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Greater sage-grouse population response to energy development and habitat loss

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Abstract: Modification of landscapes due to energy development may alter both habitat use and vital rates of sensitive wildlife species. Greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana have experienced rapid, widespread changes to their habitat due to recent coal-bed natural gas (CBNG) development. We analyzed lek-count, habitat, and infrastructure data to assess how CBNG development and other landscape features influenced trends in the numbers of male sage-grouse observed and persistence of leks in the PRB. From 2001-2005, the number of males observed on leks in CBNG fields declined more rapidly than leks outside of CBNG. Of leks active in 1997 or later, only 38% of 26 leks in CBNG fields remained active by 2004-2005, compared to 84% of 250 leks outside CBNG fields. By 2005, leks in CBNG fields had 46% fewer males per active lek than leks outside of CBNG. Persistence of 110 leks was positively influenced by the proportion of sagebrush habitat within

6.4 km of the lek. After controlling for habitat, we found support for negative effects of CBNG development within 0.8 km and 3.2 km of the lek and for a time lag between CBNG development and lek disappearance. Current lease stipulations that prohibit development within 0.4 km of sage-grouse leks on federal lands are inadequate to ensure lek persistence and may result in impacts to breeding populations over larger areas. Seasonal restrictions on drilling and construction do not address impacts caused by loss of sagebrush and incursion of infrastructure that can affect populations over long periods of time. Regulatory agencies may need to increase spatial restrictions on development, industry may need to rapidly implement more effective mitigation measures, or both, to reduce impacts of CBNG development on sage-grouse populations in the PRB.

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Large-scale modification of habitat associated with energy development may alter habitat use or vital rates of sensitive wildlife species. Populations in developed areas may decline if animals avoid specific features of infrastructure such as roads or power lines (Trombulak and Frissell 2000, Nelleman et al. 2001, 2003) or if energy development negatively affects survival or reproduction (Holloran 2005, Aldridge and Boyce 2007). For example, mortality caused by collisions with vehicles and power lines reduces adult and juvenile survival in a variety of wildlife species (reviewed in Bevanger 1998 and Trombulak and Frissell 2000). Indirect effects of energy development on populations are also possible due to changes in predator or parasite communities (Knight and Kawashima 1993, Steenhof et al. 1993, Daszak et al. 2000) or changes in vegetation structure and composition associated with disturbance (Trombulak and Frissell

2000, Gelbard and Belnap 2003). Negative impacts may be exacerbated if features of development that attract animals (e.g., ponds) simultaneously reduce survival and thereby function as ecological traps (Gates and Gysel 1978).

Rapidly expanding coal-bed natural gas (CBNG) development is a concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of northeastern Wyoming and southeastern Montana. The PRB supports an important regional population, with over 500 leks documented between 1967-2005 (Connelly et al. 2004). In the past decade, the PRB has also experienced rapidly increasing CBNG development, with impacts on wildlife habitat projected to occur over an area of approximately 24,000 km^2 (Bureau of Land Management 2003*a*, *b*). Coal-bed natural gas development typically requires construction of 2-7 km of roads and 7-22 km of power lines per km^2 as well as an extensive network of compressor stations, pipelines, and ponds (Bureau of Land Management 2003*b*). Approximately 10% of surface lands and 75% of mineral reserves in the PRB are federally owned and administered by the Bureau of Land Management (BLM) (Bureau of Land Management 2003*a*, *b*). Over 50,000 CBNG wells have been authorized for development on federal mineral reserves in northeastern Wyoming, at a density of 1 well per 16-32 ha, and as many as 18,000 wells are anticipated in southeastern Montana (Bureau of Land Management 2003*a, b*). According to data from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, by the beginning of 2005, approximately 28,000 CBNG wells had been drilled on federal (~31%), state (~11%), and private (~58%) mineral holdings in the PRB. Mitigation for sage-grouse on BLM lands typically includes lease stipulations prohibiting surface infrastructure within 0.4 km of sage-grouse leks as well as restrictions on timing of drilling and construction within 3.2 km of documented leks during the

15 March - 15 June breeding season and within crucial winter habitat from 1 December - 31 March (Montana only) (Bureau of Land Management 2003*a*, *b*). These restrictions can be modified or waived by BLM, or additional conditions of approval applied, on a case-by-case basis. In contrast, most state and private minerals have been developed with few or no requirements to mitigate impacts on wildlife.

Coal-bed natural gas development and its associated infrastructure may affect sage-grouse populations via several different mechanisms, and these mechanisms can operate at different scales. For example, males and females may abandon leks if repeatedly disturbed by raptors perching on power lines near leks (Ellis 1984), by vehicle traffic on nearby roads (Lyon and Anderson 2003), or by noise and human activity associated with energy development during the breeding season (Braun et al. 2002, Holloran 2005, Kaiser 2006). Collisions with nearby power lines and vehicles and increased predation by raptors may also increase mortality of birds at leks (Connelly et al. 2000*a*, 2000*b*). Alternatively, roads and power lines may indirectly affect lek persistence by altering productivity of local populations or survival at other times of the year. For example, sage-grouse mortality associated with power lines and roads occurs year-round (Patterson 1952, Beck et al. 2006, Aldridge and Boyce 2007), and ponds created by CBNG development may increase risk of West Nile virus (WNv) mortality in late summer (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007). Loss and degradation of sagebrush habitat can also reduce carrying capacity of local breeding populations (Swenson et al. 1987, Braun 1998, Connelly et al. 2000*b*, Crawford et al. 2004). Alternatively, birds may simply avoid otherwise suitable habitat as the density of roads, power lines, or energy development increases (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Doherty et al. 2008).

Understanding how energy development affects sage-grouse populations also requires that we control for other landscape features that affect population size and persistence, including the extent of suitable habitat. Sage-grouse are closely tied to sagebrush habitats throughout their annual cycle, and variation in the amount of sagebrush habitat available for foraging and nesting is likely to influence the size of breeding populations and persistence of leks (Ellis et al. 1989, Swenson et al. 1987, Schroeder et al. 1999, Leonard et al. 2000, Smith et al. 2005). For this reason, it is crucial to quantify and separate the effects of habitat loss from those of energy development.

To assess how CBNG development and habitat loss influence sage-grouse populations in the PRB, we conducted 2 analyses based on region-wide lek-count data. Lek counts are widely used for monitoring sage-grouse populations, and at present, are the only data suitable for examining trends in population size and distribution at this scale (Connelly et al. 2003, 2004). First, we analyzed counts of the numbers of males displaying on leks (lek counts) to assess whether trends in the number of males counted and proportion of active and inactive leks differed between areas with and without CBNG development. Second, we used logistic regression to model lek status (i.e., active or inactive) in relation to landscape features hypothesized to influence sage-grouse demographics and habitat use at 3 spatial scales. The objectives of the lek-status analysis were first, to identify the scale at which habitat and non-CBNG landscape features influence lek persistence and second, to evaluate and compare effects of CBNG development at different scales with those of non-CBNG landscape features after controlling for habitat.

Study Area

We analyzed data from sage-grouse leks within an approximately 50,000-km^2 area of northeastern Wyoming and southeastern Montana (Figure 1). This area included all areas with existing or predicted CBNG development in the PRB (Bureau of Land Management 2003*a*, *b*) as well as surrounding areas without CBNG. Land use in this region was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. Natural vegetation consisted of sagebrush-steppe and mixed-grass prairie interspersed with occasional stands of conifers. Sagebrush-steppe was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and non-native grasses and forbs. Plains silver sagebrush (*A. cana cana*) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big sagebrush in drainage bottoms.

Methods

Lek-count trend analyses

Lek-count data. We used sage-grouse lek-count data in public databases maintained by Wyoming Game and Fish Department and Montana Department of Fish, Wildlife, and Parks as the foundation for analyses. We augmented databases with lek counts provided by consultants and by the BLM's Miles City field office for 37 leks (36 in Montana, 1 in Wyoming) known to have been counted but for which data were missing. We checked for and, when possible, corrected errors in the database after consultation with database managers and regional biologists for each state. We excluded records with known errors, surveys in which lek status was not determined, leks without supporting count data, and duplicate leks prior to analysis.

Coal-bed natural gas development. We obtained data on the type, location, status, drilling date, completion date, and abandonment date of wells from public databases maintained by the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas

Conservation. Because wells are highly correlated with other features of development, such as roads, power lines, and ponds (D. E. Naugle, University of Montana, unpublished data), using well locations is a reliable way to map and measure the extent of CBNG development. We retained only those wells that were clearly in the ground, associated with energy development (gas, oil, stratification test, disposal, injection, monitoring, and water source wells), and likely to have infrastructure. We excluded wells that were plugged and abandoned, wells waiting on permit approval, wells drilled or completed in 2005 or later, and those with status reported as dry hole, expired permit, permit denied, unknown, or no report. We included wells in analyses starting in the year in which they were drilled or completed (i.e., started producing). For active wells without drilling or completion dates, we estimated start year based on approval and completion dates of nearby wells and those in the same unit lease. We included wells with status reported as dormant, temporarily abandoned, or permanently abandoned only until the year prior to when they were first reported as abandoned. Because capped wells (also commonly referred to as shut-in wells) may or may not have associated infrastructure, we included them only in years in which they were surrounded by, or within 1 km of, a producing gas field.

We estimated the extent of CBNG development around each lek in each year. We first approximated the area affected by CBNG development by creating a 350-m buffer around all well locations using ArcInfo 8.2 (ESRI, Inc., Redlands, CA) and dissolving boundaries where buffers overlapped. We then estimated the proportion of the area within 3.2 km of the lek center that was covered by the buffer around wells. At current well density (1 well per 32-64 ha), a 350-m buffer around wells estimates the extent of CBNG development more accurately than larger or smaller buffer sizes. This metric is less sensitive to variation in spacing of wells than measures such as well density and therefore more accurate for estimating the total area affected by CBNG development.

Trends in lek counts. We examined lek-count data from 1988-2005. In each year, we categorized a lek as in CBNG if ≥40% of the area within 3.2 km was developed or if ≥25% within 3.2 km was developed and ≥1 well was within 350 m of the lek center. We categorized a lek as outside CBNG if <40% of the area within 3.2 km was developed and no wells were within 350 m of the lek center. However, because few leks in CBNG were counted in consecutive years prior to 2001, we analyzed trends in lek-counts only from 2001-2005. We calculated the rate of increase in the number of males counted on leks for each year-to-year transition by summing count data across leks within each category (in CBNG vs. outside CBNG) according to their stage of development at the end of the first year of each year-to-year transition (Connelly et al. 2004). We summed data across leks to reduce the influence of geographic variation in detectability and used the maximum annual count for each lek to reduce the influence of within-year variation in detectability on the estimated rate of increase. We derived data for each transition only from leks counted in both years and known to be active in at least 1 of the 2 years of the transition. We estimated mean rates of increase in CBNG versus outside CBNG fields based on the slope of a linear regression of interval length versus rate of increase (Morris and Doak 2002). Wells completed between January and March (i.e., before lek counts were conducted) in the second year of each transition may have caused us to underestimate the amount of CBNG development around leks at the time counts were conducted. However, if CBNG development negatively affects populations, this would cause the difference between trends in lek-count data in CBNG and outside CBNG to be underestimated and would produce a conservative estimate of impacts.

Timing of lek disappearance. If CBNG development negatively affects lek persistence, most leks in CBNG fields that became inactive should have done so following CBNG development. To explore this prediction, we examined the timing of lek disappearance in relation to when a lek was first classified as being in a CBNG field (i.e., ≥40% development within 3.2 km or ≥25% development within 3.2 km and ≥1 well within 350 m of the lek center) for leks confirmed active in 1997 or later.

Lek-status analysis

Definition of leks. We defined a lek as a site where multiple males were documented displaying on multiple visits within a single year or over multiple years. We defined a lek complex as multiple leks located <2.5 km from the largest and most regularly attended lek in the complex (Connelly et al. 2004). We defined an initial set of lek complexes based on those known prior to 1990. We considered leks discovered in 1990 or later as separate complexes, even if they occurred <2.5 km from leks discovered in previous years. We did this to avoid problems with the location of already-defined leks and lek complexes shifting as new leks were discovered or if new leks formed in response to nearby CBNG development. We grouped leks discovered within 2.5 km of each other in the same year in the same lek complex. We used lek complexes as the sample unit for calculating proportion of active and inactive leks and in the lek-status analysis, but because the term lek complex can refer either to multiple leks or to a single lek, we refer to both simply as a lek.

Lek status. We determined the final status of leks by examining count data from 2002-2005. We considered a lek active if ≥ 1 male was counted in 2004 or 2005, whichever was the last year surveyed. To minimize problems with non-detection of males, we considered a lek inactive only if: 1) at least 3 consecutive ground or air visits in the last year surveyed failed to detect males, or 2) if surveys in the last 3 consecutive years the lek was checked (2002-2004 or 2003-2005) failed to detect males. We classified the status of leks that were not surveyed or were inadequately surveyed in 2004 or 2005 as unknown. Survey effort in the PRB increased 5-fold from 1997-2005 and included systematic aerial searches for new leks and repeated air and ground counts of known leks within and adjacent to CBNG fields. Therefore, it is unlikely that leks shifted to nearby sites without being detected. Many leks in the PRB disappeared during a region-wide population decline in 1991-1995 (Connelly et al. 2004), well before most CBNG development in the PRB began. To eliminate leks that became inactive for reasons other than CBNG, we calculated proportions of active and inactive leks in CBNG and outside CBNG based only on leks active in 1997 or later.

Scale. We calculated landscape metrics at 3 distances around each lek: 0.8 km (201 ha), 3.2 km (3,217 ha), and 6.4 km (12,868 ha). We selected the 0.8-km scale to represent processes that impact breeding birds at or near leks, while avoiding problems with spatial error in lek locations. We selected the 6.4-km scale to reflect processes that occur at larger scales around the lek, such as loss of nesting habitat, demographic impacts on local breeding populations, or landscape-scale avoidance of CBNG fields. The 3.2-km scale is that at which state and federal agencies apply mitigation for CBNG impacts (e.g., timing restrictions), and it is important to determine the appropriateness of managing at a 3.2-km scale versus at smaller or larger scales.

Habitat variables. Each model represented a distinct hypothesis, or combination of hypotheses, regarding how landscape features influence lek persistence. We included 2 types of habitat variables in the analysis, the proportion of sagebrush habitat and the proportion of tillage agriculture in the landscape around each lek. Because the scale at which habitat most strongly influenced lek persistence was unknown, we considered habitat variables at all 3 scales. We calculated the amount of sagebrush habitat and tillage agriculture around each lek at each scale using ArcInfo 8.2 based on classified SPOT-5 satellite imagery taken in August 2003 over an approximately 15,700 km^2 area of the PRB. We restricted the lek-status analysis to leks within the SPOT-5 satellite imagery because the only other type of classified imagery available for this region (Thematic Mapper at 30-m resolution) is unreliable for measuring the extent of sagebrush habitat (Moynahan 2004). We visually identified and manually digitized areas with tillage agriculture from the imagery. Classification accuracy was 83% for sagebrush habitat (i.e., sagebrush-steppe and sagebrush-dominated grassland). We excluded 20 leks for which >10% of classified habitat data were unavailable due to cloud cover or proximity to the edge of the imagery.

Road, power line, and CBNG variables. We hypothesized that infrastructure can affect lek persistence in 3 ways and included different variables to examine each hypothesis. Roads, power lines, and CBNG development may affect lek persistence in proportion to their extent on the landscape. Alternatively, the effects of roads and power lines may depend their distance from the lek, in which case they are expected to drop off rapidly as distance increases. Coal-bed natural gas development may also influence lek status depending on how long the lek has been in a CBNG field. If CBNG increases mortality, it may be several years before local breeding populations are reduced to the point that males no longer attend the lek (Holloran 2005). Avoidance of leks in CBNG fields by young birds (Kaiser 2006) combined with site fidelity of adults to breeding areas (Schroeder et al. 1999) would also result in a time lag between CBNG development and lek disappearance.

We used TIGER/Line® 1995 public-domain road layers for Wyoming and Montana (U.S. Census Bureau 1995) to estimate the proportion of each buffer around each lek within 350 m of a road at each of the 3 scales. We used 1995 data, rather than a more recent version, to represent roads that existed on the landscape prior to CBNG development. We obtained autumn 2005 GIS coverages of power lines directly from utility companies and used this layer to estimate the proportion of each buffer around each lek within 350 m of a power line at each scale. Year-specific power line coverages were not available, so this variable includes both CBNG and non-CNBG power lines. We estimated the extent of CBNG development around each lek at each scale by calculating the proportion of the total buffer area around the lek center covered by a dissolved 350-m buffer around well locations. If a lek was a complex, we first placed a buffer around all lek centers in the complex then dissolved the intersections to create a single buffer. We selected a 350-m buffer around roads, power lines, and CBNG wells for 2 reasons. First, quantitative estimates of the distance at which infrastructure affects habitat use or vital rates of sage-grouse were not available, and 350 m is a reasonable distance over which to expect impacts to occur, such as increased risk of predation near power lines or increased risk of vehicle collisions near roads. Second, we also wished to maintain a consistent relationship between well, road, and power line variables and the amount of area affected by each feature. We measured how long a lek was in a CBNG field as the number of years prior to 2005 during which the lek had ≥40% CBNG development within 3.2 km (or ≥25% CBNG within 3.2 km and ≥ 1 well within 350 m of the lek center).

Analyses. We used a hierarchical analysis framework to evaluate how landscape features influenced lek status (i.e., active or inactive). Our first goal was to identify the scale at which habitat, roads, and power lines affected lek persistence. Our second goal was to evaluate and compare effects of CBNG development at different scales with those of roads and power lines after controlling for habitat. In both cases, we used an information-theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model from a set of plausible candidate models. We conducted all analyses using logistic regression in R (version 2.3.1, R Development Core Team 2006). We used a logit-link function to bound persistence estimates within a (0,1) interval. Almost all CBNG development within the extent of the SPOT-5 imagery occurred after 1997, so we restricted our analysis to leks known to have been active in 1997 or later to eliminate those that disappeared for reasons other than CBNG development. We also excluded 4 leks known to have been destroyed by coal mining.

To identify the most relevant scale(s) for each landscape variable, we first allowed univariate models at different scales to compete. Variables assessed for scale effects included: (1) proportion sagebrush habitat, (2) proportion tillage agriculture, (3) proportion area affected by power lines, and (4) proportion area affected by non-CBNG roads. We then used the scale for each variable that best predicted lek status to construct the final set of candidate models. We also included models with squared distance to nearest road and squared distance to nearest power line in the final model set. To assess different possible mechanisms of CBNG impacts, we evaluated models with the extent of CBNG development or the number of years since the lek was classified as in a CBNG field. To assess the scale at which CBNG impacts occur, we included models with the extent of CBNG effects at all 3 scales. We also included models with interactions between habitat and CBNG metrics to evaluate whether effects of CBNG development are amelioriated by the amount of sagebrush habitat around the lek. To avoid problems with multicollinearity, we did not allow models with correlated variables (i.e., $r > |0.7|$) in the final model set.

We judged models based on Akaike's Information Criterion adjusted for small sample size (AIC_c) and examined beta coefficients and associated standard errors in all models to determine the direction and magnitude of effects. We estimated overdispersion by dividing the deviance of the global model by the deviance degrees of freedom. We conducted goodness-of-fit testing in R following methods described in Hosmer et al. (1997). We used parametric bootstrapping (Efron and Tibshirani 1993) to obtain means, standard errors, and 95% confidence limits for persistence estimates because coefficients of variation for most beta estimates were large (Zhou 2002). Due to model uncertainty, we used model averaging to obtain unconditional parameter estimates and variances (Burnham and Anderson 2002). We compared the relative importance of habitat, CBNG, and infrastructure in determining lek persistence by summing Akaike weights across all models containing each class of variable (Burnham and Anderson 2002). We also calculated evidence ratios to compare the likelihood of the best approximating habitat-plus-CBNG model versus the best approximating habitat-plus-infrastructure and habitat-only models.

To assess whether a known West Nile virus outbreak or habitat loss associated with tillage agriculture disproportionately influenced model selection and interpretation, we also reanalyzed the dataset after removing specific leks. The first analysis excluded 4 leks near Spotted Horse, Wyoming known to have disappeared after 2003 likely due to WNv-related mortality (Walker et al. 2004). The second analysis excluded 20 leks that had ≥5% agriculture at 1 or more of the 3 scales examined.

To evaluate the effectiveness of the stipulation for no surface infrastructure within 0.4 km of a lek, we examined the estimated probability of lek persistence without development versus that under full CBNG development with a 0.4-km buffer.

Results

Trends in lek counts. From 2001-2005, lek-count indices in CBNG fields declined by 82%, at a rate of 35% per year (mean rate of increase in CBNG = 0.65, 95% CI: 0.34-1.25) whereas indices outside CBNG declined by 12%, at a rate of 3% per year (mean rate of increase outside CBNG = 0.97, 95% CI: 0.50-1.87) (Figure 2). The mean number of males per active lek was similar for leks in CBNG and outside CBNG in 2001, but averaged 45% ± 8% (mean ± SE; range 33-55%) lower for leks in CBNG from 2002-2005 (Figure 3).

Lek status. Among leks active in 1997 or later, fewer leks remained active by 2004-2005 in CBNG fields (38%) than outside CBNG fields (84%) (Table 1). Of the 10 remaining active leks in CBNG fields, all were classified as being in CBNG in 2000 or later.

Timing of lek disappearance. Of 12 leks in CBNG fields monitored intensively enough to determine the year when they disappeared, 12 became inactive after or in the same year that development occurred (Figure 4). The average time between CBNG development and lek disappearance for these leks was 4.1 ± 0.9 years (mean ± SE).

Lek-status analysis. We analyzed data from 110 leks of known status within the SPOT-5 imagery that were confirmed active in 1997 or later. Proportion sagebrush habitat and proportion tillage agriculture best explained lek persistence at the 6.4-km scale (Table 2). Proportion power lines also best explained lek persistence at the 6.4-km scale (although power line effects at the 3.2-km scale were also supported), whereas proportion roads best explained lek persistence at the 3.2-km scale.

The final model set consisted of 19 models: 2 models based on habitat only (i.e., sagebrush, sagebrush plus tillage agriculture), 4 models with habitat plus power line variables, 4 models with habitat plus road variables, and 9 models with habitat plus CBNG variables (Table 3). Goodness-of-fit testing using the global model revealed no evidence of lack of fit (P = 0.49).

Our estimate of the variance inflation factor based on the global model ($\hat{c} = 0.96$) indicated no evidence of overdispersion, so we based model selection on AIC_c values (Burnham and Anderson 2002).

Despite substantial model uncertainty, the top 8 of 19 models all included a moderate to strong positive effect of sagebrush habitat on lek persistence and a strong negative effect of CBNG development, measured either as proportion CBNG development within 0.8 km, proportion CBNG development within 3.2 km, or number of years in a CBNG field. These 8 models were well supported, with a combined Akaike weight of 0.96. Five of the 8 models were within 2 $\Delta\mathrm{AIC}_c$ units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (> 6 $\Delta\mathrm{AIC}_c$ units lower). Evidence ratios indicate that the best habitat-plus-CBNG model was 28 times more likely to explain patterns of lek persistence than the best habitat-plus-infrastructure model and 50 times more likely than the best habitat-only model. Models 1 and 2 both included a negative effect of proportion CBNG development within 0.8 km. Models with a negative effect of number of years in CBNG (model 3) or proportion CBNG development within 3.2 km (model 4) also had considerable support. Although regression coefficients suggested that CBNG within 6.4 km also had a negative impact on lek persistence (Table 4), models with CBNG at 6.4 km showed considerably less support (~5-7 $\Delta\mathrm{AIC}_c$ units lower). Tillage agriculture appeared in 1 well-supported model (model 2), and the coefficient suggested that tillage agriculture had a strong negative effect on lek persistence. However, this effect was poorly estimated, and the same model without tillage agriculture (model 1) was more parsimonious. Regression coefficients suggested negative effects of proximity to power lines and of proportion power line development within 6.4 km (Table 4), but models with power line effects were only weakly supported (~6-8

ΔAIC_c units lower) (Table 3). Models containing effects of roads unrelated to CBNG development received little or no support. Coefficients for interaction terms did not support an interaction between habitat and CBNG variables. The best approximating model accurately predicted the status of 79% of 79 active leks and 47% of 31 inactive leks. The summed Akaike weight for CBNG variables (0.97) was almost as large as that of sagebrush habitat (1.00) and greater than that for the effects of tillage agriculture (0.26), power lines (0.02) or non-CBNG roads (0.01). Unconditional, model-averaged estimates and 95% confidence limits for beta estimates and odds ratios show that loss of sagebrush habitat and addition of CBNG development around leks had effects of similar magnitude (Table 4).

The model-averaged estimate for the effect of CBNG within 0.8 km was close to that of the best approximating model (model 1, $\beta_{\text{CBNG 0.8 km}} = -3.91 \pm 1.11$ SE) (Table 4). Thus, we illustrate the effects CBNG within 0.8 km on lek persistence using estimates from that model (Figure 5a). We also illustrate results from model 3, which indicated that leks disappeared, on average, within 3-4 years of CBNG development (Figure 5b).

The current 0.4-km stipulation for no surface infrastructure leaves 75% of the landscape within 0.8 km and 98% of the landscape within 3.2 km open to CBNG development. In an average landscape around a lek (i.e., 74% sagebrush habitat, 26% other land cover types), 75% CBNG development within 0.8 km would drop the probability of lek persistence from 86% to 24% (Figure 5a). Similarly, 98% CBNG development within 3.2 km would drop the average probability of lek persistence from 87% to 5%.

Secondary analyses. Analysis of reduced datasets did not meaningfully change model fit, model selection, or interpretation, nor did it alter the magnitude or direction of estimated CBNG effects. After excluding leks affected by WNv, the top 8 of 19 models and all 3 models within 2

ΔAIC_c units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Model-averaged estimates of CBNG effects were similar to those from the original analysis ($\beta_{\text{Sagebrush 6.4 km}} = 3.96 \pm 1.97$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.48 \pm 1.15$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.39 \pm 1.52$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.57 \pm 2.06$ SE; $\beta_{\text{Years in CBNG}} = -1.30 \pm 0.61$ SE). After excluding leks with ≥5% tillage agriculture, the top 4 of 11 models and 4 of 5 models within 2 ΔAIC_c units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Estimates of CBNG effects were again similar to the original model-averaged values ($\beta_{\text{Sagebrush 6.4 km}} = 4.03 \pm 2.29$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.34 \pm 1.41$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.83 \pm 2.06$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.76 \pm 3.21$ SE; $\beta_{\text{Years in CBNG}} = -2.44 \pm 1.25$ SE).

Discussion

Coal-bed natural gas development appeared to have substantial negative effects on sage-grouse breeding populations as indexed by male lek attendance and lek persistence. Although the small number of transitions (n = 4) in the trend analysis limited our ability to detect differences between trends, effect sizes were nonetheless large and suggest more rapidly declining breeding populations in CBNG fields. Effects of CBNG development explained lek persistence better than effects of power lines, pre-existing roads, WNv mortality, or tillage agriculture, even after controlling for availability of sagebrush habitat. Strong support for models with negative effects of CBNG at both the 0.8-km and 3.2-km scales indicate that the current restriction on surface infrastructure within 0.4 km is insufficient to protect breeding populations. Moreover, support for a lag time between CBNG development and lek disappearance suggests that monitoring effects of a landscape-level change like CBNG may require several years before changes in lek status are detected.

Although CBNG development was clearly associated with population declines, the relative contribution of different components of infrastructure to overall population impacts remains unclear. Models with power line effects were weakly supported compared to models with CBNG, but coefficients nonetheless suggested that power lines (including those associated with CBNG) had a negative effect on lek persistence. In our study, non-CBNG roads did not appear to influence lek persistence, even though collisions with vehicles and disturbance of leks near roads can have negative impacts on sage-grouse (Lyon and Anderson 2003, Holloran 2005). This may be because most roads in sage-grouse habitat in the PRB prior to CBNG development were rarely-traveled dirt tracks rather than the more heavily traveled, all-weather roads associated with CBNG development. West Nile virus has also contributed to local lek extirpations in the PRB (Walker et al. 2004). However, unless CBNG development facilitates the spread of WNv into sage-grouse habitat, impacts of the virus should be similar in areas with and without CBNG. Thus, the impact of WNv by itself cannot explain declining breeding populations in CBNG. Rather, increased WNv-related mortality may be an indirect effect of CBNG development (Zou et al. 2006). Other indirect effects, such as changes in livestock grazing due to newly-available CBNG water, or changes in predator abundance caused by addition of ponds or power lines, may also contribute to the cumulative effect of CBNG development on sage-grouse populations.

Although CBNG development and loss of sagebrush habitat both contributed to declines in lek persistence, more of the landscape in the PRB has potential for CBNG than for tillage agriculture, which suggests that CBNG may eventually have a greater impact on region-wide populations. In our analyses, we were unable to distinguish between conversion of sagebrush to cropland that would have occurred without CBNG development and that which occurred because

CBNG water became available for irrigation following development. Although sage-grouse sometimes use agricultural fields during brood-rearing (Schroeder et al. 1999, Connelly et al. 2000*b*), conversion of sagebrush habitat to irrigated cropland in conjunction with CBNG development may be detrimental (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005), particularly if birds in agricultural areas experience elevated mortality due to mowing, pesticides, or WNv (Patterson 1952, Connelly et al. 2000*b*, Naugle et al. 2004).

Accumulated evidence across studies suggests that sage-grouse populations typically decline following energy development (Braun 1986, Remington and Braun 1991, Braun et al. 2002, Holloran 2005), but our study is the first to quantify and separate effects of energy development from those of habitat loss. Our results are similar to those of Holloran (2005:49), who found that "natural gas field development within 3-5 km of an active greater sage-grouse lek will lead to dramatic declines in breeding populations," leks heavily impacted by development typically became inactive within 3-4 years, and energy development within 6.2 km of leks decreased male attendance. As in other parts of their range, sage-grouse populations in the PRB likely have declined due to cumulative impacts of habitat loss combined with numerous other known and unknown stressors. New threats, such as WNv, have also emerged (Naugle et al. 2004, Walker et al. 2007). Nonetheless, our analysis indicates that energy development has contributed to recent localized population declines in the PRB. More importantly, the scale of future development in the PRB suggests that, without more effective mitigation, CBNG will continue to impact populations over an even larger area.

It is unclear whether declines in lek attendance within CBNG fields were caused by impacts to breeding birds at the lek, reduced survival or productivity of birds in the surrounding area, avoidance of developed areas, or some combination thereof. We simultaneously observed less support for models with CBNG effects and increasing magnitude of those effects at larger scales around leks, but model uncertainty precluded identification of a specific mechanism underlying impacts. Experimental research using a before-after, control-impact design with radio-marked birds would be required to rigorously evaluate these hypotheses. Although this would allow us to identify mechanisms underlying declines, based on our findings and those of others (e.g., Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008), such an experiment would likely be detrimental to the affected populations. Nonetheless, ongoing development provides an opportunity to test mitigation measures in an adaptive management framework, with the ultimate goal of determining how to maintain robust sage-grouse populations in areas with CBNG development.

Management implications

Our analysis indicates that maintaining extensive stands of sagebrush habitat over large areas (6.4 km or more) around leks is required for sage-grouse breeding populations to persist. This recommendation matches those of all major reviews of sage-grouse habitat requirements (Schroeder et al. 1999, Connelly et al. 2000*b*, Connelly et al. 2004, Crawford et al. 2004, Rowland 2004). Our findings also refute the idea that prohibiting surface infrastructure within 0.4 km of the lek is sufficient to protect breeding populations and indicate that increasing the size of no-development zones around leks would increase the probability of lek persistence. The buffer size required would depend on the amount of suitable habitat around the lek and the level of population impact deemed acceptable. Timing restrictions on construction and drilling during the breeding season do not prevent impacts of infrastructure (e.g., avoidance, collisions, raptor predation) at other times of the year, during the production phase (which may last a decade or more), or in other seasonal habitats that may be crucial for population persistence (e.g., winter).

Previous research suggests that a more effective mitigation strategy would also include, at minimum, burying power lines (Connelly et al. 2000*b*), minimizing road and well pad construction, vehicle traffic, and industrial noise (Lyon and Anderson 2003, Holloran 2005), and managing water produced by CBNG to prevent the spread of mosquitos that vector WNv in sage-grouse habitat (Zou et al. 2006, Walker et al. 2007). The current pace and scale of CBNG development suggest that effective mitigation measures should be implemented quickly to prevent impacts from becoming more widespread.

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Literature cited

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: a habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. Wildlife Society Bulletin 34:1070-1078.

Bevanger, K. 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. Biological Conservation 86:67 -76.

Braun, C. E. 1986. Changes in sage-grouse lek counts with advent of surface coal mining. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife, Thorne Ecological Institute 2:227-231.

Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139-156.

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.

Bureau of Land Management [BLM]. 2003*a*. Final Environmental Impact Statement and Proposed Plan Amendment for the Powder River Basin Oil and Gas Project. <http://www.blm.gov/wy/st/en/info/NEPA/bfodocs/prb-feis.html>. Accessed 18 March 2007.

Bureau of Land Management [BLM]. 2003*b*. Montana Statewide Final Oil and Gas EIS and Amendment of the Powder River and Billings Resource Management Plans. <http://www.mt.blm.gov/mcfo/cbm/eis/index.html>. Accessed 18 March 2007.

Burnham, K. P, and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Connelly, J. W., A. D. Apa, R. B. Smith and K. P. Reese. 2000*a*. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

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

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. University of Idaho College of Natural Resources Experiment Station, Moscow, Idaho, USA.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Moseley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife–threats to biodiversity and human health. Science 287:443-449.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. In press. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Ellis, K. L. 1984. Behavior of lekking sage grouse in response to a perched golden eagle. Western Birds 15:37-38.

Ellis, K. L., J. R. Parish, J. R. Murphy, and G. H. Richins. 1989. Habitat use by breeding male sage grouse: a management approach. Great Basin Naturalist 49:404-407.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871-883.

Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.

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

Hosmer, D. W., T. Hosmer, S. le Cessie, and S. Lemeshow. 1997. A comparison of goodness-of-fit tests for the logistic regression model. Statistics in Medicine 16:965-980.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. Thesis, University of Wyoming, Laramie, Wyoming.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266-71.

Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse, *Centrocercus urophasianus,* on the Upper Snake River Plain of Idaho: changes from the 1950's to the 1990's. Wildlife Biology 6:265-270.

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.

Morris, W., and D. F. Doak. 2002. Quantitative Conservation Biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Moynahan, B. J. 2004. Landscape-scale factors affecting population dynamics of greater sage-grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004. Dissertation. University of Montana, Missoula, MT.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: pending crisis for greater sage-grouse. Ecology Letters 7:704-713.

Naugle, D. E., C. A. Aldridge, B. L. Walker, K. E. Doherty, M. R. Matchett, J. McIntosh, T. E. Cornish, and M. S. Boyce. 2005. West Nile virus and sage-grouse: What more have we learned? Wildlife Society Bulletin 33:616-623.

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

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

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Commission and Sage Books, Inc., Denver, Colorado.

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 3 February 2006.

Remington, T. E. and C. E. Braun. 1991. How surface coal mining affects sage grouse, North Park, Colorado. Proceedings: Issues and Technology in the Management of Impacted Western Wildlife. Thorne Ecological Institute 5:128-132.

Rowland, M. M. 2004. Effects of management practices on grassland birds: greater sage-grouse. Northern Prairie Wildlife Research Center, Jamestown, North Dakota, USA. Northern Prairie Wildlife Research Center Online. http://www.npwrc.usgs.gov/resource/literatr/grasbird/grsg/grsg.htm (Version 12AUG2004). Accessed 14 February 2007.

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

Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310-320.

Steenhof, K., M. N. Kochert, and J. A. Roppe. 1993. Nesting by raptors and common ravens on electrical transmission line towers. Journal of Wildlife Management 57:272-281.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

U. S. Census Bureau. 1995. TIGER/Line® 1995 data. Available from the Wyoming Natural Resources Data Clearinghouse. http://www.sdvc.uwyo.edu/24k/road.html. Accessed 3 August 2006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2004. Outbreak of West Nile virus in greater sage-grouse and guidelines for monitoring, handling, and submitting dead birds. Wildlife Society Bulletin 32:1000-1006.

Walker, B. L., D. E. Naugle, K. E. Doherty, and T. E. Cornish. 2007. West Nile virus and greater sage-grouse: estimating infection rate in a wild population. Avian Diseases 51: in press.

Zhou, S. 2002. Estimating parameters of derived random variables: comparison of the Delta and parametric bootstrap methods. Transactions of the American Fisheries Society 131:667-675.

Zou, L., S. Miller, and E. Schmidtmann. 2006. Mosquito larval habitat mapping using remote sensing and GIS: implications of coal-bed methane development and West Nile virus. Journal of Medical Entomology 43:1034-1041.

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Figure 1. Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, U.S.A. The dashed line shows the extent of SPOT-5 satellite imagery. This map excludes leks that became inactive or were destroyed prior to 1997 and leks whose status in 2004-2005 was unknown. The status of leks within a lek complex are depicted separately. Dot sizes of active leks represent the final count of displaying males in 2004 or 2005, whichever was the last year surveyed: small = 1-25 males, medium = 26-50 males, large = 51-75 males.

Figure 2. Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005 for leks categorized as in coal-bed natural gas fields or outside coal-bed natural gas fields on a year-by-year basis. Sample sizes in parentheses next to each year-to-year transition indicate the number of leks available for calculating rates of increase for that transition.

Figure 3. Number of male sage-grouse per active lek in coal-bed natural gas (CBNG) fields (gray) and outside (black) CBNG fields in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005. Error bars represent 95% confidence intervals (error bars for leks outside CBNG are too small to be visible). Sample sizes in parentheses above each index indicate the number of active leks available for calculating males per active lek in each year.

Figure 4. Timing of greater sage-grouse lek disappearance relative to coal-bed natural gas development in the Powder River Basin for leks confirmed active in 1997 or later. Leks above the diagonal line became inactive after CBNG development reached ≥40% within 3.2 km (or

>25% development within 3.2 km and ≥1 well within 350 m of the lek center). Small dot = 1 lek, medium dot = 2 leks, large dot = 3 leks.

Figure 5. Estimated lek persistence as a function of proportion sagebrush habitat within 6.4 km and either (a) proportion coal-bed natural gas (CBNG) development within 0.8 km or (b) number of years within a CBNG field for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on parametric bootstrapping. In (a), black lines are estimated lek persistence with no CBNG development, and gray lines are estimated lek persistence with 75% CBNG development within 0.8 km. Seventy-five percent CBNG development within 0.8 km is equivalent to full development under the Bureau of Land Management's current restriction on surface infrastructure within 0.4 km of active sage-grouse leks. In (b), black lines are estimated lek persistence prior to CBNG development, and gray lines are estimated lek persistence after 3 years in a developed CBNG field (i.e., ≥40% CBNG within 3.2 km or ≥25% CBNG within 3.2 km and ≥1 well within 350 m of the lek center).

Table 1. Status of greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A as of 2004-2005, including only leks confirmed active in 1997 or later.

	In CBNG[a]		Outside CBNG[a]	
Lek status[a]	No.	%[b]	No.	%[b]
Active	10	38	211	84
Inactive	16	62	39	16
Unknown	1		43	
Total active + inactive	26		250	

[a] See text for definitions of active and inactive leks and for how we catgorized leks as in coal-bed natural gas development (In CBNG) vs. outside coal-bed natural gas (Outside CBNG). Each lek complex counted as one lek.

[b] We calculated percentages based only on the total number of active and inactive leks.

Table 2. Univariate model selection summary for different classes of landscape variables influencing greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.[a]

Model	LL	*K*	*n*	ΔAIC_c	w_i	β	SE
Sagebrush							
6.4 km	-60.05	2	110	0.00	0.70	5.20	1.68
3.2 km	-60.95	2	110	1.81	0.28	4.38	1.53
0.8 km	-63.43	2	110	6.77	0.02	2.26	1.15
Tillage agriculture							
6.4 km	-55.52	2	110	0.00	0.79	-20.98	6.02
3.2 km	-56.83	2	110	2.63	0.21	-19.31	6.30
0.8 km	-60.92	2	110	10.81	0.00	-10.44	4.59
Power lines							
6.4 km	-58.69	2	110	0.00	0.52	-6.06	1.76
3.2 km	-58.81	2	110	0.24	0.46	-4.92	1.43
0.8 km	-62.12	2	110	6.84	0.02	-2.51	0.99
Roads							
3.2 km	-64.59	2	110	0.00	0.50	-2.50	1.99
6.4 km	-65.20	2	110	1.21	0.27	-1.52	2.35
0.8 km	-65.41	2	110	1.63	0.22	-0.08	0.87

[a] We present maximum log-likelihood (LL), number of parameters (*K*), sample size (*n*), ΔAIC_c values, AIC_c weights (w_i), estimated regression coefficients (β), and standard errors (SE) for each model in each class in order of decreasing maximum log-likelihood. AIC_c = Akaike's

Information Criterion adjusted for small sample size.

Table 3. Model selection summary for hypotheses to explain greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.[a]

No.	Model[b]	LL	K	n	$\Delta \mathrm{AIC}_c$[c]	w_i
1	Sagebrush 6.4 + CBNG 0.8	-51.16	3	110	0.00	0.24
2	Sagebrush 6.4 + Agriculture 6.4 + CBNG 0.8	-50.48	4	110	0.80	0.16
3	Sagebrush 6.4 + Years in CBNG	-51.56	3	110	0.80	0.16
4	Sagebrush 6.4 + CBNG 3.2	-51.70	3	110	1.09	0.14
5	Sagebrush 6.4 * CBNG 0.8	-50.98	4	110	1.81	0.10
6	Sagebrush 6.4 * Years in CBNG	-51.32	4	110	2.48	0.07
7	Sagebrush 6.4 + Agriculture 6.4 + CBNG 3.2	-51.52	4	110	2.88	0.06
8	Sagebrush 6.4 + CBNG 6.4	-53.69	3	110	5.07	0.02
9	Sagebrush 6.4 + Agriculture 6.4 + Dist. power line^2	-53.39	4	110	6.63	0.01
10	Sagebrush 6.4 + Agriculture 6.4 + CBNG 6.4	-53.48	4	110	6.81	0.01
11	Sagebrush 6.4 + Agriculture 6.4	-55.08	3	110	7.84	0.00
12	Sagebrush 6.4 + Power lines 6.4	-55.08	3	110	7.84	0.00
13	Sagebrush 6.4 + Agriculture 6.4 + Power lines 6.4	-54.07	4	110	7.99	0.00
14	Sagebrush 6.4 + Agriculture 6.4 + Dist. road^2	-54.47	4	110	8.78	0.00
15	Sagebrush 6.4 + Agriculture 6.4 + Roads 3.2	-54.49	4	110	8.83	0.00
16	Sagebrush 6.4 + Dist. power line^2	-57.36	3	110	12.41	0.00
17	Sagebrush 6.4	-60.05	2	110	15.67	0.00
18	Sagebrush 6.4 + Roads 3.2	-59.39	3	110	16.46	0.00
19	Sagebrush 6.4 + Dist. road^2	-59.46	3	110	16.62	0.00

[a] We present maximum log-likelihood (LL), number of parameters (K), sample size (n), $\Delta\mathrm{AIC}_c$ values, and AIC_c weights (w_i) for each model in order of increasing $\Delta\mathrm{AIC}_c$ units, starting with the best approximating model. AIC_c = Akaike's Information Criterion adjusted for small sample size.

[b] CBNG = coal-bed natural gas development. Numbers refer to the radius (km) around the lek at which the variable was measured.

[c] The AIC_c value of the best approximating model in the analysis was 108.54.

Table 4. Model-averaged estimates of regression coefficients (β) and standard errors (SE), odds ratios, and lower and upper 95% confidence limits on odds ratios for effects of landscape variables on greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.

Variable[a]	β	SE	Odds Ratio	Lower CL	Upper CL
Intercept	-1.25	1.40			
Sagebrush	4.06	2.03	58.241	1.083	3131.682
Agriculture	-8.76	8.73	1.57×10^{-4}	5.81×10^{-12}	4.22×10^{3}
Dist. power line^2	1.72	1.27	5.603	0.462	67.925
Power lines	-4.52	2.40	0.011	0.0001	1.203
Dist. road^2	0.62	0.67	1.86	0.505	6.859
Roads	-2.38	2.23	0.092	0.001	7.331
CBNG 0.8 km	-3.67	1. 18	0.026	0.003	0.257
CBNG 3.2 km	-4.72	1.50	0.009	0.001	0.169
CBNG 6.4 km	-5.11	2.04	0.006	0.0001	0.328
Years in CBNG	-1.41	0.58	0.244	0.078	0.761

[a] CBNG = coal-bed natural gas development. The estimated regression coefficient for Years in CBNG could only be derived from 1 model.

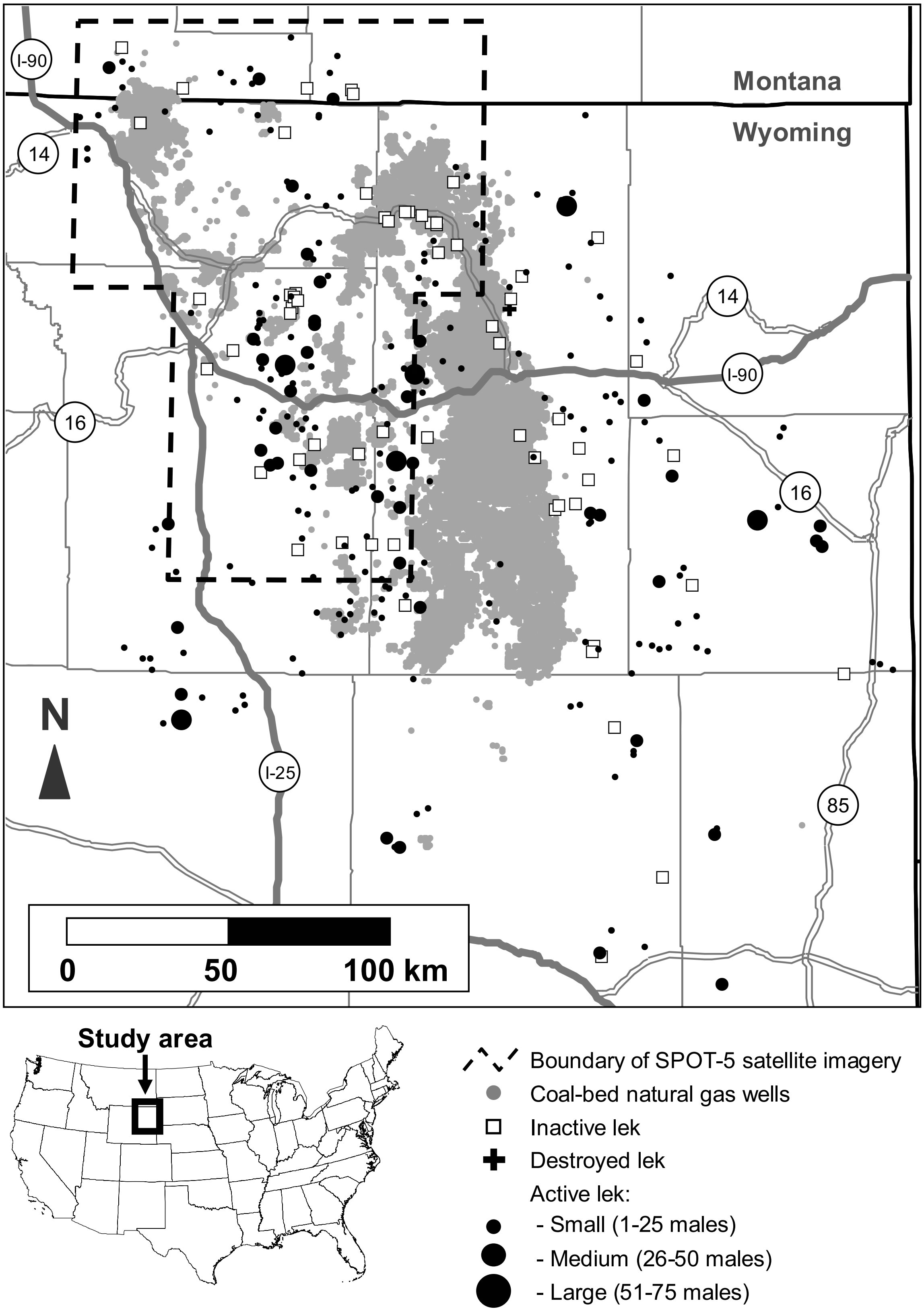
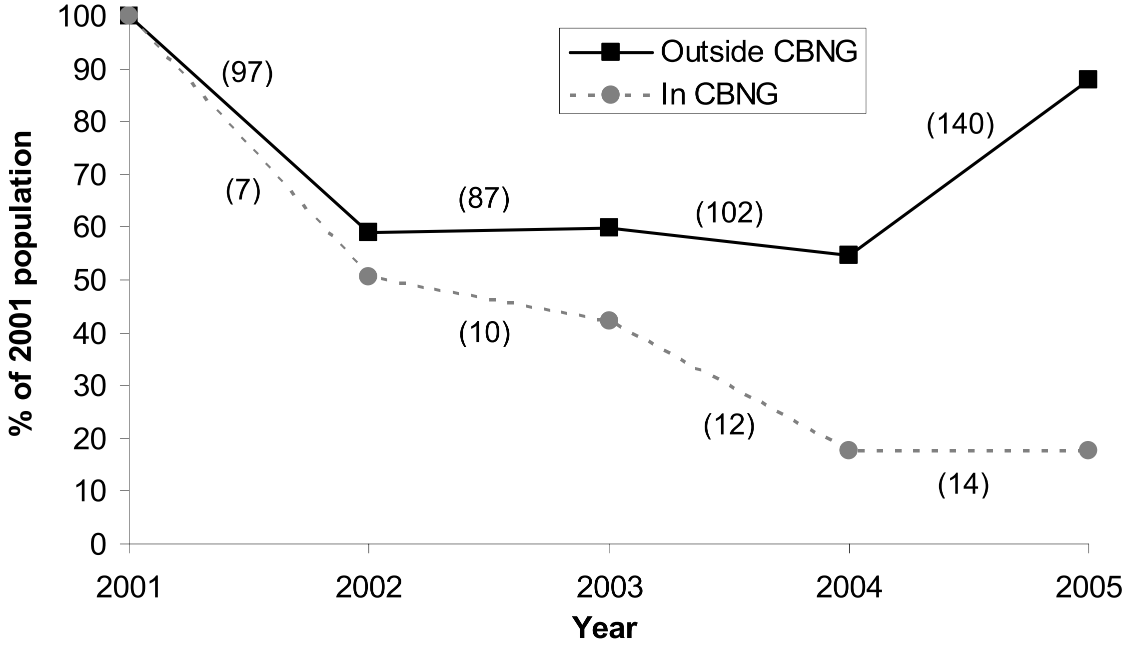

I-90
14
16
I-25
85
Montana
Wyoming
N
0
50
100 km
Study area
Boundary of SPOT-5 satellite imagery
Coal-bed natural gas wells
Inactive lek
Destroyed lek
Active lek:
- Small (1-25 males)
- Medium (26-50 males)
- Large (51-75 males)

Figure 2



100
90
80
70
60
50
40
30
20
10
0
% of 2001 population
2001
2002
2003
2004
2005
Year
Outside CBNG
In CBNG
(97)
(7)
(87)
(10)
(102)
(12)
(140)
(14)

Figure 3

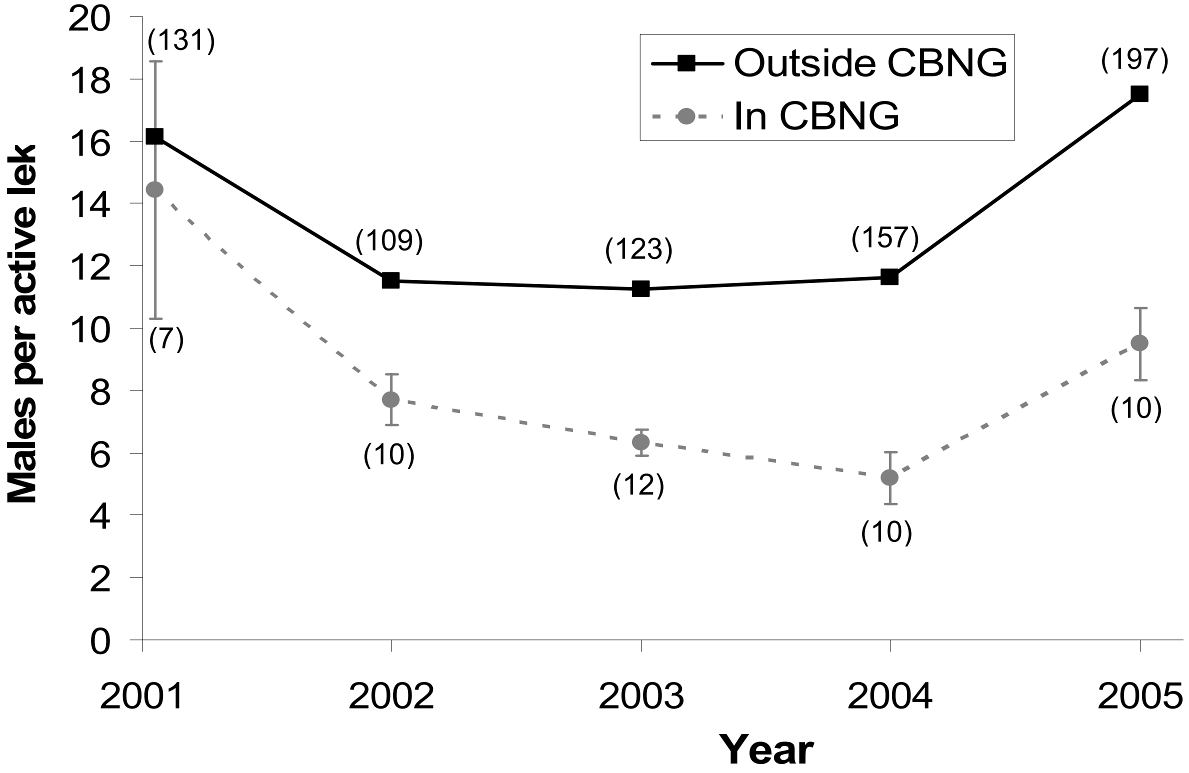
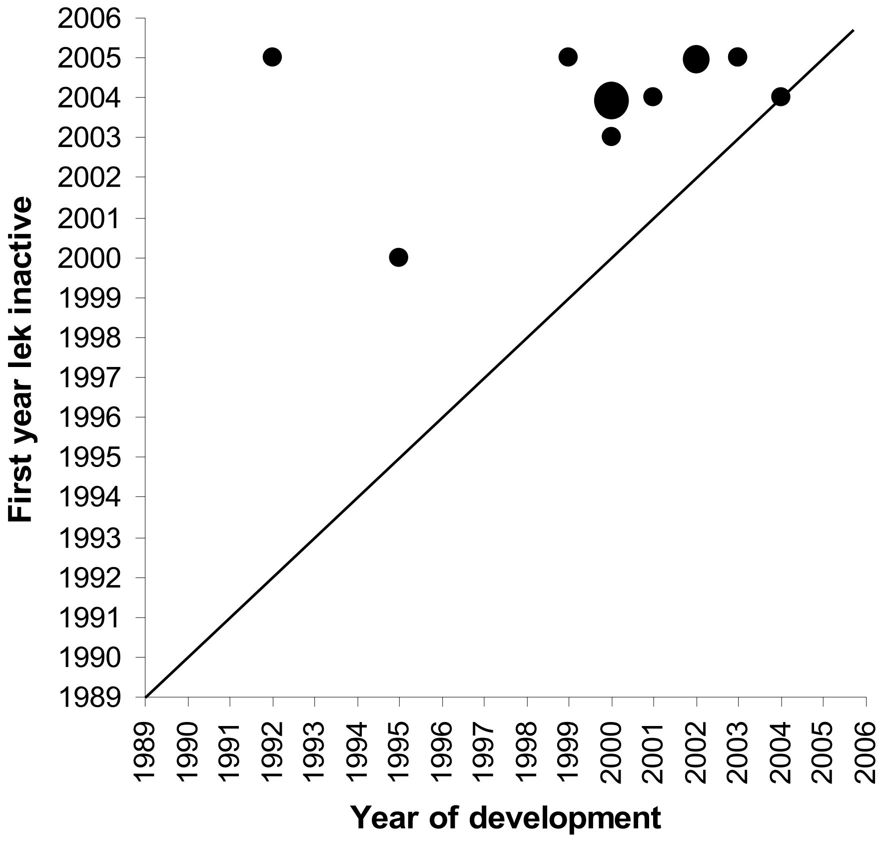

Outside CBNG
In CBNG
Males per active lek
Year
0
2
4
6
8
10
12
14
16
18
20
2001
2002
2003
2004
2005
(131)
(7)
(109)
(10)
(123)
(12)
(157)
(10)
(197)
(10)

Figure 4


First year lek inactive
2006
2005
2004
2003
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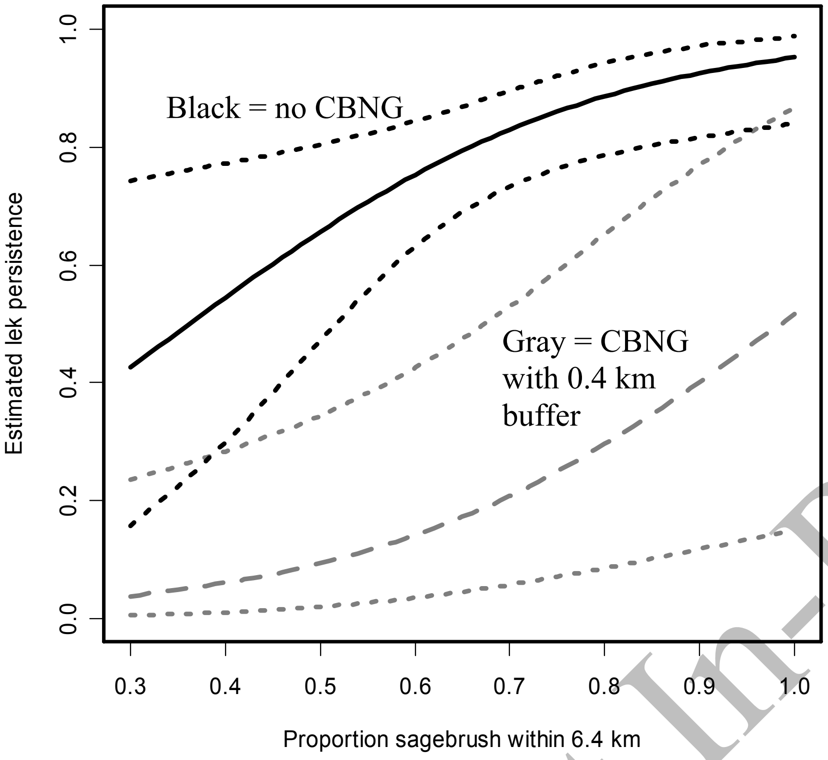
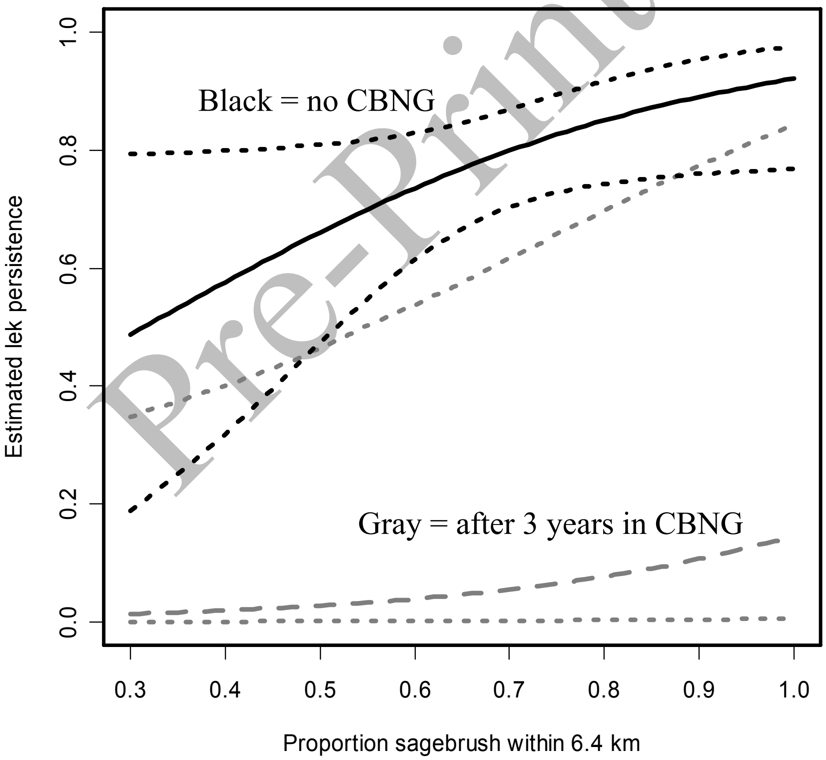
2001
2002
2003
2004
2005
2006
Year of development

Figure 5

a


Black = no CBNG
Gray = CBNG with 0.4 km buffer
Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion sagebrush within 6.4 km

b


Black = no CBNG
Gray = after 3 years in CBNG
Estimated lek persistence
0.0
0.2
0.4
0.6
0.8
1.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Proportion sagebrush within 6.4 km