



Disturbance Factors Influencing Greater Sage-Grouse Lek Abandonment in North-Central Wyoming

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ABSTRACT Detecting the disappearance of active leks is the most efficient way to determine large declines in greater sage-grouse (*Centrocercus urophasianus*) populations; thus, understanding factors that influence lek abandonment is critical. We evaluated factors that may have influenced the probability of sage-grouse lek abandonment in the Bighorn Basin (BHB) of north-central Wyoming from 1980 to 2009. Our objective was to examine lek abandonment based on landscape characteristics that explain differences between occupied and unoccupied leks. We evaluated lek abandonment from 144 occupied and 39 unoccupied leks from the Wyoming Game and Fish Department lek database with sufficient data for our 30-year analysis. We conducted our analysis with binary logistic regression using landscape predictor variables obtained from geographic coverages at 5 scales (1.0-, 3.2-, 4.0-, 5.0-, and 6.4-km radii around leks) to evaluate how these disturbances have influenced lek abandonment. Coverages included anthropogenic characteristics such as agricultural development, oil and gas development, prescribed burned treatments, and roads; and environmental characteristics such as vegetation attributes and wildfire. Our combined model included the number of oil and gas wells in a 1.0-km radius, percent area of wildfire in a 1.0-km radius, and variability in shrub height in a 1.0-km radius around sage-grouse leks. Abandoned (unoccupied) leks had 1.1-times the variability of shrub height in a 1.0-km radius, 3.1-times the percentage of wildfire in a 1.0-km radius, and 10.3-times the number of oil and gas wells in a 1.0-km radius compared to occupied leks. The model-averaged odds of lek persistence with every 1 unit increase in oil and gas wells within a 1.0-km radius was 0.66 (90% CI: 0.37–0.94), odds with every 1% increase in wildfire in a 1.0-km radius was 0.99 (90% CI: 0.85–1.12), and odds with every 1 unit increase in the standard deviation of shrub height within a 1.0-km radius around a lek was 0.77 (90% CI: 0.45–1.08). Because the 90% confidence intervals around the odds ratios of wells did not overlap 1.0, we suggest this predictor variable was most influential in our model-averaged estimates. The BHB has lower developed reserves of oil and gas than many other regions; however, our study supports findings from other studies that demonstrate energy development increases lek abandonment. Our findings indicate conservation efforts should be focused on minimizing well development and implementing wildfire suppression tactics near active sage-grouse leks. © 2012 The Wildlife Society.

KEY WORDS big sagebrush, *Centrocercus urophasianus*, cumulative disturbance factors, energy development, greater sage-grouse, lek abandonment, shrubs, wildfire.

Greater sage-grouse (*Centrocercus urophasianus*) are the largest grouse species in North America and once occupied 1,200,483 km² of sagebrush habitats in 13 of the western United States and 3 Canadian provinces (Schroeder et al. 2004). Sage-grouse are now found in Alberta, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, Saskatchewan, South Dakota, Utah, Washington, and

Wyoming (Schroeder et al. 2004). Recent studies have indicated dramatic local and range-wide declines in leks and lek attendance (Connelly and Braun 1997, Johnson et al. 2011) with some populations predicted to decline below effective population sizes ($N_e = 1/(1/N_m + 1/N_f)$; where, N_m = number of males successfully breeding and N_f = number of female breeders) within the next 30 years and others declining below effective population sizes within the next 100 years (Garton et al. 2011). The current distribution of sage-grouse represents an estimated 56% of their historical range (Schroeder et al. 2004). Sage-grouse populations have declined throughout their historical habitats through many factors related to habitat loss and fragmentation (Braun

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1998, Connelly et al. 2004) including increasing natural disturbance factors such as wildfires (Connelly and Braun 1997, Connelly et al. 2000*a, b*) and anthropogenic disturbances to sagebrush communities including agricultural development (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005, Walker et al. 2007, Aldridge et al. 2008), historical livestock-related activities (Beck and Mitchell 2000, Crawford et al. 2004), urbanization (Braun 1987, 1998; Connelly et al. 2004), energy development (Aldridge and Boyce 2007, Walker et al. 2007, Doherty et al. 2010*a*, Harju et al. 2010), invasion of exotic species (Connelly et al. 2000*b*), and prescribed fire (Connelly and Braun 1997, Connelly et al. 2000*a*, Nelle et al. 2000). Recently, the United States Fish and Wildlife Service concluded that greater sage-grouse were warranted for protection under the Endangered Species Act of 1973, but because threats were moderate in magnitude and did not occur across their range at an equal intensity, the listing was precluded to other species under severe threat of extinction (U.S. Fish and Wildlife Service 2010).

The cumulative effects of anthropogenic disturbance in landscapes surrounding leks are associated with declining sage-grouse population trends throughout their range (Johnson et al. 2011). Elevated human activity, such as an addition of a road in sagebrush habitats may directly and indirectly influence sage-grouse. Sage-grouse may directly avoid the increased anthropogenic activity associated with the road (Holloran 2005). The road may also indirectly result in a loss of habitat by accelerating the dispersal and establishment of exotic plant species such as cheatgrass (*Bromus tectorum*; Gelbard and Belnap 2003). The introduction of cheatgrass will increase frequencies of wildfire, which, in turn may rapidly lead to elimination of sagebrush dominated habitats for sage-grouse (Connelly et al. 2004). The combination of these potential effects associated with the addition of a road to habitats near a lek may relate to the probability of that lek becoming abandoned. Because disturbances can lead to indirect impacts by other factors, we believe additive effects of multiple factors influence lek abandonment, instead of impacts stemming from single factors.

We evaluated patterns of sage-grouse lek abandonment in the Bighorn Basin (BHB) of north-central Wyoming, USA based on the individual and combined effects of human disturbance factors and environmental factors that are known to influence sage-grouse by increasing habitat loss and fragmentation. Our specific objectives were to: 1) examine lek abandonment based on landscape characteristics that may explain differences between occupied and unoccupied sage-grouse leks in the BHB from 1980 to 2009, and 2) identify the relative and combined effects of landscape characteristics that were influential to lek abandonment in the BHB across the 30 years of our analysis. We developed 2 hypotheses to reflect possible influences on lek abandonment in the BHB: 1) lek abandonment increased with increasing levels of key disturbance factors, and 2) lek abandonment increased as a result of additive effects of anthropogenic and environmental disturbance factors. We applied a hierarchical model selection framework (Doherty et al. 2008, Aldridge et al.

2012) to examine the suite of factors that led to sage-grouse lek abandonment in the BHB over a 30-year period by first examining anthropogenic disturbance factors that may have contributed to lek abandonment, secondly through the addition of environmental factors potentially contributing to lek abandonment, and lastly through combining identified anthropogenic and environmental disturbance factors that best explain lek abandonment. We examined these disturbance factors over a 30-year period instead of a lek-by-lek basis because of time-lag effects on lek attendance (Walker et al. 2007, Harju et al. 2010, Holloran et al. 2010) and uncertainty about the temporal scale in which leks become abandoned. Holloran et al. (2010) suggested that the ultimate population response to influences such as development may take many sage-grouse generations to be apparent.

STUDY AREA

The BHB includes Big Horn, Hot Springs, Park, and Washakie counties and encompasses 32,002 km² of north-central Wyoming, USA (Fig. 1). The BHB is bordered by the Absoraka Mountains to the west, Beartooth and Pryor Mountains to the north, Bighorn Mountains to the east, and Bridger and Owl Creek Mountains to the south. The BHB has an average valley elevation of 1,524 m (1,116 m minimum) composed of badland topography and intermittent buttes (USGS 2008). Soil groupings include 1) aridic, coarse textured; 2) aridic, fine textured; 3) udic, cryic; and 4) ustic, frigid soils (L. Munn, University of Wyoming, personal communication). The BHB is arid to semi-arid with average annual precipitation ranging from 12.7 cm to 50.8 cm (Big Horn Basin Local Sage-Grouse Working Group 2007).

The native flora of the BHB includes perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread (*Hesperostipa comata*), and blue grama (*Bouteloua gracilis*); shrubs such as Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*A. t.* ssp. *vaseyana*), and spineless horsebrush (*Tetradymia canescens*); and forbs and subshrubs including buckwheat (*Eriogonum* spp.), prairie sagewort (*A. frigida*), milkvetch (*Astragalus* spp.), and western yarrow (*Achillea millefolium*; Big Horn Basin Local Sage-Grouse Working Group 2007). Invasive species in the BHB include cheatgrass (*B. tectorum*), Japanese brome (*B. japonicus*), Canada thistle (*Cirsium arvense*), and knapweed (*Centaurea* spp.; Big Horn Basin Local Sage-Grouse Working Group 2007). Areas in the southeastern portion of our study area were dominated by annual brome grasses following a wildfire that burned approximately 200 km² of sagebrush in 1996.

Irrigated agricultural lands typically occurred at lower elevations than sagebrush rangelands and produced approximately 30% of Wyoming's agricultural output from crops such as alfalfa, barley, dry beans, field corn, oats, spring wheat, and sugar beets (Young et al. 1999). In 2008, the BHB contributed over 80% of Wyoming's barley and sugar beet crops (Wyoming Agricultural Statistics Service 2009).

Dominant land uses in the sagebrush areas between agricultural and forested lands in the BHB included livestock

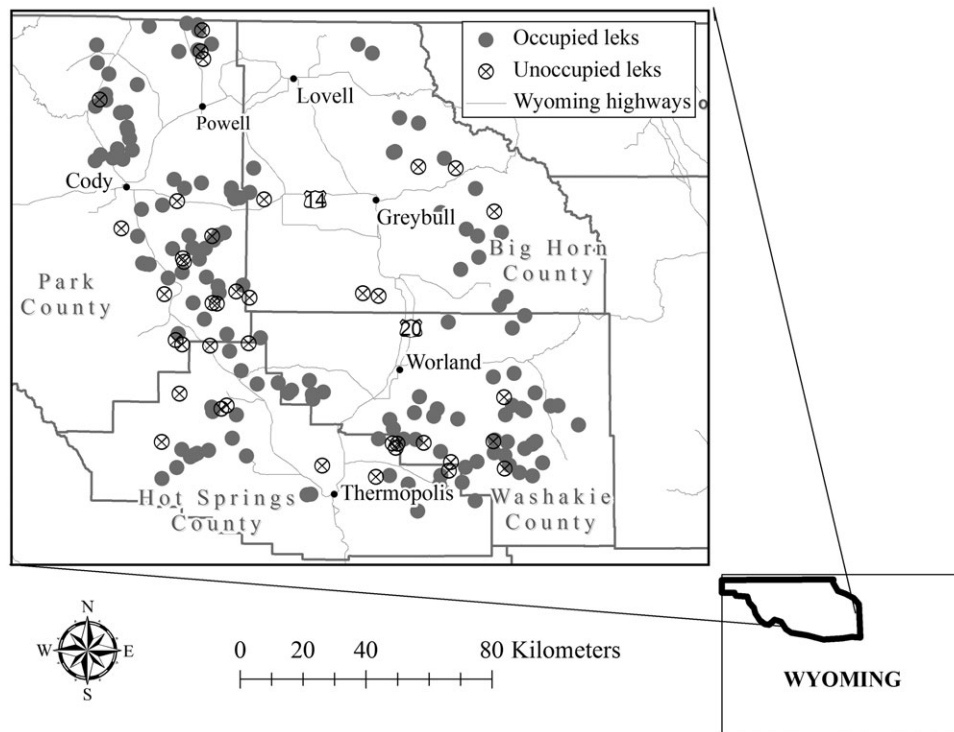


Figure 1. Greater sage-grouse lek sites (occupied and unoccupied) in the Bighorn Basin, Wyoming, USA, 1980–2009.

grazing; bentonite mining, with most current extraction occurring in lower elevation saltbush desert; and oil and gas extraction. Exploration of oil in the BHB began in the early 1900s. During our study, approximately 3,700 producing oil and gas wells operated in the BHB (Wyoming Oil and Gas Conservation Commission 2010). Oil and gas fields in the BHB produced about 28% of Wyoming's annual oil production and 1% of annual natural gas production (Big Horn Basin Local Sage-Grouse Working Group 2007). The Big Horn Basin Planning Area estimates a maximum potential of 1,865 new oil and gas wells from 2008 to 2027 (U.S. Bureau of Land Management [BLM] 2009a).

The Cody and Worland BLM Field Offices conducted 156 prescribed burns (100 km² burned) in sagebrush communities from 1980 to 2009. In addition, 91 wildfires burned 520 km² of sagebrush since 1980 (B. Wilson, BLM Cody Field Office, personal communication). Researchers have identified 256 greater sage-grouse leks in the BHB (Wyoming Game and Fish Department, unpublished data).

METHODS

Data Acquisition

We compiled landscape feature classes using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA). We categorized variables as anthropogenic or environmental characteristics.

Anthropogenic characteristics.—We compiled irrigated agricultural fields from data provided by the Wyoming

Geographic Information Science Center (WYGISC 2009). We used irrigated lands for our analysis because they were the primary form of crop agriculture in the BHB. We obtained road coverages from the Cody and Worland BLM Field Offices (B. Wilson, personal communication). We placed a 50-m buffer on roads to represent the typical area disturbed by roads in semi-arid to arid landscapes (Gelbard and Belnap 2003). We used only paved and graded roads in our analysis because of the likelihood of inadequate records of unimproved roads in the BHB (B. Wilson, personal communication). We acquired locations for producing oil and gas wells from the Wyoming Oil and Gas Conservation Commission (2010). We obtained polygons that mapped the locations of sagebrush prescribed burns from 1980 to 2009 in the BHB from the Cody and Worland BLM Field Offices (J. Mononi and T. Stephens, Cody BLM and Worland BLM, personal communication).

Environmental characteristics.—We obtained polygons that mapped the locations of sagebrush wildfires from 1980 to 2009 in the BHB from the Cody and Worland BLM Field Offices (J. Mononi and T. Stephens, personal communication). We kept wildfire and prescribed burning variables separate because of the different effects each disturbance has on sagebrush communities and because prescribed burning was applied based on land management decisions, whereas wildfire was not. The timing of fire disturbances occurred during different seasons; wildfires usually occurred in drier, hotter months and prescribed burns were normally conducted in the fall or spring (Hess 2011, Hess and Beck 2012). The majority of wildfires occurred in Wyoming big

sagebrush communities and prescribed burns were conducted in Wyoming and mountain big sagebrush communities (J. Mononi and T. Stephens, personal communication).

We included shrub characteristics including sagebrush (all *Artemisia* spp. combined) canopy cover (%) and shrub height (all species; cm) from a recent spatial sagebrush mapping product for Wyoming (Homer et al. 2012). We used a moving window to calculate the mean and standard deviation of estimated percent sagebrush canopy cover and shrub height across all scales. We used the standard deviation to represent heterogeneity in shrub characteristics. We also used a moving window to calculate mean estimated bare ground across all scales using data from Homer et al. (2012).

Lek Analysis Regions

Approximately 70% of the leks in the BHB occur on BLM land; therefore, we were able to evaluate lek abandonment in a landscape comprised of a relatively large amount of area in public ownership. The proportion of public land in the BHB is very similar to the proportion of public land (approx. 70%) providing the remaining habitat to sage-grouse across their range (Knick et al. 2003).

An index computed from the average males attending leks is the most commonly used sample statistic to monitor trends in sage-grouse populations (Beck and Braun 1980), whereas quantifying the disappearance of active leks is the most efficient way to determine large declines in populations (Connelly et al. 2004). Consequently, population-level evaluations can be conducted by comparing lek abandonment (i.e., ratio of unoccupied to occupied leks in a population) to long term changes in habitat characteristics for regional populations (e.g., Smith et al. 2005, Walker et al. 2007).

We used nested circular analysis regions to identify scales that influenced sage-grouse lek persistence in the BHB. We identified region radii from research shown to influence sage-grouse and radii used to base management and conservation strategies. We used radii of 1.0, 3.2, 4.0, 5.0, and 6.4 km around occupied and unoccupied leks to find which scale best fit a suite of anthropogenic and environmental predictor variables. Braun et al. (1977) recommended using a 3.0-km radius around leks to define sage-grouse breeding and nesting areas across their range of distribution and Connelly et al. (2000b) further recommended energy related facilities be placed >3.2-km from active leks. Sage-grouse broods have been reported to avoid visible wells in southern

Alberta at 1.0 km (Aldridge and Boyce 2007) and yearling females have avoided nesting within 0.95 km from infrastructure in natural gas fields in Wyoming (Holloran et al. 2010). Lek abandonment has been found to be greater near cultivated fields in North Dakota at a distance within 4.0 km of leks (Smith et al. 2005). Research in Wyoming has shown the majority (64%) of sage-grouse nesting may occur within 5.0 km of leks in contiguous habitats (Holloran and Anderson 2005). Walker et al. (2007) indicated that sage-grouse population persistence within areas with energy development requires maintaining sagebrush stands over larger areas (≥ 6.4 km) around leks. We converted area for roads, agriculture, prescribed burning, and wildfire within each circular analysis region into percentages (variable area divided by the area of each lek radius) and we determined the number of wells within each radius around leks for our analysis.

To maintain accuracy and transparency in summarizing lek data, our analysis relied on terminology used by the Wyoming Game and Fish Department (2010) to monitor trends in sage-grouse lek counts. By basing our lek assignment criteria on Wyoming Game and Fish Department definitions (Table 1), we removed lek observations for those leks in which counts were not recorded for ≥ 1 decade and for leks with only 1 year of data. We assumed a lek was occupied in those cases when it was observed at least once in a decade and was deemed active when male sage-grouse were observed during the strutting season; observations during the following decade also supported its status.

Data Analyses

Prior to modeling, we assessed correlations between predictor variables to ensure multicollinearity did not exist in the set of predictor variables we considered in our regression analyses. We removed 1 variable from each correlated pair when $|r| \geq 0.70$ (PROC CORR; SAS Institute 2004). If variables were highly correlated, we retained variables we felt would be most influential based on the biology of sage-grouse and findings from peer-reviewed literature. We used binary logistic regression models to provide a fit to habitat predictor variables where the dependent data were 1 for unoccupied leks and 0 for occupied leks (Boyce and McDonald 1999, PROC LOGISTIC; SAS Institute 2004). We also examined quadratic variables because this form of a variable can often identify nonlinear relationships that oth-

Table 1. Terminology used by Wyoming Game and Fish Department to monitor greater sage-grouse leks.

Term	Definition
Active lek	Lek that has attending male sage-grouse during the strutting season
Inactive lek	Lek with no attending male sage-grouse during the entire strutting season. Absence of sign (droppings or feathers) as well as visual absence of activity are needed for this designation. Aerial surveys are not sufficient for this status designation
Occupied lek	Lek that has been active during at least 1 strutting season within the prior 10 years
Unoccupied lek	Lek that has been abandoned or destroyed
Abandoned lek	Lek in suitable habitat that has not been active in a 10-year period. Must be inactive for at least 4 non-consecutive strutting seasons during the 10-year period. Abandoned leks are surveyed at least once every 10 years to ascertain whether the lek has become reoccupied by sage-grouse
Destroyed lek	Formerly active lek that has become destroyed or unsuitable for sage-grouse strutting activities. This includes sites that have been paved, converted to agricultural land, strip-mined, or have long-term habitat alteration. These leks are no longer surveyed unless the area has been reclaimed to suitable sage-grouse habitat

erwise may be undetected (Doherty et al. 2008, Aldridge et al. 2012).

We employed a hierarchical model selection framework to evaluate lek persistence by first identifying the scale at which landscape features affected lek persistence. We screened variables in anthropogenic and environmental categories by selecting the scale for each variable with the smallest log-likelihood value to prevent double representation of the same variable (Doherty et al. 2010*b*). We then developed separate models based on the best scale for anthropogenic and environmental landscape characteristics. To reduce uninformative parameters, we removed from our candidate set variables with odds ratios whose 85% confidence intervals overlapped 1.0 (Arnold 2010). We then created 2 subsets of models with variables that composed anthropogenic or environmental characteristics grouped separately. We combined the best predicting environmental model with the best predicting anthropogenic model to examine the change in variability when we added the anthropogenic model to our final candidate set. We defined our full model set as the combination of anthropogenic and environmental models (Doherty et al. 2008, Aldridge et al. 2012).

We evaluated model fit in simple models (≤ 3 predictor variables) to avoid over fitting models (Burnham and Anderson 2002). We assessed the plausibility of each model with Akaike's Information Criterion for small samples (AIC_c ; Hurvich and Tsai 1989). The null model contained no predictor variables and was used to assess whether logistic models provided a better fit for predicting lek abandonment than a model containing no predictor variables. We used the best-fitting scale (i.e., smallest log-likelihood) combinations to compete with all other variables to create the final set of candidate models for anthropogenic or environmental characteristics predicting lek abandonment. We selected the model with the smallest AIC_c value as the best-fitting model, and used the difference between AIC_c for the best model and AIC_c for the i th candidate model (Δ_i) to identify models competing with the best model. We followed the convention that models with $\Delta_i \leq 4$ were competitive with the best model (Burnham and Anderson 2002, Arnold 2010). Akaike weights (w_i) allowed us to assess the weight of evidence in favor of each model (Burnham and Anderson 2002). We ranked the relative importance of variables by summing w_i across all of the models in which they occurred (Burnham and Anderson 2002). To assess the influence of variables on lek abandonment, we created predictive probability of persistence curves for each variable from our top candidate model across the range of data for that parameter while holding other parameters in the top model at their mean value (Aldridge and Boyce 2008). Current Wyoming Game and Fish Department (2010) recommendations state that non-core sage-grouse areas should maintain habitat conditions that will sustain at least a 50% probability of lek persistence. Because portions of the BHB encompass non-core areas, we examined thresholds above 50% probability for each variable in our model-averaged estimates.

We used model averaging to address model uncertainty by averaging across the 95% confidence set for our full model set

to produce more robust spatial predictions and strengthen inference (Burnham and Anderson 2002). In addition, model averaging can minimize the effects of uninformative parameters (Arnold 2010). Following model averaging, we calculated odds ratios, probability of lek persistence, and variance decomposition with model-averaged estimates.

We used a fivefold cross validation procedure to evaluate the goodness-of-fit of our top predictive model, or in the case of model averaging, we used the variables occurring in the 95% confidence set (Boyce et al. 2002). To examine the discriminating ability of our best logistic regression model, we evaluated the area under the receiver operating curve (ROC), which in our case provided a measure of the best model's ability to discriminate between habitat characteristics at occupied leks (Hosmer and Lemeshow 2000). A perfect discrimination is represented by an ROC of 1.0 and a value of 0.5 or less represents no discrimination (Mason 1982, Manel et al. 2001). Models are considered to have low accuracy with an ROC value of 0.5–0.7; medium accuracy with an ROC value of 0.7–0.9; and high accuracy with an ROC value >0.9 (Swets 1988).

We used a variance decomposition technique to decompose relationships among our anthropogenic and environmental models (Battin and Lawler 2006). Through decomposition, variation from a full model can be split into 1) components that are purely explained individually by one subset model, and 2) components that are explained mutually by groups of models (shared components; Whittaker 1984).

RESULTS

We identified 183 leks (144 occupied leks and 39 unoccupied leks; Fig. 1) for our analysis, with most leks (37, 95.0%) becoming unoccupied from 1989 through 2004. The variables used in our models were not highly correlated ($|r| < 0.70$), thus we did not remove variables prior to model selection. We retained 1 variable for the anthropogenic model and 2 variables for the environmental model (Table 2). All other variables were uninformative (i.e., variables had 85% CIs that overlapped 1; Arnold 2010). Quadratic variables did not improve model fit and were not included in our final candidate set. Overall predictive ability of our lek abandonment model improved when we added the anthropogenic model to the environmental model (AIC_c value decreased by 4.227; Table 3). We found the top 2 models were competitive ($\Delta AIC_c = 3.071$): 1) the combined model of anthropogenic and environmental characteristics, which included the number of oil and gas wells in a 1.0-km radius, percent wildfire within a 1.0-km radius, and the variability in shrub height within a 1.0-km radius; and 2) the number of oil and gas wells in a 1.0-km radius (Table 3). Because these models were competitive, we model averaged across the 95% confidence set. Model-averaged parameter estimates based on the 95% confidence set included 4 of the 6 combined models (Table 3). The Akaike's weights for the models forming the 95% confidence set were 0.666 for the combined anthropogenic and environmental model, 0.143 for the top anthropogenic model, 0.080 for the top environmental model, and 0.067 for variability in shrub height

Table 2. Fit statistics for anthropogenic and environmental models, separately, explaining sage-grouse lek persistence in the Bighorn Basin, Wyoming, USA, 1980–2009. Each logistic regression model was based on 144 occupied and 39 unoccupied leks. Models ranked by (Δ_i), the difference between the model with the smallest Akaike's Information Criterion for small samples (AIC_c) and the AIC_c for the current model. For each logistic regression model, we present the $-2 \times \log$ likelihood ($-2LL$), number of estimated parameters (K), and Akaike weights (w_i) for each model. Circular analysis regions around leks (km) follow variable names (i.e., 1.0).

Model	K	$-2LL$	AIC_c	ΔAIC_c	w_i
Anthropogenic					
Wells 1.0	2	183.059	187.126	0.000	0.9048
Null	1	189.608	191.630	4.504	0.0952
Environmental					
Wildfire 1.0 + shrub height SD 1.0	3	182.148	188.282	0.000	0.3333
Shrub height SD 1.0	2	184.597	188.664	1.538	0.1545
Wildfire 1.0	2	186.317	190.384	3.258	0.0654
Null	1	189.608	191.630	4.504	0.0351

within a 1.0-km radius around leks (Table 3). Relative importance weights for the most influential predictor variables were number of oil and gas wells within a 1.0-km radius around leks (0.81), percentage wildfire within a 1.0-km radius around leks (0.78), and variation in shrub height within a 1.0-km radius around leks (0.81). Compared to occupied leks, unoccupied leks had 10.3-times greater number of oil and gas wells in a 1.0-km radius than occupied leks, 3.1-times greater percentage of wildfires in a 1.0-km radius, and 1.1-times greater variability in shrub height in a 1.0-km radius around leks (Table 4). The ROC value (0.67) from model-averaged estimates indicated this model was fair at discriminating between occupied and unoccupied sage-grouse leks based on the number of oil and gas wells, the amount of wildfire, and variability of shrub height within a 1.0-km radius around leks. Our cross-fold validation analysis indicated the combined model with oil and gas wells within 1.0-km, the percent of wildfire within 1.0-km, and the variability in shrub height within 1.0-km of leks performed moderately to predict lek abandonment ($r_s = 0.45$, $P = 0.189$, $n = 10$).

The model-averaged parameter estimate for number of oil and gas wells within a 1.0-km radius was -0.422 ($SE = 0.26$; 95% CI: -0.759 , -0.084), percent wildfire at the 1.0-km radius was -0.014 ($SE = 0.082$; 95% CI: -0.120 , 0.092), and standard deviation of mean shrub height at the 1.0-km radius was -0.268 ($SE = 0.245$; 95% CI: -0.584 , 0.049). Odds ratios indicated the odds of lek

abandonment increased by 34% with each additional well in a 1.0-km radius around a lek (odds ratio: 0.66, 90% CI: 0.37–0.94). Results predicted that lek abandonment would increase by 1% with every 1% increase in the area burned by wildfire in a 1.0-km radius around leks (odds ratio: 0.99, 90% CI: 0.85–1.12). The odds of lek abandonment increased by 23% with every 1 unit increase in the variation in mean shrub height in a 1.0-km radius around leks (odds ratio: 0.77, 90% CI: 0.45–1.08). Because the 90% confidence intervals around the model-averaged odds ratio of wells did not overlap 1.0, we suggest that this predictor was the most influential variable among our model-averaged estimates. The probability of persistence of sage-grouse leks dropped below 50% in the BHB when oil and gas well densities in a 1.0-km radius were >2 wells/km² (Fig. 2). The anthropogenic model explained 45.9% of the pure variation in lek abandonment, whereas the environmental model explained 52.5% of the pure variation in our models. Only 1.7% of total variation was explained by shared components.

DISCUSSION

Our approach of examining potential stressors to explain differences between occupied and unoccupied sage-grouse leks met our objective of identifying effects of disturbances influential to sage-grouse lek abandonment. We found distinguishable differences among leks in the BHB, with a greater number of oil and gas wells, percentage of wildfire, and variability in shrub height surrounding

Table 3. Fit statistics for combined anthropogenic and environmental models explaining sage-grouse lek persistence in the Bighorn Basin, Wyoming, USA, 1980–2009. Each logistic regression model was based on 144 occupied and 39 unoccupied leks. Models are ranked by (Δ_i), the difference between the model with the smallest Akaike's Information Criterion for small samples (AIC_c) and the AIC_c for the current model. For each logistic regression model, we present the $-2 \times \log$ likelihood ($-2LL$), number of estimated parameters (K), and Akaike weights (w_i) for each model. Circular analysis regions around leks (km) follow variable names (e.g., 1.0).

Model	K	$-2LL$	AIC_c	ΔAIC_c	w_i
Anthropogenic ^a + environmental ^b	4	175.830	184.055	0.000	0.666
Anthropogenic	2	183.059	187.126	3.071	0.143
Environmental	3	182.148	188.282	4.227	0.080
Shrub height SD 1.0	2	184.597	188.664	4.609	0.067
Wildfire 1.0	2	186.317	190.384	6.329	0.028
Null	1	189.608	191.630	7.575	0.015

^a Anthropogenic model = number of wells within 1.0-km radius.

^b Environmental model = percent wildfire and variability in shrub height within 1.0-km radius.

Table 4. Descriptive statistics for predictor variables potentially influencing greater sage-grouse lek persistence ($n = 144$ occupied and $n = 39$ unoccupied leks) in the Bighorn Basin, Wyoming, USA, 1980–2009. Circular analysis regions around leks (km) follow variable names (e.g., 1.0).

Variable	Occupied		Unoccupied	
	Mean	SE	Mean	SE
Shrub height 1.0 (SD)	5.1	0.1	5.7	0.2
Wells 1.0 (no.)	0.1	0.0	0.7	0.4
Wildfire 1.0 (%)	3.3	1.3	10.0	4.5

unoccupied compared to occupied leks. Model-averaged estimates predicted that increases in the number of oil and gas wells, percent area of wildfire, and variability in shrub height within 1.0-km radius around leks influenced lek abandonment in the BHB from 1980 to 2009 (Figs. 2 and 3).

In support of our second objective, our results indicate that the number of wells around leks was an influential predictor of lek abandonment, but alone, it did not explain as much of the influence on lek abandonment as when it was combined with the area of wildfire and variability of shrub height around leks. Overall predictive ability of our lek abandonment model improved when the anthropogenic model was added to the environmental model. Because these factors are interrelated, our results show some support for the cumulative influences of these 3 disturbance factors on sage-grouse lek abandonment over the 30 years of our analysis. Increasing numbers of oil and gas wells are associated with an increase in road development and other disturbances to sagebrush communities. The indirect effect of additional infrastructure required with energy development can also take a toll on sage-grouse populations. Developing roads can accelerate the dispersal and establishment of exotic plant species (Gelbard and Belnap 2003, Bergquist et al. 2007),

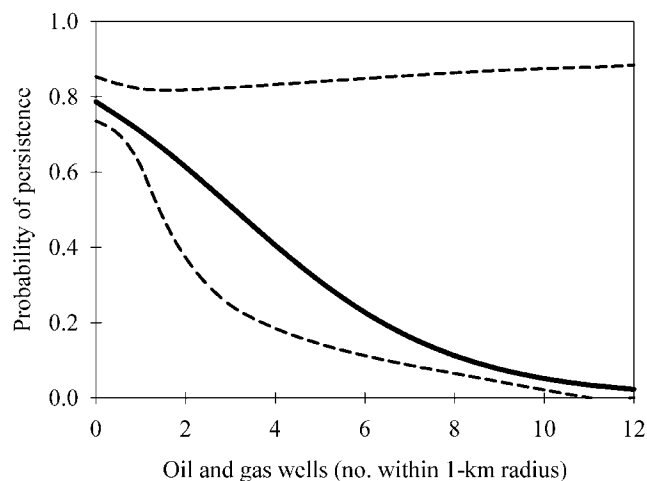


Figure 2. Probability of greater sage-grouse lek persistence as a function of model-averaged estimates of number of oil and gas wells within a 1.0-km radius with 95% confidence intervals (dashed lines) from a lek while holding the area of wildfire and the standard deviation of shrub height at their mean value within a 1.0-km radius around sage-grouse leks, Bighorn Basin, Wyoming, USA, 1980–2009.

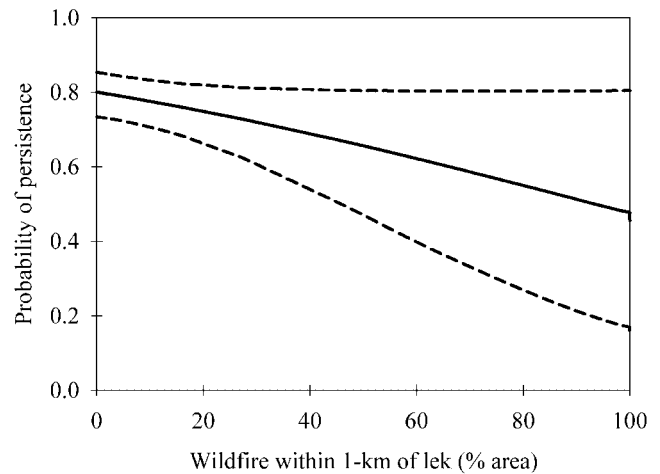


Figure 3. Probability of greater sage-grouse lek persistence as a function of model-averaged estimates of wildfire (% area in a 1.0-km radius around leks) with 95% confidence intervals (dashed lines) while holding the number of wells and standard deviation of shrub height within a 1.0-km radius around sage-grouse leks at their mean value, Bighorn Basin, Wyoming, USA, 1980–2009.

and consequently shorten fire return intervals (Levine et al. 2003) causing further habitat loss to sage-grouse. Cheatgrass has been estimated to cover >80 km² of the BHB (Wyoming Pest Detection Program 2010). Fire is even a larger threat in degraded sagebrush habitats because residual shrub patches may ultimately become dominated by exotic plants that promote longer fire return intervals and further negate efforts of restoring habitats to previous sagebrush stages because of inaccessible seed banks and inadequate recovery periods (Knick and Rotenberry 1997; Connelly et al. 2000a, b; Menakis et al. 2003; Jessop and Anderson 2007; Prev y et al. 2010). Reduction in suitable sage-grouse nesting and brood-rearing habitat in southeastern Idaho occurred when approximately 30% of a study area burned (Nelle et al. 2000). Wildfire can also have indirect effects on grouse by reducing insect populations (Fischer et al. 1996) needed by chicks for growth and development (Johnson and Boyce 1990). Fragmented shrubsteppe increases sage-grouse nest failures leading to increased risk of predation in areas with greater levels of grass-forb dominated habitat along edge habitats disturbed by fire (Shepherd 2005).

Sage-grouse nest success has been shown to be greater when nests are located within taller shrubs (Gregg et al. 1994, Connelly et al. 2000b, Popham and Guti rrez 2003). Nest predation rates were lower at artificial sage-grouse nests in Oregon with medium height (40–80 cm) and shrub cover (mean = 25%; DeLong et al. 2005) and patches of moderate sagebrush cover were selected by sage-grouse in Canada for nesting (Aldridge and Boyce 2007). As the variation in shrub height increased, the probability of lek persistence decreased in the BHB. With increasing variability in shrub height, we expect more fragmentation and patchiness of sagebrush that can ultimately have negative effects on sage-grouse. However, mean sagebrush canopy cover was not different within a 1.0-km radius around leks between occupied

(mean = 6.2, SE = 0.2) and unoccupied (mean = 6.1, SE = 0.4) leks, suggesting that the mechanisms of lek abandonment associated with shrub height variability need to be better understood.

Because no single factor has led to the decline in sage-grouse populations across their range, researchers need to examine the unintended additional stressors that result from anthropogenic activity (Johnson et al. 2011). Recent studies have documented the indirect effects of oil and gas development on sage-grouse; however, the mechanisms of these effects have rarely been reported (but see Holloran et al. 2010). Disturbances from oil and gas development include disruption in breeding (Lyon and Anderson 2003), declines in lek persistence and male lek attendance (Holloran 2005, Walker et al. 2007, Doherty et al. 2010a, Harju et al. 2010), lower yearling male recruitment to impacted leks (Kaiser 2006, Holloran et al. 2010), lower yearling male and yearling female survival (Holloran et al. 2010), avoidance of wintering habitats (Doherty et al. 2008), decreased nest initiation rates (Lyon and Anderson 2003), increased distances of nesting sites from leks (Lyon and Anderson 2003), greater chick mortality (Aldridge and Boyce 2007), and lower annual adult female survival (Holloran 2005). In addition, habitat fragmentation can lead to increasing numbers of predators that prey on nests, young, and adult sage-grouse (Steenhof et al. 1993, Connelly et al. 2000b, Vander Haegen et al. 2002, Coates and Delehanty 2010).

Our results corroborate findings on sage-grouse lek abandonment from other studies conducted in areas with much greater levels of disturbance (Connelly et al. 2000b, Holloran 2005, Walker et al. 2007, Harju et al. 2010). The BHB has fewer producing oil and gas wells (approx. 3,700) compared to the Powder River Basin of northeastern Wyoming, which had >35,000 producing wells with 68,000 wells authorized on public lands in 2007 (Naugle et al. 2011), and the Green River Basin of southwestern Wyoming, which had >7,800 active and potential wells in 2003 (Holloran 2005). Because of the greater number of wells, the impacts of development may be much more intense in the Powder River and Green River basins. Even though our study area has lower energy development pressure compared to other areas in Wyoming, our analysis nevertheless agrees with recent studies that suggest the need to reevaluate current stipulations and management practices in areas with energy development and to incorporate regional research in management decisions based on local sage-grouse populations (Walker et al. 2007, Doherty et al. 2010a, Harju et al. 2010, Holloran et al. 2010).

Biases may be associated with our analysis. Spatial data sets for road coverages are known to under represent secondary or paved roads (Aldridge et al. 2008), which may have led to our inability to detect a strong effect of roads on lek persistence. We also believe agriculture may have influenced sage-grouse lek abandonment in the BHB prior to our study because most agriculture near sagebrush habitats was established by the 1960s. We identified 2 leks that became abandoned following the development of an irrigated field encompassing these leks; however, we did not include them in our analysis

because of their abandonment in the early 1960s, which was outside of our 1980–2009 period of interest.

Across their range, sage-grouse populations have been declining because of numerous, and sometimes immeasurable, cumulative effects causing fragmentation, loss, and degradation of suitable habitat (Knick et al. 2003). Although the support for our results is not as strong as in some studies, we provided evidence suggesting that multiple factors (wells, wildfire, and variability in shrub height) were most influential to lek abandonment. Because we found greater levels of wells, wildfire, and variability in shrub height in our unoccupied lek radii, we suggest some cumulative relationship among these variables exists and that individually and combined, each factor has contributed to lek abandonment in sage-grouse populations in the BHB. Our findings confirm findings from other research indicating human disturbance and habitat loss is a leading factor in sage-grouse population decline (Lyon and Anderson 2003, Connelly et al. 2004, Smith et al. 2005, Aldridge and Boyce 2007, Walker et al. 2007).

MANAGEMENT IMPLICATIONS

Increasing energy development, wildfire, and variability in shrub height are predicted to result in loss of more sage-grouse leks in the BHB. Hess (2011) found statistical evidence suggesting that the influence of oil and gas well pads and wildfire extended as far as 1.6-km from sage-grouse leks in the BHB. These findings suggest that our results should not be explicitly used to base conservation strategies, but rather provide supportive information about the scale of disturbance on lek abandonment. Consequently, conservation efforts should be focused on mitigating disturbances associated with energy development, roads, and wildfire to stem the decline of sage-grouse leks. Wildfire suppression and minimizing well construction strategies are needed in areas with larger numbers of sage-grouse leks. The BLM (2009b) in Nevada has prioritized wildfire suppression around leks and have developed precautionary measures to reduce risks associated with wildfire to sage-grouse including localized habitat maps, suppression tactics, training programs, avoiding leks when creating wildfire suppression facilities, and proper cleaning of field vehicles to prevent spread of noxious weeds into sage-grouse habitat. Although we do not provide specific management recommendations, we do suggest that managers must understand that areas with less anthropogenic development may also affect sage-grouse populations. We thus recommend focusing management concerns on multiple disturbance factors in areas with increasing human development and developing and assessing stipulations and management strategies based on small (<1.0 km) and larger scales (>1.0 km) around leks to avoid lek abandonment.

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