Journal of Wildlife Management 74(1):65–72; 2010; DOI: 10.2193/2008-291

Management and Conservation Article

Yearling Greater Sage-Grouse Response to Energy Development in Wyoming

MATTHEW J. HOLLORAN,[1] *Wyoming Wildlife Consultants LLC, 4402 Cheyenne Drive, Laramie, WY 82072, USA*

RUSTY C. KAISER,[2] *United States Geological Survey Wyoming Cooperative Fish and Wildlife Research Unit, Department 3166, E University Avenue, Laramie, WY 82071, USA*

WAYNE A. HUBERT, *United States Geological Survey Wyoming Cooperative Fish and Wildlife Research Unit, Department 3166, E University Avenue, Laramie, WY 82071, USA*

ABSTRACT Sagebrush (*Artemisia* spp.)-dominated habitats in the western United States have experienced extensive, rapid changes due to development of natural-gas fields, resulting in localized declines of greater sage-grouse (*Centrocercus urophasianus*) populations. It is unclear whether population declines in natural-gas fields are caused by avoidance or demographic impacts, or the age classes that are most affected. Land and wildlife management agencies need information on how energy developments affect sage-grouse populations to ensure informed land-use decisions are made, effective mitigation measures are identified, and appropriate monitoring programs are implemented (Sawyer et al. 2006). We used information from radio-equipped greater sage-grouse and lek counts to investigate natural-gas development influences on 1) the distribution of, and 2) the probability of recruiting yearling males and females into breeding populations in the Upper Green River Basin of southwestern Wyoming, USA. Yearling males avoided leks near the infrastructure of natural-gas fields when establishing breeding territories; yearling females avoided nesting within 950 m of the infrastructure of natural-gas fields. Additionally, both yearling males and yearling females reared in areas where infrastructure was present had lower annual survival, and yearling males established breeding territories less often, compared to yearlings reared in areas with no infrastructure. Our results supply mechanisms for population-level declines of sage-grouse documented in natural-gas fields, and suggest to land managers that current stipulations on development may not provide management solutions. Managing landscapes so that suitably sized and located regions remain undeveloped may be an effective strategy to sustain greater sage-grouse populations affected by energy developments.

KEY WORDS *Centrocercus urophasianus*, energy development, greater sage-grouse, sage-grouse, Wyoming, yearling.

Sagebrush (*Artemisia* spp.)-dominated landscapes required to sustain greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations are experiencing unprecedented levels of energy development, resulting in widespread fragmentation and alteration of these habitats (Knick et al. 2003). Sage-grouse lek activity and numbers of males using leks are negatively influenced by the expanding infrastructure of natural-gas fields (Braun et al. 2002, Aldridge and Brigham 2003, Holloran 2005, Walker et al. 2007). Impacts of energy developments to sage-grouse nesting, brood-rearing and winter habitat selection, nesting propensity, chick survival, and population growth rates have been observed (Lyon and Anderson 2003, Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008).

Determining how a population responds to habitat fragmentation and other changes to landscapes requires an understanding of population dispersal and potential effects of anthropogenic habitat changes on dispersing cohorts in a population (Walters 2000). Wiens et al. (1986) suggested that site fidelity in breeding birds may influence short-term population responses to habitat changes, and the ultimate response requires that most site-tenacious individuals be dead. White-tailed ptarmigan (*Lagopus leucura*) in Colorado, USA, exist in naturally fragmented habitats that are linked, due to high adult philopatry to breeding sites, principally through natal dispersal among suitable areas (Giesen and Braun 1993, Martin et al. 2000). Sage-grouse adult males and females exhibit strong fidelity to breeding sites and seasonal ranges, implying that population dispersal and response of a population to habitat fragmentation depends on yearling cohorts (Wiley 1973, Gibson 1992, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005*b*).

Remington and Braun (1991) suggested that sage-grouse population declines in areas near coal mines in northern Colorado may have been caused by displacement of yearlings to leks away from development. Holloran and Anderson (2005*a*) were able to duplicate observed declines in numbers of males occupying 3 leks impacted by natural-gas development in southwestern Wyoming, USA, by assuming adult male tenacity and minimal yearling male recruitment. A delayed shift in nesting habitat selection away from infrastructure has been observed in southwestern Wyoming, a pattern consistent with adult females showing nest-site fidelity and yearling females avoiding gas fields (Holloran 2005). These studies indicate that elimination of populations from energy fields may have been due to the response of yearling cohorts to developments, but the response of yearling sage-grouse to development of natural-gas fields has not been assessed.

Our objectives were to ascertain if natural-gas development influenced 1) the distribution of, or 2) the probability of recruiting into breeding populations yearling male and female sage-grouse in southwestern Wyoming. We examined breeding habitat selection of yearling cohorts overall and breeding territory establishment, nest initiation, and annual survival probabilities of yearlings of known maternity (i.e., natal areas known) relative to locations of drilling rigs, producing well pads, and main haul roads.

[1] *E-mail: matth@wyowildlife.com*
[2] *Present address: Bureau of Land Management, 1625 W Pine Street, Pinedale, WY 82941, USA*

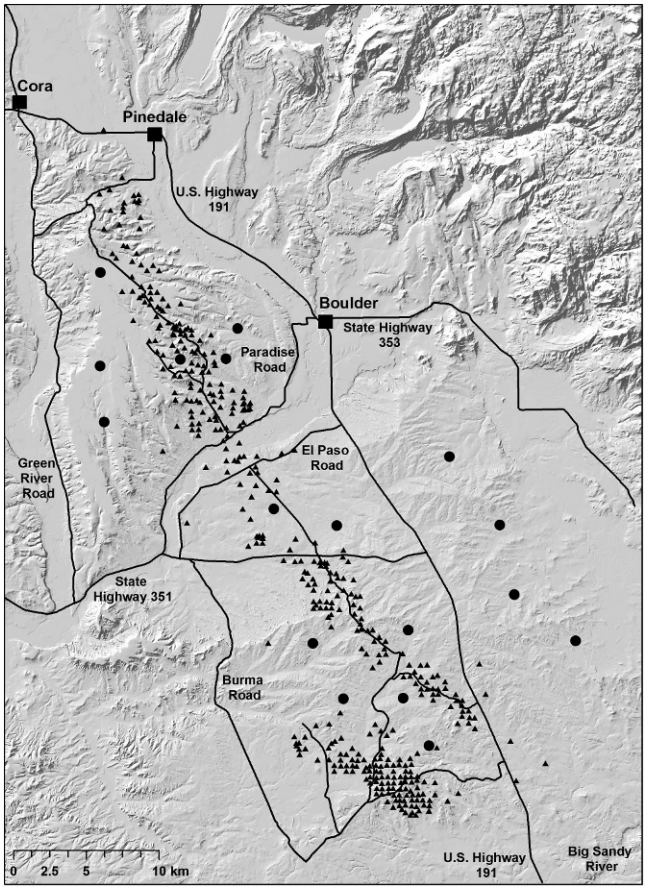

Figure 1. Yearling greater sage-grouse study area in southwestern Wyoming, USA, 2000–2006, illustrating producing well pad locations (triangles) within 5 km of displayed lek locations (circles), main haul roads (labeled), and towns (squares) present during the April 2006 breeding season.

STUDY AREA

The study area (42°60′N, 109°75′W) encompassed 17 leks near the Pinedale Anticline Project Area and northeastern portions of the Jonah II gas fields in the Upper Green River Basin in southwestern Wyoming (Fig. 1; U.S. Department of the Interior [USDI] 2000). The study area covered approximately 255,000 ha (2,550 km^2) dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) shrub–steppe habitats. Elevation was 2,100–2,350 m and annual precipitation averaged 24.1 cm (Western Regional Climate Center 2003). Natural-gas development and livestock grazing were the predominant human uses of the area (USDI 2000).

METHODS

We investigated the response of both male and female yearling sage-grouse to the infrastructure of natural-gas fields at several levels. For yearling males, we used information from 1) lek counts to investigate the response of the breeding population (Lek Recruitment), 2) radio-equipped yearling males to investigate where individuals selected breeding territories (Overall Yearling Males), and 3) radio-equipped yearling males of known maternity to investigate probability of establishing a breeding territory and annual survival responses of individuals whose natal brooding areas were within, compared to outside, developed regions (Yearling Males of Known Maternity). We used information from 4) radio-equipped yearling females to investigate where individuals selected nesting sites (Overall Yearling Females), and 5) radio-equipped yearling females of known maternity to investigate nesting propensity, natal nesting area habitat selection, and annual survival differences between individuals whose natal brooding areas were within and outside developed regions (Yearling Females of Known Maternity). We organized the methods around these 5 categories and carried this organization through the results.

We used conservative statistical approaches because of sample size constraints when comparing treatment and control groups of yearlings (Cherry 1996). Multivariate procedures were inappropriate due to highly correlated independent variables (e.g., distances to different infrastructure features). We computed statistics using MINITAB 13.1 (Minitab Inc., State College, PA). Distance variables were estimated using ArcGIS 9.

We captured female sage-grouse on or near leks from mid-March through April 2000–2005 by spotlighting and hoop-netting (Giesen et al. 1982, Wakkinen et al. 1992). We classified captured females as yearlings (first breeding season) or adults (after second breeding season) based on shape of outermost wing primaries (Eng 1955). We secured radiotransmitters to females with polyvinyl chloride (PVC)-covered wire necklaces (Advanced Telemetry Systems Inc. [ATS], Isanti, MN). Transmitters weighed 19.5 g or 25.5 g, had battery life expectancies of 530 days or 610 days, respectively, and were equipped with motion sensors (i.e., radiotransmitter pulse rate increased in response to inactivity). We included yearling females equipped with radiotransmitters during these efforts in the Overall Yearling Females sample.

We monitored brood-rearing females in late summer 2004–2005 from $\geq$100 m at least twice weekly through 10 weeks posthatch. We captured male and female chicks (e.g., hatch-yr birds) that were $\geq$10 weeks of age by spotlighting radio-equipped brood females and hoop-netting accompanying chicks (Giesen et al. 1982, Wakkinen et al. 1992). We weighed chicks to ensure that radiotransmitters did not exceed 2% of body weight and could be safely attached (Caccamise and Hedin 1985). We assigned gender to chicks based on weights or plumage, and we assigned chicks to age class to ensure captured grouse were hatch-year birds based on shape of outermost wing primaries (Eng 1955). We collected blood samples by clipping the middle toenail and stored blood on Whatman FTA® micro cards (Whatman, Florham Park, NJ). We secured 16-g or 19.5-g radio-transmitters (depending on chick wt) to chicks with PVC-covered wire necklaces (ATS). Transmitters had battery life expectancies of 500 days or 530 days, respectively, and were equipped with motion sensors. We included radio-equipped chicks that survived to 1 April of the spring following capture in the Overall Yearling Males and Overall Yearling Females samples.

We established yearling maternity using microsatellite polymerase chain reaction analyses of DNA extracted from blood samples collected during late-summer chick-trapping efforts (Taylor et al. 2003, Hawk et al. 2004); we used 5 primers in the analysis (LLSD4, LLSD8, LLST1, SGCA11, and SGCTAT1; Wyoming Game and Fish Laboratory, Laramie, WY). We obtained genotypes following Frantz et al. (2003). We ascertained maternity using CERVUS 3.0.3 (Marshall et al. 1998, Kalinowski et al. 2007). We based the simulated population genetic structure on 10,000 simulations with 5,000 potential parents, 1% of the candidate parents sampled, and 25% relatedness. We identified candidate mothers as those 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 included chicks that had maternity assigned in the Yearling Males of Known Maternity and Yearling Females of Known Maternity samples.

We mapped features of the infrastructure of natural-gas fields within 5 km of 17 leks located throughout the study area (Fig. 1; Holloran and Anderson 2005*b*). We mapped producing well pads, drilling rigs, and main haul roads; we included United States and state highways as well as the Paradise, El Paso, and Green River roads as main haul roads (Fig. 1). We obtained infrastructure location, drilling activity date, and well producing date from the Wyoming Oil and Gas Conservation Commission (Casper, WY). We verified these data using information supplied by Western Ecosystems Technology Inc. (Cheyenne, WY), Edge Environmental Inc. (Laramie, WY), individual gas companies (i.e., operators) responsible for specific wells, and through direct ground-truthing using handheld, 12-channel Global Positioning System (GPS) units. Infrastructure data were dynamic and modified to reflect the conditions encountered seasonally. We identified well pads with multiple producing wells as single active locations.

We estimated natal brooding areas to be within 1.65 km of natal nests; this area represented where chicks were raised during the early brood-rearing season. We established the area as the average of the upper 95% confidence limit of the mean distances from nest to early brood-rearing locations from studies conducted throughout southwestern Wyoming (Holloran 1999, 2005; Lyon 2000; Slater 2003; Kuipers 2004). We defined natal treatment yearlings (M and F) as any yearling whose natal area contained >1 producing well pad or >1 km of main haul road; we considered all others natal control yearlings. The inclusion of natal areas with one 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 as treatment birds.

Lek Recruitment

We conducted annual lek counts on 17 leks following standardized methods outlined by the Wyoming Game and Fish Department's (WGFD) Sage-grouse Technical Committee (Connelly et al. 2003). We estimated overall lek recruitment of males annually from 2000 to 2006 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%; Zablan et al. 2003).

We compared overall recruitment of males among leks using chi-square tests with continuity corrections (due to sample sizes <25 in some instances; Dowdy and Wearden 1991). We assumed the number of recruited males was related to lek size, but the relationship was probably not perfectly correlated. Therefore, we established expected proportions using a scaled allocation of the total recruited population. We investigated 2%, 3%, 4%, and 5% differences in proportion of the recruited population allocated to each lek size category. For example, when we investigated the 5% difference in allocation proportions, we expected each lek with $\leq$50 total males the preceding year to recruit 4%, each lek with >50 and $\leq$100 males to recruit 9%, and each lek with >100 males to recruit 14% of the total recruited population. This resulted in an annual allocation of between 2.5% and 5.9% for leks with $\leq$50 males, 6.8% and 9.1% for leks with >50 and $\leq$100 males, and 8.8% and 14.1% for leks with >100 males. We used different proportions each year because the number of leks in each size category was not constant among 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 recruitment categories by distance to closest active drilling rig, producing well pad, and main haul road using 95% confidence interval overlap. Each change in the proportion of the recruited population allocated to different lek sizes provided individual mean and 95% confidence interval estimates; we therefore investigated overlap by comparing the minimum lower limit and the maximum upper limit of the confidence intervals produced by all allocations.

Overall Yearling Males

We collected lek visitation data for radio-equipped yearling males using data-logger (ATS) stations situated near leks. Data loggers allowed for constant monitoring of leks during the breeding season, and recorded specific dates and times when radio-equipped yearlings visited a monitored lek. We did not restrict monitoring to the 17 leks situated in the study area, but used radio-equipped yearling male spring locations to establish which leks to monitor for potential establishment.

Data-logger stations consisted of one data logger run by 2 deep-cycle recreational vehicle gel batteries charged by solar panels; all equipment was housed in metal Knaack® boxes (Crystal Lake, IL). We mounted omni antennas on steel casing pipe so the top of the antenna was 3 m high. We attenuated data loggers (i.e., calibration of data-logger sensitivity) to detect the entire area used by displaying males. As much as was practical, we placed data-logger stations to minimize detection by displaying grouse and grouse using nondisplay habitat surrounding leks. Anecdotally, we did not observe behavioral changes by breeding sage-grouse in response to stations and did not observe

raptors or corvids perching on antennas. We directly accessed stations when leks were not occupied (e.g., noncrepuscular 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 to 15 May.

We distinguished radiotransmitter detection (vs. interference) signals recorded by data loggers using accumulation of evidence techniques. Initially, signal diagnostics (i.e., transmitter pulse-per-minute values and number of pulse matches [ATS algorithms]) had to match values set for the data loggers and radiotransmitters. We used pulse match to pulse detected ratios (i.e., the no. of matched pulses relative to the no. of detected pulses) and the number of logs over a given time period to further diagnose true signal detections; we established these protocols by evaluating data from reference transmitter logs. 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 used telemetry data as the final log verification. If we found an individual during the breeding season in the general area where we logged it, we considered the log verified. We considered confirmed yearling male detections between 0430 hours and 0730 hours daily lek visits.

We considered yearling males to have established on a particular lek if detected at that lek $\geq$19% of the monitoring period (Walsh et al. 2004). We estimated the probability of establishing a breeding territory on a lek as the number of yearling males with confirmed lek establishment divided by the total number of available males. We considered available males those intensively monitored by radiotelemetry during the breeding season that survived through the breeding season.

We generated minimum convex polygons around all producing well pads, and categorized monitored leks as either contained within the polygons, 0–3 km outside, or >3 km outside the polygons (Kenward 1987). We used chi-square tests with continuity corrections to compare the number of radio-equipped yearling males establishing on leks by category (i.e., obs establishment; Dowdy and Wearden 1991). We assumed equal availability among leks for each yearling male; thus, we based expected proportions on the total number of leks within each category and the total number of available yearling males.

Yearling Males of Known Maternity

We assessed the probability of establishing a breeding territory for Yearling Males of Known Maternity similarly to the Overall Yearling Male sample. We established annual survival for Yearling Males of Known Maternity from 1 April through the end of March using handheld telemetry equipment (ATS). We assessed survival between 1 April and 15 May by locating males weekly. We located males from long-range bi-weekly from 15 May through August and used transmitter pulse-rates (i.e., motion sensors) to evaluate survival. We assessed survival from 1 September through March from fixed-wing aircraft. We conducted flights at least bi-monthly and used motion sensors to evaluate whether individuals were dead or alive.

We assessed probability of establishing a breeding territory on a lek between natal brooding treatment-and-control yearling males using chi-square tests with continuity corrections (Dowdy and Wearden 1991). We estimated the expected establishment rate from the control population (i.e., results indicated a difference between natal brooding treatment and control groups).

We estimated annual (Apr–Mar) survival and standard errors of Yearling Males of Known Maternity using the staggered entry Kaplan–Meier estimator (Pollock et al. 1989). We censored birds that were not found during any monthly period. We assessed differences in annual survival by natal brooding area category using 95% confidence interval overlap.

Overall Yearling Females

We used handheld receivers and 3-element Yagi antennas (ATS) to monitor radiomarked yearling females at least twice weekly through prelaying (Apr) and nesting (May–Jun). We located nests of radiomarked birds by circling the signal source until females could be directly observed. We confirmed and marked nest locations using a GPS after long-range (>60-m) radiomonitoring indicated the female had left the area.

We investigated habitat selection of yearling females relative to infrastructure features of natural-gas fields by comparing numbers of observed and expected nests within given distances of infrastructure using chi-square tests with continuity corrections (Dowdy and Wearden 1991). We categorized nests into 0.5-km inclusive buffers around infrastructure features. We estimated the expected number of nests per buffer as the proportion of the total area of suitable nesting habitat within 5 km of trapped leks that was within or outside the buffers of infrastructure variables (Holloran and Anderson 2005*b*). We refined our distance estimate after initially establishing avoidance at a 0.5-km scale by investigating 0.1-km buffers within the identified 0.5-km buffer. We used only nests within the 5-km lek buffer in the comparison. We estimated avoidance distance as the distance between the largest buffer where observed and expected numbers of nests differed and the smallest buffer where numbers of nests did not differ; we used this avoidance distance estimate for subsequent analyses.

We assumed suitable nesting habitats were sagebrush-dominated areas within 2 standard deviations of the mean roughness (i.e., the ratio of actual surface area to planimetric area) of all nest sites (i.e., ad and yearling F) within the 5-km lek buffer between 2000 and 2006 (Holloran 2005). Jensen (2006) suggested roughness was the terrain measure best distinguishing sage-grouse nests from available locations in southwestern Wyoming. We used Landfire vegetation type layers (U.S. Department of Agriculture 2006) to identify sagebrush-dominated areas, and nearest-neighbor analysis (100-m scale) in ArcGIS Spatial Analyst to calculate roughness from 30-m digital elevation models

Table 1. Mean distance (km) from sage-grouse leks to the infrastructure of natural-gas fields in southwestern Wyoming, USA, 2001–2006. We categorized leks based on chi-square analyses of annual changes in numbers of males documented. Table depicts minimum and maximum sample size (n), mean, and confidence interval estimates produced by allocating different proportions of recruited population. Leks recruiting fewer males than expected were significantly closer to gas field infrastructure than leks recruiting more males than expected.

Relative no. of M recruited	n[a]		Distance to drill rig				Distance to well pad				Distance to haul road			
			$\bar{x}$		95% CI		$\bar{x}$		95% CI		$\bar{x}$		95% CI	
	Min.	Max.	Min.	Max.	Lower	Upper	Min.	Max.	Lower	Upper	Min.	Max.	Lower	Upper
Less than expected	26	34	2.8	3.2	2.2	4.1	1.2	1.7	0.8	2.5	1.7	1.8	1.2	2.4
Equal to expected	37	49	4.4	4.9	3.7	5.7	2.5	2.9	1.7	3.8	2.6	2.8	2.2	3.2
More than expected	19	24	6.6	7.8	5.0	9.2	4.9	6.2	3.3	7.6	4.2	4.6	3.3	5.5

[a] Total no. of lek yr.

(Wyoming Geographic Information Science Center, Laramie, WY). We used the proportion of suitable nesting habitat to generate expected nest numbers, thus standardizing for potential differences in the amount of suitable habitat within compared buffers.

Yearling Females of Known Maternity

We monitored Yearlings of Known Maternity and identified nest locations similarly to the Overall Yearling Female sample. We estimated annual survival for Yearling Females of Known Maternity from 1 April through March. We located all females twice weekly between 1 April and 1 July and visually assessed survival. Between 1 July and 31 August we located yearling females at least bi-weekly and assessed survival either visually or from long range using motion sensors. We estimated survival from 1 September through March from fixed-wing aircraft. We conducted flights at least bi-monthly and used motion sensors to evaluate whether individuals were dead or alive.

We estimated nesting propensity as the number of Yearling Females of Known Maternity initiating a nest divided by the total number intensively monitored throughout the nesting season. We did not include females found for the first time after 15 May in annual 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]). We compared nesting propensity between natal brooding treatment and control yearling females using chi-square tests with continuity corrections (Dowdy and Wearden 1991). We computed expected nesting propensity from the control population.

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. We compared the proportion of yearlings with infrastructure in natal nesting areas that nested within the avoidance distance of infrastructure to those nesting beyond the avoidance distance using chi-square tests with continuity corrections (Dowdy and Wearden 1991). We estimated the expected number of nests per category as the proportion of suitable nesting habitat in the total natal nesting area (i.e., all natal nesting areas with gas field infrastructure present combined) that was within the avoidance distance of infrastructure.

We estimated annual (Apr–Mar) survival and standard errors of yearling females of known maternity using the staggered entry Kaplan–Meier estimator (Pollock et al. 1989). We censored birds that were not found during any monthly period. We assessed differences in annual survival by natal brooding area category using 95% confidence interval overlap.

RESULTS

We radiomarked 83 yearling female sage-grouse during spring 2000–2005. We marked an additional 64 male and 76 female chicks in 2004 and 2005 (45 M and 39 F during autumn 2004, 19 M and 37 F during autumn 2005). Between capture and achieving yearling status, 41 chicks died, 7 lost the radiotransmitter (based on field sign at retrieved transmitter location), and we did not find 6. At the beginning of the breeding-season monitoring periods, 34 male and 52 female radiomarked chicks were available as yearlings. We confirmed maternity and collected breeding-season data for 15 male and 16 female yearlings.

Leks that recruited more than the expected number of males were significantly farther from drilling rigs, producing well pads, and main haul roads compared to leks that recruited fewer males than expected (Table 1). Additionally, leks that recruited more males than expected were significantly farther from main haul roads than leks that recruited the same number of males as expected.

The proportion of radiomarked yearling males that established on leks inside and outside the development boundaries (as designated by min. convex polygons around producing well pads) of natural-gas fields differed from that expected assuming equal establishment probabilities for all leks ($\chi^2_1 = 5.38$; $P = 0.02$). On leks within the interior, 2 yearling males established (expected = 9.7), compared to 22 establishing on leks outside development boundaries (expected = 23.3). The number of radiomarked yearling males that established on leks outside development did not differ from expected relative to distance to development boundary ($\chi^2_1 < 0.01$; $P = 0.94$; established 0–3 km from development observed 13 and expected 13.6 vs. established >3 km from development observed 9 and expected 9.7).

Annual survival of natal brooding treatment yearling males (54.7% [95% CI = 20.5–88.9]) was significantly lower than

Table 2. The number (n = 62) of yearling sage-grouse nests observed (obs nests in buffer) and expected (exp nests in buffer) within buffers generated around producing well pads in southwestern Wyoming, USA, 2000–2006. We estimated the expected number of nests per buffer as proportion of the total area of suitable nesting habitat within 5 km of trapped leks, and made comparisons using chi-squared analyses (χ^2_{df}) with continuity corrections. We observed fewer than expected nests in buffers <1 km.

Buffer distance (km)	Obs nests in buffer	Exp nests in buffer	χ^2_1	*P*-value
0.5	9	18.8	6.65	0.01
0.6	13	21.7	4.78	0.03
0.7	17	24.3	3.10	0.08
0.8	18	26.6	4.31	0.04
0.9	20	28.8	4.47	0.03
1.0	26	30.9	1.25	0.26
1.5	36	40.0	0.84	0.36
2.0	42	46.9	1.73	0.19
2.5	50	52.0	0.26	0.61
3.0	53	55.3	0.56	0.45

control yearling males (100%). The probability of natal brooding treatment yearling males establishing a breeding territory on a lek did not differ from expected (χ^2_1 = 1.53; P = 0.22); 4 of 8 treatment yearling males established breeding territories compared to 7 of 7 control males.

The maximum distance where the proportion of radio-marked yearling female nest locations differed from that expected was 0.9 km, assuming spatially proportional selection of nest locations within suitable habitats; the minimum distance where the proportion of nests did not differ from expected was 1.0 km (Table 2). Thus, a 950-m avoidance distance was used for subsequent analyses.

Annual survival of natal brooding treatment yearling females (69.4% [95% CI = 39.2–99.7]) was significantly lower than control yearling females (100%). Nesting propensity was not related to natal brooding area (χ^2_1 = 0.13; P = 0.71); 5 of 9 treatment yearling females initiated a nest compared to 5 of 7 control females.

The upper limit of the 95% confidence interval around mean natal nest-to-yearling nest distances for natal nesting control females indicated that a 4.0-km buffer around natal nesting locations represented the area where a yearling female typically selected a nest location (i.e., natal nesting area). There was weak evidence to support that the proportion of natal nesting treatment yearling females that selected nest locations within 950 m of infrastructure and those that nested outside the 950-m buffer differed from expected (χ^2_1 = 2.94; P = 0.09). The number of yearling female nests within 950 m of infrastructure (n = 3) was less than expected (n = 6.1); the number of nests outside the buffer (n = 7) was more than expected (n = 3.9).

DISCUSSION

Avoidance of infrastructure by breeding yearlings, decreased yearling survival, and reduced fecundity of yearling males indicate that energy development impacts the spatial distribution and numerical size of regional sage-grouse populations. A situation where adult philopatry is not influenced by energy development (Holloran 2005), but yearlings avoid areas near infrastructure indicates breeding and nesting habitat occupancy may be prolonged, and the ultimate population-level response to development may take multiple sage-grouse generations to be realized. This may explain time lags between development of gas fields and abandonment of gas fields by sage-grouse reported in previous studies (Holloran 2005, Walker et al. 2007, Doherty 2008).

Yearling male avoidance of infrastructure occurred at multiple levels. Leks recruiting more than expected numbers of males were 2.1–2.9 times as far from infrastructure compared to those recruiting fewer males than expected. A majority of the males recruited were probably yearlings because of lek tenacity exhibited by adult males (Patterson 1952, Wiley 1973, Gibson 1992). Radio-equipped yearling males were 4.6 times more likely to establish on leks outside compared to inside developed areas. We investigated post hoc the location of specific leks selected by Yearling Males of Known Maternity and found that 3 of the 4 yearling males reared within development that established breeding territories did so on leks situated on the periphery of development (i.e., within 0–3 km of infrastructure) while 3 of 5 males reared within 3 km of infrastructure established on leks >3 km from development. Dunn and Braun (1985) reported that leks selected by yearling males were spatially associated to natal areas. Thus, our results indicate that yearling males that may generally establish on leks within the developing energy field are displaced to leks on the periphery of the field. Concurrently, a portion of the yearling population that generally establishes on leks near the periphery of development moves to leks farther from infrastructure. These multiple levels of displacement may explain why leks near the periphery of development did not recruit more yearling males than expected, the probable result if displacement was occurring only from within energy fields.

Yearling males reared in areas with infrastructure features of natural-gas fields had lower annual survival and were less likely to establish a breeding territory compared to males reared in areas with limited activities associated with natural-gas fields. Although the number of yearling males establishing breeding territories did not statistically differ between natal brooding treatment and control males, the probability of treatment males establishing a breeding territory was half that of control males (i.e., 50% vs. 100%, respectively), indicating a response of biological importance. Because yearling male lek selection is spatially influenced by natal area (Dunn and Braun 1985), decreased fecundity may be in response to anthropogenic activity encountered either as chicks, or in response to conditions encountered during inaugural breeding seasons.

Yearling female avoidance responses indicate a functional loss of nesting habitats within 950 m of infrastructure. The yearling female population generally avoided nesting within 950 m of the infrastructure of natural-gas fields, and yearling females with natural-gas infrastructure present in their natal nesting area also tended to avoid nesting within

950 m of infrastructure. Holloran and Anderson (2005*b*) reported a 930-m buffer represented the upper limit of the 95% confidence interval around mean distances between consecutive year's nests in Wyoming. Because of nesting area fidelity, this indicates that a female will nest within a 272-ha area over its lifetime. Thus, yearling females appear to select nesting sites at the spatial scale of their lifetime nesting area, and avoid selecting areas with the infrastructure of natural-gas fields present.

Impacts to yearling female survival versus nesting propensity suggest energy development negatively influences population levels compared to female 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).

MANAGEMENT IMPLICATIONS

Accumulating evidence suggests the conventional development of gas resources excludes sage-grouse from developed areas (Holloran 2005, Walker et al. 2007, Doherty 2008); we provide mechanisms for these population-level responses. Yearling dispersal distances indicate that viable management solutions may not be to expand current development stipulations (e.g., no surface occupancy distances around leks; USDI 2000), but to manage landscapes where sagebrush-dominated regions within those landscapes remain undeveloped for sage-grouse. Because sage-grouse are a landscape-scale species, managers may rely on seasonal habitat selection and movement information collected from individual sage-grouse residing in proposed undeveloped regions to assign appropriate spatial scales for these areas (Patterson 1952, Connelly et al. 2000). For example, seasonal distribution information exists that suggests the region depicted in Fig. 1 east of United States Highway 191 and south of State Highway 353 to the Big Sandy River encompasses the seasonal habitats required by the population currently residing in that region. In situations where large landscapes are developed (e.g., Powder River Basin, WY), preplanning and adaptive management would be required to ensure suitably located and sized regions are protected (Walker et al. 2007, Doherty 2008). Undeveloped regions may have to be maintained until the infrastructures in developed areas are removed if impacts of gas field development phases continue through production phases as suggested by Aldridge and Brigham (2003) and Walker et al. (2007; total life-of-project for Jonah II Natural Gas Field Infill estimated at 76 yr [USDI 2006]). We suggest habitat management in undeveloped regions maintain or enhance populations in the short term because of impacts of development to yearling survival. This implies that these areas be managed conservatively (see Connelly et al. 2000) and that large-scale habitat manipulations, habitat manipulations focused on enhancing productivity, and habitat management alternatives with unproven results be avoided.

ACKNOWLEDGMENTS

This work is dedicated to Dr. S. H. Anderson, former leader of the Wyoming Cooperative Fish and Wildlife Research Unit, who was instrumental in initiating and sustaining sage-grouse research throughout Wyoming. Financial support was provided by the Bureau of Land Management, United States Department of Energy, WGFD, Yellowstone-to-Yukon Initiative, EnCana Oil & Gas Inc., Ultra Resources Inc., and Shell Rocky Mountain Production. We thank all the landowners in the upper Green River Basin that allowed access to private lands. Field assistance was provided by J. Anderson, D. Edmunds, R. Holloran, B. Holtby, S. Huber, D. Jacobson, L. Knox, J. Michalak, T. Parker, S. Slater, R. Stewart, J. Swift, C. Taber, J. Vick, G. Wilson, and D. Woolwine. Technical assistance was provided by Western EcoSystems Technology Inc. (Cheyenne, WY), Edge Environmental Inc. (Laramie, WY), Bureau of Land Management Pinedale field office (Pinedale, WY), and the WGFD Jackson–Pinedale regional office (Pinedale, WY). Telemetry flights and lek surveys were conducted with the assistance of Mountain Air Research (Driggs, ID) and Sky Aviation (Dubois, WY). This manuscript was greatly improved by critical reviews from C. E. Braun, T. J. Christiansen, K. E. Doherty, D. E. Naugle, E. T. Rinkes, B. L. Walker, and M. J. Willis.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 117:508–526.

Aldridge, C. L., and R. M. Brigham. 2003. Distribution, abundance, and status of the greater sage-grouse, *Centrocercus urophasianus*, in Canada. Canadian Field-Naturalist 117:25–34.

Braun, C. E., O. O. Oedekoven, and C. L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions of the North American Wildlife and Natural Resources Conference 67:337–349.

Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97:306–318.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use–availability studies. Journal of Wildlife Management 60:653–658.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Publication No. 979, University of Idaho, Moscow, USA.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

Doherty, K. E. 2008. Sage-grouse and energy development: integrating science with conservation planning to reduce impacts. Dissertation, University of Montana, Missoula, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Dowdy, S. M., and S. Wearden. 1991. Statistics for research. Second edition. John Wiley & Sons, New York, New York, USA.

Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621–627.

Eng, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, and K. P. Reese. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95:1038–1041.

Frantz, A. C., L. C. Pope, P. J. Carpenter, T. J. Roper, G. J. Wilson, R. J. Delahay, and T. Burke. 2003. Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. Molecular Ecology 12:1649–1661.

Gibson, R. M. 1992. Lek formation in sage grouse: the effect of female choice on male territory settlement. Animal Behaviour 43:443–450.

Giesen, K. M., and C. E. Braun. 1993. Natal dispersal and recruitment of juvenile white-tailed ptarmigan in Colorado. Journal of Wildlife Management 57:72–77.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Hagen, C. A. 2003. A demographic analysis of lesser prairie-chicken populations in southwestern Kansas: survival, population viability, and habitat use. Dissertation, Kansas State University, Manhattan, USA.

Hawk, D., K. Sargeant, and S. Sharpe. 2004. Wyoming Game and Fish laboratory forensic procedure manual and molecular diagnostic protocols for fish health. Wyoming Game and Fish Department, Laramie, USA.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Holloran, M. J., and S. H. Anderson. 2005*a*. Greater sage-grouse population response to natural gas development in western Wyoming: are regional populations affected by relatively localized disturbances? Transactions of the North American Wildlife and Natural Resources Conference 70:160–170.

Holloran, M. J., and S. H. Anderson. 2005*b*. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. Condor 107:742–752.

Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis, University of Wyoming, Laramie, USA.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 6:1099–1106.

Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London, United Kingdom.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611–634.

Kuipers, J. L. 2004. Grazing system and linear corridor influences on greater sage-grouse (*Centrocercus urophasianus*) habitat selection and productivity. Thesis, University of Wyoming, Laramie, USA.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. Thesis, University of Wyoming, Laramie, USA.

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

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639–655.

Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. Condor 102:503–516.

Patterson, R. L. 1952. The sage grouse in Wyoming. Sage, Denver, Colorado, USA.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Remington, T. E., and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings, issues and technology in management of impacted western wildlife. Thorne Ecological Institute 5:128–132.

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

Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildlife Biology 9:291–299.

Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). Account 425 *in* A. Pool and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Slater, S. J. 2003. Sage-grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. Thesis, University of Wyoming, Laramie, USA.

Taylor, S. E., S. J. Oyler-McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). Molecular Ecology Notes 3:262–264.

U.S. Department of Agriculture. 2006. Landfire.existing_vegetation_type. U.S. Department of Agriculture Forest Service, Missoula, Montana, USA.

U.S. Department of the Interior [USDI]. 2000. Record of decision, environmental impact statement for the Pinedale anticline oil and gas exploration and development project Sublette County, Wyoming. U.S. Bureau of Land Management, no. BLM/WY/PL-00/026+1310, Pinedale, Wyoming, USA.

U.S. Department of the Interior [USDI]. 2006. Final environmental impact statement: Jonah infill drilling project Sublette County, Wyoming. U.S. Bureau of Land Management, no. BLM/WY/PL-06/006+1310, Pinedale, Wyoming, USA.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

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

Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56–68.

Walters, J. R. 2000. Dispersal behavior: an ornithological frontier. Condor 102:479–481.

Western Regional Climate Center. 2003. Western U.S. climate historical summaries page. <http://www.wrcc.dri.edu/summary/Climsmwy.html>. Accessed 21 Feb 2008.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365–376.

Wiley, R. H. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. Animal Behavior Monographs 6:85–169.

Zablan, M. A., C. E. Braun, and G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67:144–154.

Associate Editor: Vangilder.