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**POPULATION RESPONSE OF YEARLING GREATER SAGE-GROUSE TO THE
INFRASTRUCTURE OF NATURAL GAS FIELDS IN SOUTHWESTERN WYOMING**

Completion Report

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ABSTRACT

Energy development throughout the western United States has caused habitat changes resulting in local sage-grouse population declines. Sagebrush-dominated habitats in the Green River Basin of southwestern Wyoming have experienced extensive, rapid changes due to the development of natural gas fields. It is unclear whether population declines in natural gas fields are caused by avoidance or demographic impacts, and which age classes are most affected. We investigated habitat selection during the breeding season and demographics of greater sage-grouse to determine if natural gas development has influenced yearling male and yearling female populations in the Upper Green River Basin of southwestern Wyoming. Yearling males avoided leks near the infrastructure of natural gas fields when establishing breeding territories. Additionally, yearling males reared in areas influenced by infrastructure established breeding territories less often, were observed on leks during the breeding period less often, and had lower annual survival rates compared to yearling males reared in areas with no infrastructure. Yearling females avoided nesting within 930 m of the infrastructure of natural gas fields. Additionally, yearling females reared in areas influenced by infrastructure had lower annual survival rates than females reared in areas with no infrastructure. Our results suggest that development of natural gas fields will result in the loss of leks within developed areas and in the functional loss of nesting habitat within 930 m of infrastructure. Because both yearling dispersal from infrastructure and reduced demographics are contributing to abandonment of leks and nesting habitat within natural gas fields, we suggest that peripheral areas be protected from energy development and managed to sustain robust populations to ensure that greater sage-grouse may be available to re-colonize disturbed areas following reclamation.

INTRODUCTION

Populations of greater sage-grouse (*Centrocercus urophasianus*) throughout North America are one-half to one-third the size of those during the late 1960s (Connelly et al. 2004), and the species currently occupies 56% of its pre-European settlement distribution (Schroeder et al. 2004). Throughout Wyoming, greater sage-grouse populations declined an average of 5.2% annually between 1965 and 2003, and the average number of males per lek declined by 49% over that 38-year period (Connelly et al. 2004). Although factors responsible for declines vary regionally, Braun (1998) suggested that declines are primarily a result of human-caused habitat changes. The development of gas and oil fields throughout the western United States (U.S.) has been recognized as one of several anthropogenic changes associated with reduced sage-grouse (*Centrocercus* spp.) populations (U.S. Fish and Wildlife Service 2005).

Approximately 2.7 million ha of land managed by the U.S. Bureau of Land Management (BLM) in the western U.S. are currently in production status for oil, natural gas, or geothermal energy (Knick et al. 2003). A minimum of 25-28% of the total area delineated by a 50-km buffer around the pre-settlement distribution of sage-grouse was influenced by the infrastructure of oil or natural gas developments in 2003 (Connelly et al. 2004). Extraction of oil resources in Wyoming began in the early 1880s (Salt Creek and Dallas Dome oil fields), but industry emphasis has shifted to extraction of natural gas resources since the 1960s (Braun et al. 2002, Connelly et al. 2004; E. T. Rinkes, BLM Lander, Wyoming Field Office; personal communication). Connelly et al (2004) estimated that in 2003, 6 major fields producing oil and gas in the Greater Green River Basin of southwestern Wyoming covered over 8,740 km², and active and potential wells numbered approximately 7,890. The infrastructure associated with natural gas developments in the region is expected to increase by 40% by 2015 (Connelly et al. 2004). Existing and proposed oil and gas wells in Wyoming are primarily within landscapes dominated by sagebrush (*Artemisia* spp.; Knick et al. 2003), which are essential for persistence of greater sage-grouse populations.

In southwestern Wyoming, researchers have observed that as the distances between leks and the infrastructure of natural gas fields decrease and as the level of development surrounding leks increase, declines in lek attendance by males approached 100% (Holloran 2005). Walker et al. (2007) reported that only 38% of greater sage-grouse leks active in 1997 or later within coal-bed methane (CBM) fields in the Powder River Basin (PRB) of northeastern Wyoming and

southeastern Montana were still active in 2004-2005, compared to 84% of leks outside CBM fields. Active leks in CBM fields had 46% fewer males per lek than leks outside the fields (Walker et al. 2007). Similarly, Braun et al. (2002) found that the average number of males on leks within 0.4 km of CBM wells was significantly lower than leks greater than 0.4 km from CBM wells. Between 1983 and 1985, 3 lek complexes in southern Canada were disturbed by oil and gas activities within 200 m, and none of these leks have been active since disturbance (Braun et al. 2002, Aldridge and Brigham 2003). In northern Colorado, the overall decline in the number of males on 4 leks near the infrastructure of coal mines was 73% from peak numbers prior to development to approximately 3 years after an increase in mining activity; declines in the number of males were significantly higher than changes witnessed on non-impacted leks (Braun 1986, Remington and Braun 1991).

Impacts of energy developments on sage-grouse can include behavioral avoidance of anthropogenic disturbance and/or increased risk of mortality (Connelly et al. 2004). Lyon and Anderson (2003) observed that female greater sage-grouse nested significantly farther from leks disturbed by roads associated with natural gas fields compared to birds on leks in undisturbed areas in southwestern Wyoming. Significantly fewer females from disturbed leks nested within 3 km of the lek where they were captured compared to birds from undisturbed leks (Lyon and Anderson 2003). Additionally, Holloran (2005) suggested that nesting females avoided areas with high densities of natural gas wells (i.e., 16 ha well spacing). In the PRB, Doherty et al. (2008) concluded that greater sage-grouse avoided CBM wells located in otherwise suitable wintering habitat. At CBM well densities of 12.3 wells/4 km² greater sage-grouse were 1.3 times more likely to occupy sagebrush habitats with no CBM wells (Doherty et al. 2008). Greater sage-grouse in Canada avoided nesting in areas with high proportion of non-natural edge habitats, and brood-rearing females avoided areas with high densities of visible wells within 1 km (Aldridge and Boyce 2007). The authors noted that avoidance of human features effectively removed nesting habitat within a 1-km² area of these structures (i.e., functional habitat loss).

In Colorado, the probability of detecting Gunnison sage-grouse (*Centrocercus minimus*) declined as sagebrush patches became smaller and were situated closer to roads (Oyler-McCance 1999). Similarly, in southwestern Kansas, lesser prairie-chickens (*Tympanuchus pallidicinctus*) avoided wells and power lines, and the presence of high densities of either type of feature in areas with otherwise suitable habitat precluded use (Hagen 2003). The odds of a power line or

road occurring within a monthly-range were 3 times and 11% less likely than in a non-use range. Additionally, lesser prairie-chickens selected nesting sites farther from wellheads, improved roads, buildings (including natural gas compressor stations), and transmission lines than was expected at random (Pitman et al. 2005). Avoidance of anthropogenic features resulted in a functional loss of 58% of the total amount of suitable lesser prairie-chicken nesting habitat (Robel et al. 2004).

Adverse impacts of energy development to demographic parameters have also been noted. Lyon and Anderson (2003) suggested that nesting propensity was significantly lower for females breeding on leks disturbed by roads associated with natural gas fields compared to females in undisturbed areas. The risk of chick mortality among greater sage-grouse increased by a factor of 1.5 for each additional well visible within 1 km of brooding locations (Aldridge and Boyce 2007). Population growth rates of greater sage-grouse and lesser prairie-chickens influenced by energy development were less than growth rates of non-impacted populations (Hagen 2003, Holloran 2005). Both authors suggested that lower population growth rates were primarily due to lower survival and nesting success in the impacted populations.

Research has suggested that energy developments can cause the loss of affected populations. Remington and Braun (1991) suggested that greater sage-grouse population declines in areas near coal mines may have been caused by displacement of yearlings to leks situated away from development. Holloran and Anderson (2004) were able to reproduce observed declines in the number of males occupying 3 natural gas development-impacted leks in southwestern Wyoming by assuming adult male tenacity and minimal yearling male recruitment. A delayed shift in nesting habitat selection away from the infrastructure has been documented in southwestern Wyoming, a pattern consistent with adult females showing nest-site fidelity and yearling females avoiding gas fields (Holloran 2005). Although these studies suggest that the elimination of populations from energy fields may have resulted from the reaction of the yearling cohorts to developments, the response of yearling greater sage-grouse to development of natural gas fields has not been quantified. It is important to determine if yearlings are being primarily displaced or if development negatively influences demographics as these scenarios suggest different mitigation alternatives.

Our objectives were to determine if natural gas development influences habitat selection and demographics of yearling male and yearling female greater sage-grouse in southwestern

Wyoming. We investigated habitat selection and demographics relative to the locations of drilling rigs, producing well pads, and main haul roads. For males, we investigated the location of leks where yearlings established breeding territories, date of territory establishment, breeding-period lek tenacity, and annual and seasonal survival probabilities for both the yearling male cohort overall and for yearlings of known maternity. For females, we investigated nesting habitat selection, nesting propensity, dates-of-nest establishment, nest success, chick productivity, and annual and seasonal survival for both the overall yearling female cohort and for yearlings of known maternity.

STUDY AREA

The study area (42°60' N, 109°75' W) encompassed 17 leks primarily within the boundaries of the Pinedale Anticline Project Area (PAPA) and portions of the Jonah II gas field in the upper Green River Basin in southwestern Wyoming (Figure 1; Bureau of Land Management 2000). The study area covered approximately 255,000 ha (2,550 km²) dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) shrub-steppe habitats. Elevation ranged from 2,100 to 2,350 m and annual precipitation averaged 27.3 cm (Western Regional Climate Center, Reno, NV). Natural gas development and livestock grazing were the predominant human uses of the area (Bureau of Land Management 2000).

FIELD METHODS

We captured female greater sage-grouse on and near leks from mid-March through April in 2004 and 2005 by spot-lighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We secured radio transmitters to females with PVC-covered wire necklaces (Advanced Telemetry Systems Inc. [ATS], Isanti, MN, USA). Transmitters weighed 19.5 g, had a battery life expectancy of 530 days, and were equipped with motion sensors (i.e., radio-transmitter pulse rate increased in response to inactivity).

We used hand-held receivers and 3-element Yagi antennas (ATS) to monitor radio-marked females at least twice weekly through pre-laying (April) and nesting (May-June). We located nests of radio-marked birds by circling the signal source until females could be directly observed. We monitored incubating females after nest identification from a distance of ≥ 60 m to minimize chances of human-induced nest predation or nest abandonment. We established nest

fate (successful or unsuccessful) when radio monitoring indicated that the female had left the area. We considered nests successful if ≥ 1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). We monitored unsuccessful females twice weekly for 2 weeks following nest failure to detect re-nests.

We located females that nested successfully 14 days post-hatch. We considered females with ≥ 1 chick to have been successful through the early brood-rearing stage. We based chick existence on either visual confirmation of chick(s) or the reaction of brooding females to the presence of a potential predator (i.e., the researcher; Schroeder et al. 1999). We relocated females for which no live chicks were detected at 14 days post-hatch 2 to 4 days following the initial location to confirm brood loss.

We monitored females that successfully raised ≥ 1 chick through the early brood-rearing stage from ≥ 100 m at least twice weekly through 10 weeks post-hatch. In late summer 2004 and 2005, we captured male and female chicks (e.g., hatch-year birds) that were ≥ 10 weeks old by spot-lighting radio-equipped brood-rearing females. We captured chicks with the brooding females using hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). We weighted captured chicks to ensure that radio transmitters could be safely attached (Caccamise and Hedin 1985). We sexed captured chicks based on weights or plumage and aged the birds (to ensure captured grouse were hatch-year birds) based on the shape of the outermost wing primaries (Eng 1955). We collected blood samples by clipping the middle toenail and stored blood on Whatman FTA micro cards (Whatman 2005). We secured 16- or 19.5-g radio transmitters (depending on chick weight) to chicks with PVC-covered wire necklaces (ATS). Transmitters had battery life expectancies of 500 or 530 days, respectively, and were equipped with motion-sensors. We considered radio-equipped male chicks that survived to 1 March and female chicks that survived to 1 April the spring following capture the yearling sample.

Yearling Males

We collected lek visitation data for yearling males using data-logger stations (ATS) situated near 17 leks throughout the study area (Figure 1). Data loggers allowed for constant monitoring of leks during the breeding season. Radio-equipped yearlings visiting a monitored lek were recorded as being on or near that lek at specific dates and times.

Data Loggers.--Data-logger stations consisted of 1 data logger run by 2 deep-cycle recreational vehicle (RV) gel batteries charged by solar panels; all equipment was housed in metal Knaack® boxes. We mounted omni antennas on steel casing pipe such that the top of the antenna was 3 m high. Data loggers were attenuated (i.e., calibration of data logger sensitivity) to detect the entire area utilized by strutting males, and situated to minimize detection of birds using non-strutting habitat surrounding leks. We set data loggers to scan for ATS transmitters (Model A4000) with 35 and 45 pulse per minute (PPM) signals. Due to the possible effects of cold weather on transmitter pulse rates, we allowed a tolerance of 1 (e.g., 35 PPM: 34-36 was recorded; 45 PPM: 44-46 was recorded). We directly accessed stations when leks were not occupied (e.g., non-crepuscular periods) and downloaded data loggers to a laptop computer at least twice during the breeding season. We placed reference transmitters at each data-logger station to verify logging accuracy on all downloads. We monitored leks annually from 1 April to 15 May.

Lek Counts.--Annual lek counts on the 17 monitored leks were conducted by personnel from the Wyoming Cooperative Fish and Wildlife Research Unit (COOP), the Wyoming Game and Fish Department (WGFD), and the Pinedale field office of the BLM. Lek counts were conducted according to standardized methods outlined by the WGFD's Sage-Grouse Technical Committee (Cheyenne, WY, USA; also see Connelly et al. 2003:19-20).

Survival.--We used hand-held telemetry equipment (ATS) to locate yearling males during the breeding season to assess survival. Annual survival for yearling males was assessed from 1 March through the end of February. We assessed survival directly between 1 April and 15 May by locating males weekly. From 15 May through August, we located males from long-range bi-weekly and used transmitter pulse-rates (e.g., motion sensors) to assess survival. Survival from 1 September through March was assessed using fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA; Sky Aviation, Dubois, WY, USA). Flights were conducted at least bi-monthly and we used motion-sensors to evaluate whether individuals were dead or alive.

Yearling Females

Demographics.--We assessed yearling female demographics similarly to those described for the original sample of radio-equipped females. We used hand-held telemetry equipment (ATS) to locate nests by circling the signal source until females could be directly observed. We

monitored incubating females from a distance of ≥ 60 m to minimize abandonment risks. Nest fate (successful or unsuccessful) was established when radio monitoring indicated that the female had left the area; we considered nests successful if ≥ 1 egg hatched, indicated by presence of detached eggshell membranes (Wallestad and Pyrah 1974). We monitored unsuccessful yearling females twice weekly for 2 weeks following nest failure to assess re-nesting attempts.

We located yearling females that nested successfully weekly from hatch through 35 days post-hatch. We considered females with ≥ 1 live chick to have been successful through each brooding stage. We based chick existence during the early brooding stage (i.e., hatch through 2 weeks post-hatch) on either visual confirmation of chick(s) or the reaction of brooding females to the presence of a potential predator (i.e., the researcher; Schroeder et al. 1999). During the 2005 late-brooding stages, we obtained fledge estimates (i.e., the number of chicks per brood) by spot-light surveys conducted during trapping. In 2006, we obtained fledge estimates from spot-light surveys conducted 35 days post-hatch (Walker et al. 2006). We relocated females found without live chicks during any of these stages 2 to 4 days following the initial location to confirm brood loss.

Survival.--We assessed annual survival for yearling females from 1 April through March. We located all females twice weekly between 1 April and hatch (approximately 15 June), and brooding females weekly from hatch through August. We assessed survival directly from observations during these periods. We monitored barren females from long-range weekly from nest loss through June, and bi-weekly from July 1 through August; motion sensors were used to evaluate barren female survival during these stages. We assessed survival from 1 September through March for all females from fixed-wing aircraft (Mountain Air Research, Driggs, ID, USA; Sky Aviation, Dubois, WY, USA). Flights were conducted at least bi-monthly and we used the motion sensors to evaluate whether individuals were dead or alive.

STATISTICAL METHODS

Infrastructure of Natural Gas Fields

We mapped features of the infrastructure of natural gas fields within 5 km (Holloran and Anderson 2005) of the 17 monitored leks using ArcGIS 9 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA). We mapped producing well pads, drilling rigs, and main haul roads; state highways, the Paradise Road, and the Green River Road were included as main

haul roads (Figure 1). We obtained infrastructure location, drilling activity date, and well producing date information from the Wyoming Oil and Gas Conservation Commission and verified these data using information supplied by Western Ecosystems Technology, Inc. (Cheyenne, WY, USA), Edge Environmental, Inc. (Laramie, WY, USA), individual gas companies (i.e., operators) responsible for specific wells, and through direct ground-truthing using hand-held, 12 channel, Garmin RINO 110 Global Positioning System units (Garmin International, Olathe, KS, USA). Infrastructure data were dynamic and were modified to reflect the conditions encountered seasonally. We considered well pads with multiple producing wells single active locations.

Maternity

We established yearling maternity using microsatellite polymerase chain reaction (PCR) analyses of DNA extracted from blood samples collected during trapping (Taylor et al. 2003, Hawk et al. 2004); 5 primers were used in the analysis (LLSD4, LLSD8, LLST1, SGCA11, and SGCTAT1; Wyoming Game and Fish Laboratory, Laramie, WY, USA). We obtained genotypes following methods described by Frantz et al. (2003). We determined maternity using program Cervus 3.0.3 (Marshall et al. 1998). The simulated population genetic structure was based on 10,000 simulations with 5,000 potential parents, 1% of the candidate parents sampled, and 25% relatedness. Candidate mothers were all females identified by the analysis with $\geq 80\%$ confidence in parentage assignment. We based final maternal assignment on trap location; if a chick was trapped from the same flock as a candidate mother, maternity was assigned.

We estimated natal areas as the area within 1.9 km of natal nests. We used this distance because 1.9 km represents the mean radius of home ranges during early brood-rearing (Drut et al. 1994) and the upper 95% confidence limit of the mean distance from nest to early brood-rearing locations (Lyon 2000, Slater 2003). We defined natal treatment yearlings as any yearling whose natal area contained >1 producing well pad or >1 km of main haul road; all others were considered natal control yearlings. The inclusion of natal areas with 1 well or a short distance of main haul road in the control population was to guard against including yearlings raised in areas with isolated well pads (e.g., wildcat wells) as treatment birds.

Greater Sage-grouse Yearling Variables

Survival.--We estimated yearling male annual (March-February), yearling female annual (April-March), and monthly survival estimates and standard errors using the staggered entry Kaplan-Meier estimator (Pollock et al. 1989). We censored birds that were not found during any monthly period. We combined monthly survival estimates into sexually distinct seasonal periods: for males, breeding (Mar.-May), summer (June-Aug.) and winter (Sept.-Feb.); and for females nesting (April-June), summer (July-Aug.) and winter (Sept.-Mar.).

Overall Lek Recruitment.--We estimated overall lek recruitment of males annually from lek counts. We estimated the number of males recruited to a lek as the annual change in the maximum number of males minus the number of adult males expected to return to a lek the following year (37%; Zablán et al. 2003).

Yearling Male Demographics.--We based lekking demographics of yearling males on information from data loggers or telemetry. Logged signals consisted of the date, time, transmitter frequency, signal strength, number of pulses recorded in 15 seconds, transmitter pulse-per-minute (PPM) value, and the number of pulse matches (ATS algorithms). The steps taken for distinguishing radio-transmitter detection versus interference included: (1) signals that logged at a PPM outside the range of values set for the data-logger were discounted as interference (e.g., PPM <34, 37-43, >47). (2) Given transmitter pulse rates of either 35 or 45 PPM, the data-loggers accepting pulse rates of 36 and 46 PPM, respectively for these transmitter types, and a 15 second scan time, the number of pulses detected for 35 PPM transmitters had to be ≤ 9 ($[36 \text{ PPM}/60 \text{ sec}] \times 15$) and for 45 PPM transmitters ≤ 12 ($[46 \text{ PPM}/60 \text{ sec}] \times 15$); if the number of pulses matched was outside these ranges, logged signals were discounted as interference. Logged signals remaining were potential birds. We primarily used pulse match to pulse detected ratios (e.g., the number of matched pulses relative to the number of detected pulses) and the number of logs over a given time period to validate remaining detections as birds. We established the protocol for assessing bird probabilities using pulse match-to-detected ratios and the number of detections by evaluating data from reference collar logs. Reference collar downloads suggested a high pulse match-to-detected ratio, numerous detections, and a recorded pulse count >4 and <30 was a validated detection of a radio-transmitter and not interference. Numerous logs by the same frequency, especially numerous within the same relative time period, with high pulse match-to-detected ratios, had higher potential to be a confirmed bird detection.

We did not consider those frequencies only logged once as bird detections until compared with future data and telemetry locations. We consulted ATS experts for verification of questionable data. We considered confirmed yearling male detections between 0430 and 0730 hours daily lek visits.

The average date that radio-equipped yearling males were first documented on established leks was April 8; thus yearlings were available to be logged for 37 days. Because yearling male daily lek attendance rates in a previous study averaged 19% (Walsh et al. 2004), we considered a bird to have established on a particular lek if it had ≥ 7 confirmed daily lek visits during the monitoring period. We assessed lek establishment of males not detected on data-logger-monitored leks using telemetry data. A yearling male had to be detected on a lek ≥ 3 times during the crepuscular daily breeding period between 1 April and 15 May to verify establishment. The date of establishment was estimated as the first day yearling males were documented on the lek where established. Yearling male lek tenacity was estimated as the total number of confirmed daily lek visits on the lek where established. The number of different leks visited by yearling males was estimated as the number of leks with ≥ 1 confirmed daily lek visit(s), and included leks where established. We only estimated establishment dates, lek tenacity, and number of different leks visited for yearlings that visited leks monitored by data-loggers.

Distance from natal nest-to-established lek was estimated as the straight-line distance from the nest site where a yearling male hatched to the lek where he established the following spring. The probability of establishing a breeding territory on a lek was estimated as the number of yearling males with confirmed lek establishment divided by the total number of available males. Available males survived the breeding season and were those we actively attempted to document establishment leks using telemetry (i.e., those monitored during the breeding season).

Nest Site Designations (Yearling Females).--Females that nested within 930 m of an infrastructure feature of a natural gas field were considered to have been potentially influenced by infrastructure (i.e., nesting treatment females); those nesting outside the 930-m buffer were considered nesting control females (Figure 2). The 930-m buffer represented the upper limit of the 95% confidence interval around mean distances between consecutive year's nests and, due to nesting area fidelity, represented a female's life-time nesting area (Holloran and Anderson 2005).

Natal nesting areas were an estimate of the area around the natal nest where a yearling female will usually select a nest location. We used the upper limit of the 95% confidence interval around the mean natal nest-to-yearling nest distances for females raised in areas without the infrastructure of natural gas fields to establish the natal nesting area.

Yearling Female Demographics.--Nesting propensity was estimated as the number of females initiating a nest divided by the total number of yearlings intensively monitored throughout the entire nesting season. We did not include females found for the first time after 15 May annually in nesting propensity estimates (15 May represented the latest date of incubation initiation based on mean latest hatch date and 27 days to incubate a clutch [Schroeder et al. 1999]). The date of nest establishment was the first day females were documented on a nest. Apparent nest success was the number of successfully hatched nests divided by the total number of known nests. Early brood-rearing success was the number of females successfully raising ≥ 1 chick through 14 days post-hatch divided by the total number of successfully nesting females monitored through the early brood-rearing period. Overall brood-rearing success was the number of females successfully fledging ≥ 1 chick divided by the total number of successfully nesting females that were monitored throughout the entire brood-rearing period. Natal nest-to-yearling nest distances were estimated as the straight-line distance from the nest site where a yearling female hatched to her first nest the following spring.

Yearling Male Comparisons

We investigated overall male recruitment to monitored leks and radio-equipped yearling male lek establishment relative to the distance of leks to infrastructure of natural gas fields. We also investigated yearling male lek establishment demographics and survival relative to infrastructure impacts to natal areas.

Overall Recruitment.--We used Chi-square tests with continuity corrections (due to sample sizes < 25 in certain instances; Dowdy and Wearden 1991) to compare overall recruitment of males among leks. Although we assumed that the number of recruited males was related to lek size, the relationship was probably not 100% correlated. Therefore, we established expected proportions using a scaled allocation of the total recruited population. Leks with ≤ 50 total males the preceding year were expected to recruit either 4.5 or 5%, leks with > 50 and ≤ 100 males were expected to recruit either 7 or 8.5%, and leks with ≥ 100 males were expected to recruit either 9.5

or 12.25% of the total recruited population. We used different proportions annually because some of the leks changed size categories between years, and we needed the total proportion of the expected population to sum to 100%. We categorized leks as those recruiting more, less, or equal to the expected number of males. We compared categories by distance to closest active drilling rig, producing well pad, and main haul road using 95% confidence interval overlap.

Lek Establishment.--We generated minimum convex polygons (Kenward 1987) around all producing well pads, and categorized monitored leks as either: contained within the polygon, ≤ 2 km outside, between 2 and 5 km outside, or >5 km outside the polygon. We used Chi-square tests with continuity corrections (Dowdy and Wearden 1991) to compare the number of radio-equipped yearling males establishing on leks by category (i.e., observed establishment). We assumed equal availability between leks for each yearling male, thus expected proportions were based on the total number of leks within each buffer. We compared dates-of-establishment, lek tenacity, and annual and seasonal survival by buffer using 95% confidence interval overlap.

Natal Areas.--We compared the probability of establishing a breeding territory on a lek between natal treatment and natal control yearling males using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We determined the expected establishment rate from the control population (e.g., results suggest a difference between natal treatment and natal control groups). We compared the number of different leks visited during the breeding season, the distance from natal nest-to-established lek, dates-of-establishment, lek tenacity, and annual and seasonal survival by natal area category using 95% confidence interval overlap.

Yearling Female Comparisons

General Habitat Selection.--We investigated habitat selection of yearling females relative to infrastructure features of natural gas fields by comparing nesting treatment and nesting control females using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We estimated the expected number of nests per category as the proportion of the total area within 5 km of trapped leks (Holloran and Anderson 2005) that was within 930 m of an infrastructure variable (Figure 2). We only considered nests located within the 5-km buffer in the comparison.

We assumed suitable nesting habitats were sagebrush and desert shrub-dominated areas within 2 standard deviations of the mean roughness of nest sites located within the 5-km buffer

between 2000 and 2006 (Holloran 2005). Jensen (2006) suggested roughness (i.e., the ratio of actual surface area to planimetric area) was the terrain measure best distinguishing greater sage-grouse nests from available locations in southwestern Wyoming. We used Gap Analysis Program (GAP) landcover layers (Wyoming Geographic Information Science Center (WyGISC), University of Wyoming, Laramie, WY, USA) to identify sagebrush and desert shrub-dominated areas, and Hawth's Analysis Tools 3 (Beyer 2004) within ArcView 3 (ESRI, Redlands, CA, USA) to calculate roughness from digital elevation models (DEM; WyGISC). We compared the proportion of suitable nesting habitat within 930 m of infrastructure and outside of the 930-m buffer but within the 5-km buffer to investigate if the proportion of suitable habitat in compared areas differed.

Overall Demographics.--We used nesting or spring locations to categorize all yearling females as treatment (i.e., within 930 m of infrastructure) or control individuals (Figure 2). Differences in nesting propensity, apparent nest success, early brood-rearing success, and overall brood-rearing success were investigated using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We established expected proportions from the control population (e.g., results suggest a difference between treatments and controls). The date of nest establishment, and annual and seasonal survival were compared between categories using 95% confidence interval overlap.

Natal Areas.--We compared nesting propensity and apparent nest success between natal treatment and control yearling females using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We determined expected nesting propensity and success rates from the control population. Distances from the natal nest to the yearling's nest, date of nest initiation, and annual and seasonal survival differences between treatment and control populations were compared using 95% confidence interval overlap.

To examine nest site selection of yearling females relative to where they were raised and the existence of infrastructure features of natural gas fields, we compared the proportion of yearlings with infrastructure in the natal nesting area (i.e., the area around the natal nest where a yearling female will usually select a nest location) that nested within and beyond 930 m of infrastructure using Chi-square tests with continuity corrections (Dowdy and Wearden 1991). We used all natal nesting areas with infrastructure present in the analysis. We estimated the expected number of nests per category (i.e., within or beyond 930 m of infrastructure) as the

proportion of the total natal nesting area (i.e., all natal nesting areas with gas field infrastructure present combined) within 930 m of infrastructure.

Because of relatively small sample sizes and the possibility that single measures could disproportionately influence results, we identified influential observations and considered those when interpreting results. We performed statistical procedures with MINITAB 13.1 (Minitab Inc., State College, PA, USA). We estimated distance variables (km) using ArcGIS 9 (ESRI).

RESULTS

We radio-tagged 64 male and 76 female chicks (45 males and 39 females during fall 2004; 19 males and 37 females during fall 2005). Between capture and yearling status designation, 41 chicks died, 7 lost the radio-transmitter (based on field sign at retrieved transmitter location), and 6 were never found. Thirty-four male and 52 female radio-equipped chicks were available as yearlings at the beginning of the breeding season monitoring periods. Maternity was confirmed for 16 male and 17 female yearlings, and breeding-season data were collected on 15 males and 16 females with known maternity.

Because of sample size constraints, we chose to use conservative statistical approaches when comparing treatment and control groups of yearlings.

Yearling Male Comparisons

Overall Recruitment.--Leks that recruited fewer than expected males were significantly closer to producing well pads, and tended to be closer to main haul roads compared to leks that recruited the same number of males as expected. Generally, greater sage-grouse leks that recruited significantly less than expected numbers of males were closer to infrastructure features of natural gas fields than those that recruited equal to or significantly more males than expected. Leks that recruited more than expected males were consistently closer to infrastructure than those that recruited the same number of males as expected (Table 1; Figure 3).

Lek Establishment.--The proportion of radio-equipped yearling males that established on leks inside and outside the development boundaries (as designated by minimum convex polygons around producing well pads) of the natural gas field differed significantly from that expected assuming equal establishment probabilities for all leks ($\chi^2_1 = 4.54$; $P = 0.03$; Table 2). Yearling males establishing on leks within the interior (2) were less than expected (7.4), while numbers

establishing on leks outside the development boundaries (23) were more than expected (17.6). The number of radio-equipped yearling males that established on leks outside development and categorized by distance to the development boundary did not differ from expected ($\chi^2_2 = 0.12$; $P = 0.94$; Table 2).

Mean date of establishment, lek tenacity, and annual survival of yearling males did not differ inside and outside gas fields (Table 2).

Natal Areas.--Lek tenacity of natal treatment and natal control yearling males did not differ. However, after removing a natal treatment male (e.g., male reared in an area with infrastructure of natural gas fields present) that was documented on a lek 2.5 times as often as any other treatment male, lek tenacity of treatment males (9.3 days) was significantly less than control males (22.8 days; Table 3). Annual survival of natal treatment yearling males (52.5%) was significantly lower than natal control yearling males (100%; Table 3). Additionally, although not significantly different ($\chi^2_1 = 1.53$; $P = 0.22$), the estimated probability of natal treatment yearling males establishing on a lek was half that of natal control yearling males; 7 of 7 control yearling males and 4 of 8 treatment yearling males established breeding territories. The number of different leks visited during the breeding season, distance from natal nest-to-established lek, dates-of-establishment, and seasonal survival probabilities did not differ between natal treatment and control yearling males (Table 3).

Yearling Female Comparisons

General Habitat Selection.--The proportion of radio-equipped yearling females that selected nest locations within 930 m of an infrastructure feature of the natural gas fields and those nesting outside the 930-m buffer differed significantly from that expected assuming spatially proportional selection of nest locations ($\chi^2_1 = 4.10$; $P = 0.04$). The number of yearling female nests located within 930 m of infrastructure (6) was less than expected (11.5), while nest numbers located outside the buffer (19) were more than expected (13.5). The proportions of area assessed to be suitable nesting habitat within (75.1%) and outside (80.9%) the 930-m buffer were similar.

Overall Demographics.--Nesting propensity, apparent nest success, early brood-rearing success, and overall brood-rearing success did not differ between treatment (i.e., nesting within 930 m of gas field infrastructure) and control individuals ($\chi^2_1 < 0.12$; $P > 0.72$; Table 4). Date of

nest establishment and annual survival were not related to nest location treatment status (Table 4).

Natal Areas.--Annual survival of natal treatment yearling females (69.4%) was significantly lower than natal control yearling females (100%; Table 5). Nesting propensity and nest success probabilities were not related to natal area ($\chi^2_1 < 0.13$; $P > 0.71$; Table 5). Natal nest-to-yearling nest distances, nest initiation dates, and seasonal survival did not differ between natal treatment and control yearling females (Table 5).

The upper limit of the 95% confidence interval around the mean natal nest-to-yearling nest distances for natal control females suggested that a 4.0-km buffer around natal nesting locations represented the area around the natal nest where a yearling female typically selected a nest location (i.e., natal nesting area; Table 5). There was weak evidence that the proportion of natal yearling females reared near infrastructure that selected nest locations within 930 m of infrastructure and those that nested outside the 930-m buffer differed from that expected assuming spatially proportional selection of nest locations ($\chi^2_1 = 3.49$; $P = 0.06$). The number of yearling female nests located within 930 m of infrastructure (3) was less than expected (6.3), while nest numbers located outside the buffer (7) were more than expected (3.7).

DISCUSSION

Energy development impacts to greater sage-grouse populations typically result from a combination of demographic and behavioral responses (i.e., cumulative effects) affecting different age classes. Our results suggest that avoidance of infrastructure by breeding yearlings, decreased yearling survival, and reduced fecundity of yearling males contribute to abandonment of leks and nesting habitat within natural gas fields.

Greater sage-grouse leks situated near the infrastructure of natural gas fields recruited fewer males than expected. Because of lek tenacity by adult males (Patterson 1952, Wiley 1973, Gibson 1992), a majority of the birds recruited were probably yearling males. There was also a tendency for leks situated on the periphery of the fields to recruit a higher proportion of yearling males than those farther from disturbance, suggesting that yearling males avoid natural gas fields and move to the periphery of the fields when establishing breeding territories. Additionally, yearling males reared in areas with infrastructure features of natural gas fields were less likely to establish a breeding territory, did not occupy leks during the breeding period as tenaciously, and

had lower annual survival than males reared in areas with no activities associated with natural gas fields. Dunn and Braun (1985) suggested that leks selected by yearling males were spatially associated to natal areas. Thus, decreased fecundity may be in response to anthropogenic activity encountered either as chicks, or in response to conditions encountered during inaugural breeding seasons. Regardless, natural gas development appeared to influence negatively both the breeding-season distribution and success of the yearling male population.

Greater sage-grouse yearling females generally avoided nesting within 930 m of the infrastructure of natural gas field. Yearling females with natural gas infrastructure present in their natal nesting area also generally avoided nesting within 930 m of infrastructure; this general avoidance results in the functional loss of at least the habitats within 930 m of infrastructure. However, distance from natal-nest to first-year-nest locations did not differ, suggesting that yearling females did not vacate natal areas but simply avoided nesting near infrastructure within natal areas. Holloran (2005) suggested that the eventual response of greater sage-grouse nesting populations will be avoidance of natural gas development, but the avoidance response would be driven by habitat selection of yearling females due to nesting-area fidelity of adult females. Further, Wiens et al. (1986) suggested that site fidelity in breeding birds could delay population response to habitat changes, and that a clear response required that most site-tenacious individuals be dead. Fidelity of adults to nesting areas and fidelity of yearlings to natal areas may delay a population-level avoidance response, and may explain time lags between the development of gas fields and the abandonment of gas fields by greater sage-grouse found in previous studies (Holloran 2005, Walker et al. 2007).

Yearling females reared in areas with natural gas infrastructure had lower annual survival rates than females reared in areas without infrastructure. However, we detected no negative effects of natal-area condition on productivity. These results are similar to analyses investigating population growth differences between anthropogenically disturbed and undisturbed populations that attributed differences in population growth to lower female annual survival in impacted populations (Hagen 2003, Holloran 2005). Natural gas development appeared to influence negatively both the nesting-season distribution and annual survival of the yearling female population.

MANAGEMENT IMPLICATIONS

The results from this study suggest that dispersal of yearling greater sage-grouse from the infrastructure of natural gas fields and demographic impacts are contributing to abandonment of leks and nesting habitat within natural gas fields. This implies that developing a natural gas field reduces the extent of the landscape used by sage-grouse populations. Sage-grouse populations typically inhabit large, unbroken expanses of sagebrush and are characterized as a landscape-scale species (Patterson 1952, Connelly et al. 2004). Thus, preserving sagebrush-dominated areas within an impacted landscape as refugia may be necessary to maintain remnant sage-grouse populations. To ensure that viable populations are conserved, we recommend managers rely on seasonal habitat selection and movement information collected from individual sage-grouse residing in proposed refugia to determine appropriate refugia size and configuration. Additionally, if impacts continue through the gas field production phases as suggested by Aldridge and Brigham (2003) and Walker et al. (2007), refugia will have to be maintained until developed areas are re-occupied by sustainable sage-grouse populations (gas well life-expectancy estimated at 25 to 40 years for the types of formations encountered in the PAPA; Wyoming Oil and Gas Conservation Commission, personal communication 2005).

Dispersal corridors may be needed to ensure the maintenance of the genetic diversity of sage-grouse populations potentially isolated into refugia, and to allow for immigration if a stochastic natural event (i.e., drought, fire, disease outbreak) eliminates a protected population. Sage-grouse can disperse long distances between seasonal ranges (Connelly et al. 2000*b*), and are physically capable of traversing natural gas fields. However, because of strong adult fidelity to breeding sites (Patterson 1952, Wiley 1973, Gibson 1992, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005) and the propensity of yearling females to nest near natal areas, large-scale movements of individuals does not necessarily equate to the dispersal of genetic material nor the functional immigration of individuals. If genetic diversity is maintained through the dispersal of yearling males, and yearlings tend to establish breeding territories on leks near natal areas, the abandonment of leks situated between distinct population segments may genetically isolate those segments. We recommend research investigating the mechanisms responsible for the dispersal of greater sage-grouse genetic information throughout a landscape.

Sage-grouse survival and fecundity have been linked to sagebrush-steppe habitat quality, and the dependence of the species on sagebrush through all seasonal periods has been well

documented (see Connelly et al. 2004 for review). Sagebrush habitat enhancements typically entail manipulation of shrub overstories in an attempt to increase herbaceous understories and improve brood survival (e.g., prescribed fire, herbicide application). However, no research to date has shown a positive response of sage-grouse populations to sagebrush treatment (Wallestad 1975, Martin 1990, Fischer et al. 1996). In fact, large-scale shrub manipulations, particularly in winter, nesting, or year-round habitats may result in population declines (Swenson et al. 1987, Connelly et al. 2000a, Nelle et al. 2000). We recommend that land managers exercise extreme caution in applying shrub manipulations (Connelly et al. 2000b, Dahlgren et al. 2006), and focus instead on management options that enhance or restore herbaceous understories within sagebrush stands (e.g., via livestock grazing management [Beck and Mitchell 2000]). The establishment of interconnected refugia managed to sustain robust populations will help ensure that greater sage-grouse are present to re-colonize natural gas fields following reclamation.

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Table 1. Mean (95% confidence interval [95% CI]) distance (km) from greater sage-grouse leks to natural gas field infrastructure in southwestern Wyoming, 2005-06. Leks were categorized as recruiting significantly less than, equal to, or more than expected numbers of males based on Chi-squared analyses of annual changes in the maximum number of males documented on leks during lek count procedures. Notice that leks recruiting fewer than expected males were those relatively close to gas field infrastructure and that leks recruiting more than expected males tended to be closer to development than those recruiting the same number of males as expected (suggesting yearling dispersal to the periphery of developing energy fields).

Relative Number of Males Recruited	n ^a	Distance Drill Rig		Distance Well Pad		Distance Haul Road	
		mean	95% CI	mean	95% CI	mean	95% CI
Less than expected	11	3.6	(2.4, 4.8)	1.7	(0.6, 2.7)	2.2	(1.0, 3.4)
Equal to expected	10	6.1	(4.0, 8.2)	5.0	(2.9, 7.1)	4.0	(3.2, 4.8)
More than expected	9	5.9	(3.8, 8.0)	4.0	(2.0, 5.9)	3.6	(2.0, 5.1)

^a Total number of lek years.

Table 2. Establishment locations and breeding season demographics (means and 95% confidence intervals [95% CI]) of yearling male greater sage-grouse establishing breeding territories on leks categorized by lek-to-natural gas field development distances in southwestern Wyoming, 2005-06. Notice that leks situated within the development boundaries of the natural gas fields recruited fewer yearling males than expected.

Lek-to-Development Distance Categories ^a	Number of Males		Date of Establishment ^e		Lek Tenacity ^f		Annual Survival ^g	
	n ^b	Established ^c Expected ^d	mean	95% CI	mean	95% CI	mean	95% CI
Within Development	10	2 7.4	4/1	N/A ^h	37.5	(24.8, 50.2)		
Between 0 and 2 km of development	10	11 7.4	4/9	(4/3, 4/16)	21.9	(15.1, 28.7)	83.3	(64.8, 101.8)
Between 2 and 5 km of development	4	3 2.9	4/11	(3/23, 4/30)	27.3	(14.9, 39.7)		
More than 5 km from development	10	9 7.4	4/8	(4/2, 4/14)	19.6	(13.5, 25.6)	100	N/A ^h

^a Development represents the area within a minimum convex polygon (Kenward 1987) around all producing well pads.

^b Total number of lek years within buffer distance.

^c Number of yearling males documented on a lek for at least 7 days.

^d Number of yearling males expected on leks with the buffer based on the total number of lek years (i.e., leks equally available for establishment by yearling males).

^e First date established yearling males documented on lek.

^f Total number of days established yearling males documented on lek.

^g Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989); because of sample sizes, annual survival was not estimated for males establishing within the buffer, and males establishing on leks more than 2 km from development were combined.

^h Standard error = 0.

Table 3. Mean (95% confidence interval [95% CI]) of breeding season demographics of yearling male greater sage-grouse reared within 1.9 km of natural gas field infrastructure (natal treatment males) compared to yearling males reared in areas with limited natural gas field infrastructure (natal control males) in southwestern Wyoming, 2005-06. Notice that lek tenacity and annual survival were lower for natal treatment yearling males.

Male Demographic	Natal Treatment Males			Natal control Males		
	n	mean	95% CI	n	mean	95% CI
Leks visited ^a	7	1.86	(1.3, 2.4)	7	1.57	(1.2, 2.0)
Natal nest-to-lek distance ^b	4	4.76	(1.2, 8.3)	7	7.38	(1.5, 13.3)
Natal nest-to-lek distance_2 ^c	4	4.76	(1.2, 8.3)	6	5.02	(1.5, 8.5)
Date of establishment ^d	4	4/5	(3/28, 4/12)	6	4/11	(4/2, 4/19)
Lek tenacity ^e	4	14.5	(4.2, 24.8)	6	22.8	(15.1, 30.6)
Lek tenacity_2 ^f	3	9.3	(6.5, 12.2)	6	22.8	(15.1, 30.6)
Annual survival ^g	8	52.5	(27.4, 77.6)	7	100	N/A ^h

^a Total number of leks yearling males documented visiting.

^b Straight line distance from natal nest to lek where yearling males established.

^c One natal control male established on a lek 2.0 times as far from the natal nest than any other male; confidence intervals were re-computed after removing that observation.

^d First date established yearling males documented on lek.

^e Total number of days established yearling males documented on lek.

^f One natal treatment male was documented on a lek 2.5 times as often as any other treatment male; confidence intervals were re-computed after removing that observation.

^g Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

^h Standard error = 0.

Table 4. Breeding demographic probabilities and means (95% confidence intervals [95% CI]) of yearling female greater sage-grouse nesting within 930 m of natural gas field infrastructure (nesting treatment females) or nesting beyond 930 m of development (nesting control females) in southwestern Wyoming, 2005-06. Notice no differences in demographic probabilities.

Female Demographic	Nesting Treatment Females			Nesting Control Females		
	Available ^a	Documented ^b	95% CI	Available ^a	Documented ^b	95% CI
Nesting propensity ^c	12	8		31	22	
Nesting success ^d	8	4		21	10	
Early brood success ^e	4	3		9	8	
Overall brood success ^f	4	1		8	4	
Nest establishment date ^g	8	5/6	(5/1, 5/12)	21	5/7	(5/4, 5/9)
Annual survival (%) ^h	8	80.0	(55.2, 104.8)	21	61.8	(45.5, 78.1)

^a Total number of yearling females available for the demographic (e.g., the denominator for estimating demographic probability).

^b Total number of yearling females documented successful (e.g., the numerator).

^c Number of females documented nesting versus the number monitored during the nesting season.

^d Number of females hatching at least 1 egg versus the total number initiating a nest

^e Number of successfully nesting females with at least 1 chick to 2 weeks post-hatch.

^f Number of successfully nesting females with at least 1 chick 35 days or 10 weeks post-hatch (see methods).

^g Date females first documented on nest.

^h Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

Table 5. Breeding demographic probabilities and means (95% confidence intervals [95% CI]) of yearling female greater sage-grouse reared within 1.9 km of natural gas field infrastructure (natal treatment females) compared to yearling females reared in areas with limited natural gas field infrastructure (natal control females) in southwestern Wyoming, 2005-06. Notice that annual survival of natal treatment yearling females was lower than natal control yearlings.

Female Demographic	Natal Treatment Females			Natal Control Females		
	Available ^a	Documented ^b	95% CI	Available ^a	Documented ^b	95% CI
Nesting propensity ^c	9	5		7	5	
Nesting success ^d	4	1		6	2	
Natal nest-to-yearling						
nest distance (km) ^e	5	3.33	(1.1, 5.6)	6	2.83	(1.6, 4.0)
Nest establishment date ^f	5	5/6	(5/1, 5/10)	6	5/8	(5/1, 5/16)
Annual survival (%) ^g	9	69.4	(44.4, 94.5)	7	100	N/A ^h

^a Total number of yearling females available for the demographic (e.g., the denominator for estimating demographic probability).

^b Total number of yearling females documented successful (e.g., the numerator).

^c Number of females documented nesting versus the number monitored during the nesting season.

^d Number of females hatching at least 1 egg versus the total number initiating a nest

^e Straight line distance from natal nest to yearling female nest.

^f Date females first documented on nest.

^g Annual survival estimated using Kaplan-Meier estimator (Pollock et al. 1989).

^h Standard error = 0.

Figure 1. Yearling greater sage-grouse study location in southwestern Wyoming, 2005-06. The figure illustrates producing well pads and main haul roads present during the breeding seasons of 2005 and 2006; well pads within 5 km of trapped leks are included.

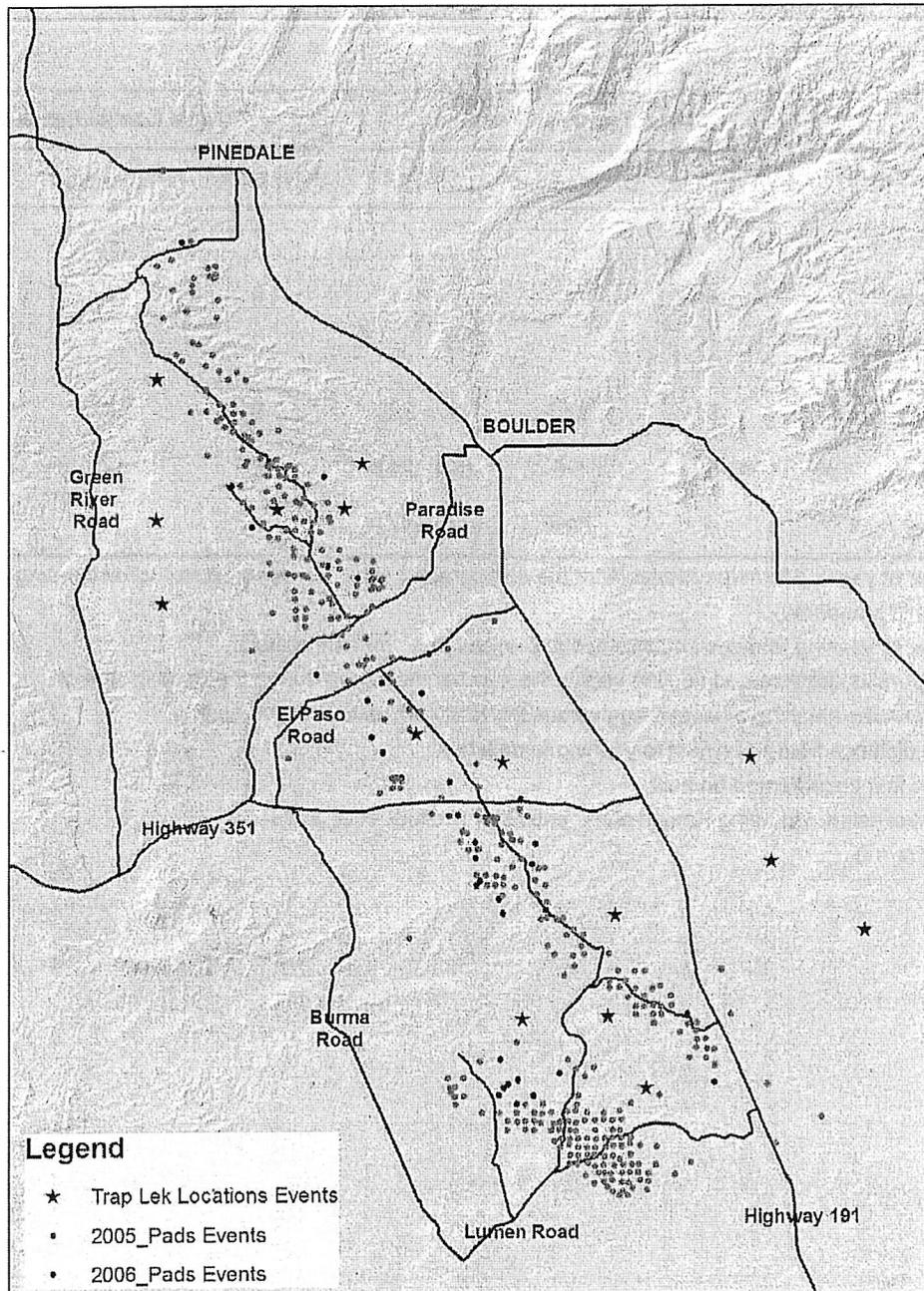


Figure 2. Yearling greater sage-grouse study location in southwestern Wyoming, 2005-06. The figure illustrates producing well pads and main haul roads present during the breeding seasons of 2005 and 2006; well pads within 5 km of trapped leks are included. Natural gas field infrastructure were buffered by 930 m (hatched areas) to determine areas of potential influence to nesting yearling females within the area of interest (i.e., within 5 km of trapped leks).

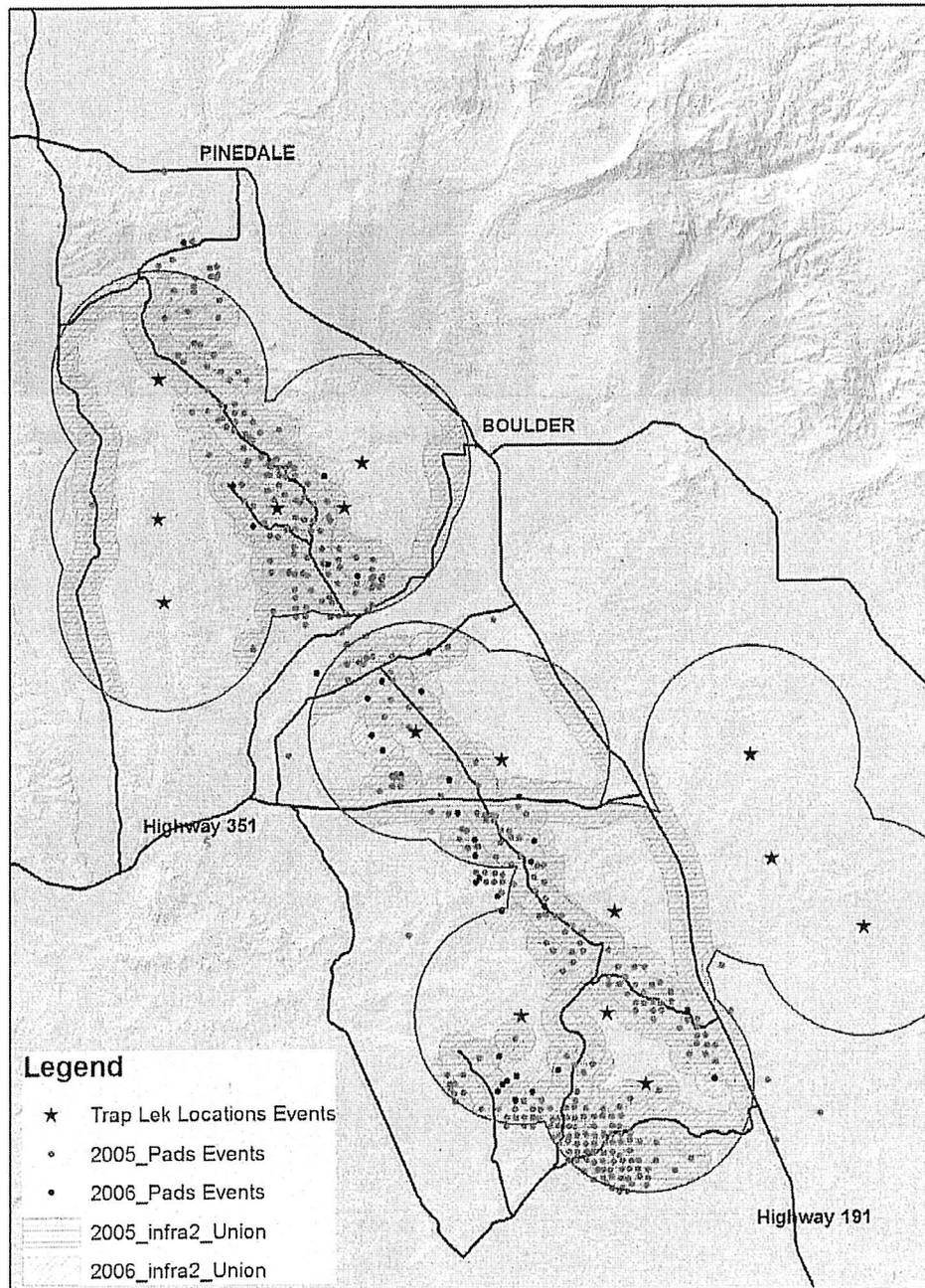


Figure 3. Mean (standard error) distances (km) from greater sage-grouse leks to natural gas field infrastructure in southwestern Wyoming, 2005-06. Leks were categorized as recruiting significantly less than, equal to, or more than expected numbers of males based on Chi-squared analyses of annual changes in the maximum number of males documented on leks during lek count procedures.

