chronic leaking components.

LDAR is a work practice designed to identify leaking equipment so that emissions can be reduced through repairs. A component that is subject to LDAR requirements must be monitored at specified, regular intervals to determine whether or not it is leaking. Any leaking component must then be repaired or replaced within a specified time frame.

Table 3.1 – Sources of equipment leaks.

Pumps are used to move fluids from one point to another. Two types of pumps extensively used in petroleum refineries and chemical plants are centrifugal pumps and positive displacement, or reciprocating pumps.	**Leaks from pumps** typically occur at the seal.
Valves are used to either restrict or allow the movement of fluids. Valves come in numerous varieties and with the exception of connectors, are the most common piece of process equipment in industry.	**Leaks from valves** usually occur at the stem or gland area of the valve body and are commonly caused by a failure of the valve packing or O-ring.
Connectors are components such as flanges and fittings used to join piping and process equipment together. Gaskets and blinds are usually installed between flanges.	**Leaks from connectors** are commonly caused from gasket failure and improperly torqued bolts on flanges.
Sampling connections are utilized to obtain samples from within a process.	**Leaks from sampling connections** usually occur at the outlet of the sampling valve when the sampling line is purged to obtain the sample.
Compressors are designed to increase the pressure of a fluid and provide motive force. They can have rotary or reciprocating designs.	**Leaks from compressors** most often occur from the seals.
Pressure relief devices are safety devices designed to protect equipment from exceeding the maximum allowable working pressure. Pressure relief valves and rupture disks are examples of pressure relief devices.	**Leaks from pressure relief valves** can occur if the valve is not seated properly, operating too close to the set point, or if the seal is worn or damaged. Leaks from rupture disks can occur around the disk gasket if not properly installed.
Open-ended lines are pipes or hoses open to the atmosphere or surrounding environment.	**Leaks from open-ended lines** occur at the point of the line open to the atmosphere and are usually controlled by using caps, plugs, and flanges. Leaks can also be caused by the incorrect implementation of the block and bleed procedure.

Table 3.2 – Equipment component counts at a typical refinery or chemical plant.

Component	Range	Average
Pumps	10 360	100
Valves	150 - 46,000	7,400
Connectors	600 - 60,000	12,000
Open-ended lines	1 - 1,600	560
Sampling connections	20 - 200	80
Pressure relief valves	5 - 360	90

Source: "Cost and Emission Reductions for Meeting Percent Leaker Requirements for HON Sources." Memorandum to Hazardous Organic NESHAP Residual Risk and Review of Technology Standard Rulemaking docket. Docket ID EPA-HQ-OAR-2005-0475-0105.

Table 3.3 – Uncontrolled VOC emissions at a typical facility.

Component	Average Uncontrolled VOC Emissions (ton/yr)	Percent of Total Emissions
Pumps	19	3
Valves	408	62
Connectors	201	31
Open-ended lines	9	1
Sampling connections	11	2
Pressure relief valves	5	1
Total	653	

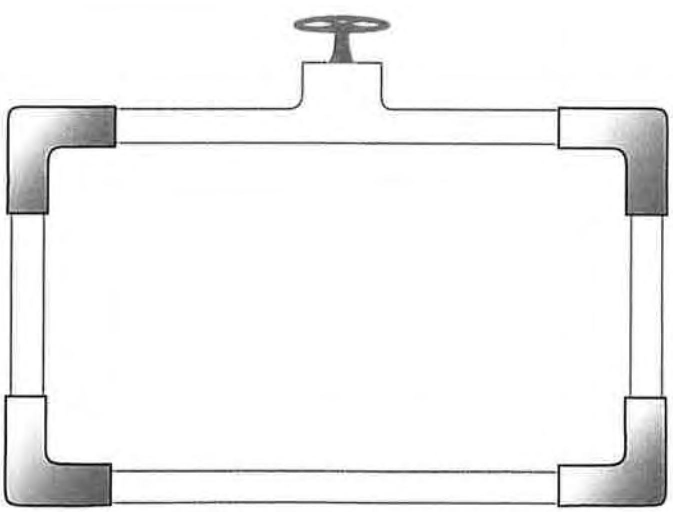
Source: Emission factors are from Protocol for Equipment Leak Emission Estimates, EPA-453/R-95-017, Nov 1995, and equipment counts in Table 3.2.

More recent data indicates that open ended lines and sampling connections each account for approximately 5-10% of total VOC emissions.

3.2 What regulations incorporate LDAR programs?

LDAR programs are required by many New Source Performance Standards (NSPS), National Emission Standards for Hazardous Air Pollutants (NESHAP), State Implementation Plans (SIPs), the Resource Conservation and Recovery Act (RCRA), and other state or local requirements. There are 25 federal standards that require facilities to implement LDAR programs. Appendix A shows the 25 federal standards that require the implementation of a formal LDAR program using Method 21. Appendix B lists 28 other federal regulations that require some Method 21 monitoring, but do not require LDAR programs to be in place.

- NSPS (40 CFR Part 60) equipment leak standards are related to fugitive emissions of VOCs and apply to stationary sources that commence construction, modification, or reconstruction after the date that an NSPS is proposed in the Federal Register.
- NESHAP (40 CFR Parts 61, 63, and 65) equipment leak standards apply to both new and existing stationary sources of fugitive VHAPs.
- RCRA (40 CFR Parts 264 and 265) equipment leak standards apply to hazardous waste treatment, storage, and disposal facilities.
- Many state and local air agencies incorporate federal LDAR requirements by reference, but some have established more stringent LDAR requirements to meet local air quality needs.



A facility may have equipment that is subject to multiple NSPS and NESHAP equipment leaks standards. For example, a number of manufacturing processes listed in the Hazardous Organic NESHAP (HON) equipment leak standard (40 CFR 63, Subpart H) may utilize equipment for which other NESHAP or NSPS equipment leak standards could apply (such as 40 CFR 60, Subpart VV). In addition, one process line may be subject to one rule and another process line subject to another rule. Facilities must ensure that they are complying with the proper equipment leak regulations if multiple regulations apply.

4.0 What Are the Benefits of an LDAR Program?

When the LDAR requirements were developed, EPA estimated that petroleum refineries could reduce emissions from equipment leaks by 63% by implementing a facility LDAR program. Additionally, EPA estimated that chemical facilities could reduce VOC emissions by 56% by implementing such a program.

Table 4.1 presents the control effectiveness of an LDAR program for different monitoring intervals and leak definitions at chemical process units and petroleum refineries.

Emissions reductions from implementing an LDAR program potentially reduce product losses, increase safety for workers and operators, decrease exposure of the surrounding community, reduce emissions fees, and help facilities avoid enforcement actions.

Example – Emissions reductions at a typical SOCMI facility.

Applying the equipment modifications and LDAR requirements of the HON to the sources of uncontrolled emissions in the typical facility presented in Tables 3.2 and 3.3 would reduce the emissions per facility by approximately 582 tons per year of emissions, an 89% reduction.

Table 4.1 – Control effectiveness for an LDAR program at a chemical process unit and a refinery.

Equipment Type and Service	Control Effectiveness (% Reduction) Monthly Monitoring 10,000 ppmv Leak Definition	Quarterly Monitoring 10,000 ppmv Leak Definition	500 ppm Leak Definition[a]
Chemical Process Unit			
Valves – Gas Service[b]	87	67	92
Valves – Light Liquid Service[c]	84	61	88
Pumps – Light Liquid Service[c]	69	45	75
Connectors – All Services			93
Refinery			
Valves – Gas Service[b]	88	70	96
Valves – Light Liquid Service[c]	76	61	95
Pumps – Light Liquid Service[c]	68	45	88
Connectors – All Services			81

Source: Protocol for Equipment Leak Emission Estimates, EPA-453/R-95-017, Nov 1995

[a] Control effectiveness attributable to the HON-negotiated equipment leak regulation (40 CFR 63, Subpart H) is estimated based on equipment-specific leak definitions and performance levels. However, pumps subject to the HON at existing process units have a 1,000 to 5,000 ppm leak definition, depending on the type of process.

[b] Gas (vapor) service means the material in contact with the equipment component is in a gaseous state at the process operating conditions.

[c] Light liquid service means the material in contact with the equipment component is in a liquid state in which the sum of the concentration of individual constituents with a vapor pressure above 0.3 kilopascals (kPa) at 20°C is greater than or equal to 20% by weight.

4.1 Reducing Product Losses

In the petrochemical industry, saleable products are lost whenever emissions escape from process equipment. Lost product generally translates into lost revenue.

4.2 Increasing Safety for Facility Workers and Operators

Many of the compounds emitted from refineries and chemical facilities may pose a hazard to exposed workers and operators. Reducing emissions from leaking equipment has the direct benefit of reducing occupational exposure to hazardous compounds.

4.3 Decreasing Exposure for the Surrounding Community

In addition to workers and operators at a facility, the population of a surrounding community can be affected by severe, long-term exposure to toxic air pollutants as a result of leaking equipment. Although most of the community exposure may be episodic, chronic health effects can result from long-term exposure to emissions from leaking equipment that is either not identified as leaking or not repaired.

4.4 Potentially Reducing Emission Fees

To fund permitting programs, some states and local air pollution districts charge annual fees that are based on total facility emissions. A facility with an effective program for reducing leaking equipment can potentially decrease the amount of these annual fees.

4.5 Avoiding Enforcement Actions

In setting Compliance and Enforcement National Priorities for Air Toxics, EPA has identified LDAR programs as a national focus. Therefore, facilities can expect an increased number and frequency of compliance inspections and a closer review of compliance reports submitted to permitting authorities in an effort by the Agency to assess LDAR programs and identify potential LDAR problems. A facility with an effective LDAR program decreases the chances of being targeted for enforcement actions and avoids the costs and penalties associated with rule violations.

Example – Cost of product lost.

In previous rulemaking efforts, EPA has estimated that the average value of product lost due to equipment leaks is $1,370 per ton.[a]

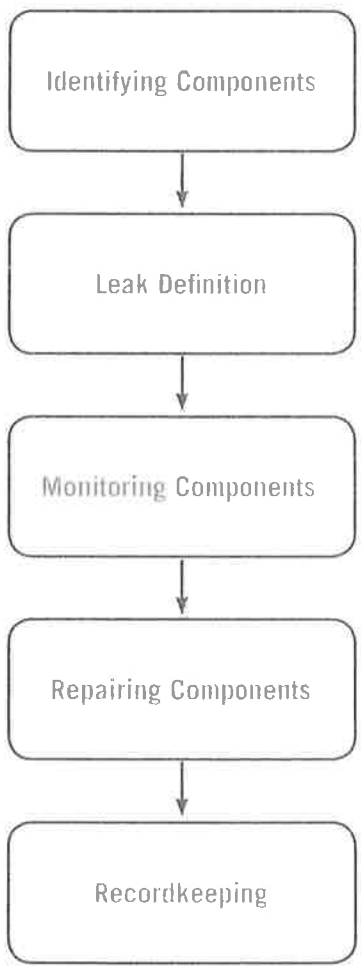
Applying this cost factor results in a potential savings of $730,000 per year per facility.

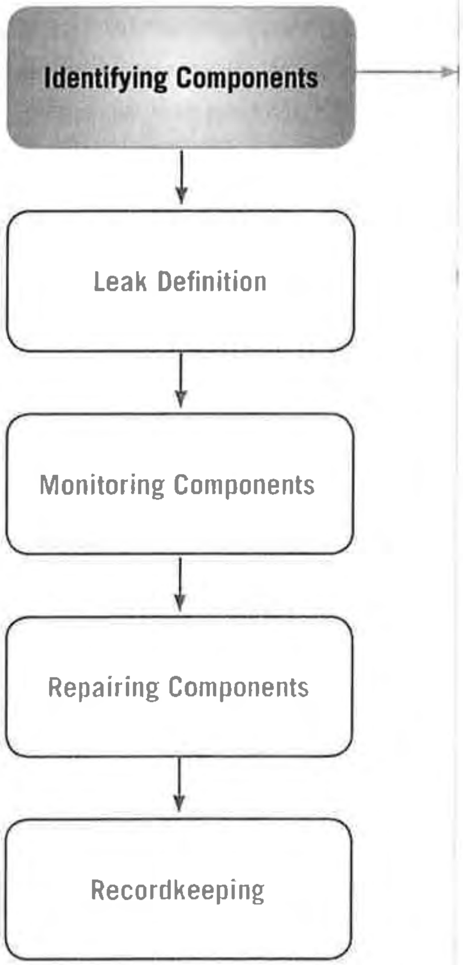
[a] Source: Hazardous Air Pollutant Emissions From Process Units in the Synthetic Organic Chemical Manufacturing Industry-Background Information for Proposed Standards, Vol 1C-Model Emission Sources, Emission Standards Division, US EPA, Office of Air and Radiation, OAQPS, Research Triangle Park, NC, Nov 1992

5.0 Elements of an LDAR Program

The requirements among the regulations vary, but all LDAR programs consist of five basic elements, which are discussed in detail in Sections 5.1 through 5.5.

For each element, this section outlines the typical LDAR program requirements, common compliance problems found through field inspections, and a set of best practices used by facilities with effective LDAR programs.





Current Requirements

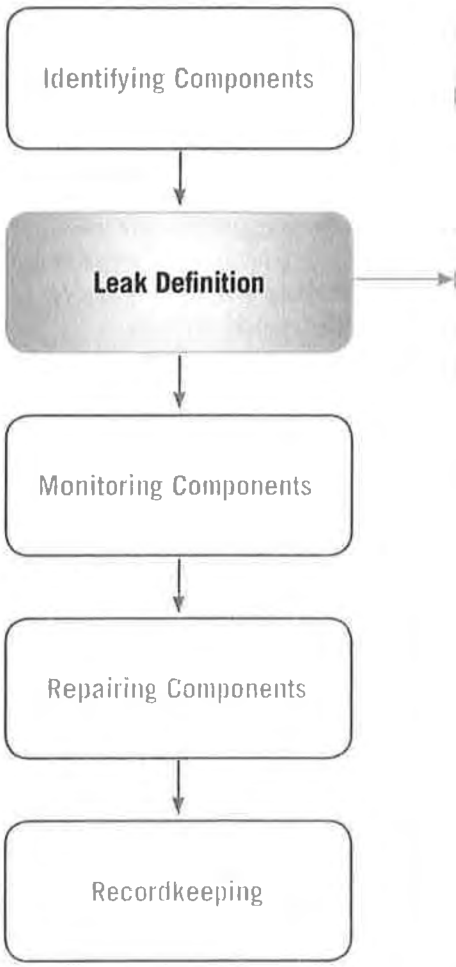
- Assign a unique identification (ID) number to each regulated component.
- Record each regulated component and its unique ID number in a log.
- Physically locate each regulated component in the facility, verify its location on the piping and instrumentation diagrams (P&IDs) or process flow diagrams, and update the log if necessary. Some states require a physical tag on each component subject to the LDAR requirements.
- Identify each regulated component on a site plot plan or on a continuously updated equipment log.
- Promptly note in the equipment log when new and replacement pieces of equipment are added and equipment is taken out of service.

Common Problems

- Not properly identifying all regulated equipment components.
- Not properly documenting exempt components (e.g., <300 hour exemption and <5 (or <10) weight % HAP).

Best Practices

- Physically tag each regulated equipment component with a unique ID number
- Write the component ID number on piping and instrumentation diagrams.
- Institute an electronic data management system for LDAR data and records, possibly including the use of bar coding equipment
- Periodically perform a field audit to ensure lists and diagrams accurately represent equipment installed in the plant



Current Requirements

- Method 21 requires VOC emissions from regulated components to be measured in parts per million (ppm). A leak is detected whenever the measured concentration exceeds the threshold standard (i.e., **leak definition**) for the applicable regulation.
  - Leak definitions vary by regulation, component type, service (e.g., light liquid, heavy liquid, gas/vapor), and monitoring interval.
  - Most NSPS have a leak definition of 10,000 ppm. Many NESHAP use a 500-ppm or 1,000-ppm leak definition
- Many equipment leak regulations also define a leak based on visual inspections and observations (such as fluids dripping, spraying, misting or clouding from or around components), sound (such as hissing), and smell.

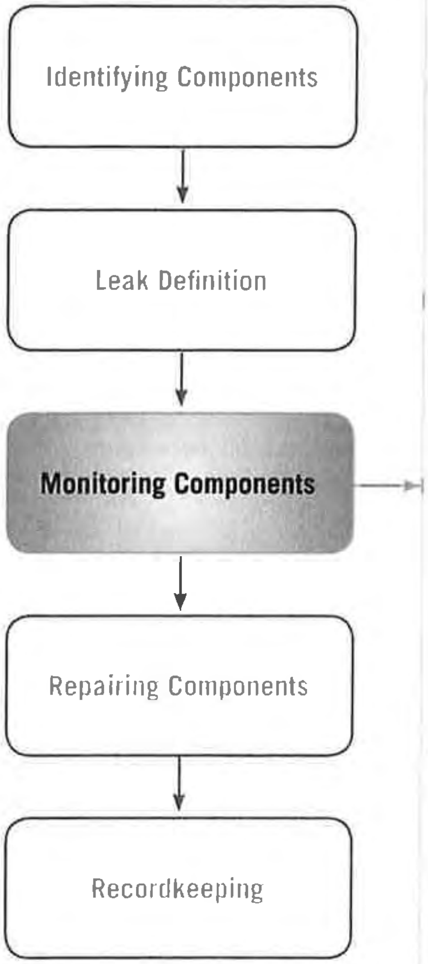
  Note: The LDAR requirements specify weekly visual inspections of pumps, agitators, and compressors for indications of liquids leaking from the seals.

Common Problems

- Using the wrong leak definition for a particular component due to confusion at facilities where multiple LDAR regulations apply.

Best Practices

- Utilize a leak definition lower than what the regulation requires
- Simplify the program by using the lowest leak definition when multiple leak definitions exist
- Make the lowest leak definition conservative to provide a margin of safety when monitoring components
- Keep the lowest leak definition consistent among all similar component types. For example, all valves in a facility might have a leak definition of 500 ppm



The **monitoring interval** is the frequency at which individual component monitoring is conducted. For example, valves are generally required to be monitored once a month using a leak detection instrument, but the monitoring interval may be extended (e.g. to once every quarter for each valve that has not leaked for two successive months for Part 60 Subpart VV, or on a process unit basis of once every quarter for process units that have less than a 2% leak rate for Part 63 Subpart H).

Current Requirements

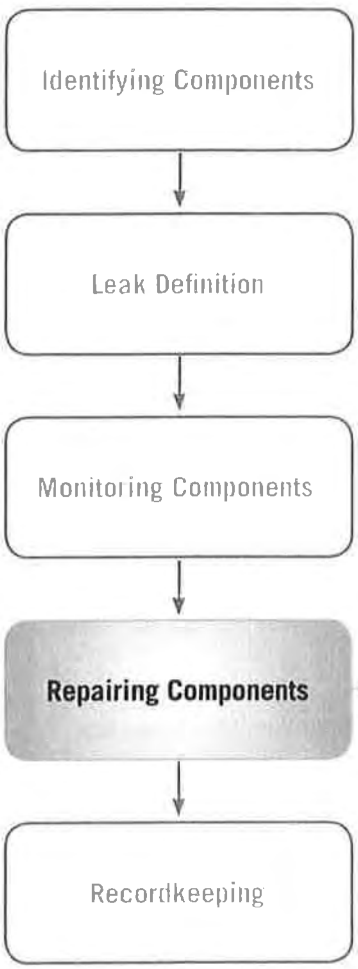
- For many NSPS and NESHAP regulations with leak detection provisions, the primary method for monitoring to detect leaking components is EPA Reference Method 21 (40 CFR Part 60, Appendix A)
- Method 21 is a procedure used to detect VOC leaks from process equipment using a portable detecting instrument.
- Appendix C of this guide explains the general procedure and Appendix D presents the complete Method 21 requirements.
- Monitoring intervals vary according to the applicable regulation, but are typically weekly, monthly, quarterly, and yearly. For connectors, the monitoring interval can be every 2, 4. or 8 years. The monitoring interval depends on the component type and periodic leak rate for the component type.

Common Problems

- Not following Method 21 properly.
- Failing to monitor at the maximum leak location (once the highest reading is obtained by placing the probe on and around the interface, hold the probe at that location approximately two times the response rate of the instrument).
- Not monitoring long enough to identify a leak
- Holding the detection probe too far away from the component interface The reading must be taken at the interface
- Not monitoring all potential leak interfaces
- Using an incorrect or an expired calibration gas
- Not monitoring all regulated components
- Not completing monitoring if the first monitoring attempt is unsuccessful due to equipment being temporarily out of service.

Best Practices

- Although not required by Method 21, use an automatic (electronic) data logger to save time, improve accuracy, and provide an audit record
- Audit the LDAR program to help ensure that the correct equipment is being monitored Method 21 procedures are being followed properly. and the required records are being kept
- Monitor components more frequently than required by the regulations
- Perform QA/QC of LDAR data to ensure accuracy, completeness, and to check for inconsistencies.
- Eliminate any obstructions (e.g. grease on the component interface) that would prevent monitoring at the interface
- If a rule allows the use of alternatives to Method 21 monitoring, Method 21 should still be used periodically to check the results of the alternative monitoring method.



Current Requirements

- Repair leaking components as soon as practicable but not later than a specified number of calendar days (usually 5 days for a first attempt at repair and 15 days for final attempt at repair) after the leak is detected
- First attempts at repair include, but are not limited to, the following practices where practicable and appropriate:
- Tightening bonnet bolts
- Replacing bonnet bolts
- Tightening packing gland nuts
- Injecting lubricant into lubricated packing
- If the repair of any component is technically infeasible without a process unit shutdown, the component may be placed on the Delay of Repair list, the ID number is recorded, and an explanation of why the component cannot be repaired immediately is provided. An estimated date for repairing the component must be included in the facility records

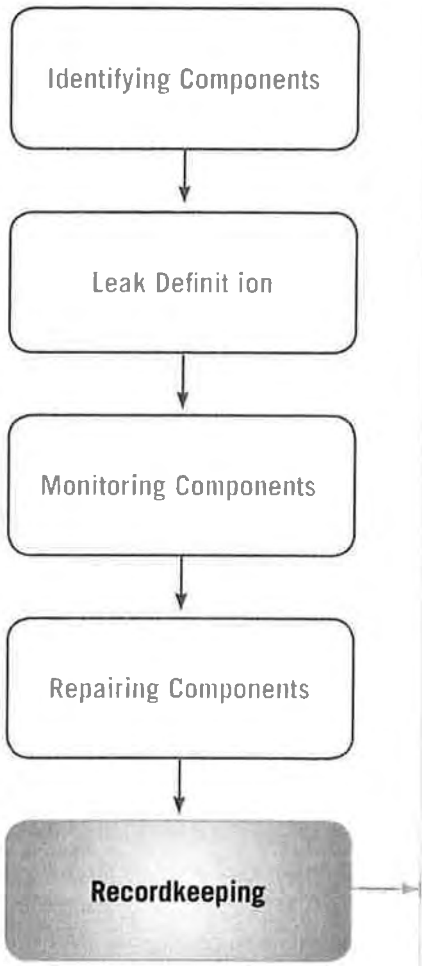
  Note: The "drill and tap" method for repairing leaking valves is generally considered technically feasible without requiring a process unit shutdown and should be tried if the first attempt at repair does not fix the leaking valve. See section 6.7 for a discussion of "drill and tap"
- The component is considered to be repaired only after it has been monitored and shown not to be leaking above the applicable leak definition

Common Problems

- Not repairing leaking equipment within the required amount of time specified by the applicable regulation
- Improperly placing components on the Delay of Repair list.
- Not having a justifiable reason for why it is technically infeasible to repair the component without a process unit shutdown
- Not exploring all available repair alternatives before exercising the Delay of Repair exemption (specifically as it pertains to valves and "drill and tap" repairs)

Best Practices

- Develop a plan and timetable for repairing components
- Make a first attempt at repair as soon as possible after a leak is detected.
- Monitor components daily and over several days to ensure a leak has been successfully repaired
- Replace problem components with "leakless" or other technologies.



Current Requirements

For each regulated process:

- Maintain a list of all ID numbers for all equipment subject to an equipment leak regulation.
- For valves designated as "unsafe to monitor," maintain a list of ID numbers and an explanation/review of conditions for the designation.
- Maintain detailed schematics, equipment design specifications (including dates and descriptions of any changes), and piping and instrumentation diagrams.
- Maintain the results of performance testing and leak detection monitoring, including leak monitoring results per the leak frequency, monitoring leakless equipment, and non-periodic event monitoring.

For leaking equipment:

- Attach ID tags to the equipment
- Maintain records of the equipment ID number, the instrument and operator ID numbers, and the date the leak was detected
- Maintain a list of the dates of each repair attempt and an explanation of the attempted repair method
- Note the dates of successful repairs
- Include the results of monitoring tests to determine if the repair was successful

Common Problems

- Not keeping detailed and accurate records required by the applicable regulation.
- Not updating records to designate new components that are subject to LDAR due to revised regulations or process modifications.

Best Practices

- Perform internal and third-party audits of LDAR records on a regular basis to ensure compliance.
- Electronically monitor and store LDAR data including regular QA/QC audits.
- Perform regular records maintenance.
- Continually search for and update regulatory requirements.
- Properly record and report first attempts at repair.
- Keep the proper records for components on Delay of Repair lists.

6.0 What Compliance Problems Have Been Found With Current LDAR Programs?

Many regulatory agencies determine the compliance status of LDAR programs based on a review of submitted paperwork. Some conduct walk-through inspections to review LDAR records maintained on site and perform a visual check of monitoring practices. However, a records review will not show if monitoring procedures are being followed. Similarly, the typical walkthrough inspection will not likely detect improper monitoring practices since operators will tend to ensure that they are following proper procedures when they are being watched.

EPA's National Enforcement Investigations Center (NEIC) conducted a number of sampling investigations of LDAR programs at 17 petroleum refineries. Appendix E summarizes the comparative monitoring results, and Appendix F contains a copy of the 1999 Enforcement Alert that explains the monitoring results. The investigations consisted of records review and comparative leak monitoring (comparing the leak rate found by NEIC to the facility's historic leak rate) at a subset of the facility's total components. These investigations have shown a pattern of significantly higher equipment leak rates (5%) than what the refineries reported (1.3%). While there have been improvements since 1999, facility audits are still showing significantly elevated leak rates, especially in the chemical manufacturing industries.

The discrepancy in leak rates indicates that monitoring staff may not be complying with Method 21 procedures. Failure to accurately detect leaks may be due to a lack of internal quality control oversight or management accountability for the LDAR programs regardless of whether the monitoring is done by contractors or in-house personnel.

Each leak that is not detected and repaired is a lost opportunity to reduce emissions. In the October 1999 Enforcement Alert, EPA estimates that an additional 40,000 tons of VOCs are emitted annually from petroleum refineries because leaking valves are not found and repaired.

Several important factors contribute to failing to identify and repair leaking components:

1. **Not identifying all regulated components/units in inventory**

   If a facility does not properly identify all of its regulated components, some leaks may go unidentified. Unidentified components may leak or have existing leaks that will worsen over time if the components are not properly identified, monitored and repaired. Facilities can fail to identify regulated components when new processes are constructed, existing process are modified, or new or revised equipment leak regulations are published.

2. **Not monitoring components**

   In some cases, the number of components reported to have been monitored may indicate problems with monitoring procedures. What facility inspectors have found:

   - A data logger time stamp showed valves being monitored at the rate of one per second with two valves occasionally being monitored within the same 1-second period.

- At one facility, a person reported monitoring 8,000 components in one day (assuming an 8-hour work day, that represents one component every 3.6 seconds).
- Records evaluations showed widely varying component monitoring counts, suggesting equipment might not always be monitored when required.
- Equipment was marked "temporarily out of service" because the initial inspection attempt could not be performed. However, the equipment was in service for most of the period, and no subsequent (or prior) inspection attempts were performed to meet the monitoring requirement.

However, even when records show a realistic number of components are being monitored, if there are no oversight or accountability checks, then there is no guarantee that components are actually being monitored.

> A well-trained LDAR inspection team (two people) can monitor approximately 500-700 valves per day.

3. Insufficient time to identify a leak

In other cases, facilities are not following proper monitoring procedures, resulting in a lower number of leaking components being reported.

- If a worker moves the probe around the component interface so rapidly that the instrument does not have time to properly respond, then a component may never be identified as leaking.
- If a worker fails to find the maximum leak location for the component and then does not spend twice the response time at that location, then the monitoring instrument will not measure the correct concentration of hydrocarbons and the leak may go undetected. **Optical leak imaging shows the importance of identifying the maximum leak location, as hydrocarbons are quickly dispersed and diluted by air currents around the component**.

4. Holding the probe away from the component interface

The probe must be placed at the proper interface of the component being analyzed. Placing the probe even 1 centimeter from the interface can result in a false reading, indicating that the component is not leaking, when in fact it is leaking. Eliminate any issues (e.g., grease on the component interface) that prevent monitoring at the interface (e.g., remove excess grease from the component before monitoring or use a monitor that won't be impacted by the grease and is easy to clean.

For equipment with rotating shafts (pumps and compressors), Method 21 requires the probe be placed within 1 centimeter of the shaft-seal interface. Placing the probe at the surface of the rotating shaft is a safety hazard and should be avoided.

> Typical TVA (Toxic Vapor Analyzer) response times are around 2 4 seconds.

5. Failing to properly maintain monitoring instrument

Factors that may prevent the instrument from identifying leaks are:

- Not using an instrument that meets the specifications required in Method 21, section 6.
- Dirty instrument probes;
- Leakage from the instrument probes;
- Not zeroing instrument meter;
- Incorrect calibration gases used; and
- Not calibrating the detection instrument on a daily basis.

6. Improperly identifying components as "unsafe" or "difficult" to monitor

Components that are identified as being "unsafe to monitor" or "difficult to monitor" must be identified as such because there is a safety concern or an accessibility issue that prevents the component from being successfully monitored.

All unsafe or difficult-to-monitor components must be included on a log with identification numbers and an explanation of why the component is "unsafe to monitor" or "difficult to monitor." Monitoring can be deferred for all such components, but the facility must maintain a plan that explains the conditions under which the components become safe to monitor or no longer difficult to monitor.

7. Improperly placing components/units on the "Delay of Repair" list

Generally, placing a leaking component on the "Delay of Repair" list is permissible only when the component is technically infeasible to repair without a process unit shutdown (e.g., for valves the owner/operator must demonstrate that the emissions from immediate repair will be greater than waiting for unit shutdown).

Repair methods may exist, such as "drill and tap" for valves, that allow leaks to be fixed while the component is still in service. Failing to consider such repair methods before exercising the "Delay of Repair" list may constitute noncompliance with repair requirements (usually 15 days under federal LDAR standards).

Components placed on the "Delay of Repair" list must be accompanied by their ID numbers and an explanation of why they have been placed on the list. These components cannot remain on the list indefinitely – they must be repaired by the end of the next process unit shutdown.

Drill and Tap is a repair method where a hole is drilled into the valve packing gland and tapped, so that a small valve and fitting can be attached to the gland. A packing gun is connected to this fitting and the small valve is opened allowing new packing material to be pumped into the packing gland.

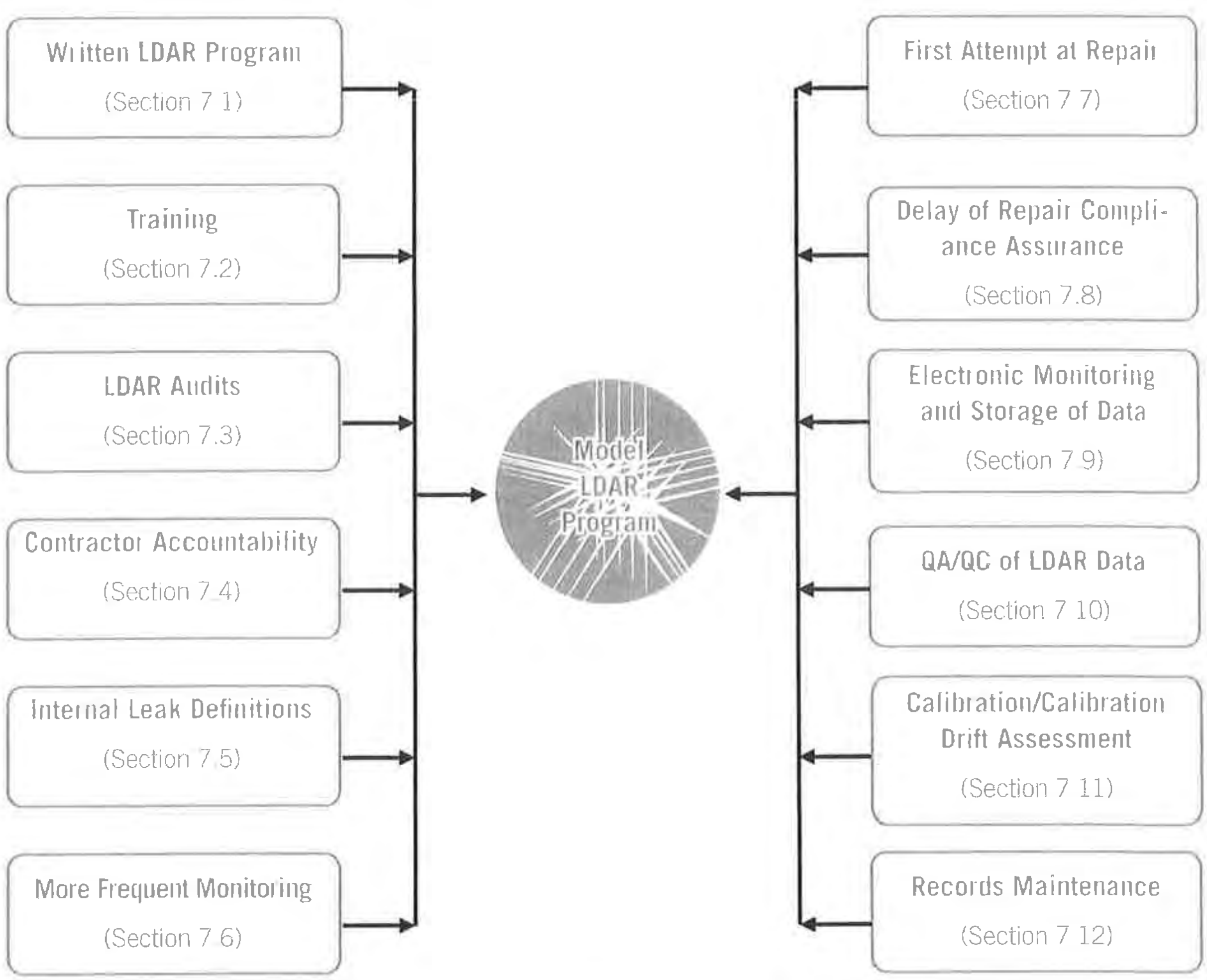
Many companies consider this a permanent repair technique, as newer pumpable packing types are frequently superior to the older packing types they replace. Packing types can be changed and optimized for the specific application over time.

7.0 Model LDAR Program

Experience has shown that facilities with an effective record of preventing leaks integrate an awareness of the benefits of leak detection and repair into their operating and maintenance program. This section outlines some of the major elements of successful LDAR programs. These program elements were developed from:

- Evaluation of best practices identified at facilities with successful LDAR programs, and
- Analysis of the root causes of noncompliance at facilities that were found to have recurring violations of LDAR regulatory requirements.

LDAR programs that incorporate most or all of the elements described in the following sections have achieved more consistent results in their LDAR programs, leading to increased compliance and lower emissions.



7.1 Written LDAR Program

A written LDAR program specifies the regulatory requirements and facility-specific procedures for recordkeeping certifications, monitoring, and repairs. A written program also delineates the roles of each person on the LDAR team as well as documents all the required procedures to be completed and data to be gathered, thus establishing accountability. The plan should identify all process units subject to federal, state, and local LDAR regulations and be updated as necessary to ensure accuracy and continuing compliance.

Elements:

- An overall, facility-wide leak rate goal that will be a target on a process-unit-by-process-unit basis;
- A list of all equipment in light liquid and/or in gas/vapor service that has the potential to leak VOCs and VHAPs, within process units that are owned and maintained by each facility;
- Procedures for identifying leaking equipment within process units;
- Procedures for repairing and keeping track of leaking equipment,
- A process for evaluating new and replacement equipment to promote the consideration of installing equipment that will minimize leaks or eliminate chronic leakers;
- A list of "LDAR Personnel" and a description of their roles and responsibilities, including the person or position for each facility that has the authority to implement improvements to the LDAR program, and
- Procedures (e.g. a Management of Change program) to ensure that components added to each facility during maintenance and construction are evaluated to determine if they are subject to LDAR requirements, and that affected components are integrated into the LDAR program.

Within thirty (30) days after developing the written facility-wide LDAR program, submit a copy of the Program to EPA and to the appropriate state agency.

7.2 Training

A training program will provide LDAR personnel the technical understanding to make the written LDAR program work. It also will educate members of the LDAR team on their individual responsibilities. These training programs can vary according to the level of involvement and degree of responsibility of LDAR personnel.

Elements:

- Provide and require initial training and annual LDAR refresher training for all facility employees assigned LDAR compliance responsibilities, such as monitoring technicians, database users, QA/QC personnel, and the LDAR Coordinator
- For other operations and maintenance personnel with responsibilities related to LDAR, provide and require an initial training program that includes instruction on aspects of LDAR that are relevant to their duties (e.g. operators and mechanics performing valve packing and unit supervisors that approve delay of repair work). Provide and require "refresher" training in LDAR for these personnel at least every three years.
- Collect training information and records of contractors, if used

7.3 LDAR Audits

Whether LDAR monitoring is done in house or contracted to third parties outside the company, the potential exists for LDAR staff not to adhere correctly to the LDAR program. Internal and third-party audits of a facility LDAR program are a critical component of effective LDAR programs. The audits check that the correct equipment is being monitored, Method 21 procedures are being followed, leaks are being fixed, and the required records are being kept. In short, the audits ensure that the LDAR program is being conducted correctly and problems are identified and corrected.

Elements:

- Review records on a regular cycle to ensure that all required LDAR-related records, logs, and databases are being maintained and are up to date.
- Ensure and document that the correct equipment is included in the LDAR program and that equipment identified as leaking is physically tagged with the equipment ID number
- Observe the calibration and monitoring techniques used by LDAR technicians, in particular to ensure the entire interface is checked and the probe is held at the interface, not away from the interface.
- Retain a contractor to perform a third-party audit of the facility LDAR program at least once every four (4) years.
- Perform facility-led audits every four (4) years.
  - Use personnel familiar with the LDAR program and its requirements from one or more of the company's other facilities or locations (if available).
  - Perform the first round of facility-led LDAR audits no later than two (2) years after completion of the third party audits outlined above, and every four (4) years thereafter
  - This rotation ensures that the facility is being audited once every two (2) years.
- If areas of noncompliance are discovered, initiate a plan to resolve and document those issues.
- Implement, as soon as practicable, steps necessary to correct causes of noncompliance, and prevent, to the extent practicable, a recurrence of the cause of the noncompliance.
- Retain the audit reports and maintain a written record of the corrective actions taken in response to any deficiencies identified

7.4 Contractor Accountability

Contractors performing monitoring are frequently compensated for the number of components they monitor, which might provide an incentive to rush through monitoring procedures and not adhere to Method 21 requirements for response time, monitoring distance, etc. If this happens, some equipment leaks may not be detected. To overcome this potential problem, facilities should have in place sufficient oversight procedures to increase the accountability of contractors.

Elements:

- Write contracts that emphasize the quality of work instead of the quantity of work only.
- Require contractors to submit documentation that their LDAR personnel have been trained on Method 21 and facility-specific LDAR procedures.
- Ensure that the contractor has a procedure in place to review and certify the monitoring data before submitting the data to the facility.
- Review daily results of contractor work to ensure that a realistic number of components are being monitored.
- Perform spot audits in the field to ensure that Method 21 procedures are being followed. This can include spot-checking monitored components with another hydrocarbon analyzer or following LDAR personnel as they perform monitoring.
- Have periodic reviews of contractor performance (e.g., quarterly or semi-annually) to resolve issues and correct problems.

7.5 Internal Leak Definition for Valves and Pumps

The varying leak definitions that can apply to different process units and components can be confusing and lead to errors in properly identifying leaks. To counter this potential problem, operate your LDAR program using an internal leak definition for valves and pumps in light liquid or gas vapor service. The internal leak definition would be equivalent to or lower than the applicable definitions in your permit and the applicable federal, state, and local regulations. Monitoring against a uniform definition that is lower than the applicable regulatory definition will reduce errors and provide a margin of safety for identifying leaking components. The internal leak definition would apply to valves and pumps (and possibly connectors) in light liquid or gas vapor service.

Elements:

- Adopt a 500-ppm or lower internal leak definition for VOCs for all valves in light liquid and/or gas vapor service, excluding pressure relief devices.
- Adopt a 2,000-ppm or lower internal leak definition for pumps in light liquid and/or gas/vapor service.
- Record, track, repair, and monitor leaks in excess of the internal leak definition. Repair and monitor leaks that are greater than the internal leak definitions but less than the applicable regulatory leak definitions within thirty (30) days of detection.

Consent Decrees between EPA and many chemical facilities subject to the HON require using a 250-ppm leak definition for valves and connectors and a 500-ppm leak definition for pumps.

Note: If a state or local agency has lower leak definitions, then the internal leak definition should be set to the lowest definition or even lower to include/allow for margin of error.

7.6 More Frequent Monitoring

Many regulations allow for less frequent monitoring (i.e. skip periods) when good performance (as defined in the applicable regulation) is demonstrated. Skip period is an alternative work practice found in some equipment leak regulations and usually applies only to valves and connectors. After a specified number of leak detection periods (e.g., monthly) during which the percentage of leaking components is below a certain value (e.g., 2% for NSPS facilities), a facility can monitor less frequently (e.g., quarterly) as long as the percentage of leaking components remains low. The facility must keep a record of the percentage of the component type found leaking during each leak detection period.

Experience has shown that poor monitoring rather than good performance has allowed facilities to take advantage of the less frequent monitoring provisions. To ensure that leaks are still being identified in a timely manner and that previously unidentified leaks are not worsening over time, implement a plan for more frequent monitoring for components that contribute most to equipment leak emissions.

Elements:

- Monitor pumps in light liquid and/or gas vapor service on a monthly basis.
- Monitor valves in light liquid and/or gas vapor service — other than difficult-to-monitor or unsafe-to-monitor valves — with no skip periods.

Consent Decrees between EPA and many chemical facilities subject to the HON require semiannual monitoring of connectors.

7.7 Repairing Leaking Components

To stop detected leaks while they are still small, most rules require a first attempt at repair within 5 days of the leak detection and a final repair within 15 days. However, any component that cannot be repaired within those time frames must be placed on a "Delay of Repair" list to be repaired during the next shutdown cycle.

First attempts at repair include, but are not limited to, the following best practices where practicable and appropriate:

- Tightening bonnet bolts;
- Replacing bonnet bolts;
- Tightening packing gland nuts; and
- Injecting lubricant into lubricated packing.

Elements:

- Schedule the "first attempt at repair" of those components that the monitoring personnel are not authorized to repair consistent with the existing regulatory requirements.
- Monitor the component for which a "first attempt at repair" was performed no later than the next regular business day to ensure the leak has not worsened.
- If the first attempt at repair has not succeeded then other methods, such as "drill and tap" should be employed where feasible. Drill and tap procedures are no longer considered extraordinary practices.

7.8 Delay of Repair Compliance Assurance

Any component that cannot be repaired during the specified repair interval must be placed on a "Delay of Repair" list to be repaired during the next shutdown cycle. Delay of repair compliance assurance procedures ensure that the appropriate equipment is justifiably on the "Delay of Repair" list and that facilities have a plan to fix these components.

Elements:

- Have the unit supervisor approve in advance and certify all components that are technically infeasible to repair without a process unit shutdown.
- Continue to monitor equipment that is placed on the "Delay of Repair" list in the facility's regular LDAR monitoring. For leaks above the internal leak definition rate and below the regulatory rate, put the equipment on the "Delay of Repair" list within 30 days.
- Implement the following repair policies and procedures within 15 days of implementing the written LDAR program:

  For valves, other than control valves or pressure relief valves, that are leaking at a rate of 10,000 ppm or greater and cannot be feasibly repaired without a process unit shutdown, use "drill and tap" repair methods to fix the leaking valve, unless you can determine and document that there is a safety, mechanical, or major environmental concern posed by repairing the leak in this manner.

  Perform up to two "drill and tap" repair attempts to repair a leaking valve, if necessary, within 30 days of identifying the leak.

7.9 Electronic Monitoring and Storage of LDAR Data

Electronic monitoring and storage of LDAR data will help evaluate the performance of monitoring personnel (via time/date stamps), improve accuracy, provide an effective means for QA/QC, and retrieve records in a timely manner for review purposes. Incorporate and maintain an electronic database for storing and reporting LDAR data. Use data loggers or other data collection devices during all LDAR monitoring.

Elements:

- Use best efforts to transfer, on a daily basis, electronic data from electronic data logging devices to the database.
- For all monitoring events in which an electronic data collection device is used, include a time and date stamp, operator identification, and instrument identification.
- Paper logs can be used where necessary or more feasible (e.g., small rounds, re-monitoring fixed leaks, or when data loggers are not available or broken), and should record, at a minimum, the monitoring technician, date, and monitoring equipment used.
- Transfer any manually recorded monitoring data to the database within 7 days of monitoring.
- Review records to identify "problem" components for preventative maintenance (repair prior to anticipated failure) or for replacement with "leakless" technology.

7.10 QA/QC of LDAR Data

QA/QC audits ensure that Method 21 procedures are being followed and LDAR personnel are monitoring the correct components in the proper manner. Develop and implement a procedure to ensure QA/QC review of all data generated by LDAR monitoring technicians on a daily basis or at the conclusion of each monitoring episode.

Elements:

Some QA/QC procedures include:

- Daily review/sign-off by monitoring technicians of the data they collected to ensure accuracy and validity.
- Periodic review of the daily monitoring reports generated in conjunction with recordkeeping and reporting requirements.
- Quarterly QA/QC of the facility's and contractor's monitoring data including:
  - Number of components monitored per technician;
  - Time between monitoring events; and
  - Abnormal data patterns.

7.11 Calibration/Calibration Drift Assessment

Always calibrate LDAR monitoring equipment using an appropriate calibration gas, in accordance with 40 CFR Part 60, EPA Reference Test Method 21.

Elements:

- Conduct calibration drift assessments of LDAR monitoring equipment at the end of each monitoring shift, at a minimum.
- Conduct the calibration drift assessment using, at a minimum, approximately 500 ppm of calibration gas.
- If any calibration drift assessment after the initial calibration shows a negative drift of more than 10% from the previous calibration, re-monitor all valves that were monitored since the last calibration with a reading of greater than 100 ppm. Re-monitor all pumps that were monitored since the last calibration with a reading of greater than 500 ppm.

7.12 Records Maintenance

Organized and readily available records are one potential indication of an effective LDAR program. Well-kept records may also indicate that the LDAR program is integrated into the facility's routine operation and management. The equipment leak regulations specify recordkeeping and reporting requirements; incorporating the elements below will help ensure your facility LDAR records are thorough and complete.

Elements:

Records to maintain:

- A certification that the facility implemented the "first attempt at repair" program
- A certification that the facility implemented QA/QC procedures for review of data generated by LDAR technicians.
- An identification of the person/position at each facility responsible for LDAR program performance as defined in the written program.
- A certification that the facility developed and implemented a tracking program for new valves and pumps added during maintenance and construction defined in the written program
- A certification that the facility properly completed calibration drift assessments.
- A certification that the facility implemented the "delay of repair" procedures.
- The following information on LDAR monitoring:
  (1) The number of valves and pumps present in each process unit during the quarter,
  (2) The number of valves and pumps monitored in each process unit,
  (3) An explanation for missed monitoring if the number of valves and pumps present exceeds the number of valves and pumps monitored during the quarter
  (4) The number of valves and pumps found leaking;
  (5) The number of "difficult to monitor" pieces of equipment monitored;
  (6) A list of all equipment currently on the "Delay of Repair" list and the date each component was placed on the list;
  (7) The number of repair attempts not completed promptly or completed within 5 days;
  (8) The number of repairs not completed within 30 days and the number of components not placed on the "Delay of Repair" list, and
  (9) The number of chronic leakers that do not get repaired
- Records of audits and corrective actions. Prior to the first third-party audit at each facility, include in your records a copy of each audit report from audits conducted in the previous calendar year and a summary of the actions planned or taken to correct all deficiencies identified in the audits.
- For the audits performed in prior years, identification of the auditors and documentation that a written plan exists identifying corrective action for any deficiencies identified and that this plan is being implemented

8.0 Sources of Additional Information

Inspection Manual: Federal Equipment Leak Regulations for the Chemical Manufacturing Industry, EPA/305/B-98/011, December 1998.
http://cfpub.epa.gov/compliance/resources/publications/assistance/sectors/chemical/index.cfm

Vol 1: Inspection Manual
http://www.epa.gov/compliance/resources/publications/assistance/sectors/insmanvol1.pdf

Vol 2: Chemical Manufacturing Industry Regulations (3 parts on the Internet)
http://www.epa.gov/compliance/resources/publications/assistance/sectors/insmanvol2pt1.pdf
http://www.epa.gov/compliance/resources/publications/assistance/sectors/insmanvol2pt2.pdf
http://www.epa.gov/compliance/resources/publications/assistance/sectors/insmanvol2pt3.pdf

Vol 3: Petroleum Refining Industry Regulations
http://www.epa.gov/compliance/resources/publications/assistance/sectors/insmanvol3.pdf

1995 Protocol for Equipment Leak Emission Estimates, EPA-453/R-95-017, Nov 1995.
http://www.epa.gov/ttnchie1/efdocs/equiplks.pdf

Enforcement Alert, EPA Office of Enforcement and Compliance Assurance, EPA 300-N-99-014, Oct 1999.
http://www.epa.gov/compliance/resources/newsletters/civil/enfalert/emissions.pdf

National Petroleum Refinery Initiative, EPA.
http://www.epa.gov/compliance/resources/cases/civil/caa/refineryinitiative032106.pdf

Petroleum Refinery Initiative Fact Sheet, EPA.
http://www.epa.gov/compliance/resources/cases/civil/caa/petroleumrefinery-fcsht.html

Petroleum Refinery National Priority Case Results.
http://www.epa.gov/compliance/resources/cases/civil/caa/oil/

Draft Staff Report, Regulation 8, Rule 18, Equipment Leaks, Bay Area Air Quality Management District, Jul 1997.
http://www.baaqmd.gov/pln/ruledev/8-18/1997/0818_sr_071097.pdf

Standards of Performance for Equipment Leaks of VOC in the Synthetic Organic Chemicals Manufacturing Industry; Standards of Performance for Equipment Leaks of VOC in Petroleum Refineries; Proposed Rule, [EPA-HQ-OAR-2006-0699; FRL-] RIN 2060-AN71.
http://www.epa.gov/ttn/oarpg/t3/fr_notices/equip_leak_prop103106.pdf

Industrial Organic Chemicals Compliance Incentive Program, EPA Compliance and Enforcement.
http://www.epa.gov/compliance/incentives/programs/ioccip.html

Leak Detection and Repair Program Developments.
http://www.epa.gov/compliance/neic/field/leak.html

Compliance and Enforcement Annual Results: Important Environmental Problems / National Priorities.
http://www.epa.gov/compliance/resources/reports/endofyear/eoy2006/sp-airtoxics-natl-priorities.html

Portable Instruments User's Manual For Monitoring VOC Sources, EPA-340/1-86-015.
Inspection Techniques For Fugitive VOC Emission Sources, EPA 340/1-90-026a,d,e,f (rev May 1993) Course #380.

Environmental compliance assistance resources can be found at:

http://cfpub.epa.gov/clearinghouse/
http://www.assistancecenters.net/
http://www.epa.gov/compliance/assistance/sectors/index.html

Appendix A Federal Regulations That Require a Formal LDAR Program With Method 21

40 CFR Part	40 CFR Subpart	Regulation Title
60	VV	SOCMI VOC Equipment Leaks NSPS
60	DDD	Volatile Organic Compound (VOC) Emissions from the Polymer Manufacturing Industry
60	GGG	Petroleum Refinery VOC Equipment Leaks NSPS
60	KKK	Onshore Natural Gas Processing Plant VOC Equipment Leaks NSPS
61	J	National Emission Standard for Equipment Leaks (Fugitive Emission Sources) of Benzene
61	V	Equipment Leaks NESHAP
63	H	Organic HAP Equipment Leak NESHAP (HON)
63	I	Organic HAP Equipment Leak NESHAP for Certain Processes
63	J	Polyvinyl Chloride and Copolymers Production NESHAP
63	R	Gasoline Distribution Facilities (Bulk Gasoline Terminals and Pipeline Breakout Stations)
63	CC	Hazardous Air Pollutants from Petroleum Refineries
63	DD	Hazardous Air Pollutants from Off-Site Waste and Recovery Operations
63	SS	Closed Vent Systems, Control Devices, Recovery Devices and Routing to a Fuel Gas System or a Process
63	TT	Equipment Leaks – Control Level 1
63	UU	Equipment Leaks – Control Level 2
63	YY	Hazardous Air Pollutants for Source Categories: Generic Maximum Achievable Control Technology Standards
63	GGG	Pharmaceuticals Production
63	III	Hazardous Air Pollutants from Flexible Polyurethane Foam Production
63	MMM	Hazardous Air Pollutants for Pesticide Active Ingredient Production
63	FFFF	Hazardous Air Pollutants: Miscellaneous Organic Chemical Manufacturing
63	GGGGG	Hazardous Air Pollutants: Site Remediation
63	HHHHH	Hazardous Air Pollutants: Miscellaneous Coating Manufacturing
65	F	Consolidated Federal Air Rule – Equipment Leaks
264	BB	Equipment Leaks for Hazardous Waste TSDFs
265	BB	Equipment Leaks for Interim Status Hazardous Waste TSDFs

Note: Many of these regulations have identical requirements, but some have different applicability and control requirements.

Appendix B Federal Regulations That Require the Use of Method 21 But Do Not Require a Formal LDAR Program

40 CFR		Regulation Title
Part	Subpart	
60	XX	Bulk Gasoline Terminals
60	QQQ	VOC Emissions from Petroleum Refinery Wastewater Systems
60	WWW	Municipal Solid Waste Landfills
61	F	Vinyl Chloride
61	L	Benzene from Coke By-Products
61	BB	Benzene Transfer
61	FF	Benzene Waste Operations
63	G	Organic Hazardous Air Pollutants from SOCMI for Process Vents, Storage Vessels, Transfer Operations, and Wastewater
63	M	Perchloroethylene Standards for Dry Cleaning
63	S	Hazardous Air Pollutants from the Pulp and Paper Industry
63	Y	Marine Unloading Operations
63	EE	Magnetic Tape Manufacturing Operations
63	GG	Aerospace Manufacturing and Rework Facilities
63	HH	Hazardous Air Pollutants from Oil and Gas Production Facilities
63	OO	Tanks – Level 1
63	PP	Containers
63	QQ	Surface Impoundments
63	VV	Oil/Water, Organic/Water Separators
63	HHH	Hazardous Air Pollutants from Natural Gas Transmission and Storage
63	JJJ	Hazardous Air Pollutant Emissions: Group IV Polymers and Resins
63	VVV	Hazardous Air Pollutants: Publicly Owned Treatment Works
65	G	CFAR – Closed Vent Systems
264	AA	Owners and Operators of Hazardous Waste Treatment, Storage, and Disposal Facilities - Process Vents
264	CC	Owners and Operators of Hazardous Waste Treatment, Storage and Disposal Facilities - Tanks, Surface Impoundments, Containers
265	AA	Interim Standards for Owners and Operators of Hazardous Waste Treatment, Storage, and Disposal Facilities – Process Vents
265	CC	Interim Standards for Owners and Operators of Hazardous Waste Treatment, Storage, and Disposal Facilities - Tanks, Surface Impoundments, Containers
270	B	Hazardous Waste Permit Program – Permit Application
270	J	Hazardous Waste Permit Program – RCRA Standardized Permits for Storage Tanks and Treatment Units

Appendix C Method 21 General Procedure

Failure of facilities to follow Method 21 can lead to them not properly identifying and subsequently repairing leaking components. It is critical for facilities to refer to the complete text of Method 21 (see Appendix D) for detailed explanations of each general procedure found below and how to properly perform each step.

1. **Evaluate Instrument Performance**

   Performance criteria for the monitoring instrument:

   - For each VOC measured, the response factor should be <10 unless specified in the applicable regulation. Response factor is the ratio of the known concentration of a VOC compound to the observed meter reading when measured using an instrument calibrated with the reference compound specified in the applicable regulation.
   - The calibration precision should be <10 percent of the calibration gas value. Calibration precision is the degree of agreement between measurements of the same known value, expressed as the relative percentage of the average difference between the meter readings and the known concentration to the known concentration.
   - The response time should be ≤30 seconds. Response time is the time interval from a step change in VOC concentration at the input of the sampling system to the time at which 90% of the corresponding final value is reached as displayed on the instrument readout meter.

2. **Calibrate Instrument**

   Before each monitoring episode:

   - Let the instrument warm up.
   - Introduce the calibration gas into the instrument probe.
   - Adjust the instrument meter readout to match the calibration gas concentration value.

3. **Monitor Individual components**

   When monitoring components:

   - Place the probe at the surface of the component interface where leakage could occur.
   - Move the probe along the interface periphery while observing the instrument readout.
   - Locate the maximum reading by moving the probe around the interface.
   - Keep the probe at the location of the maximum reading for 2 times the response factor.
   - If the concentration reading on the instrument readout is above the applicable leak definition, then the component is leaking and must be repaired.

Appendix D Method 21—Determination of Volatile Organic Compound Leaks

1.0 Scope and Application

1.1 Analytes.

Analyte	CAS No.
Volatile Organic Compounds (VOC)..........	No CAS number assigned.

1.2 Scope. This method is applicable for the determination of VOC leaks from process equipment. These sources include, but are not limited to, valves, flanges and other connections, pumps and compressors, pressure relief devices, process drains, open-ended valves, pump and compressor seal system degassing vents, accumulator vessel vents, agitator seals, and access door seals.

1.3 Data Quality Objectives. Adherence to the requirements of this method will enhance the quality of the data obtained from air pollutant sampling methods.

2.0 Summary of Method

2.1 A portable instrument is used to detect VOC leaks from individual sources. The instrument detector type is not specified, but it must meet the specifications and performance criteria contained in Section 6.0. A leak definition concentration based on a reference compound is specified in each applicable regulation. This method is intended to locate and classify leaks only, and is not to be used as a direct measure of mass emission rate from individual sources.

3.0 Definitions

3.1 Calibration gas means the VOC compound used to adjust the instrument meter reading to a known value. The calibration gas is usually the reference compound at a known concentration approximately equal to the leak definition concentration.

3.2 Calibration precision means the degree of agreement between measurements of the same known value, expressed as the relative percentage of the average difference between the meter readings and the known concentration to the known concentration.

3.3 Leak definition concentration means the local VOC concentration at the surface of a leak source that indicates that a VOC emission (leak) is present. The leak definition is an instrument meter reading based on a reference compound.

3.4 No detectable emission means a local VOC concentration at the surface of a leak source, adjusted for local VOC ambient concentration, that is less than 2.5 % of the specified leak definition concentration. That indicates that a VOC emission (leak) is not present.

3.5 Reference compound means the VOC species selected as the instrument calibration basis for specification of the leak definition concentration. (For example, if a leak definition concentration is 10,000 ppm as methane, then any source emission that results in a local concentration that yields a meter reading of 10,000 on an instrument meter calibrated with methane would be classified as a leak. In this example, the leak definition concentration is 10,000 ppm and the reference compound is methane.)

3.6 Response factor means the ratio of the known concentration of a VOC compound to the observed meter reading when measured using an instrument calibrated with the reference compound specified in the applicable regulation.

3.7 Response time means the time interval from a step change in VOC concentration at the input of the sampling system to the time at which 90 percent of the corresponding final value is reached as displayed on the instrument readout meter.

4.0 Interferences [Reserved]

5.0 Safety

5.1 Disclaimer. This method may involve hazardous materials, operations, and equipment. This test method may not address all of the safety problems associated with its use. It is the responsibility of the user of this test method to establish appropriate safety and health practices and determine the applicability of regulatory limitations prior to performing this test method.

5.2 Hazardous Pollutants. Several of the compounds, leaks of which may be determined by this method, may be irritating or corrosive to tissues (e.g., heptane) or may be toxic (e.g., benzene, methyl alcohol). Nearly all are fire hazards. Compounds in emissions should be determined through familiarity with the source. Appropriate precautions can be found in reference documents, such as reference No. 4 in Section 16.0.

6.0 Equipment and Supplies

A VOC monitoring instrument meeting the following specifications is required:

6.1 The VOC instrument detector shall respond to the compounds being processed. Detector types that may meet this requirement include, but are not limited to, catalytic oxidation, flame ionization, infrared absorption, and photoionization.

6.2 The instrument shall be capable of measuring the leak definition concentration specified in the regulation.

6.3 The scale of the instrument meter shall be readable to ±2.5 % of the specified leak definition concentration.

6.4 The instrument shall be equipped with an electrically driven pump to ensure that a sample is provided to the detector at a constant flow rate. The nominal sample flow rate, as measured at the sample probe tip, shall be 0.10 to 3.0 l/min (0.004 to 0.1 ft 3 /min) when the probe is fitted with a glass wool plug or filter that may be used to prevent plugging of the instrument.

6.5 The instrument shall be equipped with a probe or probe extension or sampling not to exceed 6.4 mm (1/4 in) in outside diameter, with a single end opening for admission of sample.

6.6 The instrument shall be intrinsically safe for operation in explosive atmospheres as defined by the National Electrical Code by the National Fire Prevention Association or other applicable regulatory code for operation in any explosive atmospheres that may be encountered in its use. The instrument shall, at a minimum, be intrinsically safe for Class 1, Division 1 conditions, and/or Class 2, Division 1 conditions, as appropriate, as defined by the example code. The instrument shall not be operated with any safety device, such as an exhaust flame arrestor, removed.

7.0 Reagents and Standards

7.1 Two gas mixtures are required for instrument calibration and performance evaluation:

7.1.1 Zero Gas. Air, less than 10 parts per million by volume (ppmv) VOC.

7.1.2 Calibration Gas. For each organic species that is to be measured during individual source surveys, obtain or prepare a known standard in air at a concentration approximately equal to the applicable leak definition specified in the regulation.

7.2 Cylinder Gases. If cylinder calibration gas mixtures are used, they must be analyzed and certified by the manufacturer to be within 2 % accuracy, and a shelf life must be specified. Cylinder standards must be either reanalyzed or replaced at the end of the specified shelf life.

7.3 Prepared Gases. Calibration gases may be prepared by the user according to any accepted gaseous preparation procedure that will yield a mixture accurate to within 2 percent. Prepared standards must be replaced each day of use unless it is demonstrated that degradation does not occur during storage.

7.4 Mixtures with non-Reference Compound Gases. Calibrations may be performed using a compound other than the reference compound. In this case, a conversion factor must be determined for the alternative compound such that the resulting meter readings during source surveys can be converted to reference compound results.

8.0 Sample Collection, Preservation, Storage, and Transport

8.1 Instrument Performance Evaluation. Assemble and start up the instrument according to the manufacturer's instructions for recommended warmup period and preliminary adjustments.

8.1.1 Response Factor. A response factor must be determined for each compound that is to be measured, either by testing or from reference sources. The response factor tests are required before placing the analyzer into service, but do not have to be repeated at subsequent intervals.

8.1.1.1 Calibrate the instrument with the reference compound as specified in the applicable regulation. Introduce the calibration gas mixture to the analyzer and record the observed meter reading. Introduce zero gas until a stable reading is obtained. Make a total of three measurements by alternating between the calibration gas and zero gas. Calculate the response factor for each repetition and the average response factor.

8.1.1.2 The instrument response factors for each of the individual VOC to be measured shall be less than 10 unless otherwise specified in the applicable regulation. When no instrument is available that meets this specification when calibrated with the reference VOC specified in the applicable regulation, the available instrument may be calibrated with one of the VOC to be measured, or any other VOC, so long as the instrument then has a response factor of less than 10 for each of the individual VOC to be measured.

8.1.1.3 Alternatively, if response factors have been published for the compounds of interest for the instrument or detector type, the response factor determination is not required, and existing results may be referenced. Examples of published response factors for flame ionization and catalytic oxidation detectors are included in References 1–3 of Section 17.0.

8.1.2 Calibration Precision. The calibration precision test must be completed prior to placing the analyzer into service and at subsequent 3-month intervals or at the next use, whichever is later.

8.1.2.1 Make a total of three measurements by alternately using zero gas and the specified calibration gas. Record the meter readings. Calculate the average algebraic difference between the meter readings and the known value. Divide this average difference by the known calibration value and multiply by 100 to express the resulting calibration precision as a percentage.

8.1.2.2 The calibration precision shall be equal to or less than 10 % of the calibration gas value.

8.1.3 Response Time. The response time test is required before placing the instrument into service. If a modification to the sample pumping system or flow configuration is made that would change the response time, a new test is required before further use.

8.1.3.1 Introduce zero gas into the instrument sample probe. When the meter reading has stabilized, switch quickly to the specified calibration gas. After switching, measure the time required to attain 90 % of the final stable reading. Perform this test sequence three times and record the results. Calculate the average response time.

8.1.3.2 The instrument response time shall be equal to or less than 30 seconds. The instrument pump, dilution probe (if any), sample probe, and probe filter that will be used during testing shall all be in place during the response time determination.

8.2 Instrument Calibration. Calibrate the VOC monitoring instrument according to Section 10.0.

8.3 Individual Source Surveys.

8.3.1 Type I—Leak Definition Based on Concentration. Place the probe inlet at the surface of the component interface where leakage could occur. Move the probe along the interface periphery while observing the instrument readout. If an increased meter reading is observed, slowly sample the interface where leakage is indicated until the maximum meter reading is obtained. Leave the probe inlet at this maximum reading location for approximately two times the instrument response time. If the maximum observed meter reading is greater than the leak definition in the applicable regulation, record and report the results as specified in the regulation reporting requirements. Examples of the application of this general technique to specific equipment types are:

8.3.1.1 Valves. The most common source of leaks from valves is the seal between the stem and housing. Place the probe at the interface where the stem exits the packing gland and sample the stem circumference. Also, place the probe at the interface of the packing gland take-up flange seat and sample the periphery. In addition, survey valve housings of multipart assembly at the surface of all interfaces where a leak could occur.

8.3.1.2 Flanges and Other Connections. For welded flanges, place the probe at the outer edge of the flange-gasket interface and sample the circumference of the flange. Sample other types of nonpermanent joints (such as threaded connections) with a similar traverse.

8.3.1.3 Pumps and Compressors. Conduct a circumferential traverse at the outer surface of the pump or compressor shaft and seal interface. If the source is a rotating shaft, position the probe inlet within 1 cm of the shaft-seal interface for the survey. If the housing configuration prevents a complete traverse of the shaft periphery, sample all accessible portions. Sample all other joints on the pump or compressor housing where leakage could occur.

8.3.1.4 Pressure Relief Devices. The configuration of most pressure relief devices prevents sampling at the sealing seat interface. For those devices equipped with an enclosed extension, or horn, place the probe inlet at approximately the center of the exhaust area to the atmosphere.

8.3.1.5 Process Drains. For open drains, place the probe inlet at approxima tely the center of the area open to the atmosphere. For covered drains, place the probe at the surface of the cover interface and conduct a peripheral traverse.

8.3.1.6 Open-ended Lines or Valves. Place the probe inlet at approximately the center of the opening to the atmosphere.

8.3.1.7 Seal System Degassing Vents and Accumulator Vents. Place the probe inlet at approximately the center of the opening to the atmosphere.

8.3.1.8 Access door seals. Place the probe inlet at the surface of the door seal interface and conduct a peripheral traverse.

8.3.2 Type II—"No Detectable Emission". Determine the local ambient VOC concentration around the source by moving the probe randomly upwind and downwind at a distance of one to two meters from the source. If an interference exists with this determination due to a nearby emission or leak, the local ambient concentration may be determined at distances closer to the source, but in no case shall the distance be less than 25 centimeters. Then move the probe inlet to the surface of the source and determine the concentration as outlined in Section 8.3.1. The difference between these concentrations determines whether there are no detectable emissions. Record and report the results as specified by the regulation. For those cases where the regulation requires a specific device installation, or that specified vents be ducted or piped to a control device, the existence of these conditions shall be visually confirmed. When the regulation also requires that no detectable emissions exist, visual observations and sampling surveys are required. Examples of this technique are:

8.3.2.1 Pump or Compressor Seals. If applicable, determine the type of shaft seal. Perform a survey of the local area ambient VOC concentration and determine if detectable emissions exist as described in Section 8.3.2.

8.3.2.2 Seal System Degassing Vents, Accumulator Vessel Vents, Pressure Relief Devices. If applicable, observe whether or not the applicable ducting or piping exists. Also, determine if any sources exist in the ducting or piping where emissions could occur upstream of the control device. If the required ducting or piping exists and there are no sources where the emissions could be vented to the atmosphere upstream of the control device, then it is presumed that no detectable emissions are present. If there are sources in the ducting or piping where emissions could be vented or sources where leaks could occur, the sampling surveys described in Section 8.3.2 shall be used to determine if detectable emissions exist.

8.3.3 Alternative Screening Procedure.

8.3.3.1 A screening procedure based on the formation of bubbles in a soap solution that is sprayed on a potential leak source may be used for those sources that do not have continuously moving parts, that do not have surface temperatures greater than the boiling point or less than the freezing point of the soap solution, that do not have open areas to the atmosphere that the soap solution cannot bridge, or that do not exhibit evidence of liquid leakage. Sources that have these conditions present must be surveyed using the instrument technique of Section 8.3.1 or 8.3.2.

8.3.3.2 Spray a soap solution over all potential leak sources. The soap solution may be a commercially available leak detection solution or may be prepared using concentrated detergent and water. A pressure sprayer or squeeze bottle may be used to dispense the solution. Observe the potential leak sites to determine if any bubbles are formed. If no bubbles are observed, the source is presumed to have no detectable emissions or leaks as applicable. If any bubbles are observed, the instrument techniques of Section 8.3.1 or 8.3.2 shall be used to determine if a leak exists, or if the source has detectable emissions, as applicable.

9.0 Quality Control

Section	Quality control measure	Effect
8.1.2	Instrument calibration precision check.	Ensure precision and accuracy, respectively, of instrument response to standard.
10.0	Instrument calibration.	

10.0 Calibration and Standardization

10.1 Calibrate the VOC monitoring instrument as follows. After the appropriate warmup period and zero internal calibration procedure, introduce the calibration gas into the instrument sample probe. Adjust the instrument meter readout to correspond to the calibration gas value.

Note: If the meter readout cannot be adjusted to the proper value, a malfunction of the analyzer is indicated and corrective actions are necessary before use.

11.0 Analytical Procedures [Reserved]

12.0 Data Analyses and Calculations [Reserved]

13.0 Method Performance [Reserved]

14.0 Pollution Prevention [Reserved]

15.0 Waste Management [Reserved]

16.0 References

1. Dubose, D.A., and G.E. Harris. Response Factors of VOC Analyzers at a Meter Reading of 10,000 ppmv for Selected Organic Compounds. U.S. Environmental Protection Agency, Research Triangle Park, NC. Publication No. EPA 600/2-81051. September 1981.
2. Brown, G.E., et al. Response Factors of VOC Analyzers Calibrated with Methane for Selected Organic Compounds. U.S. Environmental Protection Agency, Research Triangle Park, NC. Publication No. EPA 600/2-81-022. May 1981.
3. DuBose, D.A. et al. Response of Portable VOC Analyzers to Chemical Mixtures. U.S. Environmental Protection Agency, Research Triangle Park, NC. Publication No. EPA 600/2-81-110. September 1981.
4. Handbook of Hazardous Materials: Fire, Safety, Health. Alliance of American Insurers. Schaumberg, IL. 1983.

17.0 Tables, Diagrams, Flowcharts, and Validation Data [Reserved]

Appendix E Summary of NEIC Comparative Monitoring Results of Leaking Valves at 17 Refineries

	Refineries Total	NEIC Total
Valves Monitored	170,717	47,526
Number of Leaks	2,266	2,372
Leak Rate (%)	1.3	5.0 (avg)
Emissions Rate (lb/hr)	1,177.0	2,775.5
Potential Emissions from Undetected Leaks (lb/hr)[a]	**1,598.5**	

Source: Enforcement Alert – Proper Monitoring Essential to Reducing 'Fugitive Emissions' Under Leak Detection and Repair Programs, EPA 300-N-99-014. US EPA Office of Enforcement and Compliance Assurance. Vol. 2, No. 9, Oct 1999.

[a] Potential Emissions from Undetected Leaks (lb/hr) = NEIC Total Emissions Rate (lb/hr) – Refineries Total Emissions Rate (lb/hr)

Appendix F Enforcement Alert

United States Environmental Protection Agency | Office of Enforcement and Compliance Assurance (2201A) | EPA 300-N-99-014

EPA Enforcement Alert

Volume 2, Number 9 | Office of Regulatory Enforcement | October 1999

Proper Monitoring Essential to Reducing 'Fugitive Emissions' Under Leak Detection and Repair Programs

The Clean Air Act requires refineries to develop and implement a Leak Detection and Repair (LDAR) program to control fugitive emissions. Fugitive emissions occur from valves, pumps, compressors, pressure relief valves, flanges, connectors and other piping components.

Comparison monitoring conducted by the U.S. Environmental Protection Agency's (EPA) National Enforcement Investigations Center (NEIC) shows that the number of leaking valves and components is up to 10 times greater than had been reported by certain refineries *(see Table, Page 2)*. EPA believes this great disparity between what refineries are reporting and what EPA is finding may be attributable to refineries not monitoring in the manner prescribed in 40 CFR Part 60, Appendix A, Method 21.

Federal regulations require refiners to routinely monitor for leaks and to fix any equipment found leaking. Failure to identify leaking equipment results in necessary repairs not being made and continuing fugitive emissions of volatile organic chemicals (VOCs) and other hazardous chemicals. EPA estimates that the failure to identify and repair leaks at petroleum refineries could be resulting in additional VOC emissions of 80 million pounds annually. VOCs contribute to ground-level ozone, a principal component of smog, which can cause significant health and environmental problems.

> EPA estimates that leaks not found and repaired could be resulting in additional volatile organic chemical emissions of 80 million pounds annually.

What the Law Requires

Specific requirements for refinery fugitive emissions are identified in 40 CFR Part 60, New Source Performance Standards (NSPS), and 40 CFR Parts 61 and 63, National Emission Standards for Hazardous Air Pollutants (NESHAP). Many State and local air agencies incorporate federal requirements, but some have established more stringent requirements as authorized by law. The various regulations require refineries to implement an LDAR program to reduce fugitive emissions from valves, pumps, compressors, pressure relief valves, flanges, connectors, and other piping components.

Valves are usually the single largest source of fugitive emissions. Emissions from any single piece of equipment are usually small. Based on the large number of equipment components that can leak and are subject to LDAR requirements, however, cumulative emissions can be very large. To obtain a proper reading of emissions from leaking components, the monitoring equipment must be calibrated cor-

Continued on page 2

About Enforcement Alert

"Enforcement Alert" is published periodically by the Office of Regulatory Enforcement to inform and educate the public and regulated community of important environmental enforcement issues, recent trends and significant enforcement actions.

This information should help the regulated community anticipate and prevent violations of federal environmental law that could otherwise lead to enforcement action. Reproduction and wide dissemination of this newsletter is encouraged.

See Page 4 for useful EPA Websites and additional resources.

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Enforcement Alert

Continued from page 1

rectly and held at the component interface where leakage could occur (e.g., at the seal between the valve stem and housing) for a sufficient length of time to obtain a valid measurement.

LDAR Programs Should Consist of Several Processes

LDAR programs are generally comprised of four processes. Regulations vary, but usually require refineries to:

- Identify components to be included in the program;
- Conduct routine monitoring of identified components;
- Repair any leaking components; and
- Report monitoring results.

Compliance issues associated with each of these processes have resulted in numerous enforcement actions by EPA Regional offices, State agencies, or local air boards, depending on the specific regulations. Common violations include:

- Failure to identify process units and components that must be monitored;
- Failure to follow prescribed monitoring procedures;
- Use of incorrect or expired calibration gases;
- Failure to repair components within specified timeframes; and
- Failure to submit quarterly reports and maintain appropriate calibration and/or monitoring records.

Comparative Monitoring Results

Refinery	Company Monitoring: Valves/Leaks	NEIC Monitoring: Valves/Leaks	Leak Rate: Company/NEIC (%)	Emissions Rate: Company/NEIC (lb/hr)	Potential Emissions: Undetected Leaks (lb/hr)
A	7,694/170	3,363/354	2.3/10.5	38.8/106.6	67.8
B	7,679/223	3,407/216	2.8/6.3	44.0/73.5	29.5
C	3,913/22	2,008/108	0.6/5.4	18.3/90.1	71.8
D	2,229/26	1,784/24	1.2/1.4	15.5/17.1	1.6
E	5,555/96	2,109/112	0.7/5.3	50.7/125.8	75.1
F	42,505/124	3,053/53	0.3/1.7	154.7/382.3	227.6
G	14,307/226	3,852/236	1.6/6.1	122.2/369.7	247.5
H	20,719/736	3,351/179	3.6/5.3	332.2/469.7	137.5
I	5,339/9	2,754/84	0.2/3.1	16.9/76.6	59.7
J	8,374/78	2,981/55	0.9/1.8	50.8/78.5	27.7
K	6,997/101	1,658/114	1.4/6.9	56.1/201.2	145.1
L	12,686/26	3,228/125	0.2/3.8	34.9/84.0	49.1
M	4,160/40	1,926/222	1.0/11.5	25.7/192.2	166.5
N	5,944/29	2,487/106	0.5/4.3	26.1/112.3	86.2
O	7,181/112	2,897/130	1.6/4.5	60.8/140.9	80.1
P	8,532/203	4,060/181	2.4/4.5	98.8/167.5	68.7
Q	6,640/36	2,608/74	0.5/2.8	30.5/87.5	57.0
Total	170,717/2,266	47,526/2,372	1.3/5.0 (avg)	1,177.0/ 2,775.5	1,598.5

Refinery Monitoring Reports: What EPA is Finding

During the past several years, NEIC has monitored for leaking components at refineries. For 17 facilities investigated by NEIC, the average leak rate reported by the facilities was 1.3 percent. The average leak rate determined by NEIC and confirmed by the facilities was 5.0 percent. One explanation for this difference in leak rates may be found in a report published by the Bay Area Air Quality Management District ("Rule Effectiveness Study"). The Bay Area Air Quality Management District determined that when valves were inspected at a distance of one centimeter (0.4 inches) from the component instead of at the interface with the component, as the regulations require,

Continued on page 3

Enforcement Alert

Continued from page 2

57 percent of the leaking valves would be missed when monitoring above the 500 ppm level.

Fugitive emissions account for 22 percent of all emissions from non-refineries but account for more than 55 percent of all refinery emissions identified in the 1996 Toxic Release Inventory (TRI). Since TRI includes only "reportable" hydrocarbons, total fugitive emissions were significantly larger than the 33 million pounds then identified by reporting refineries.

The failure to identify leaks means that they remain unrepaired and will continue to release VOCs and hazardous substances into the atmosphere. Emission estimates using a 50/50 split between components in gas light liquid service (*see Table, Page 2*) suggest that these 17 refineries' annual fugitive emissions could be more than 6,000 tons per year greater than previously believed. Extrapolating this difference to all refineries larger than the smallest refinery investigated by NEIC also suggests that there may be an additional 80 million pounds of VOCs being emitted each year because refinery leaks are not being identified properly and repaired promptly, as required by LDAR programs. Significantly and as recognized by industry, fugitive emissions can be reduced by up to 90 percent if leaks are detected and repaired in a timely manner.

EPA Policies for Reducing, Eliminating Penalties for Self-Policing

EPA has adopted two policies designed to encourage the regulated community to comply with environmental laws.

For more information, see EPA's Audit Policy Website at: http://www.epa.gov/oeca/auditpol.html, and the Small Business Policy at: http://www.epa.gov/oeca/smbusi.html.

Regulatory Impacts of Inadequate Fugitive Monitoring

By not fully identifying all leaking components, refineries are likely causing the unnecessary release of excess hydrocarbons. The impacts of these additional hydrocarbon releases may result in:

- Additional VOC emissions that could worsen local or transboundry smog problems;
- Under reporting of fugitive emissions on the annual Toxic Reporting Inventory;
- Under reporting of various TRI chemicals on annual Form R submissions; and
- Delayed or denied permits for expansion.

Most LDAR regulations allow for decreased monitoring frequency if certain performance standards are consistently achieved. Monitoring frequency is decreased from quarterly to annual monitoring if less than two percent of the valves within a process unit are found leaking. Conversely, if greater than two percent of the valves are found to be leaking, monitoring must be conducted quarterly. EPA monitoring showing a greater than two percent leak rate has resulted in refineries reverting back to quarterly monitoring.

Improving Leak Detection Monitoring Reliability

Although not required under current LDAR programs, several practices appear to improve the reliability of monitoring data and LDAR compliance

- Energetic LDAR coordinators (advocates) with the responsibility and authority to make things happen;
- Continuing education/refresher programs for plant operators. Plant operators can have a major impact on LDAR compliance;
- Diligent and well-motivated monitoring personnel.
- Use of a lower than required leak definition. Several refineries use a leak definition lower than the regulatory limit. For example, several refineries use a 500 ppm limit rather than the regulatory limit of 10,000 ppm;
- More frequent monitoring than required. Rather than monitoring annually, some refineries monitor quarterly. More frequent monitoring also may permit lower emissions to be reported on the annual Toxic Reporting Inventory and/or Form Rs; and
- Established Quality Assurance/Quality Control procedures. Several refineries have initiated a program to check the monitoring results submitted by the monitoring team (in-house or contractor).

EPA's Office of Enforcement and Compliance Assurance is encouraged by efforts currently underway by the National Advisory Committee on Environmental Policy and Technology (NACEPT) petroluem refining workgroup to find more cost-effective ways to identify significant leaks

Continued on page 4

EPA
United States
Environmental Protection Agency
Office of Regulatory Enforcement
2248A
Washington, D.C. 20460

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Continued from page 3

through new technology that allows for quick identification of the most significant losses. Meanwhile, however, the regulated industry is expected to comply fully with existing LDAR requirements.

Contact Ken Garing, National Enforcement Investigations Center, (303)236-6658; Email: garing.ken@epa.gov; Tom Ripp, Office of Compliance, Manufacturing, Energy and Transportation Division, (202)564-7003; Email: ripp.tom@epamail.epa.gov; or Jim Jackson, Office of Regulatory Enforcement, Air Enforcement Division, (202) 564-2002; Email: jackson.james@epamail.epa.gov.

EPA'S Y2K Enforcement Policy

EPA's Y2K Enforcement Policy is designed to encourage the expeditious testing of computer associated hardware and software that may be potentially vulnerable to Y2K problems.

Under this policy, which was published in the Federal Register on March 10, 1999, EPA intends to waive 100 percent of the civil penalties and recommend against criminal prosecution for environmental violations resulting from Y2K testing designed to identify and eliminate Y2K-related malfunctions. To receive the policy's benefits (e.g. waiver of penalties due to testing), regulated entities must address specific criteria and conditions identified in the policy.

For more about the Y2K Enforcement Policy, contact *Gary Jonesi, Office of Regulatory Enforcement, (202) 564-4002 or E-mail jonesi.gary@epa.gov*

Useful Websites

EPA's Technical Web site for Information Transfer and Sharing Related to Air Pollution Topics: http://www.epa.gov/ttn/

Toxics Release Inventory (TRI): http://www.epa.gov/opptintr/tri/

EPA Home Page: http://www.epa.gov/epahome

National Enforcement Investigations Center: http://www.epa.gov/oeca/oceft/neic/index.html

EPCRA Hotline: 1-800-424-9346. For callers in the DC area, please call (703) 412-9810. Also, the TDD is (800) 553-7672.

Office of Regulatory Enforcement http://www.EPA.gov/oeca/ore.html

EPA Compliance Assistance Centers: http://www.epa.gov/oeca/mfcac.html

Small Business Gateway: http://www.epa/gov/smallbusiness

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United States
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Office of Compliance
Office of Enforcement and Compliance Assurance
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EPA-305-D-07-001
October 2007
www.epa.gov/compliance

Comment Letter I9

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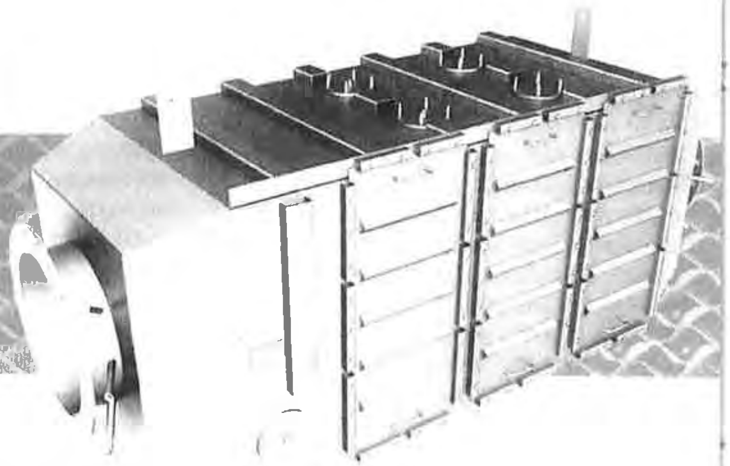


FORMULATIONS

SCR Selective Catalyst Reduction System

WHY THE MIRATECH SCR SYSTEM?

- **NOx Reduction For Tier 4 Compliance**
- **Up to 99% NOx Reduction**
- **Noise Reduction: up to 52 dB(A)**
- **Global Experience**
  - Over 2,000 SCR Systems Installed
- **U.S. Based Service & Support**
  - Fast Response Field Service & Technical Support
  - U.S. Based Engineering & Product Support

APPLICATIONS

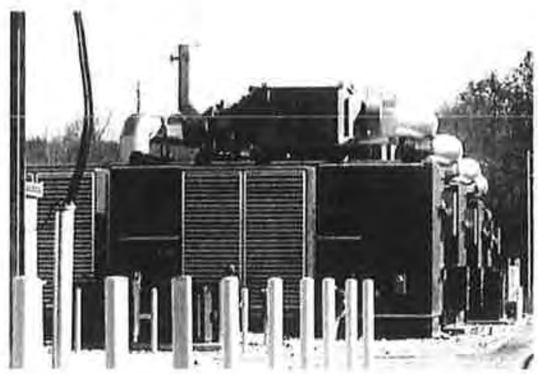
- **Stationary Reciprocating Engines**
  - Lean-Burn Natural Gas
  - Diesel and Dual-Fuel
- **Power Generation**
- **Gas Compression**
- **Greenhouse CO_2 Augmentation**

FEATURES & BENEFITS

- **Two-Stage System: SCR & Oxidation**
  - Compliance-Levels For All Emissions: NOx, CO, HAPs, VOCs
  - Three Stage System: DOC/DPF + SCR NOx, CO, VOC, HAPs, PM
- **Efficient Reactant Atomization**
  - Choice Urea or Ammonia Reductant
  - Purge Lines & Air-Assisted Injection Nozzle
- **Designed for Serviceability**
  - Easy Access to Injector for Cleaning & Maintenance
  - Catalyst Access Door
- **Designed for Durability**
  - Carbon or Stainless Steel Housing
  - Aluminum or Galvanized Insulation Sheathing
  - Simple, Quick Bulkhead Connections for Wiring & Plumbing
- **Designed for Easy of Use**
  - Advanced, User-Friendly Controls
  - Safety Shutdown & Alarm Controls
  - Data Storage
  - Data Transfer
  - Network Communications

PRODUCT ADVANTAGE

Where NOx control is a challenge, MIRATECH delivers the best SCR system, service and product support, for both diesel (Tier 4) and natural gas engine applications.



SCR Installation

DESIGN, DELIVER, SUPPORT

Experience

Along with unsurpassed technical expertise, vast real-world experience goes into every MIRATECH SCR project gained in nearly two decades of SCR experience, with more than 2,000 units installed worldwide in power, water pumping and gas compression applications. If there's a problem, or a potential problem—MIRATECH probably has already solved it. If a new issue arises, no one will get to the bottom of it faster.

Bottom-Line Value

When you install MIRATECH's SCR system equipped with advanced injection control, your engine will run efficiently, with low fuel costs, and ongoing compliance assured every step of the way. Your catalyst will work harder, longer, with greater flexibility to handle varying loads, and with less risk of non-compliance fines or operational shutdowns.

World-Class Technology

It starts with the world's best SCR technology. MIRATECH, an acknowledged world leader in the field, provides customers with all the benefits of best available control technology.

- Consistently set the standards for Best Available Control Technology (BACT)
- Simple, user-friendly control and communication technology connects to any building's communication systems
- U.S. based Service & Support
  - Fast-response field service and technical support
  - Replacement components stocked in Tulsa, OK
  - In-house engineering and custom product support

Innovative Emissions Solutions

ORMULATIONS SCR Selective Catalyst Reduction System

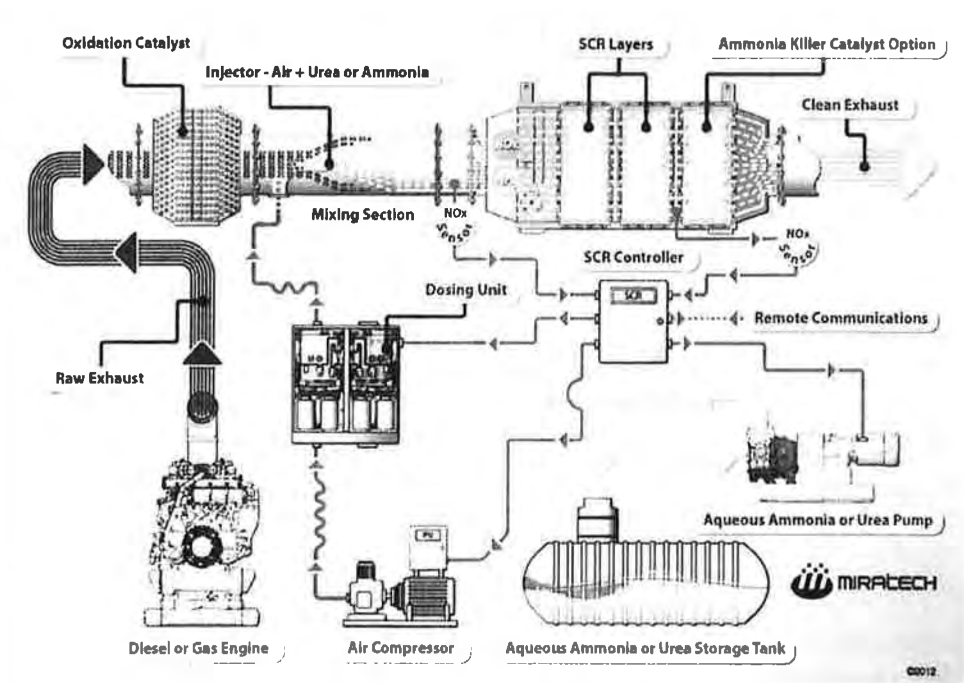
EMISSIONS: CONTROLLED

MIRATECH's SCR catalytic converters reduce regulated exhaust pollutants for stationary reciprocating diesel, dual-fuel and lean-burn natural gas engines. These pollutants include oxides of nitrogen, (NOx), carbon monoxide (CO), and unburned hydrocarbons (HC) comprising Hazardous Air Pollutants (HAPs) and Volatile Organic Compounds (VOCs). The MIRATECH SCR systems work in two efficient stages: the NOx Reduction Stage and the Oxidation Stage for CO and HC reduction. Both stages work together, drastically reducing harmful emissions to satisfy the strictest regulatory requirements. In the mixing section, either ammonia or aqueous urea is injected into the exhaust stream. Urea is often used instead of ammonia; since it's much less toxic than ammonia, it's generally easier to transport and store, and it allows easier permitting. This urea is hydrolyzed and breaks down in the exhaust stream to form ammonia. Ammonia, whether injected directly or formed from urea, reacts with NOx at the SCR catalyst to form harmless water and nitrogen. The Oxidation Stage uses oxidation catalyst elements, with surface coatings impregnated with precious metals, to reduce CO, HAPs, and VOCs—oxidizing these pollutants to form water and carbon dioxide.

COMPLIANCE AND MORE

Most important of all, MIRATECH's SCR solutions give you assured compliance with less cost, less disruption of your operation and full support you can count on over the long haul. With MIRATECH's SCR system, you don't have to deal with complex controls assembly; panels include microprocessor-controlled hardware. MIRATECH's SCR systems give you a choice of reactant, ammonia or urea, for efficient atomization. And MIRATECH's SCR gives you a level of operations control that's simply unique to the industry.

PROCESS DIAGRAM



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MIRATECH

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Tulsa, OK 74108 · USA · +1 918 794 0341
info@miratechcorp.com · www.miratechcorp.com

WHY MIRATECH?

- Advanced Technology
- Product Range: 20 to 20,000+ hp
- Innovative, Cost-Effective, Comprehensive Emissions Solutions
- RICE NESHAP Compliant
- Turnkey Projects
- Unsurpassed Experience & Expertise
- Fast, Responsive, Customer-Focused Service and Support
  - Prevent Non-Compliance Fines
  - Improve Engine & Catalyst Performance
  - Cut Maintenance Costs
  - Maximize Catalyst Life
- Full Service Catalyst Wash & Repair
  - 'Free Wash for Life' on Next® & Vortex® Substrates
- Project Management
- Onsite Services
  - Supervision
  - Technical
  - Skilled
- Product O&M Training
- Replacement Parts

EMISSIONS SOLUTIONS

- Catalysts
  - 3-Way
  - Oxidation (Natural Gas & Diesel)
  - HAPs
  - Selective Catalytic Reduction (SCR)
  - Urea Hydrolysis
  - DPF
- Housings
  - NX Series
  - IQ
  - CBS
  - CBL
  - Silencer Combinations
    - VX Series
    - RX Series
    - ZX Series
    - Ground Access
- Controls
  - SCR
  - Active DPF
  - Air Fuel Ratio (Rich & Lean Burn)
  - Monitors
    - RICE NESHAP
    - DPF

Specification: SCR CATALYTIC CONVERTERS

PART 1 GENERAL

1.0 SUBMITTALS

A. Provide drawings and product data including the following:

1. Drawings, catalog cuts, brochures, and other materials required to completely describe the systems and equipment being furnished.

2. Project specific drawings detailing the Converter Housing(s), Control System, General Arrangement and Interconnects shall be submitted in hard copy and electronic format within one week of award of order.

3. Ten-Year Life Cycle Cost Analysis for general operation & maintenance costs with associated assumptions.

4. SCR System design shall be based on the following engine exhaust data:

   a. Nitrogen Oxides (NOx) in grams/BHP-hr
   b. Carbon Monoxide (CO) in grams/BHP-hr
   c. Non Methane, Non Ethane Hydrocarbons (NMNEHC) in grams/BHP-hr
   d. Formaldehyde (CH_2O) in grams/BHP-hr
   e. Exhaust Temperature in °F
   f. Exhaust Flow Rate in lbs/hr

5. Guaranteed exhaust gas emission data at the stable design point following selective catalytic reduction system include:

   a. Nitrogen Oxides (NOx) in grams/BHP-hr
   b. Carbon Monoxide (CO) in grams/BHP-hr
   c. Non Methane, Non Ethane Hydrocarbons (NMNEHC) in grams/BHP-hr
   d. Formaldehyde (CH_2O) in grams/BHP-hr
   e. Ammonia (NH_3) in ppm@15%O_2

6. O&M Manuals including installation guidelines for the converter, catalyst, and control system shall be provided in hard copy with the equipment and available electronically for review.

1.1 QUALITY ASSURANCE

A. The selective catalytic reduction system shall be successfully proven in similar stationary applications and a reference list supporting an installation base of at least 1200 natural gas and or diesel fueled engines shall be provided for vendor qualification.

B. Manufacturer/Supplier to have successfully commissioned at least (200) SCR units installed on Internal Combustion Engines within North America and at least (1200) units worldwide.

C. The control system is to be designed, manufactured and assembled under the direct control and supervision of the SCR System manufacturer and shall have an integrated measuring system. For system continuity and dependability the use of measuring systems designed and or manufactured by those other than the SCR System manufacturer are prohibited.

D. The following shall be tested for operation and accuracy by the SCR Manufacturer prior to shipment:
1. Control System I/O
2. Air Compressor Flow Rate and Pressure
3. Reactant Metering Flow Rate and Pressure

4. Converter and Catalyst Dimensions

1.2 DELIVERY, STORAGE AND HANDLING

A. Ship equipment, material and spare parts complete except where partial disassembly is required by transportation regulations, for protection of components or customer request.

B. All mechanical and electrical equipment should be crated such that it is protected from snow, rain, dust, dirt, mud, and condensed water vapor during shipment and while in place during construction.

C. Carriage and Insurance to job site shall be Pre-paid the supplier in accordance with INCO Terms 2000 CIP

1.3 MAINTENANCE

A. The SCR System supplier shall maintain an adequate stock, within North America, of maintenance/replacement parts for the system, including catalyst and all control system sub-components.

1.4 WARRANTY

A. All equipment supplied under this Section shall be warranted by the manufacturer for a period of 24 months from startup of the equipment, or 26 months from the date the equipment is available for shipment, whichever occurs first. The specifics of the warranty should be included within the quotation.

B. The supplier shall provide a written guarantee of performance tied directly to the engine manufacturer's written guarantee and shall be evaluated on stated levels of pollutants.

1.5 COMMISSIONING AND FIELD SERVICE SUPPORT

A. Supplier/Manufacturer shall have a North American based service department staffed with factory trained and certified emissions technicians. Service technician qualifications must be available for review and approval upon request.

B. Service technicians must be qualified to train operating personnel on the general operating, maintenance and troubleshooting of the system.

PART 2 PRODUCTS

2.0 CATALYTIC REDUCTION SYSTEMS FOR ENGINE EXHAUST

A. Available Selective and Oxidative Catalyst Reduction System Manufacturers:

1. MIRATECH Corporation, Tulsa, OK

B. The engine(s) shall be furnished with a catalytic reduction system to reduce engine exhaust emissions detailed in 1.0.A.5 of this specification.

2.1 SCR System Components

A. SCR Reactor Housing

1. Shall be designed to contain the catalyst blocks on a shelf system. The housing shall be a rigid structure, which will not warp or deform significantly during normal operation. The housing shall be designed to allow for thermal expansion differences within the housing, while preventing exhaust gas from leaking past the catalyst.

2. Shall be designed as a free-standing, self-supported structure. The housing shall be complete with inlet and outlet transition sections designed for bolting to the exhaust gas ductwork. Connection to the engine exhaust system will be via standard ANSI 150 lb bolt pattern flat face flanges. The reactor shall be

provided with an integrated mounting base so that the housing itself is isolated from vibration and can accommodate thermal expansion.

3. Shall be equipped with access doors to the catalyst. The doors shall be easily removed without the assistance of lifting equipment and be on top or the side of the housing and shall provide access to each layer of catalyst without removal of any catalyst. Doors shall be designed with gaskets to prevent exhaust gas from leaking to the atmosphere.

4. Shall be constructed of heat, corrosion, and scaling resistant steel, or stainless steel, based on the recommendation of the manufacturer.

5. Shall be provided with internal catalyst support structure, perforated plates, inlet and outlet flat face flanged openings.

6. Shall provide instrumentation ports for differential pressure and temperature upstream and downstream of the catalyst beds. Additional test ports shall be provided between each layer of catalyst to allow for future testing of layer performance.

B. Catalyst

1. General
   a. Shall be extruded, ceramic blocks with square monolithic channels (honeycomb type). The catalyst material shall be mixed into the substrate prior to extrusion. The catalyst material composition shall be tungsten, vanadium, titanium and other base metals. The catalyst shall have a proven track record in similar applications.
   b. Shall operate and perform properly without the use of a guard bed or filter which may become masked, coated and clogged and require frequent cleaning and/or change-out due to compounds and particulates such as soot or ash.
   c. Shall be shop assembled with a high temperature fiberglass gasket material. The modules should be approximately 150mm x 150mm in cross section and 150, 300 or 450mm in depth for ease of field installation and removal from the reactor housing.
   d. Shall be designed to minimize the SO_2 to SO_3 conversion rate.
   e. Shall be of sufficient mass such that the natural frequency in or around the engine is far above the resonant frequency of the engine firing so it will not resonate.

2. SCR Catalyst
   a. Shall have a minimum active surface area of 890 m^2/m^3
   b. Shall have an operating range of 572°F to 986°F

3. Ammonia Reduction Catalyst
   a. Shall have a minimum active surface area of 890 m^2/m^3
   b. Shall have an operating range of 572°F to 986°F
   c. Shall reduce the concentration of residual ammonia in the exhaust gas without creation of NO_x

4. Oxidation Catalyst
   a. Shall have an operating range of 572°F to 986°F
   b. May be located within the SCR Converter Housing or in a separate housing upstream of the injection lance.

C. Mixing Section

1. Static mixers shall be supplied for installation in the exhaust piping down stream of the reducing agent injection lance. The mixers shall have low pressure drop, designed to be welded into the exhaust duct. The supplier shall determine the quantity, type, and location of the mixers. The mixers shall be of

corrosion resistant materials, and designed to provide long operating life in the temperature conditions that will exist within the exhaust system.

2. A flow dresser shall be installed up stream of the reducing agent injection lance to assist in proper distribution of the reducing agent.

3. The residence time from the reactant injection lance to the first mixer shall be no less than 0.05 sec

D. Injection Lance

1. The reducing agent injection lance constructed of 304 Stainless Steel shall be installed on the engine exhaust upstream from the reactor housing at a location to achieve proper reducing agent distribution and atomization. Injection nozzles shall be oriented with respect to engine exhaust gas flow for optimum dispersion of the reducing agent into the engine exhaust gas upstream of the catalyst bed.

2. The injection lance shall be of the two-phase type using compressed air to atomize the reducing agent.

3. The injection lance assembly shall be designed for ease of installation and service. The catalyst manufacturer shall supply mating flange for saddle connection of the lance to the exhaust duct.

E. Reducing Agent Injection Control System

1. General
   a. All Control system components shall be designed to operate on 230VAC, Single Phase, 60Hz power with a maximum current draw of 10 Amps per engine set.
   b. The control system shall be Programmable Logic Controller based and provide automatic SCR system start-up, operation, shutdown, monitoring and annunciation of abnormal conditions.
   c. All tubing within the system shall be either Type 316 stainless steel tubing or heavy wall Teflon. Tubing shall be laid out to minimize elbows and bends, and to present neat, orderly assembly.
   d. Wiring within the panel shall be arranged in wire tray to not interfere with routine servicing. All wiring shall be numbered at both ends. Analog signal wiring shall be routed away from power wiring to avoid potential interference. All wiring to and from the metering panel shall terminate on easily accessible, numbered terminal blocks. All components shall be identified with a device tag corresponding to the wiring diagrams and P&ID supplied with the equipment.
   e. The control system shall control and provide automatic SCR system start-up, operation, shutdown, monitoring and annunciation of abnormal conditions.
   f. The metering panel shall control the amount of reducing agent injected into the exhaust gas stream. The panel shall contain the reducing agent metering equipment and their controls. Controls shall include a main disconnect breaker for power supply; indication of operating status; a PLC to perform all interlock, sequencing, alarm, and injection rate control functions; 24 Volt DC power supply.
   g. The reducing agent to be used in the SCR system shall be technical grade urea dissolved in demineralized water to provide a 32 to 40 percent aqueous solution or 19% aqueous ammonia solution.

2. Closed Loop Control Unit
   a. Reactant injection rate shall be based on NO emission values and may not be solely dependant on engine speed or power output feed back.
   b. Analysis of the NO concentration shall be via a redundant integrated electrochemical cell based sample system. Interfacing with 3rd party analysis systems shall not be allowed
   c. Measuring system accuracy and zero must be confirmed on 5 minute intervals by the control system without the use of external calibration/span gas.
   d. Data shall be available to the operator via an LCD display. The following data shall be included:

      1. Emission Value

2. Emission Target

3. Reactant Injection Rate

4. Operational Alarms with ID Number and Description

e. The system shall automatically stop and re-start under the following conditions:

1. Catalyst bed temperature less than 572 °F

2. Engine shutdown

f. Data Logging capabilities. The Controller should be able to data log every 5 minutes and store up to 3 months of data for troubleshooting purposes the following items.

1. Date
2. Time
3. Engine Load (%)
4. Dosing Valve Opening
5. NO after SCR (ppm)
6. NO emissions (ppm)
7. Reactant flow (l/hr)
8. Temperature after converter (C)
9. Temperature in Converter (C)
10. Pressure drop across converter (mbar)

g. Networking: The controller platform will utilize TCP / IP networking and can accommodate up to 16 control panels and 2 pump controllers on the same network. This network will allow visualization of the network from any controller. Remote access to network via internet for visualization or troubleshooting should be available via dedicated IP address.

SCR Catalysts For Greenhouse Plants Provide A Microcosm Of Earth

By William Clary, Dr. Jean-Paul Stringaro

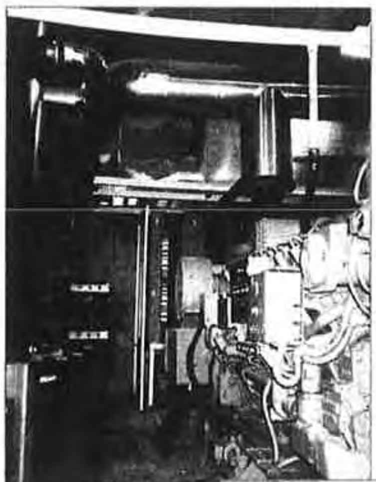
Rosa Flora Limited, a greenhouse in Dunnville, Ontario, Canada, is dedicated to growing roses, alstromeria, stephanotis, and gardenias. Established in the spring of 1978 under the sole management and ownership of Otto and Corine Bulk, additions to the greenhouse have been built every year, to where the facility now has a total of 449,462 sq.ft. under cover.

Due to cool ambient temperatures, Rosa Flora had used natural gas burners to heat and provide carbon dioxide (CO_2) to the greenhouses. In 1992, Rosa Flora replaced the burners with a power generation station driven by two natural gas-fueled Caterpillar G3516LE engines supplied by Toromont Caterpillar. The station produces electricity, heat and CO_2. The engines run at 1200 rpm, generate about 770 kW, and have a heat rate of less than 7300 BTU/bhp-hr.

Power from the generators is utilized to run pumps and lights, with excess power sold to the local utility, Ontario Hydro. The heat from the engines is used to keep a warm climate inside the greenhouses. Furthermore, the exhaust gases are catalytically purified and the engine exhaust, with its high (about 7.2 percent) CO_2 content, is plumbed directly into the greenhouses. Higher CO_2 levels promote plant growth by enhancing the kinetics of the plants' photosynthesis.

By raising the greenhouse atmosphere level of CO_2 from 350 ppm to 900-1000 ppm, while also adding water vapor and heat, plant growth rates can be increased by up to 20 percent. In this manner, about 107,526 sq.ft. of flowers can be fertilized with CO_2 by combusting 1236 cu.ft. of natural gas per hour, while 107,526 sq.ft. of vegetables can be fertilized by combusting 2130 cu.ft. per hour. With these two Caterpillar G3516LE engines, 268,817 sq.ft. of flowers benefit from this system. The catalytic treatment of the exhaust gases is necessary to reduce unwanted exhaust components like oxides of nitrogen, carbon monoxide (CO), ethylene and other uncombusted hydrocarbons which would otherwise be harmful to the plants and operating personnel.

The catalyst system for this application is a novel design incorporating Selective Catalytic Reduction (SCR) and oxidation catalysts to reduce oxides



(Left) A look one of the two gas-fueled Caterpillar G3516LE engines that provide electricity, heat and CO_2 for the Rosa Flora Limited greenhouse in Dunnville, Ontario. The engine power station was installed in 1992 to replace natural gas burners and utilizes a selective catalytic reduction system developed by Hug Engineering and sold in the U.S. through Miratech. (Below) The CO_2 fertilizing system used at the Rosa Flora greenhouse is designed and packaged by HUG Engineering of Switzerland, which has supplied over 400 units throughout the world for soot filtering, No_x reduction, and catalytic oxidation of exhaust from engines fueled with natural gas and propane.

William Clary is vice president of Miratech Corp. and Dr. Jean-Paul Stringaro is a representative for HUG Engineering.

Otto Bulk, owner of Rosa Flora, grows a variety of flowers and vegetables in his greenhouse complex, which has a total of 449,462 sq.ft. under cover.

of nitrogen (NO_x), CO, ethylene (C_2H_4), and other hydrocarbon (HC) emissions. NO_x reduction is accomplished through the reaction of ammonia with NO_x on the surface of the SCR catalysts. Ammonia is generated through thermal hydrolysis of urea, which upon decomposition inside a specially designed mixing duct, yields ammonia (NH_3) and CO_2. The catalytic reduction of NO_x with ammonia on the SCR catalyst surface forms nitrogen (N_2) and water. The catalytic oxidation of CO, ethylene, and other hydrocarbons on the oxidation catalyst forms CO_2 and water.

The emissions are carefully monitored and controlled, so that the exhaust gas quality comes close to the quality of breathable air. NO_x emissions with this system are less than 15 g/GJ or 0.054 g/kW-hr. CO and ethylene are oxidized with excess oxygen in the exhaust across a proprietary oxidation catalyst to form CO_2 and water. CO emissions are less than 5 g/GJ or 0.018 g/kW-hr and ethylene (C_2H_4) emissions are less that 0.35 g/GJ or 0.001 g/kW-hr. Constant monitoring of NO_x and CO levels with a self calibrating analyzer package is necessary to control the quality of the exhaust gas to be injected in the greenhouses, as well as to fine tune the amount of urea to be injected upstream of the catalysts.

The capital cost for this system was $175,000. Operating 10 hours per day, the annual urea costs are $3100. The control system requires maintenance on filters and pumps which is scheduled every 1500 hours of operation. When compared to the CO_2 burners that were used prior to the installation of the engines and SCR catalyst, operation of the system was extended to 350 days versus 250 days per year, operating costs were reduced by $63,000, resulting in a simple payback of less than two years. Net thermal efficiency of the plant is 96 to 97 percent, and greenhouse gas emissions are significantly reduced through the catalysts and subsequent absorption of the CO_2 by the plants.

The CO_2 fertilizing system is designed and packaged by Hug Engineering of Switzerland, a leader in urea-based, small-scale catalytic off-gas treatment plants. To date, Hug has supplied over 400 units throughout the world for soot filtering, NO_x reduction, and catalytic oxidation of exhaust from engines fueled with natural gas; propane; landfill and digester gas; No. 2, No. 6, and bunker C oil. Applications include power generation, cogeneration, propulsion engines for ships and ferries, greenhouses, railroad engines, and construction equipment with a wide variety of engine sizes and manufacturers.

In 1986, Hug Engineering developed the urea process for use with engine exhaust gases, and works mainly with urea as the reactant material. Urea offers considerable advantages over ammonia in terms of transport, storage and handling procedures. Urea is not subject to the dangerous substance regulations, is not poisonous and can be used without any special protective measures. Urea costs are typically about $0.33 per kg of pure urea in pellet form, and approximately 1 kg of urea is required to reduce 1 kg of NO_x.

Miratech Corp., Tulsa, Okla., has been appointed North American distributor for Hug's SCR catalyst technology. To receive more information, or to request a free consultation, call Miratech at (918) 622-7077 or fax (918) 663-5737, or visit Hug's web site at http://www.hug-eng.ch. ★

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MIRATECH

CASE STUDY 1074

SCR

PROJECT GOALS

- Keep new co-generating plant compliant with strict emission and air quality requirements
- Design and construct a computer controlled, low maintenance emissions control solution

INSTALLATION DETAILS

- Location: Orange County, CA
- Engine: (4) Cummins QSV81
  - Rating: 1750 kW
  - Speed: 1500 rpm
  - Fuel: Natural Gas
- Chillers:
  - (2) Broad 535 ton absorption chillers
  - (3) Carrier 750 ton water cooled centrifugal chillers
- Duty: Cogeneration
  - 8000 hours per year
  - N+1 Configuration

PRODUCT SPECS

- Product: MIRATECH SCR
  - NOx Reduction Stage and Oxidation Stage for CO and HC reduction
  - Automated Urea Injection
  - Sound Attenuation: 30 dB(A)
- Emissions Reduction
  - NOx: 5 ppm @ 15% O_2
  - CO: 33 ppm @ 15% O_2
  - VOC: 15 ppm @ 15% O_2
- Type of Catalyst Health Monitoring
  - Pre & Post Catalyst Temperature
  - Catalyst Pressure Drop
  - Datalogging

SERVICES PROVIDED

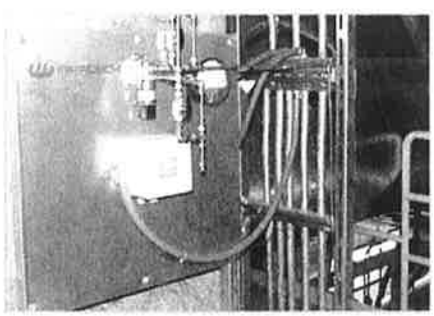
- Design, Manufacture and Logistics
- Onsite Project Management
- Installation
- Emissions Compliance Test

SCRs Keep California Airport Compliant

Busy John Wayne Airport in Orange County, California, uses a new cogeneration plant to make 95% of the power needed for the airport's concessions, baggage handling, parking structure and terminal common areas, plus provide 80% of the chilled water for air-conditioning using waste heat from natural gas fueled reciprocating engines. The plant relies on a computer controlled engine emission system using a urea injection component supplied by MIRATECH, a leader in SCR innovative emission solutions, that allows it to comply with stringent South Coast Air Quality Management District (SCAQMD) regulations.

The $30.7 million utility plant came online in March 2011. It employs four natural gas fueled Cummins QSV81 G 18-cylinder, reciprocating engine driven gen-sets, each producing 1750 kW for a total of seven megawatts of electricity, two 535 ton Broad absorption chillers, and three Carrier 750 ton water cooled centrifugal chillers. The plant has Siemens controls. The plant uses an "N+1" engine/generator configuration.

The airport has to meet both noise abatement rules along with the strictest air quality requirements found anywhere in the nation.



SCR Catalyst and Silencer Injection System

To meet the emissions standards MIRATECH SCR catalytic converters reduce regulated exhaust stream pollutants including oxides of nitrogen, (NOx), carbon monoxide (CO), and unburned hydrocarbons (HC) comprising Hazardous Air Pollutants (HAPs) and Volatile Organic Compounds (VOCs).

SCR Catalyst and Silencer Central Plant installation
Photo Credit: John Wayne Airport

The systems work in two efficient stages: the NOx Reduction Stage and the Oxidation Stage for CO and HC reduction. In the mixing section, aqueous urea is injected into the exhaust stream. In the process, the urea is hydrolyzed and breaks down in the exhaust stream to form ammonia. The ammonia reacts with NOx at the SCR catalyst to form harmless water and nitrogen. In the Oxidation Stage, oxidation catalyst elements, with surface coatings impregnated with precious metals, reduce CO, HAPs, and VOCs – oxidizing these pollutants to form water and carbon dioxide. The SCR net effect is NOx emitting under 5 ppm.

Learn More: Phone Email Web "The Emissions Monitor" Subscription

NSCR SCR DPF Silencers AFRC NESHAP CPMS Field Service Training Turnkey

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info@miratechcorp.com • www.miratechcorp.com

BY DAN VNUK

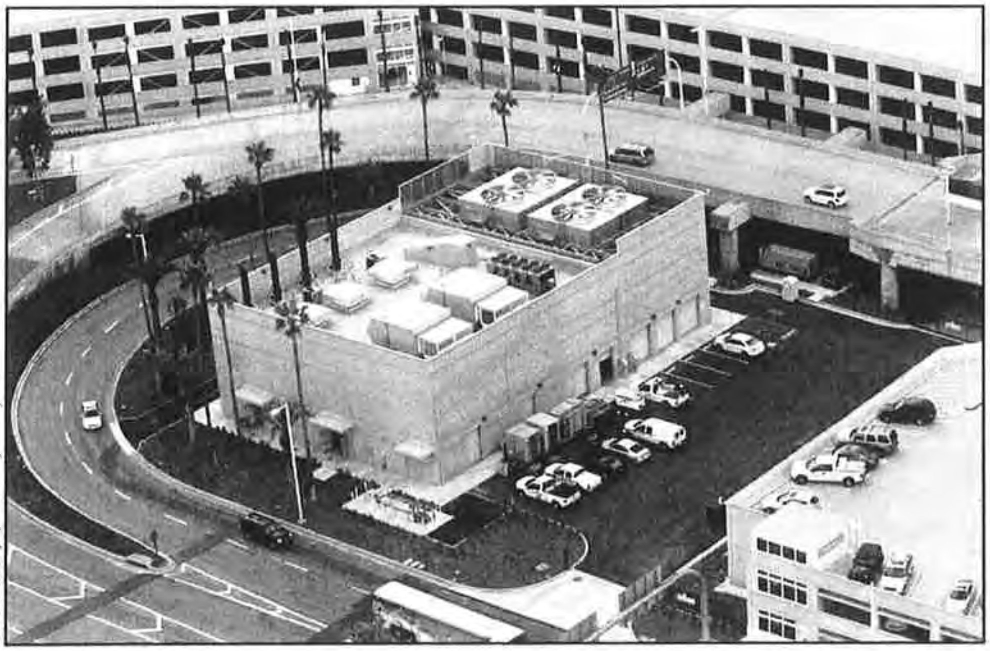


Photo courtesy of John Wayne Airport.

The new John Wayne Airport Terminal cogen facility in Orange County, California, U.S.A.

Inside The Engine Room: Central Utility Plant, John Wayne Airport

New cogeneration plant utilizes Miratech solutions to meet strict emissions regulations

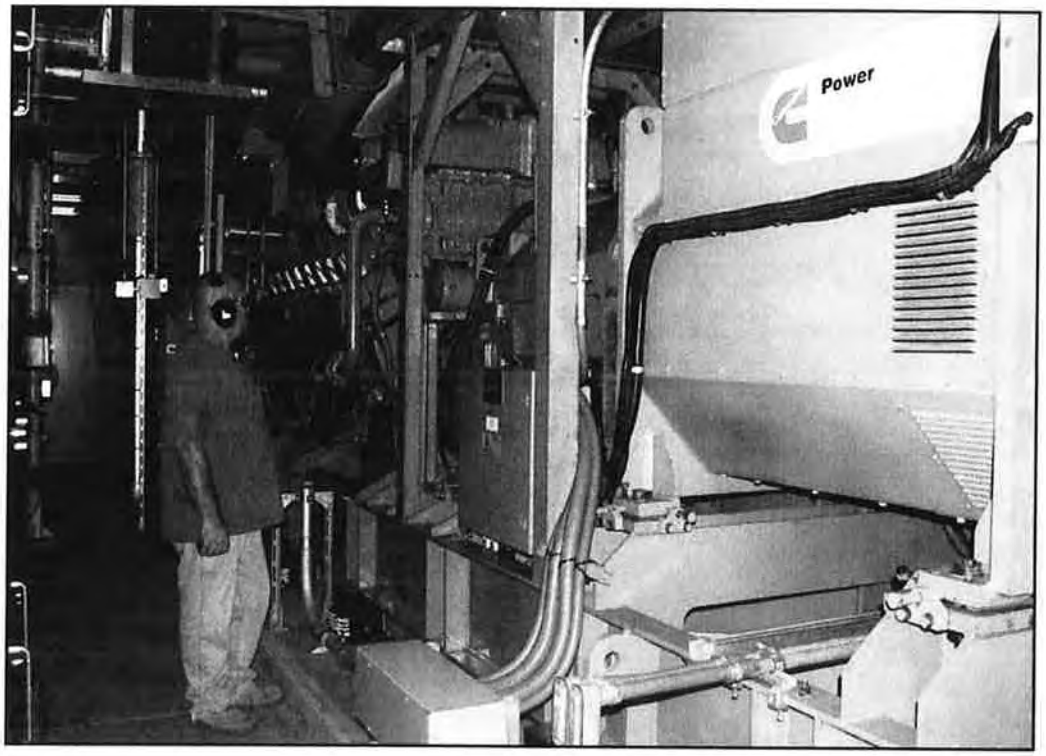
Renamed after The Duke (John Wayne) in 1979 and owned and operated by the County of Orange, California, U.S.A., John Wayne Airport is a modern, busy facility that served nearly 11 million passengers in 2011. It's the second-busiest airport in southern California (LAX is only 64 km away), yet it has the shortest runway of any major airport in the United States.

Sharing a border with posh Newport Beach, John Wayne Airport strives to be a positive reflection of the sleek, modern, "ahead of the curve" area in which it is located. Evidence of this is an ongoing improvement plan that includes a new central utility plant using natural gas-fueled engines for cogeneration to provide 95% of the electrical power needs and most of the thermal load of the airport. The plant captures waste heat from the engines to produce chilled water to provide cooling for the airport. It's important to note that the airport has to meet both stringent noise abatement rules along with the strictest air-quality requirements found anywhere in the nation.

According to Britt Griffith, manager, airport maintenance, "John Wayne Airport continues to grow in the number of passengers each year, yet we're land-locked on a very small 'footprint' of less than 202 ha and can't expand."

The airport had an electrical substation on-site and purchased power at a large-user rate from the local utility, which it then stepped-down for use on-site. "We had heard that our utility rates could possibly double after we removed the substation site in order to expand," Griffith explained. "Once we lost it and our ability to step-down power, we would be buying power at the 12 kV rate, or twice the cost. We had not done cogeneration before, but it gave us a redundancy factor because

Dan Vnuk is a writer with Marketing & Technology Insights.



An operator at John Wayne Airport inspects the Cummins gen-set operations.

we could use natural gas or still get electricity from the grid."

The idea of a cogeneration plant was considered in 2003 when a local engineering company, Popov Engineers, was asked by airport personnel to determine the most efficient way to keep utility rates in check with the planned airport expansion and produce the chilled water it would need.

Recommending the construction of a cogeneration facility using natural gas-fueled reciprocating engines, Popov Engineers developed the bridging document of the original plant design used by the contractor, West Coast Air Conditioning Company Inc., as a model to complete the design of the central utility plant. In addition, Parsons Transportation Group handled management and oversight of architect-engineer and construction agreements, which include monitoring, reporting and making recommendations regarding program costs, schedules and budgets.

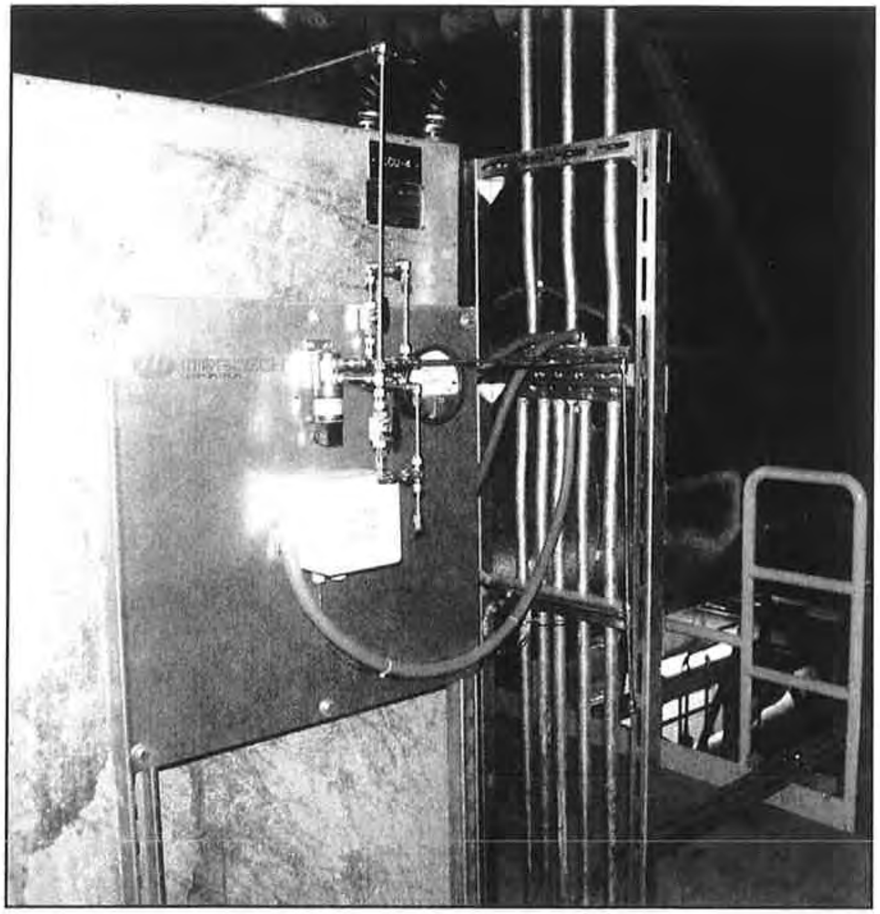
Work on the Central Utility Plant began in September 2009 as part of an airport improvement program that includes an additional third terminal and parking structure. The US$30.5 million utility plant project is funded by airport revenues and is a design-build project that allows contractors to both design and construct the facility.

The plant, which came online in March 2011, supplies the Thomas F. Riley Terminal complex with power and with chilled water to serve the air-conditioning system. It employs four natural gas-fueled Cummins QSV81 G 18-cylinder, reciprocating engine-driven gen-sets, each rated 1750 kW with a total rating of 7 MW; two 535 ton Broad absorption chillers and three Carrier 680 tonne water-cooled centrifugal chillers were included. The plant uses Siemens controls.

In California, a constant supply of chilled air is vital to meet the terminal's HVAC needs. The new system was designed to support chilled water to the terminal that's made by chillers using waste heat or by traditional electricity. The waste heat is preferred because it boosts the system's overall efficiency. If enough waste heat isn't available, then the electric chillers are turned on by the system's computer, but this doesn't happen very often. "80% of our normal chilled water needs are covered by waste heat," said Mike O'Leary, project manager at the plant. "The plant was sized large enough to handle an addition to the new terminal, but the overall airport is limited to 202 ha, so it's doubtful that it will ever need to be enlarged."

The cogen plant's engine emissions control uses a urea injection component supplied by Miratech Corp. in a computer-controlled system that allows the plant to comply with all South Coast Air Quality Management District (SCAQMD) regulations. The SCAQMD air emission standards are among the strictest in the world and the toughest in the nation, according to Griffith.

The plant relies on a Miratech selective catalytic reduction (SCR) emissions compliance system to reduce exhaust pollutants including oxides of nitrogen (NO_x), carbon monoxide (CO) and unburned hydrocarbons (HC) comprising hazardous air pollutants (HAPs) and volatile organic compounds (VOCs). The systems work in two efficient stages: the oxidation stage for CO and HC reduction and then the NO_x reduction stage. Between the oxidation and SCR catalysts, aqueous urea is injected into the exhaust stream via



The Miratech selective catalytic reduction (SCR) urea injection system.

mixing pipe section. In the process, the urea is hydrolyzed and breaks down in the exhaust stream to form ammonia. Urea is often preferred instead of ammonia because it's nontoxic, and easier to transport and store. Permitting for urea is easier too. The ammonia reacts with NO_x inside the proprietary SCR catalyst formulation to form harmless water and nitrogen.

In the oxidation stage, oxidation catalyst elements with surface coatings impregnated with precious metals reduce CO, HAPs and VOCs — oxidizing these pollutants to form water and carbon dioxide. The SCR net effect is to meet engine exhaust targets of 5/33/15 ppm at 15% O_2 NO_x/CO/VOC. The overall benefit of the Miratech system is that it allows the plant to operate 365 days a year providing power and chilled water to the airport, all within strict emissions compliance.

The cogeneration plant's power is supplied to the airport's concessions, baggage handling, parking structure and terminal common areas but not to airfield areas like the tower. The airport traffic operations rely on grid power with a UPS backup system. "It's not an FAA requirement. It's just that the economics weren't there," Griffith said. "In the past, up to 85% of the power purchased from the utility (Southern California Edison) went to supply the terminal and parking structure. We continue to get approximately 5% of our power supply from Southern California Edison Co. via a 12 kV feed. This source of power can be used if the engine generator service is interrupted for any reason."

The plant uses an "N+1" engine/generator configuration in that there are four units on-site but only three engines are needed to meet the anticipated demands of the airport. "Although the combined rating is 7 MW for the gen-sets, we are only permitted for 5 MW but the airport's normal demand is 3.6 MW," said O'Leary. "The idea is that we would run a maximum of three units under all normal circumstances. But in an emergency, we could bring on the fourth engine. We have tested the plant in 'island' mode to make sure that if something ever did happen to the utility grid we would not be affected."

The central utility plant is equipped with waste heat recovery equipment typically associated with the natural gas engine/generator sets. The recovered waste heat can generate up to 970 tonnes refrigeration capacity via absorption chillers, which satisfies most of the airport's need for chilled water year-round. The central utility plant is also equipped with three Carrier chillers running on electricity to help satisfy any extra chilled water demands. Two Broad heat exchangers capture the waste heat for hot-water absorption chillers using heat from the exhaust and the engine's water jacket.

"The facility came online in March of 2011," Griffith said. "The start-up had its challenges, as any start-up does, because we are merging so many technologies in building a combined heat and power plant. The cogeneration really helps boost our overall efficiency."

"We are permitted for three engines, the fourth engine aids in uptime and maintenance, and all four are run in rotation to keep the hours the same on all. It's like an installed spare, acting as a buffer," said O'Leary. "This is a critical facility so the expense of a fourth engine redundancy is justified, and it's also there for peak demand times. If we lost Edison completely and a gen-set were to fail, the computer can turn off non-essential, nonmission-critical loads, and turn off power to the parking structure first. In a catastrophic failure, the plant is designed to save itself — with the most important thing being not losing the plant itself. A catastrophic event would be seismic-oriented in this area, but terrorist activity is not out of the question."

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CATALYST FORMULATIONS
3-Way | HAPs Oxidation | Diesel Oxidation
DPF | SCR | Urea Hydrolysis | Ammonia Killer

WHY MIRATECH CATALYST FORMULATIONS?

- **Consistently Sets the Standard for Best Available Control Technology (BACT)**
- **Better Designed, Built & Value**
- **Cost-Effective, No-Hassle Compliance for both Natural Gas & Diesel**
  - NOx, CO, HC, VOCs, HAPs, PM10, PM2.5
- **Available in NEXT™ and VORTEX™ Element Configurations with**
  - Free Washes for Life
  - Two-Year Warranty

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- **Stationary Natural Gas & Diesel Engines**
  - Gas Compression
  - Power Generation
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PRODUCT ADVANTAGE

MIRATECH provides straightforward solutions to the emissions needs of all industrial engine applications. The unique combinations of substrates, formulations and housings is often the standard for Best Available Control Technology (BACT) which allows end users to achieve first-time compliance. MIRATECH's catalysts substrates are reliable, high-performance elements with superior mechanical and thermal durability. MIRATECH's catalyst technology cuts natural gas and diesel exhaust NOx, CO, hydrocarbons, VOCs, HAPs and particulates emissions to federal and state compliance levels at minimum cost with minimum space requirements, pressure drop and impact on your operation.

YOUR BEST BET

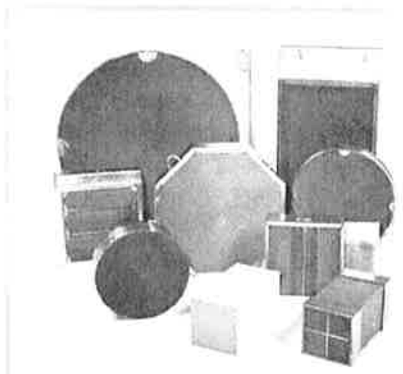
Running an industrial engine means running the risk of costly non-compliance fines. MIRATECH's catalyst keeps emissions in check in applications ranging from gas compression; continuous, prime and stand-by power generation to liquids pumping; air compression; marine power and more. Count on MIRATECH catalysts to keep your operation in compliance and on the right side of the "fine" line.

INNOVATIVE DESIGN: VERSATILITY

Sensible, Cost-Effective Solutions

Standard-setting design, expert craftsmanship and top-quality fabrication mean that each MIRATECH catalyst element delivers long-lasting, problem-free performance you can bank on, year after year.

To determine the correct MIRATECH formulation configuration, review the 'Catalyst Formulations' to determine options to cut your emission levels.



CATALYST FORMULATIONS

CATALYST TYPE *	3-WAY	NATURAL GAS OXIDATION	DIESEL OXIDATION	DPF	SCR		UREA HYDROLYSIS		AMMONIA KILLER	
NOx	99%*				99%*	98%*				
CO	99%*	99%*	99%*	70%*						
HAPs	99%*	99%*	99%*	90%*						
VOCs	95%*	95%*	95%*	70%*						
PM10	30%*	30%*	30%*	99%*						
PM2.5	30%*	30%*	30%*	99%*						
Urea to NH3							100%	100%		
NH3 Slip									99%*	99%*

* Emissions reduction percentages (%) are typical maximum performance values

4SLB/2SLB = 4-Stroke and 2-Stroke Lean Burn; Natural Gas Spark Ignited (SI) Engines with Exhaust Oxygen greater than 4%

4SRB = 4-Stroke, Rich Burn; Natural Gas Spark Ignited (SI) Engines with Exhaust Oxygen less than 1%

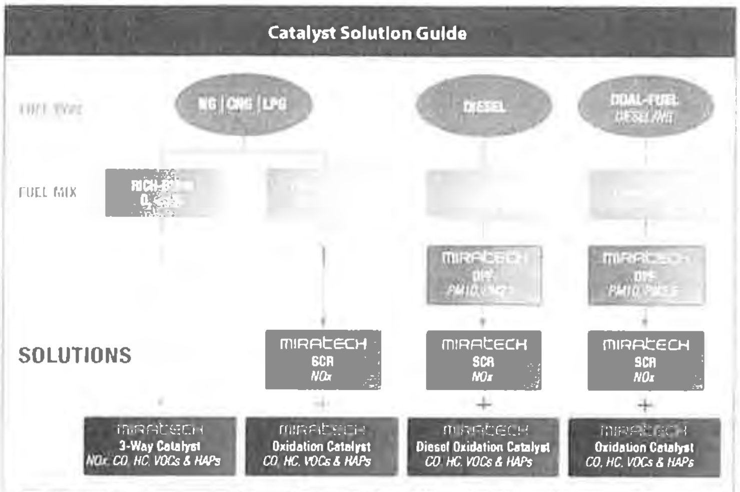
CI = Diesel and Dual Fuel 4-Stroke and 2-Stroke; Compression Ignition (CI) Engines

Innovative Emissions Solutions

FORMULATIONS 3-Way | HAPs | Oxidation | Diesel Oxidation DPF | SCR | Urea Hydrolysis | Ammonia Killer

CHOOSE FORMULATION

Use the *Catalyst Solution Guide* below to determine the application 'Fuel Type' and 'Fuel Mix' to help identify the combination of formulation 'Solutions' required.



ELEMENTARY GEOMETRY:

The right fit for any system, the MIRATECH catalyst comes in a wide variety of shapes and sizes to match a wide range of engine sizes, applications, catalyst system requirements, and budgets... The final system selection will be based on specific air regulations. To determine the correct MIRATECH housing, choose the right Catalyst Formulation, Substrate Configuration, Sound Attenuation and Horsepower Range. Match the horsepower with the right MIRATECH housing. Next contact MIRATECH Sale or specify the project at the www.miratechcorp.com Emissions Solutions Guide.

Diesel gensets with a combined SCR & Diesel Oxidation Catalyst package

HOUSINGS	CATALYST FORMULATIONS: 3-WAY	NG OXI	DIESEL OXI	UREA HYDR	DPF	SCR	AMMONIA KILLER	CATALYST SUBSTRATE CONFIGURATIONS: METAL: NEXT	VORTEX	OPEN	HERRING-BONE			SILENCER Sound Attenuation dB(A)	HP RANGE
NX Series	X		X					X		X		X			26-325
VX Series	X		X						X					25-37	26-325
IQ	X	X	X					X		X					200-8000
RX Series	X	X	X					X		X				25-35	200-8000
ZX Series	X	X	X						X		X			22-52	1200-4500
CBS w/ OXI(DOC/DPF)			X		X			X	X	X	X	X	X	25-30	100-6000
CBL w/ DOC(DOC/SCR)		X	X	X		X	X	X	X	X	X	X		20-35	100-20,000+
Ground Access		X	X						X		X			25-52	1400-20,000+

WHY MIRATECH?

- Advanced Technology
- Product Range: 20 to 20,000+ hp
- Innovative, Cost-Effective, Comprehensive Emissions Solutions
- RICE NESHAP Compliant
- Turnkey Projects
- Unsurpassed Experience & Expertise
- Fast, Responsive, Customer-Focused Service & Support
  - Prevent Non-Compliance Fines
  - Improve Engine & Catalyst Performance
  - Cut Maintenance Costs
  - Maximize Catalyst Life
- Full Service Catalyst Wash & Repair
  - 'Free Wash for Life' on NEXT™ & VORTEX™ Substrates
- Project Management
- Onsite Services
  - Supervision
  - Technical
  - Skilled
- Product O&M Training
- Replacement Parts

EMISSIONS SOLUTIONS

- Catalysts
  - 3-Way
  - Oxidation (Natural Gas & Diesel)
  - HAPs
  - Selective Catalytic Reduction (SCR)
  - Urea Hydrolysis
  - DPF
- Housings
  - NX Series
  - IQ
  - CBS
  - CBL
  - Silencer Combinations
    - VX Series
    - RX Series
    - ZX Series
    - Ground Access
- Controls
  - SCR
  - Active DPF
  - Air Fuel Ratio (Rich & Lean Burn)
  - Monitors
    - RICE NESHAP
    - DPF

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MIRATECH REPORT

Overcoming the Hurdle of Emissions Control, Creative Co-Generation Cuts Calif. Foundry's Costs

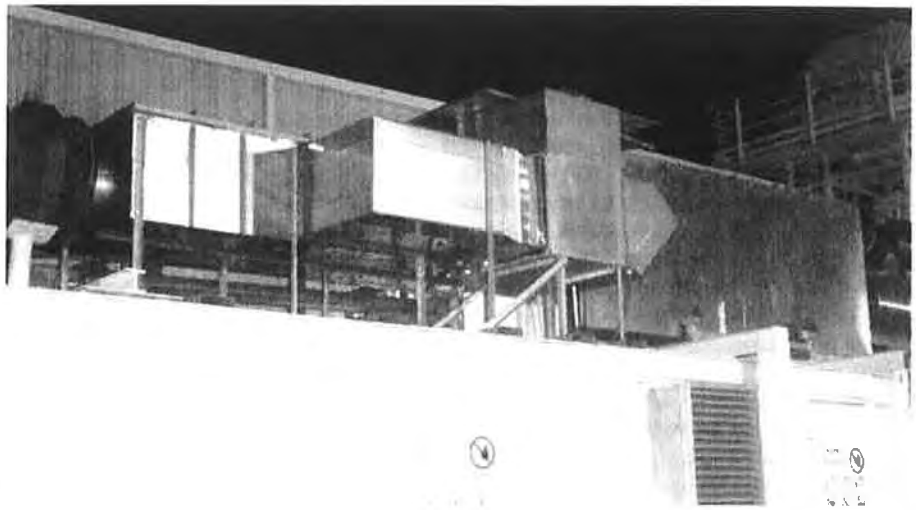
Techni-Cast Corp., a foundry and machined products firm in South Gate, California, shaved its energy bills by generating power on-site with a natural gas-fueled co-generation system that "recycles" waste heat and meets some of the toughest exhaust emissions limits in the U.S. Even with today's high natural gas prices, the project saves the company about 33 percent on electricity, according to president Bryn Van Hiel.

A key challenge in the Techni-Cast co-generation project was meeting the strict emissions control requirements of the South Coast Air Quality Management District (SCAQMD), an area that includes Los Angeles. With the help of Oklahoma-based MIRATECH Corp. and its subsidiary, MIRATECH SCR Corp., Techni-Cast found innovative ways to meet and sometimes exceed these requirements without jeopardizing bottom-line co-generation savings, Van Hiel said.

Techni-Cast product lines are centrifugally cast in aluminum, copper, iron, nickel and cobalt base alloys and include both rough alloy castings and machined products such as cylinders, washers, bushings, bearings, seat rings, valve bodies, and solid bar stock. Customers are in the petrochemical, valves, pumps, food products, machinery, hydraulics, recreational vehicles, commercial aircraft and military industries.

Van Hiel, a mechanical engineer, developed the Techni-Cast co-generation system after the California energy crisis of 2000 – 2001, when "rolling blackouts" and utility rate hikes rocked Golden State industry. "During the three to four years after 9-11, business took a dive. If we hadn't put in a generator, I don't know if we'd be alive today," Van Hiel said.

The Techni-Cast cogeneration system is driven by a GE/Jenbacher 320 engine, a V20 natural gas-fueled unit. Techni-Cast operates its



Techni-Cast emissions solutions include both a MIRATECH Selective Catalytic Reduction (SCR) system for NOx compliance, and a Non-Selective Catalytic Reduction System, the MIRATECH Oxidation Catalyst, for CO, HC, VOCs and HAPs compliance.

Techni-Cast Corp., a foundry based in South Gate, Calif., has met some of the nation's toughest emissions requirements in a creative combined-heat-and-power project, with emissions solutions provided by MIRATECH.

Jenbacher six days a week, 24 hours a day, Van Hiel said. "We're good Christian people so we give it a rest on Sundays."

Lean-Burn Emissions Control

The Techni-Cast Jenbacher, like most current natural-gas engines used to drive generators, runs "lean," partly to hold down fuel costs. This complicates emissions compliance, said MIRATECH Sales Manager Nick Detor.

SCAQMD emissions regulations require reduction of three air pollutants, Detor explained: oxides of nitrogen (NOx), carbon monoxide (CO), and hydrocarbons (HC). HC regulations include Volatile Organic Compounds (VOCs) and EPA-listed Hazardous Air Pollutants (HAPs), such as formaldehyde and acrolein.

With rich-burn engines, a "3-Way" Non-Selective Catalytic Reduction (NSCR) system can ensure compliance for all three classes of pollutant, added MIRATECH Engineering Manager John Sartain. But when an engine runs lean, excess air in the exhaust stream requires a Selective Catalytic Reduction (SCR) system to meet NOx requirements, Sartain said.

The emissions control solution MIRATECH installed at the Techni-Cast plant combines technology developed by MIRATECH's Swiss-based partner, HUG Engineering, a leader in the field, and a MIRATECH NSCR Oxidation Catalyst system, said MIRATECH SCR Project Manager Mike Owings.

"As HUG Engineering's sole North American partner, MIRATECH can deliver the world's most advanced SCR technology to customers, backed by full service and support based here in the U.S.," Owings said. Van Hiel attests to the benefits: "We've had things come up from time to time and MIRATECH has always been very responsive, from the VP of operations down to their engineers."

MIRATECH SCR: Reducing Hard NOx

The MIRATECH SCR system offers the option of using either ammonia or aqueous urea and a catalyst to break down NOx into harmless nitrogen, oxygen and water. Sartain noted that the MIRATECH SCR catalyst also significantly reduces formaldehyde. Techni-Cast chose to use urea in its SCR system, since urea is both less expensive and easier to store and handle than ammonia. Though ammonia is classified by the U.S. Occupational Safety & Health Administration as a flammable and hazardous material, it does not have the temperature and volume storage requirements of aqueous urea, Sartain pointed out.

Techni-Cast's SCR system automatically monitors "tailpipe" exhaust NOx levels. This allows adjustment of reactant injection rates to ensure compliance and cost-effective reactant use, Detor said.

NSCR: CO, HC, VOCs & HAPS

To control CO and hydrocarbon emissions, Van Hiel chose the MIRATECH Oxidation Catalyst, housed in a MIRATECH catalyst-silencer combo unit placed upstream of the Techni-Cast SCR system. A version of the MIRATECH QCC catalyst-silencer modified to allow catalyst element replacement, the unit reduces noise as well as air pollutants, Detor said. MIRATECH catalyst-silencers offer two grades of noise reduction: the QCC and RCS reduce sound by 25-30 decibels (dBA), while the QCH and RHS "hospital grade" units cut noise by an additional five dBA for total sound attenuation of 30 to 35 dBA.

The MIRATECH Oxidation Catalyst simultaneously reduces CO, HC, VOCs, HAPs and particulates, Sartain said. For Techni-Cast, the company developed a custom-version of its standard catalyst element design. The element is constructed of corrugated metal foil wash-coated with a slurry containing precious-metal-group catalysts such as platinum and rhodium. This wash-coated foil is tightly wound around a steel spool-post, forming a "honeycomb" pattern that maximizes catalyst contact with exhaust gasses while resisting shock and vibration as well as fouling and catalyst "poisoning" by materials such as lead in the exhaust stream. The patented MIRATECH banding and pinning process adds durability and strength.

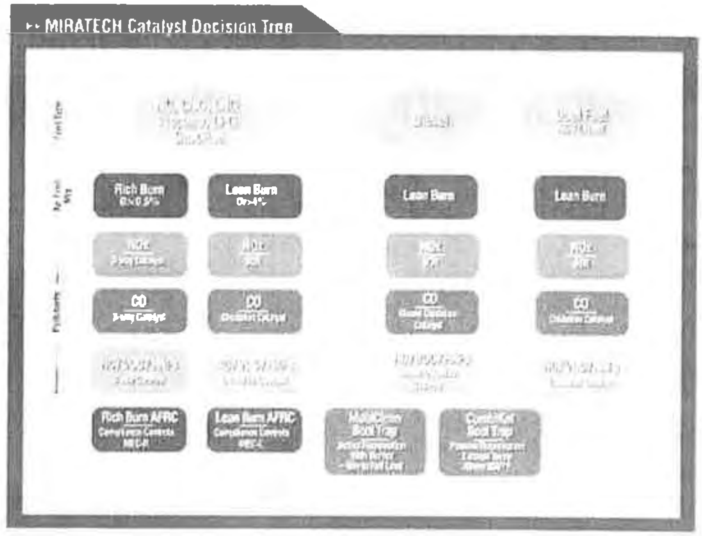
Before the Oxidation Catalyst could be put to work, Techni-Cast needed to overcome yet another challenge: the Jenbacher's 1,100° exhaust temperature. The catalyst is designed to withstand temperatures as high as 932° – ample for most applications, but not high enough for the Techni-Cast system, Owings said.

To solve the problem, Van Hiel and MIRATECH distributor Bill Rosentreter,

Techni-Cast's combined-heat-and-power system uses waste-heat from electrical generation to pre-heat metal before melting, thus reducing the overall energy requirements of foundry operations.

president of Otto H. Rosentreter Co., developed a forced-air duct system to cool the exhaust to 880° before it enters the catalyst-silencer combo. The Techni-Cast engine, generator, ductwork, and emissions control system are housed in a 45' x 8' x 8' structure. Van Hiel said it looks like a cargo container.

The company's cogeneration emissions control system cuts NOx by more than 90 percent and reduces other regulated air pollutants to less than five parts per million, according to Detor. Since current regulations cap these emissions at 13 parts per million, Techni-Cast is prepared if regulations tighten – "and just about everybody I know expects the regs will tighten," Detor added.



The "MIRATECH Catalyst Decision Tree" illustrates the different types of emission solution needed by stationary engines operating with different types of fuel and air-fuel mix.

Energy "Recycling"

When treated exhaust exits the system, Techni-Cast pipes it into a preheating oven, which raises to 800° the temperature of metal to be melted down in foundry operations. This metal includes crushed and washed chips, scrap returns and ingots, all placed in the preheating oven in 55-gallon metal drums. Pre-heating saves Techni-Cast money with every degree: the hotter the metal gets, the less energy Techni-Cast has to buy or produce to melt it.

From the preheating oven, Techni-Cast's cogen system exhaust flows through a "bag house" where a 1,500-filter dust collection system eliminates particulates it might have picked up in the preheating process. After the bag house, the exhaust goes through a HEPA filter, which Van Hiel said is 99.97 efficient. Then, the exhaust is dispersed into the California environment. "The air we're releasing into the atmosphere is a lot cleaner than the air going into our engine," Van Hiel surmised.

Techni-Cast's creative use of its combined-heat-and-power system doesn't stop there. Engine jacket water, used to cool the company's generator, does double-duty in an absorption chiller system that provides heating, cooling and humidity control for Techni-Cast offices, metrology and chemical analytical labs, Van Hiel said.

Bottom-Line Benefits

Techni-Cast now produces about 82 percent of the electricity it uses, and has cut energy requirements both through its use of exhaust gas for metal preheating and generator jacket water for air conditioning. Plus, when commercial customers combine co-gen with "energy-recycling" measures, as Techni-Cast has done, the local utility, Southern California Edison (SoCal Edison), exempts them from certain fees for ten years. Techni-Cast is now in its fourth year of exemption.

"We started generating our own electricity after SoCal Edison more than doubled its rates. Back then, gas prices were around $2.50/mmbtu. Now, we're paying $6.25 to $6.50. Even with the high gas prices, we're producing electricity for a little less than 10 cents per kilowatt-hour. If we were buying utility electricity, it would cost 16 to 17 cents per kilowatt-hour. So our net cost is still a third less than what we were paying before we made the change," Van Hiel said.

Rosentreter, who has helped Van Hiel with Techni-Cast's exhaust systems for more than 30 years, said the project fits the Techni-Cast mold: "Bryn Van Hiel is conscientious about the environment. He's been innovative and aggressive in solving his energy problems in a way that's friendly to the environment."

Beyond the bankable benefits, Techni-Cast's effective use of electricity has brought it national recognition. In 2002, Techni-Cast was awarded the National Electrical Contractors Association's Electrical Excellence Award. With a little help from friends like Rosentreter and MIRATECH, the company has shown that creative cogen can meet emissions control requirements, benefit the environment and pay off in net cost-savings all at the same time.

According to Rosentreter, Techni-Cast is the only centrifugal foundry on the West Coast. Techni-Cast employs 100 people and has a long history in Southern California. Van Hiel's father started the company in 1950 and it was re-named Techni-Cast in 1954. It has been in its present location in South Gate since 1972.

A privately held company, MIRATECH Corp. and its subsidiary MIRATECH SCR Corp. are leaders in the development and engineering of emission control and engine performance technology for industrial engines. Both companies are based in Tulsa, OK, with sales offices located across North America.

For more information about MIRATECH emissions solutions, call 1-800-640-3141, or visit www.MIRATECHcorp.com

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Emissions

NO_x Reduction at a Vermont Ski Resort

Miratech SCR system used to reduce engine emissions from snowmaking activities

To a skier, there is nothing quite like the feel of fresh snow and the sound of cutting skis as one glides down picturesque mountains with perfect snow conditions. Each year from late November through early April, that feeling is replayed thousands of times at the Okemo Mountain Resort, located near the town of Ludlow in the mountains of south central Vermont, U.S.A.

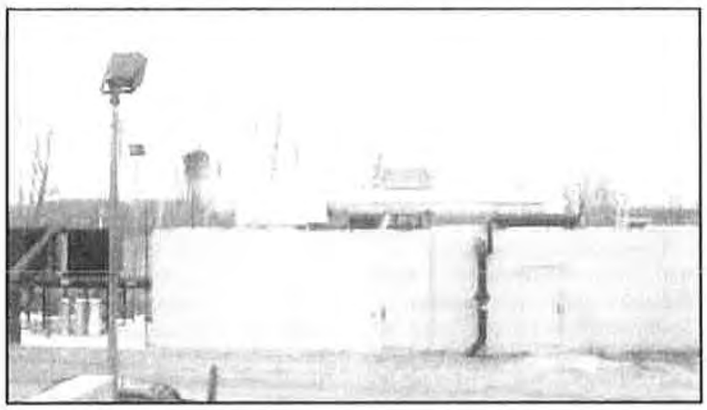
For years, the best ski resorts have known that success depends on their ability to do one thing — create and consistently maintain the best possible snow conditions. And in Vermont, Okemo Mountain Resort is one of the best. In terms of snow quality and grooming, the resort is consistently ranked as the best in the state (SKI Magazine). Its snowmaking coverage capabilities are listed at 95%. Needless to say, The Okemo Mountain Resort takes its snow seriously.

One of the resort's primary engine-driven air compressors for snowmaking is powered by a 69 L displacement Caterpillar V-16 3516B diesel. The eight-year old engine operates approximately 1500 hours annually while driving an Ingersoll-Rand Centac centrifugal model 2ACII57D3 compressor. The compressor produces 2832 inlet m^3/s of compressed air at 6 9 bar. While the compressor requires 935 kW of power, the engine can produce 1104 kW at 1550 r/min.

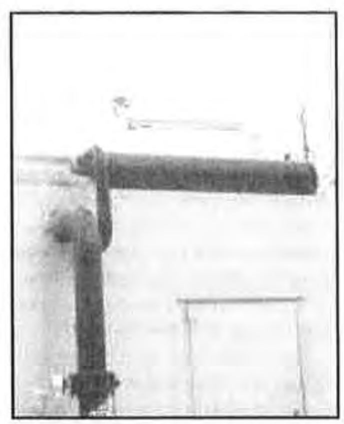
Due to the lack of extensive natural gas distribution in southern Vermont, most ski areas use #2 diesel fuel for snowmaking equipment purposes.

Three years ago, the State of Vermont approached the Okemo Mountain Resort and asked it to develop and implement a comprehensive program to reduce NO_x emissions resulting from its large-scale snowmaking activities. The resort takes pride in its willingness and ability to improve ski industry methods and was eager to find an emissions solution that reduced NO_x levels, while maintaining engine use and optimum snow conditions. Further, it was vital to implement the emission solution during the summer shutdown period to insure the system could be fully operational before the start of ski season.

While searching for emissions control options for the Cat 3516B, the resort found that although selective catalytic reduction (SCR) technology for diesel engines was in widespread use in Europe, there were relatively few applications in the United States. The resort's

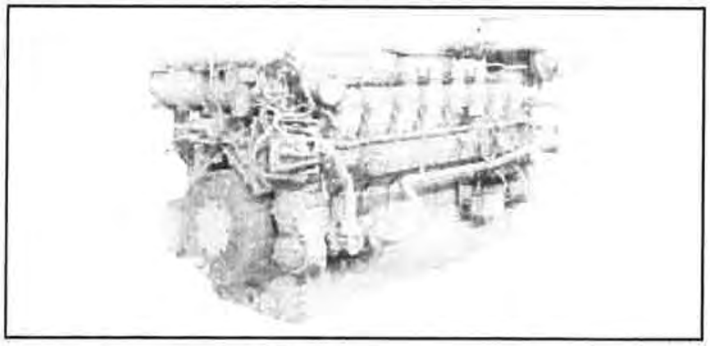


The Okemo Mountain Resort constructed a separate building (entered through doorway at left) to house the Miratech SCR system reactant storage tank, injection panel and all other components, next to the Cat 3516B engine-IR Centac compressor package enclosure (entered through doorway at right).



A closeup view of the urea injector wand location in the exhaust pipe. The exhaust piping was insulated to maintain exhaust temperatures for the catalytic reactions, and a straight run of pipe was necessary for proper mixing and urea hydrolysis.

Emissions



One of the Okemo Mountain Resort's primary engine-driven air compressors for snowmaking comprises a Caterpillar 3516B diesel similar to the unit pictured, driving an Ingersoll-Rand Centac 2ACII57D3 compressor. The Miratech SCR system reduced NO_x by 85% on the engine without any operational problems.

research eventually took it to the Miratech Corporation's website. Intrigued by the company's emissions technology and ability to deliver solutions in a timely and competitive manner, the resort began a dialog and ultimately a partnership with Miratech's emissions control experts.

To provide a viable emissions solution, Tulsa, Oklahoma, U.S.A.-based Miratech solicited the assistance of Southworth-Milton Power Systems, Milford, Massachusetts, U.S.A., the authorized Caterpillar dealer in Vermont and other New England states and upstate New York. The partnership with Southworth-Milton proved beneficial, because the Cat dealer already provided all the maintenance on the engine and lease rental generation for the mountain's electrical needs. Together, the companies designed a system-specific emissions control application.

Installation of the application proved to be a challenge. The Cat engine-IR Centac compressor package is located on a ski slope and therefore is exposed to an extreme and harsh environment throughout the year. Winter daytime temperatures average between -8 and -9°C, and summer daytime temperatures average between 20 and 21°C.

Also, Miratech and Southworth-Milton chose urea as the reductant for its ease of handling and storage. Urea must be stored at temperatures above 1.7°C to avoid crystallization, so the team installed an insulated tank and submersion heater as part of the system. The exhaust piping had to be insulated to maintain exhaust temperatures for the catalytic reactions, and a straight run of pipe was necessary for proper mixing and urea hydrolysis (conversion of urea to ammonia after injection in the exhaust pipe). The resort constructed a separate building to house the storage tank, injection panel and all other components next to the engine-compressor enclosure.

The SCR system itself consists of three main components. The urea injection panel is a prepackaged unit containing the urea pump, air compressor and PLC for the proper metering of the aqueous urea reductant.

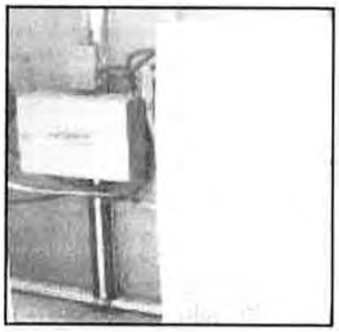
In this application, a higher degree of difficulty was encountered because unlike a base-loaded electrical generator, a compressor application has some engine load swings. The PLC component of this system must track load swings with an engine mapping procedure performed at start-up. The injector wand is placed in the exhaust pipe upstream of the converter, and the urea is sprayed with a very fine mist with the air compressor assisting in the process. The compressor also purges the urea lines during system shutdown to avoid urea crystallization when these lines are exposed to the elements.

Featuring an insulated housing, the converter also contains three layers of SCR catalyst and one layer of oxidation catalyst. Although the Vermont State Air Board requirements were for NO_x reduction only, the oxidation catalyst also provided an additional 90% reduction of carbon monoxide, hydrocarbon reduction, hazardous air pollutant (HAPs) reductions and served as a failsafe device to avoid any potential of ammonia slip if the SCR catalyst becomes coated or damaged.

In the end, the three-week project was a success. "The system provided the resort an 85% reduction in NO_x on the Caterpillar 3516B without any operational problems," said Allen Fortier, manager of snowmaking at Okemo. "We are proud to be the first in the state to have taken the initiative to make such a step in the reduction of emissions and implement new ways to work in conjunction with our environment."

With Miratech and Southworth-Milton developing and implementing the system as a team, the resort received the benefit of a single-point guarantee on emissions. Miratech provided an emissions-conversion percentage guarantee and Southworth-Milton, through Caterpillar, guaranteed the engine's raw emissions levels.

Thanks to the foresight of The Okemo Mountain Resort and the partnership between Miratech Corporation and Southworth-Milton Power Systems offering total emissions solutions, skiers will continue to enjoy excellent skiing conditions in an environmentally friendly setting for years to come.



The urea injection panel is a prepackaged unit containing the urea pump, air compressor and PLC for the proper metering of the aqueous urea reductant. Miratech sells, specifies and supports SCR catalytic systems from the Swiss company HUG Engineering.

For more information visit www.miratechcorp.com or contact jmcdonald@miratechcorp.com

Comment Letter I9

ACIS

ANALYSIS CONTROLLED INJECTION SYSTEM.

Urea/Ammonia Injector
Developed For SCR Systems

TAKE CONTROL OF SCR.

The Analysis Controlled Injection System. Only From MIRATECH SCR.

Running a Selective Catalytic Reduction system at peak efficiency can be a complicated, demanding job. But it's a job that has to be done right if you want to get the most out of your SCR system at least cost, and steer clear of non-compliance.

ACIS
Analysis Controlled Injection System

Now, a new, automated solution makes SCR control a whole lot easier: ACIS – the Analysis-Controlled Injection System, brought to you by MIRATECH SCR. With ACIS, one state-of-the-art system integrates monitoring and control functions – and payback starts the minute you switch ACIS on.

The key? ACIS continuously monitors actual post-catalyst exhaust, and automatically adjusts reactant injection accordingly, in real time. That keeps actual NOx emission levels within compliance, whether you're running a base-load or load-following application.

The payoff? Continuous, on-going compliance, guaranteed – with maximum efficiency in reactant use. Plus, with features like remote website monitoring and troubleshooting, ACIS cuts man-hours needed for SCR, and helps your personnel work more efficiently and reliably.

CONTACT MIRATECH.

Find out more about ACIS and other advanced, cost-effective MIRATECH SCR Emissions Solutions. Give us a call or visit our website: www.miratechcorp.com

WHY MIRATECH?

- Advanced Technology
- Cost-Effective, Comprehensive Solutions
- Unsurpassed Experience & Expertise
- Fast, Responsive, Customer-Focused Service & Support
  - *Prevent Non-Compliance Fines*
  - *Improve Engine & Catalyst Performance*
  - *Cut Maintenance Costs*
  - *Maximize Catalyst Life*

EMISSIONS SOLUTIONS

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  - *3-Way Catalyst Systems*
  - *Oxidation Catalysts*
  - *HAPs Catalysts*
  - *Diesel Oxidation Catalysts*
- Catalyst Housings
  - *MN/MBA*
  - *IQ*
- Catalyst-Silencer Combos
  - *QCC/QCH*
  - *RCS/RHS*
- Active Regeneration Soot Traps
- SCR Catalyst Systems
- NX Analyzers
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Comment Letter I9

MAKE ACIS THE BASIS OF SCR – BROUGHT TO YOU BY MIRATECH SCR

ACIS

ANALYSIS CONTROLLED INJECTION SYSTEM.

FAILSAFE COMPLIANCE 24-7-365.

Count on the Analysis Controlled Injection System to make sure your lean-burning engine is fully NOx compliant all the time. Rather than using base load or engine speed set points or other fixed criteria to govern your SCR system, ACIS continuously monitors actual post-catalyst exhaust, and adjusts reactant injection accordingly – in real time. No load curve or signal is required. Your system is more responsive, performs more efficiently – and on-going compliance is assured, in any and all real-world operating conditions.

ACIS TRUMPS FINES.

MIRATECH ACIS measures actual NO when and where you need monitoring most: post-catalyst, every minute, every day. That way, what actually comes out of the exhaust pipe will always be within compliance – and you avoid non-compliance fines.

SCR: ON-SITE

SAVE ON REACTANT, TOO.

With ACIS, injection rates are based on actual process conditions, not preset values that may not match changing engine load or other operational factors. At all times, you use exactly the right amounts of reactant to achieve compliance – no less and no more. With ACIS, you don't waste a drop of the reactant you've paid for. So you save money each and every time you buy ammonia or urea.

LESS LABOR. MORE VALUE.

ACIS takes labor and hassles out of SCR – automatically maximizing efficiency. That way, your employees can focus on what matters most: running your operation. Easy to install and quick to set up, ACIS even saves you time, trouble and dollars on the front-end.

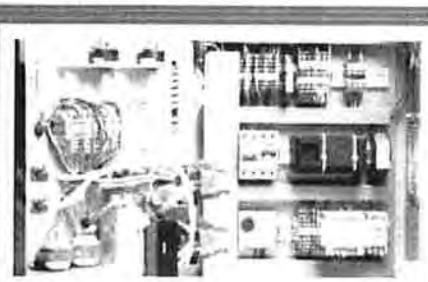
REMOTE MONITORING & TROUBLESHOOTING.

You can monitor and troubleshoot ACIS and your SCR system from any location you choose – on-site or off-site, virtually anywhere in the world – via a secure website. Plus, ACIS opens secure access from any location to rich data for Continuous Assurance Monitoring (CAM) or other uses.

WORLD-CLASS SOLUTIONS.

ACIS was developed by Swiss-based HUG Engineering, the acknowledged world leader in advanced SCR technology. As HUG's sole North American partner, we can put the world's most advanced solutions to work for our customers, backed by expert MIRATECH engineering as well as technical support close to home. And we back ACIS – and every other product we ship – with service and support that set standards for the industry. If there's a question, we'll answer it. If there's a problem, we'll fix it – whatever it takes. No *ifs, ands,* or *buts.*

MIRATECH also offers a full spectrum of ongoing service contracts, on-site technical support and training programs designed to take emission control issues off your busy agenda.



ACIS By MIRATECH SCR
Continuous Assurance Monitoring (CAM)

EMISSIONS SOLUTIONS: CONTACT MIRATECH.

For more than a decade, MIRATECH has been at the forefront in helping industries handle emissions standards. Whatever your emission control needs may be, count on MIRATECH SCR for solutions. Just give us a call – or visit our website: www.miratechcorp.com. *Ask for your FREE subscription to our useful, fact-filled electronic newsletter, THE EMISSIONS MONITOR.*

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ONGOING Compliance

WHY MIRATECH ACIS?

Integrated Solution: SCR Exhaust Gas Analysis & Injector Control In One Package

- Continuously Monitors Actual, Post-Catalyst Exhaust & Adjusts Reactant Injection Accordingly
- Continuous Compliance Assured: 24-7-365
- Maximum Efficiency
- Cuts Costs On Reactant & Labor

APPLICATIONS

- SCR Systems For Lean-Burn Engines, Natural Gas, LPG, Diesel, Dual-Fuel
  - *Power Generation*
  - *Chillers*
  - *Gas Compression*
  - *Air Compression*
  - *Water Pumps & Irrigation*
  - *Quick, Easy Installation & Setup*

FEATURES & BENEFITS

- Automatically Monitors:
  - *Exhaust Gas Temperature*
  - *Post-Catalyst NO*
  - *Operating Hours*
  - *Reactant Injection Flow Rate*
- Automatically Adjusts Reactant Injection Based On Actual Exhaust Gas NO Levels
- Remote Monitoring & Troubleshooting Via Website
- Standard ACIS Components
  - *Main Control Panel*
  - *Alarms*
  - *Booster Pump Skid Supplies Constant 1-Bar Reactant Pressure To The Dosing Valve*
  - *Dosing Control Box*
  - *Injector*
- No Load Curve Or Signal Required
- Available In Dosing Rate Ranges From 3 – 115 L/HR
- ACIS Options
  - *Post-Catalyst Carbon Monoxide (CO) Monitoring*
  - *PE Differential Converter Pressure Switch*
  - *USM US Modem*
  - *ACU Air Conditioning Unit*
  - *AN4 Analog Output*