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Linking Landscape Disturbance to the Population Ecology of Great Basin Rattlesnakes (*Crotalus oreganus lutosus*) in the Upper Snake River Plain

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Summary

Sagebrush steppe ecosystems throughout the Great Basin and Interior Columbia Basin are experiencing widespread landscape conversion due to livestock overgrazing, invasive plants, and fire. Previous studies have documented the effects of landscape conversion on birds and mammals but there is little information on the effects on reptiles. The Great Basin rattlesnake is a good species to study the potential influence of landscape conversion on reptiles because they are widely distributed, sympatric with many other species of reptiles, move long distances relative to other reptiles, and have life histories that are sensitive to variation in prey availability. We developed a study that links landscape disturbance to rattlesnake populations through a series of trophic interactions. We studied disturbance, substrate, vegetation, prey, and rattlesnakes at two study sites in the Upper Snake River Plain of southeastern Idaho. We used radio telemetry to track rattlesnakes while concurrently conducting habitat sampling and small mammal trapping in areas used by snakes and in random locations. We found lower biological crust cover, shrub cover, shrub height, and shrub dispersion and higher grass and bare soil cover in disturbed areas (i.e., areas with grazing and/or burning). In addition, at one study site, grass cover in disturbed areas was dominated by non-native invasive grasses such as cheatgrass and crested wheatgrass. Habitat characteristics associated with disturbance levels, such as shrub cover and shrub height, were important predictors of prey resources for snakes. We found lower small mammal biomass, abundance, and rabbit index values in disturbed areas. Small mammal species richness was lower in disturbed areas at only one site. Disturbed areas had lower proportions of large prey species (such as least chipmunks) and higher proportions of small prey species (such as pocket mice). Rattlesnake movements were not significantly different among disturbance categories. Snakes displayed preference for habitat characteristics typical of undisturbed sites, with the exception of a preference for areas with lower biological crust cover. Rattlesnake diets differed between study sites, and snakes showed preference for certain small mammals at the Crater Butte study site. Small mammal biomass within the rattlesnakes' home range influenced how much weight the snakes gained during the active season. Overall, our study suggests that disturbance in sagebrush steppe ecosystems may cause a series of interactions that result in less energy acquisition by a top predator, the Great Basin rattlesnake. The results from this study have important implications for the conservation of sagebrush steppe habitats and wildlife. For example, management prescriptions that do not provide sufficient cover, or that promote altered disturbance regimes will have a negative impact on sagebrush steppe reptiles. This study highlights the importance of finding effective ways to prevent further landscape conversion and restoring previously converted areas of sagebrush steppe.

Introduction

The sagebrush steppe of western North America is one of the most endangered ecosystems in the world (Noss et al. 1995). Sagebrush steppe is threatened by a combination of factors such as livestock overgrazing, invasive plants, and fire. Specifically, the synergistic effects of livestock overgrazing and invasive annual vegetation (such as cheatgrass, *Bromus tectorum*) have altered historic fire regimes in sagebrush steppe (Whisenant 1990). Historically, small infrequent fires with return intervals of approximately every 25 (more xeric areas) to 110 (more mesic areas) years occurred throughout the Snake River Plain of southern Idaho (Whisenant 1990). Long fire return intervals allowed perennial vegetation to recover between fires. However, the spread of invasive annual plants (accelerated by soil disturbance associated with overgrazing) has altered the historical fire regime to one with much larger and more frequent fires (return intervals of 3 to 5 years in southern Idaho). The larger size of fires has disrupted the historical patch mosaic of substrate characteristics (e.g., cryptogamic crusts), perennial grasses, forbs, and shrubs and created large areas that are dominated almost solely by invasive annual vegetation (Harniss and Murray 1993, Belnap et al. 2001).

Changes in sagebrush steppe ecosystems due to disturbance are having negative effects on wildlife species (Wisdom et al. 2000, Vander Haegen et al. 2001). These effects range from the loss of nesting habitat for breeding birds to the loss of forage that mammals depend on for winter survival (Green and Flinders 1980, Knick and Rotenberry 2000). In addition, many of the small mammals that snakes and other carnivores depend on for food are also negatively affected (e.g., Knick and Dryer 1997). Despite the wide range of documented negative effects on wildlife species and the fact that 21 of the 23 reptiles in Idaho are found in sagebrush steppe ecosystems, few studies have evaluated the effect of these disturbances on reptiles (Guyer 1978, Beck 1997, Cossel 2003).

By studying how disturbance and landscape conversion influence a single reptile that serves as a potential ‘umbrella’, we can provide management recommendations that will benefit many reptiles and other wildlife species. The Great Basin rattlesnake (*Crotalus oreganus lutosus*) is an effective umbrella species for other reptiles and carnivores in sagebrush steppe ecosystems. First, they are one of the most common snakes with one of the widest distributions, hence they are sympatric with many of Idaho’s reptiles (St. John 2002). Second, they share winter hibernacula with many other snake species including gopher snakes (*Pituophis catenifer*), terrestrial garter snakes (*Thamnophis elegans*), racers (*Coluber constrictor*), striped whipsnakes (*Masticophis taeniatus*), and night snakes (*Hypsiglena torquata*) (Peterson unpublished data). These communal areas are also suitable habitat for a number of lizard species including western skinks (*Eumeces skiltonianus*) and common sagebrush lizards (*Sceloporus graciosus*). Third, Great Basin rattlesnakes move great distances from hibernacula [up to 8 km on the Idaho National Laboratory (INL), (Cobb 1994)], and are one of the most vagile reptiles in sagebrush steppe ecosystems. As a result of their extensive movements they may be more susceptible to disturbance than other reptiles. Finally, they have life history characteristics such as slow growth, late age at maturity, giving birth once every 3-5 years, and low fecundity that may make them more susceptible to disturbances relative to other reptiles (Diller and Wallace 1984, McCartney and Gregory 1988, Brown 1993, Martin 2002,). All of these characteristics suggest that by meeting the needs of rattlesnakes in southeast Idaho we will help protect other reptiles and potentially other species.

Rattlesnakes have life histories (see above) that should make them especially sensitive to changes in the environment that result in lower prey availability. As a result, the overall goal of this project is to determine if landscape change in sagebrush steppe ecosystems is influencing the population ecology of Great Basin rattlesnakes by altering prey resources. To achieve our goal, we developed a conceptual framework that links landscape disturbance to rattlesnake life histories (Figure 1). We developed specific objectives based on our conceptual framework including, 1) describing broad scale patterns in disturbance in two study areas used by rattlesnake populations, 2) describing how disturbance influences substrate and vegetation characteristics, 3) describing how disturbance and habitat characteristics influence small mammal communities, 4) describing how disturbance influences rattlesnake movements, 5) describing habitat preferences of rattlesnakes, 6) describing rattlesnake diets and prey preferences, and 7) describing how prey availability influences weight gain of rattlesnakes.

Study Area

The INL is administered by the United States Department of Energy (DOE) and is located in the Upper Snake River Plain of southeast Idaho. The INL includes 2,564 km^2 of predominately sagebrush steppe habitat. The landscape has received minimal disturbance as compared to adjacent lands. Human development and access is limited on the INL with only peripheral areas (~ 40%) receiving grazing. The United States Bureau of Land Management (BLM) administers grazing on the INL.

Topography in the study area is generally flat with dispersed volcanic features including buttes, cinder cones, lava flows, and collapsed lava tubes. Climate is characteristic of cold deserts with high daily fluctuations in temperature and low levels of precipitation (Anderson et al. 1996). Similarly, there are dramatic seasonal fluctuations in temperature with hot summers and cold winters. The average annual temperature is 5.6 degrees Celsius and annual precipitation is approximately 220 mm. Precipitation peaks are in the months of April, May, and June.

Two study sites were selected as the focus of this study, Crater Butte (CRAB) and Rattlesnake Cave (RCAV) (Figure 2). Each site contains a Great Basin Rattlesnake hibernaculum where populations have been monitored by the Herpetology Laboratory at Idaho State University for 11 years. Each site is centered on a rattlesnake overwintering site and includes a 5 km radius buffer of surrounding desert (5 km was selected to represent the furthest distance snakes will move from either overwintering site). The Crater Butte hibernaculum is located in the southwest portion of the INL; surrounding areas receive extensive human disturbance in the form of sheep and cattle grazing. In addition, fires have burned a significant portion of the area surrounding the hibernaculum. The Rattlesnake Cave hibernaculum is located in the southeastern portion of the INL; some surrounding areas receive livestock grazing and have burned.

Sampling Methods and Data Analysis

Disturbance- To quantify the extent of landscape disturbance in the study area, we use ArcMap GIS software to intersect fire (from the Bureau of Land Management) and grazing coverages (from the Department of Energy) to develop a disturbance category layer that characterized the landscape into 4 cover types; undisturbed, grazed, burned, and grazed and burned. We then used a personal geodatabase in ArcMap to determine the proportion of each study site (i.e., Crater Butte and Rattlesnake Cave) in each disturbance category.

Habitat Characteristics- We measured a suite of substrate and vegetation characteristics in a series of randomly distributed plots (50 locations at Rattlesnake Cave in 2003, 33 locations at Rattlesnake Cave in 2004, and 33 locations at Crater Butte in 2004). We determined the locations of random plots using the Animal Movements extension in ArcView GIS. Specifically, we generated random points within a 5 km radius buffer around each hibernaculum to sample the areas available to snakes during the summer active period. We used hand held GPS units (Geoexplorer, Trimble Navigation Limited, 749 North Mary Ave, Sunnyvale, CA 94085) to navigate to each habitat plot. At each plot, we measured the following characteristics: biological crust cover, bare soil cover, litter cover (downed plant material), rock cover, average shrub height, average shrub dispersion (only measured in 2004), shrub cover, grass cover, and forb cover. We also recorded the dominant shrub species (i.e., the shrub species that dominated the shrub canopy layer) and whether the plot was dominated by native or nonnative grasses.

Each habitat plot was 20 meters by 20 meters and centered on the snake location or random point. Plots were oriented so the four sides faced the four cardinal directions. We measured habitat cover values (bare soil, biological crust, litter, rock, shrub, grass, and forb) using the line intercept method along two perpendicular 20 meter transects that crossed at the center of the plot. Specifically, we counted the number of centimeters of each cover type that intersected the transects. Each cover type was measured independently. For example, a given centimeter could intercept the foliage of a shrub and also intercept bare soil beneath the shrub foliage. To measure shrub height and dispersion, we divided the plot into four quadrats delineated by the perpendicular transects. Within each quadrat, we visually assessed the average canopy height and measured a representative shrub height. Similarly, the average distance between shrubs was visually assessed and a distance between a representative pair of shrubs measured. To assure that visual assessments of average canopy height and distance between shrubs were precise we conducted blind tests where all field workers took measurements separately and results were compared. In general, the measurements were precise among field workers but to further assure precision, at least two field workers would conduct each visual assessment.

We used a combination of geospatial and descriptive statistics to quantify how habitat characteristics varied by disturbance category. First we used ArcMap to intersect the disturbance category layer with a point file of habitat sampling locations. We then characterized each sampling location by disturbance category (e.g., burned) and calculated mean and standard error values for each habitat and small mammal variable by disturbance category, study site, and year.

Small Mammals- After taking habitat measurements, we conducted small mammal sampling at each random habitat plot. We used small mammal trapping and a rabbit scat index to characterize small mammal and rabbit communities. We trapped small mammals by placing 16 Sherman live traps within each plot. We set one trap every 2 meters along both line transects, beginning at the 2 meter mark. Traps were baited with a peanut butter, oat, bird seed, and bacon mixture. We trapped each plot for two nights and checked them between 05:00 and 10:00 Hrs. each morning to prevent excessive heat induced mortality. Each small mammal we captured was identified to species, weighed, and marked with a hair clip on the lower back. To measure the rabbit scat index, we walked eight perpendicular 20 meter transects (north to south) within each plot, each two meters apart, beginning at the 2 meter mark. Along each transect we counted the number of rabbit pellets observed and categorized those numbers into an index (0 = no pellets, 1 = 1-20 pellets, 2 = 21-50 pellets, 3 = 51-100 pellets, and 4 = > 100 pellets).

From small mammal trapping data, we quantified the species richness, abundance, and total biomass of small mammals captured at each plot. We described differences in small mammal metrics between disturbance categories, study sites, and years using mean and standard error values. We characterized overall prey community composition as the proportion of deer mice (*Peromyscus maniculatus*), least chipmunks (*Tamias minimus*), and other small mammal species captured relative to the total number captured by study site and disturbance category.

To determine the habitat characteristics that best predicted small mammal biomass we used multiple linear regression. Specifically, we ran three models, the first for Rattlesnake Cave (including both years), the second for Crater Butte, and a third model on data collected in 2004 to compare differences among hibernacula. In all models small mammal biomass was used as the dependant variable and habitat characteristics were used as independent variables. Due to multiple comparisons we used Bonferoni corrections to assess significance. We used forward stepwise selection to develop each model. We examined residuals for normality and made transformations as necessary.

We used principal component analysis to characterize disturbance categories by habitat and prey characteristics. We described the 2 principal components that explain the most variation in the multivariate data set. To characterize the two principal components, we used separate Spearman correlations comparing each habitat variable to each axis. For example, if shrub height was positively correlated with axis 1, then axis 1 would be characterized by increasing shrub height values.

Rattlesnake Movements- In the spring of 2003, we initiated radio telemetry studies on Great Basin rattlesnakes (10 snakes) from the Rattlesnake Cave hibernaculum. We continued telemetry at Rattlesnake Cave (11 snakes) in 2004 and began telemetry studies on snakes from the Crater Butte hibernaculum (9 snakes). Transmitters were surgically implanted into the body cavity of snakes following procedures outlined in Reinert and Cundall (1982). We located snakes every 24-48 hours in 2003 and every 48-72 hours in 2004 using a hand held radio receiver (Model R-1000, Communications Specialist Inc., 426 West Taft Ave. Orange, California 92865) and a Yagi antenna (Wildlife Materials International Inc., 1202 Walnut Street Murphysboro, Illinois 62966 USA). To visually locate snakes before disturbing them, we used binoculars to scan for individuals and made only careful movements as we approached. Using this approach, we were often able to observe snakes with no apparent influence on behavior. For example, snakes approached in this manner would often continue specialized activities such as drinking. Once a snake was located, we noted any behavioral observations (e.g., coiled in foraging posture or in rodent burrow), marked the location with labeled flagging, and recorded a location using a GPS receiver. We later post processed (i.e., differentially corrected) the GPS locations to improve location accuracy.

We used geospatial techniques to describe movements of individual snakes. We used the Animal Movements extension in ArcView GIS to calculate the total and average distances moved and to estimate kernel density home range statistics. We used fixed kernels and estimated 50% and 95% use areas. Subsequently we refer to snake locations within 50% use areas as core areas and all other points as migration areas. We used the measurement tool in ArcGIS to measure the maximum distance snakes moved away from hibernacula. To determine if disturbance category, study site, year, sex, and/or study site influenced rattlesnake movements, we used a series of one way ANOVAs. Movement characteristics were dependant variables and category, study site, year, sex, and study site were independent variables in ANOVAs.

Habitat Preferences of Rattlesnakes- In conjunction with random habitat plots described previously, we also conducted habitat and small mammal sampling at snake locations. Snake plots were surveyed following the exact procedures outlined previously. We sampled plots at snake locations approximately 1-3 days after the snake had left the location to minimize disturbance to the snake and maximize the safety of the individuals recording the habitat data. In cases when the snake stayed in the same location for 7 days, we measured habitat characteristics at a time when the snake was not active on the surface (e.g., at the warmest time of the day).

We used logistic regression to determine if rattlesnakes preferred certain habitats. We ran two models for each study site. The first model used all snake locations as indicators of preference and the second model used only those snake locations in the core area of the snakes' home range (as determined from movement analyses). In all models biological crust, rock, bare soil, litter, shrub, grass, and forb cover and shrub height and small mammal richness, biomass, and abundance were used as independent variables. We used forward stepwise selection in each model to select the habitat variables that best predicted rattlesnake preference. We examined residuals for normality and made transformations as necessary.

Rattlesnake Diet- We opportunistically captured all rattlesnakes encountered while conducting field work. We palped each rattlesnake to acquire scat samples. Scat samples were dried, dissected, and any material that could be used to identify prey (i.e.., hair) was saved. We worked with David Hilliard to identify prey items in snake scats; Hilliard conducted prey identification as part of an independent research project at Idaho State University. Mammal hairs were the only items found in all scat samples. We used two keys to identify mammal hairs to species (Moore et al. 1974, Blew 1988). We used cuticular scale patterns, medulla configuration, banding patterns, and hair width and length to identify mammal hairs to species. Specifically, hairs from scat samples were compared to hairs from reference collections supplied by the Idaho Museum of Natural History and the Environmental Surveillance, Education, and Research Program (operated by Stoller Corporation for the DOE). Banding patterns and hair width and length were examined using a dissecting microscope. To examine cuticular scale patterns we made impression slides of 5 guard hairs from each scat sample following procedures outlined by Blew (1988). To examine medulla configuration, we made temporary slide mounts following procedures outlined in Blew (1988).

We first described rattlesnake diet at each study site by developing a list of prey items. We then examined prey selection by comparing the proportion of deer mice, least chipmunks, and other species (all other small mammal species) found in scat samples to the proportions of the same groups of small mammals captured at random habitat plots with exact tests (one test for each study site).

Prey Availability and Rattlesnake Population Ecology- Once per month during the summer activity period, we attempted to capture each snake. Snakes were then measured and weighed at the location of capture and released after 2-5 minutes of handling. We used multiple linear regression to quantify how well small mammal biomass predicted weight gain in rattlesnakes. Before running the analysis we refined our estimate of prey availability based on known movement and foraging patterns in Great Basin rattlesnakes and other closely related rattlesnakes. Prairie rattlesnakes, *Crotalus viridis* (a species closely related to Great Basin rattlesnakes) typically leave hibernacula and move along a straight bearing until they reach an area of high prey availability (Duvall et al. 1985). To account for this we used our kernel density home range estimates to separate those area snakes are moving through (i.e., migration areas) and those that are spending the majority of the active season in (i.e., core areas). For a given snake, we calculated the average prey biomass of all plots within their core area (i.e., plots that were contained within the 50% isopleth of the kernel home range estimate). We then used the average prey biomass in a snake's core area as an independent variable and the amount of weight gained by a snake over the course of the active season as the dependent variable. We only included snakes in analyses if they were captured and weighed at both the beginning and the end of the active season. In many cases it was not possible to capture snakes towards the end of the active season because rattlesnakes often spent long periods of time underground.

Results

Disturbance- We found variation in the amount and types of disturbance between our two study sites. The Crater Butte study site was entirely disturbed with 42% of the area grazed and 58% of the area grazed and burned. A portion of the Rattlesnake Cave study site was undisturbed (22%) but the majority was disturbed, specifically 37% was grazed, 40% burned, and 1% was grazed and burned. Note the spatial distribution of disturbances in each study site (Figure 2). Disturbances at each site are generally clustered due to the large size of grazing allotments and fires. At the Crater Butte study site most of the western portion is grazed and most of the eastern portion is grazed and burned. Whereas, at the Rattlesnake Cave study site most of the western portion is burned, most of the eastern portion grazed, and undisturbed areas are patchily distributed.

Habitat Characteristics- We found that disturbance (i.e., grazing and fire) influenced substrate and vegetation characteristics (Table 1). Biological crust was lower and bare soil was higher in disturbed areas (Figure 3A and B). We observed lower shrub cover in disturbed areas at Crater Butte in 2004 and Rattlesnake Cave in 2003, however shrub cover was not different among disturbance categories at Rattlesnake Cave in 2004 (Table 1). Shrub dispersion was lower in disturbed areas. Shrub height was lower (Figure 3C) and the dominant shrub species was green rabbit brush in burned and grazed and burned areas (whereas the dominate shrub was big sagebrush in undisturbed and grazed areas). Differences in shrub characteristics among disturbance categories were accompanied by higher grass cover and higher proportions of nonnative grasses (e.g., cheatgrass, *Bromus tectorum* and crested wheatgrass, *Agropyron cristatum*) in more disturbed areas (Table 1).

Small Mammals- Results from linear regression models show that disturbance and associated changes in habitat characteristics influence prey availability. Small mammal biomass was higher in areas with higher shrub and biological crust cover (Table 2). Both high shrub and biological crust cover are characteristics of areas with lower levels of disturbance (Table 1). In addition, linear regression models showed that the categorical variable year had a significant influence on small mammal biomass. We sampled higher small mammal biomass in 2003 than 2004.

Small mammal biomass and abundance as well as rabbit scat index were higher in less disturbed areas (Table 3, Figure 3D). However, prey richness was only lower in disturbed areas at Rattlesnake Cave; species richness did not vary among disturbance categories at Crater Butte. The majority of small mammals captured were deer mice and least chipmunks, although the composition of small mammals varied based on disturbance category (Table 4). In more disturbed areas the proportion of least chipmunks was lower and the proportion of other species was higher.

To provide an overall summary of the habitat and prey characteristics available to Great Basin rattlesnakes, we used principal components analysis. Results showed that principal component 1 (PCA 1) is characterized by higher levels of biological crust cover, shrub cover, small mammal biomass, small mammal abundance, and small mammal richness and lower levels of bare soil cover, while principal component 2 (PCA 2) is characterized by higher levels of rock cover and shrub height and lower levels of grass cover (Table 5). Relatively undisturbed sites, sites from 2003, and sites from Rattlesnake Cave loaded high on PCA 1 (Figure 4). There were not notable differences among disturbance categories, sites, or years on PCA 2 with the exception of burned sites from Rattlesnake Cave in 2003 which loaded significantly lower than all other sites (Figure 4).

Rattlesnake Movements- We followed 30 snakes during the 2003 and 2004 active seasons (see Appendix I). Snakes were tracked for an average of 64 days, ranging between 30 and 102 days. Snakes moved an average total distance of 3611 meters, an average of 1378 meters from hibernacula, and an average of 53 meters per day. Snakes had an average core activity area (i.e., as determine from kernel density home range estimates) of 10 hectares. We found no significant differences in movement patterns among different disturbance categories, sex, or years (Table 6). However, we observed notable differences in movements between large males and females. Large males were approximately 1 meter long (snout vent length) and had high body condition. They tended to move longer total distances; for example snakes RCAV12, RCAV15, and RCAV17 moved the furthest and were all large males. Indeed, the female (CRAB9) that moved the longest total distance did not even move half the total distance of most large males. However, all the farthest movements from the hibernacula were by females (e.g., CRAB5, CRAB7, CRAB9, RCAV1, and RCAV12).

Habitat Preferences of Rattlesnakes- Using all rattlesnake locations, we found no habitat preference by snakes from either study site. However, when using only those snake locations within their core activity area we observed habitat preference. Snakes from Rattlesnake Cave preferred habitat characteristics typical of less disturbed areas such as low bare soil cover, high shrub height, and high small mammal biomass whereas snakes from Crater Butte did not show these preferences (Table 7). Snakes from both study sites selected areas with low biological crust cover.

Rattlesnake Diet- We collected 7 scat samples from Rattlesnake Cave Snakes and 6 scat samples from Crater Butte snakes. We found significant differences in rattlesnake diet between the two study sites. Snakes from the Rattlesnake Cave hibernaculum fed on deer mice (*Peromyscus maniculatus*), least chipmunks (*Tamias minimus*), and sagebrush voles (*Lemmiscus curtatus*) and snakes from the Crater Butte hibernacula fed on kangaroo rats (*Dipodomys ordii*), harvest mice (*Reithrodontomys megalotis*), pocket mice (*Perognathus parvus*), sagebrush voles (*Lemmiscus curtatus*), and wood rats (*Neotoma cinerea*) (Table 8). Snakes from Crater Butte fed on other species more than expected and deer mice and least chipmunks less than expected based on availability ($P < 0.0001$). Snakes from Rattlesnake Cave fed on small mammals in proportion to their availability ($P = 0.2282$; Table 9).

Prey Availability and Rattlesnake Population Ecology- We found that snakes with high small mammal biomass in their core activity area gained more weight (Figure 5). This analysis also supports the idea that disturbance-caused changes to prey availability influence snakes. Snakes that used undisturbed areas had high prey biomass in their home range and as a result gained more weight.

Discussion

<u>Disturbance</u>- We found that the Crater Butte landscape was more disturbed (i.e., due to grazing and fire) than the Rattlesnake Cave landscape (Figure 2). We also observed lower small mammal biomass, abundance, and species richness at Crater Butte (Table 3) suggesting that broad scale landscape patterns can influence the availability of rattlesnake prey. Similar studies on small mammal communities on the INL show that broad scale patterns in grazing can influence small mammal communities (Johnson 1982). We also found that the spatial distributions of disturbances were clumped in both study areas. Our study did not address the spatial structure of disturbed and undisturbed habitats; future studies should examine the influence of spatial patch structure on prey resources. In addition, other unmeasured factors such as weather, topography, competition, and/or predation may also be having an effect on broad scale patterns in prey resources and should be the focus of future research projects.

<u>Habitat Characteristics</u>- We found that biological crust cover was lower in grazed areas than undisturbed areas and almost absent in burned disturbance categories (Table 1). Instead substrates in disturbed areas were characterized by higher bare soil cover. These changes can have important effects on sagebrush steppe communities. Biological crusts serve as a critical component of healthy sagebrush ecosystems by functioning as nursery areas for new plants, increasing water retention in soils, and fixing nitrogen from atmosphere (Belnap 2001). The loss and regeneration of biological crusts occurs naturally in sagebrush ecosystems. However, in our study area as well as much of the western United States, vegetation is not recovering naturally; instead non-native herbaceous plants are invading. Fire frequencies associated with non-native herbaceous plants (3-5 years, Whisenhant 1990) are shorter than the time needed for most biological crusts to regenerate and could result in the disappearance of biological crusts from much of the sagebrush steppe (regeneration rates reported for crusts vary widely but at least 40 years has been observed in many studies, Belnap et al. 2001).

The loss of sagebrush is an important conservation issue in the region (Knick et al. 2003). Many species of sagebrush (especially Wyoming big sagebrush in our study area) are critical for maintaining natural processes in sagebrush steppe ecosystems. Sagebrush makes water available to other plants through uplift, provides favorable microclimates for other plants and animals, and is an important winter food source for wildlife (Green and Flinders 1980, Huber-Sannwald and Pyke 2005). We found that shrub cover, height, and dispersion varied among disturbance categories (Table 1). Sagebrush is being removed by fire and replaced by rabbit brush. Early seral rabbit brush stands are generally short in height and dense relative to late seral sagebrush. These changes in vegetation occur naturally, however, the invasion of non-native hebaceous plants can cause permanent changes to shrub communities (Humphrey and Schupp 2004). Similar to issues discussed with biological crust, frequent fires associated with invasive plants do not give sagebrush enough time to mature and could ultimately result in the loss of sagebrush or a shift to early seral species such as rabbit brush (Whisenant 1990).

Contrary to the general trend we observed in shrub cover (i.e., lower shrub cover in disturbed areas), we did not find lower shrub cover in disturbed areas at Rattlesnake Cave in 2004. We attribute this to clumped patchy distributions of green rabbit brush observed in the field. In burned areas surrounding Rattlesnake Cave many dispersed clumps of dense rabbit brush can be found. We suspect that due to chance we may have randomly sampled a high proportion of these sites and measured high shrub cover values.

We found higher grass cover in disturbed sites (Table 1), however this is only of great concern at the Rattlesnake Cave study site because most of the new grasses at this site are non-native invasive species. Cheatgrass and crested wheatgrass are widespread in burned areas surrounding Rattlesnake Cave and uncommon in disturbed areas surrounding Crater Butte. Previous studies show that invasion by these grasses has negative impacts on native wildlife communities (e.g., Knick and Rotenberry 2000). In addition, some of the wildlife affected by non native grasses are important prey species for Great Basin rattlesnakes.

Disturbance has the potential to influence Great Basin rattlesnakes in a variety of ways. First, the observed changes in substrate and vegetation will affect the availability of microclimates (the influence on microclimates is the focus of another study we are currently conducting). Specifically, less crust and sagebrush and more bare soil and grass may result in drier hotter environments that restrict rattlesnake activity. Second, the changes could influence prey availability. Specifically, as substrate and vegetation change, food resources (e.g., seeds and forbs) and microclimates can influence small mammal communities (Parmenter and MacMahon 1983). Indeed we found that habitat characteristics associated with disturbance influence prey biomass available to snakes (Table 2).

<u>Small Mammals</u>- We found that disturbed areas had fewer prey, lower prey biomass, and fewer large prey items (e.g., rabbits and chipmunks). These results are similar to other studies in sagebrush steppe that observed declines of small mammal populations in disturbed areas (e.g., McGee 1982). However, other studies have also shown a decrease in diversity with disturbance in sagebrush steppe (Olson et al. 2003) whereas we found no difference in species richness among disturbance categories at the Crater Butte site. We did not observe differences in species richness among disturbance categories despite the disappearance of chipmunks from disturbed habitats. Instead some less common small mammal species such as pocket mice and harvest mice made up larger portions of the small mammal community. The disappearance of large prey items in disturbed areas is similar to results from previous studies. Least chipmunks move out of areas after shrubs are removed by fire whereas other species such as deer mice and pocket mice decreased in abundance but remained in burned areas (Parmenter and MacMahon 1983).

<u>Rattlesnake Movements</u>- In environments with limited resources, we would predict that snakes need to travel longer distances and cover larger areas to find food. However, we

found no difference in movements among snakes using areas with different disturbance levels (i.e., different prey resources). Instead it appears that snakes are philopatric to summer activity areas and that they do not increase movements in search of food in disturbed areas. Indeed we observed multiple snakes that were philopatric to their summer activity area from year to year. However, we never followed a snake that had its summer range disturbed while being tracked to see if it would then change their movement patterns.

We observed that large males moved further distances and covered more area than females and smaller males but did not travel as far from hibernacula. In addition, based on examination for the presence of meals and significant weight loss, we think that none of these large males fed despite often occupying habitats with abundant prey resources. We suspect that instead of feeding through the first half of the active season like typical males (King and Duvall 1990) these large males have built up resources over previous seasons and are spending an entire season searching for mates. Indeed one of these large males was tracked in consecutive years and he did not feed in the first year when he was in good condition but did feed the second season when he was not in as good of condition.

<u>Habitat Preferences of Rattlesnakes</u>- Snakes from Rattlesnake Cave preferred habitat characteristics typical of areas with low disturbance (Table 7). However, snakes from Crater Butte did not show similar preferences. Duvall et al. (1985) suggests that Prairie rattlesnakes move along straight bearings until they reach areas with high prey availability. Once they reach these areas they change their movements and focus their activities on foraging. Our results suggest that the snakes from Rattlesnake Cave may be displaying the behaviors suggested by Duvall et al. (1985) but snakes from Crater Butte are not. We also suggest that snakes may be philopatric to summer activity areas despite annual variation in prey abundance. Movement data from snakes tracked in consecutive years support this idea. Specifically, 4 of 5 snakes tracked for multiple years were philopatric to summer activity areas despite changes in prey availability from 2003 to 2004. The one snake that was not philopatric was pregnant during one of the years she was tracked and thus would not be expected to use the same summer range (Cobb 1994) and one snake used the same summer range for three consecutive years. However it is also important to note that if prey resources change proportional across the landscape over time, than being philopatric to a summer range may be advantageous to snakes because they will still be selecting areas with the highest prey availability even if prey changes year to year.

<u>Rattlesnake Diet</u>- We found that snake diet varied between Crater Butte and Rattlesnake Cave (Table 8) and that snakes from Crater Butte preferred some prey resources and avoided others. Snakes from Crater Butte avoided the two most abundant species (i.e., deer mice and least chipmunks). Snakes from Crater Butte may be avoiding larger small mammal species such as chipmunks because they are smaller snakes than those from Rattlesnake Cave (Jenkins unpublished data). Snakes are gape limited predators and larger snakes are known to eat larger prey items (Arnold 1993). Snakes from Crater Butte may also not have the opportunity to eat these more common prey items due to the

activity patterns or spatial distribution of small mammals. Specifically, if snake activity times or space use do not overlap with those of small mammals such as chipmunks they would not be available prey items. Finally, increasing sample sizes used in scat analyses is important for understanding differences in snake diets between sites.

Prey Availability and Rattlesnake Population Ecology- We found that prey availability within the home range of rattlesnakes influenced their weight gain (Figure 5). Rattlesnakes can be considered energy limited systems and as a result changes in weight gain can significantly affect life history characteristics such as age to maturity, interval between pregnancies, and fecundity (Taylor et al. 2005). These life history traits are often used for estimating population viability. Thus our results show that landscape disturbance is influencing weight gain in rattlesnakes and suggest that landscape disturbance could ultimately, influence rattlesnake population viability.

General Conclusions and Recommendations- The results from this project suggest that landscape disturbances (i.e., livestock grazing, fire, and invasive plants) in sagebrush steppe ecosystems are altering habitat characteristics, prey communities, and ultimately the population ecology of Great Basin rattlesnakes. Similar studies in the Snake River Birds of Prey Area and on the INL found that spatial and temporal changes in small mammal populations were having negative impacts on reproductive success in golden eagles and bobcats (Kochert et al. 1999 and Knick 1990). Based on these studies it is becoming apparent that landscape change is influencing top level predators of multiple taxa (reptiles, birds, and mammals) in sagebrush steppe ecosystems by altering habitat and prey resources. In addition, by using management practices that promote suitable habitat conditions and minimize alteration of natural fire regimes, we may have a positive affect on sagebrush steppe reptiles. Future conservation and management efforts should focus on maintaining and restoring sagebrush ecosystems and associated natural disturbance regimes to provide the prey base necessary to support top predators.

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TABLES

Table 1. Mean and standard error values for habitat characteristics grouped by study site, year, and disturbance category.

	Crater Butte		Rattlesnake Cave					
	2004		2004			2003		
Habitat	Grazed	Grazed and Burned	Undisturbed	Grazed	Burned	Undisturbed	Grazed	Burned
Number of Plots	17	16	11	11	11	20	12	18
Rock Cover (cm)	501.3 ± 138.2	317.9 ± 72.1	323.4 ± 61.6	207.5 ± 91.9	313.6 ± 110.8	341.3 ± 73.7	211.3 ± 118.5	185.7 ± 50.6
Baresoil Cover (cm)	1200.3 ± 124.9	2136.6 ± 156.0	1210.2 ± 159.8	1413.6 ± 204.6	1855.5 ± 137.6	1350.2 ± 96.4	1599.8 ± 191.3	1686.2 ± 176.3
Crust Cover (cm)	113.0 ± 23.7	11.7 ± 8.7	321.4 ± 61.6	239.6 ± 50.4	9.5 ± 6.2	808.5 ± 36.4	505.7 ± 104.5	49.5 ± 11.6
Litter Cover (cm)	602.6 ± 101.2	273.4 ± 34.8	278.1 ± 42.9	340.0 ± 45.4	281.5 ± 55.1	326.3 ± 35.3	239.9 ± 56.8	455.4 ± 73.4
Shrub (cm)	369.6 ± 46.0	193.4 ± 36.4	400.3 ± 91.5	401.1 ± 48.2	419.4 ± 103.0	784.0 ± 71.1	720.9 ± 104.1	420.4 ± 95.5
Grass (cm)	230.25 ± 33.0	278.2 ± 33.8	206.1 ± 28.8	242.7 ± 31.5	261.2 ± 68.3	476.8 ± 62.8	431.1 ± 51.0	782.5 ± 158.3
Forb (cm)	59.7 ± 13.5	67.4 ± 13.6	58.3 ± 28.6	38.9 ± 11.8	46.6 ± 21.3	19.6 ± 32.6	66.4 ± 15.9	63.7 ± 18.9
Shrub Height (cm)	52.6 ± 6.7	31.6 ± 3.2	54.6 ± 5.6	52.6 ± 3.7	25.7 ± 4.6	50.5 ± 7.2	32.5 ± 3.2	13.2 ± 2.3
Shrub Dispersion (cm)	112.8 ± 18.2	86.7 ± 11.0	108.3 ± 11.5	92.1 ± 22.5	41 ± 9.8	Not Measured	Not Measured	Not Measured
Dominant Shrub	Big Sagebrush	Green Rabbitbrush	Big Sagebrush	Big Sagebrush	Green Rabbitbrush	Big Sagebrush	Big Sagebrush	Green Rabbitbrush
Proportion Plots Dominated by Native Grasses	0.81	0.82	0.91	0.73	0.36	Not Measured	Not Measured	Not Measured

Table 2. Linear regression models predicting small mammal biomass.

Model	Variable	Coefficient	R2	F value	P value
Crater Butte	Shrub Cover	0.965	0.16	5.75	0.0227
Rattlesnake Cave	Year	-0.299	0.06	6.43	0.0130
	Crust Cover	1.640	0.15	8.71	0.0001
2004	Shrub Cover	0.592	0.12	8.54	0.0048

Table 3. Mean and standard error values for prey community characteristics grouped by study site, year, and disturbance category. Values were calculated per plot then averaged across plots by categories (e.g., disturbance).

	Crater Butte		Rattlesnake Cave					
	2004		2004			2003		
Small Mammal	Grazed	Grazed and Burned	Undisturbed	Grazed	Burned	Undisturbed	Grazed	Burned
Total Biomass (g)	45.6 ± 14.7	16.0 ± 3.9	69.9 ± 18.3	59.2 ± 13.3	43.8 ± 16.9	134.7 ± 14.5	91.3 ± 18.0	84.4 ± 16.02
Total Abundance	2.3 ± 0.6	1.3 ± 0.4	3.0 ± 0.8	2.7 ± 0.6	1.3 ± 0.2	7.3 ± 0.8	5.3 ± 1.0	4.7 ± 0.8
Species Richness	0.8 ± 0.1	0.8 ± 0.2	1.4 ± 0.2	1.45 ± 0.2	1.0 ± 0.1	1.9 ± 0.1	1.8 ± 0.2	1.6 ± 0.2
Rabbit Scat Index	1.3 ± 0.3	0.5 ± 0.2	2.0 ± 0.4	0.91 ± 0.4	0.6 ± 0.2	Not Measured	Not Measured	Not Measured

Table 4. Proportion of deer mice (*Peromyscus maniculatus*), least chipmunks (*Tamias minimus*), and other small mammal species by study site, year, and disturbance category.

	Crater Butte		Rattlesnake Cave					
	2004		2004			2003		
Species	Grazed	Grazed and Burned	Undisturbed	Grazed	Burned	Undisturbed	Grazed	Burned
Deer Mice	0.73	0.76	0.67	0.63	0.64	0.75	0.83	0.77
Least Chipmunks	0.22	0.06	0.33	0.37	0.21	0.24	0.15	0.14
Other Species	0.05	0.18	0	0	0.15	0.01	0.02	0.09

Table 5. Spearman correlation coefficients of each independent variable by axis combination. *, P $\leq$ 0.05.

Variable	Axis 1	Axis 2
Small Mammal Biomass	0.884*	-0.222
Small Mammal Abudnance	0.902*	-0.250
Small Mammal Richness	0.881*	-0.177
Biological Crust Cover	0.782*	0.180
Rock Cover	-0.061	0.538*
Bare Soil Cover	-0.364*	-0.242
Litter Cover	0.019	-0.186
Shrub Cover	0.555*	0.236
Grass Cover	0.303*	-0.689*
Forb Cover	0.111	0.138
Shrub Height	0.322*	0.543*

Table 6. Mean and standard errors comparing characteristics of rattlesnake movements among disturbance categories, study sites, and years.

	Crater Butte		Rattlesnake Cave			
	2004		2004		2003	
Species	Grazed	Grazed and Burned	Undisturbed	Burned	Undisturbed	Burned
Number of Snakes	5	4	1	10	6	4
Total Distance (m)	1977 ± 1067	1728 ± 580	2220	2337.9 ± 455	8145 ± 1663	4268 ± 636
Maximum Distance from Den (m)	1474 ± 553	1198 ± 366	1339	1410 ± 200	1521 ± 231	1154 ± 179
Mean Distance per Day (m)	29 ± 15	31 ± 7	31	50 ± 9	94 ± 17	54 ± 11
Core Area (hectares)	9 ± 5.8	8.7 ± 4.3	11.3	14.9 ± 7	6.5 ± 1.6	5.9 ± 2.5

Table 7. Logistic regression models of habitat preference for Great Basin rattlesnakes.

Model	Variable	Coefficient	Chi-square	P > Chi-square
Crater Butte	Biological Crust	-1.108	6.19	0.0128
Rattlesnake Cave	Bare Soil Cover (cm)	-3.821	17.58	<0.0001
	Biological Crust Cover (cm)	-1.280	30.03	<0.0001
	Small Mammal Biomass	0.704	3.76	0.0522
	Shrub Height	1.843	8.28	0.0040

Table 8. Diet of Great Basin rattlesnakes from the Crater Butte and Rattlesnake Cave study sites based of analysis of scat samples.

Crater Butte		Rattlesnake Cave	
Species	Frequency	Species	Frequency
Bushy-tailed Woodrat	1	Deer Mouse	5
Great Basin Pocket Mouse	2	Least Chipmunk	1
Ord's Kangaroo Rat	1	Sagebrush Vole	1
Sagebrush Vole	1		
Western Harvest Mouse	1		

Table 9. The number and proportion (in parentheses) of deer mice, least chipmunks, and all other species combined in the diet of Great Basin rattlesnakes relative to availability.

	Crater Butte		Rattlesnake Cave	
	Diet	Available	Diet	Available
Deer Mouse	0 (0)	43 (0.73)	5 (0.71)	50 (0.65)
Least Chipmunk	0 (0)	10 (0.17)	1 (0.14)	25 (0.32)
Other	6 (1)	6 (0.10)	1 (0.14)	2 (0.30)

FIGURES

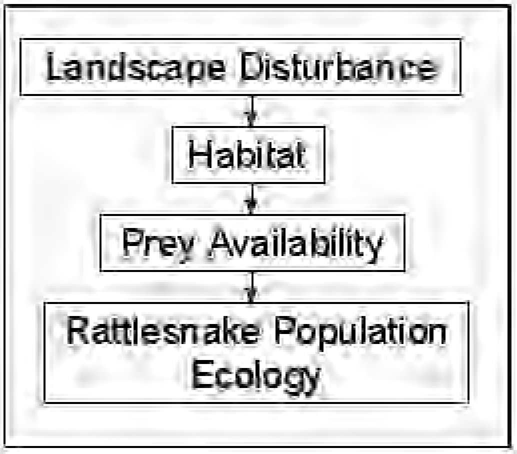

Figure 1. Conceptual framework linking landscape disturbance to rattlesnake populations.

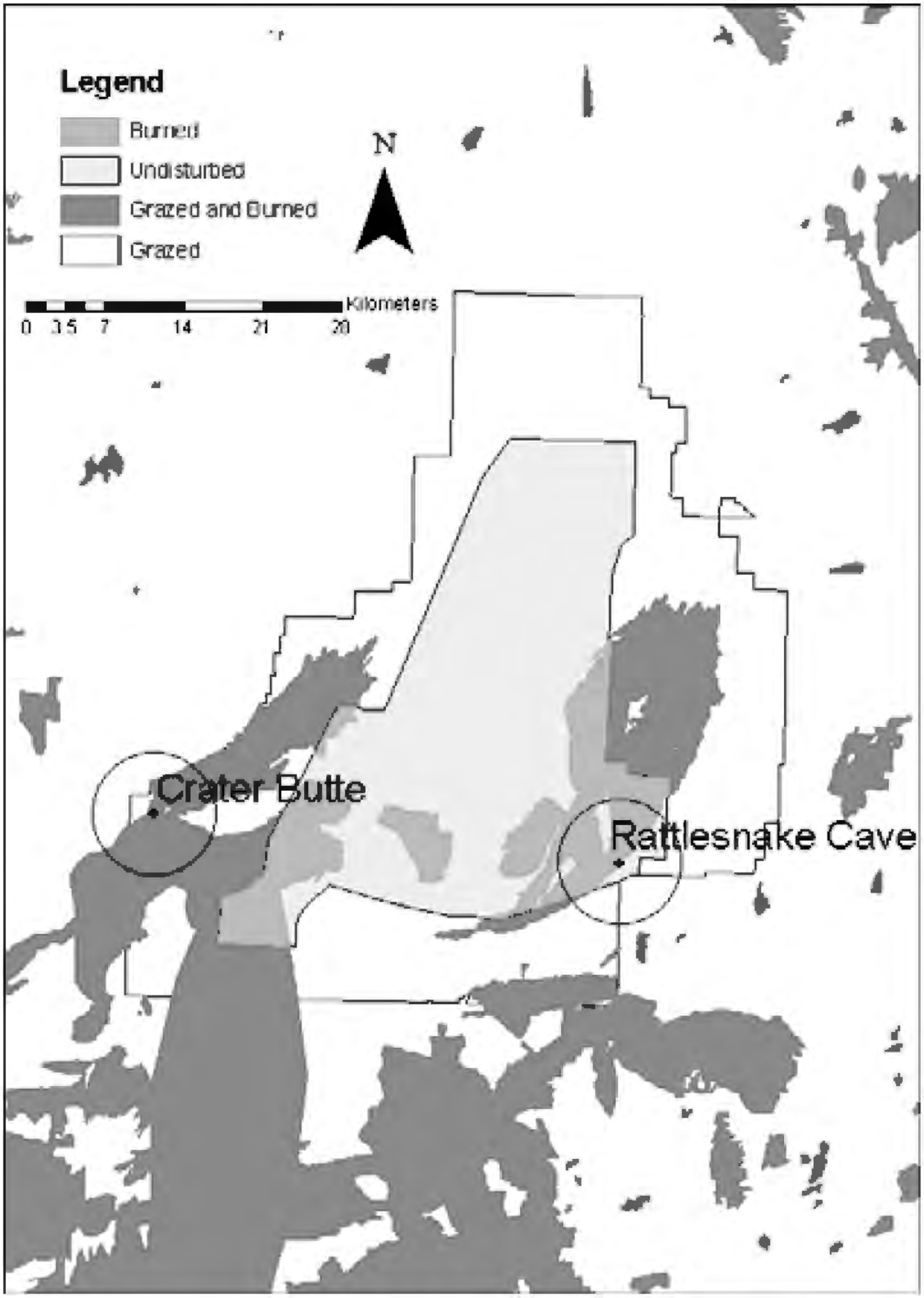

Figure 2. Map of the study area showing the boundary of the Idaho National Laboratory, the location of the two study sites (with 5-km buffers), and the distribution of disturbance categories.

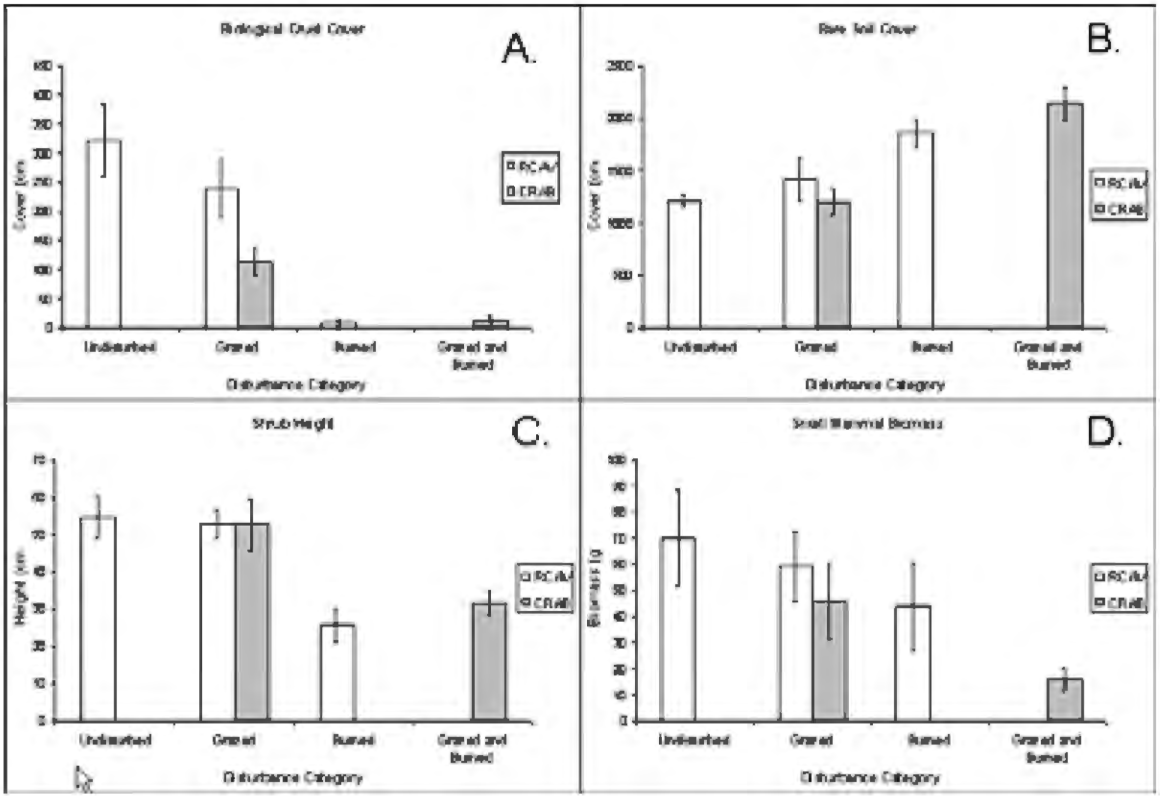

Figure 3. Bar graphs displaying mean and standard error values for biological crust cover, bare soil cover, shrub height, and small mammal biomass by study site and disturbance category for 2004.

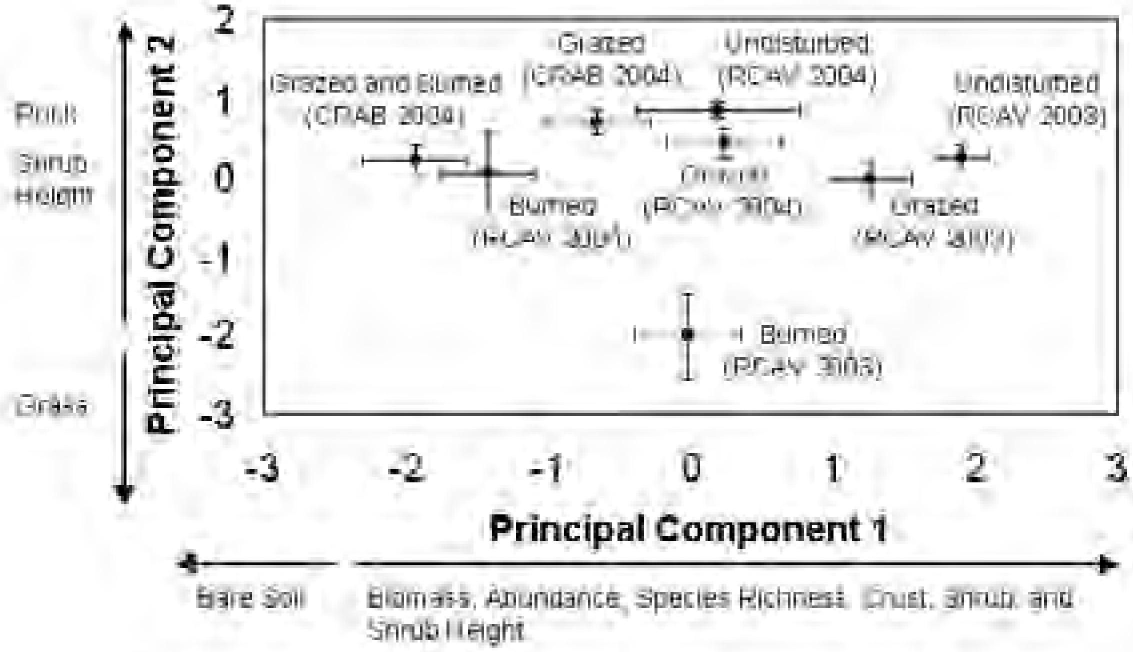

Figure 4. Plot characterizing disturbance categories (by study site and year) along principal components developed from habitat and prey characteristics. See Table 5 for description of principal components.

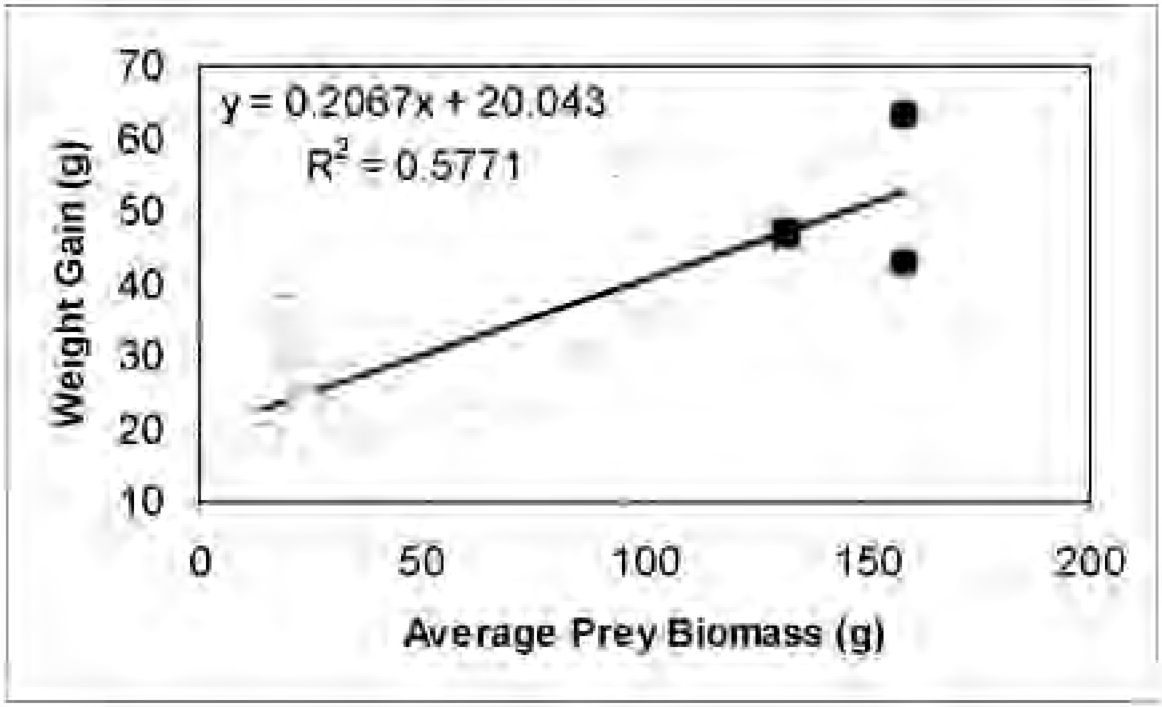

Figure 5. Weight gain by Great Basin rattlesnakes plotted against the average prey biomass in the core area of the snakes' home ranges. Circles represent snakes tracked in 2003 and squares represent snakes tracked in 2004. Shaded shapes represent snakes that used undisturbed areas and unshaded represent snakes that used distrubed areas (i.e., grazed, burned, or grazed and burned).

Appendix I. Movement characteristics of 30 Great Basin rattlesnakes tracked during 2003 and 2004.

Snake	Sex	Year	Days followed	Total Distance Moved (m)	Maximum Distance moved from Den (m)	Mean Distance moved per day (m)	Core Area (hectares)	Disturbance Category
CRAB1	F	2004	33	922	733	28	1.74	GB
CRAB2	F	2004	71	723	225	10	0.12	G
CRAB3	M	2004	39	334	1365	9	0.06	G
CRAB4	M	2004	59	967	611	16	2.32	GB
CRAB5	F	2004	65	2434	2220	37	28.97	G
CRAB6	F	2004	66	430	402	7	0.31	G
CRAB7	F	2004	67	3400	2220	51	20.28	GB
CRAB8	F	2004	52	1624	1227	31	10.42	GB
CRAB9	F	2004	71	5964	3160	84	15.68	G
RCAV1	F	2004	30	2986	2954	100	77.41	B
RCAV2	M	2004	31	1496	966	48	4.05	B
RCAV3	M	2004	69	5422	1524	79	11.90	B
RCAV4	F	2004	45	2765	1482	61	6.27	B
RCAV5	F	2004	71	2220	1339	31	11.33	U
RCAV6	M	2004	63	2885	911	46	3.5	B
RCAV7	F	2004	61	114	864	2	0.04	B
RCAV8	F	2004	48	995	880	21	5.6	B
RCAV9	F	2004	59	2915	1308	49	7.58	B
RCAV10	F	2004	51	1812	1418	36	11.96	B
RCAV11	F	2004	34	1989	1796	59	20.30	B
RCAV12	F	2003	102	12678	2495	124	11.58	U
RCAV6	M	2003	69	5502	1267	79	9.82	B
RCAV13	F	2003	98	4616	1364	47	5.22	U
RCAV14	F	2003	101	2534	652	25	0.92	B
RCAV15	M	2003	88	11525	967	130	3.41	U
RCAV16	M	2003	73	6364	1708	81	4.59	U
RCAV17	M	2003	80	10845	1596	135	11.29	U
RCAV18	M	2003	58	2844	995	49	3.09	U
RCAV19	F	2003	99	4831	1499	48	10.65	B
RCAV3	M	2003	67	4204	1199	62	2.05	B