Management and Conservation Article

Greater Sage-Grouse Winter Habitat Selection and Energy Development

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ABSTRACT Recent energy development has resulted in rapid and large-scale changes to western shrub-steppe ecosystems without a complete understanding of its potential impacts on wildlife populations. We modeled winter habitat use by female greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana, USA, to 1) identify landscape features that influenced sage-grouse habitat selection, 2) assess the scale at which selection occurred, 3) spatially depict winter habitat quality in a Geographic Information System, and 4) assess the effect of coal-bed natural gas (CBNG) development on winter habitat selection. We developed a model of winter habitat selection based on 435 aerial relocations of 200 radiomarked female sage-grouse obtained during the winters of 2005 and 2006. Percent sagebrush (*Artemisia* spp.) cover on the landscape was an important predictor of use by sage-grouse in winter. The strength of habitat selection between sage-grouse and sagebrush was strongest at a 4-km^2 scale. Sage-grouse avoided coniferous habitats at a 0.65-km^2 scale and riparian areas at a 4-km^2 scale. A roughness index showed that sage-grouse selected gentle topography in winter. After controlling for vegetation and topography, the addition of a variable that quantified the density of CBNG wells within 4 km^2 improved model fit by 6.66 Akaike's Information Criterion points (Akaike wt = 0.965). The odds ratio for each additional well in a 4-km^2 area (0.877; 95% CI = 0.834–0.923) indicated that sage-grouse avoid CBNG development in otherwise suitable winter habitat. Sage-grouse were 1.3 times more likely to occupy sagebrush habitats that lacked CBNG wells within a 4-km^2 area, compared to those that had the maximum density of 12.3 wells per 4 km^2 allowed on federal lands. We validated the model with 74 locations from 74 radiomarked individuals obtained during the winters of 2004 and 2007. This winter habitat model based on vegetation, topography, and CBNG avoidance was highly predictive (validation $R^2 = 0.984$). Our spatially explicit model can be used to identify areas that provide the best remaining habitat for wintering sage-grouse in the PRB to mitigate impacts of energy development. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):187–195; 2008)

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Understanding landscape-scale habitat selection during critical life stages is essential for developing conservation plans for sensitive species. Studies of habitat selection at small scales further our ecological understanding of species–habitat relationships but do not convey spatially explicit information about habitat quality at a scale useful for prioritizing landscapes for conservation. Recent advances in modeling habitat selection from high-resolution satellite imagery using resource selection functions (RSF) offers the ability to rank specific areas by their relative probability of use (Manly et al. 2002). Resulting probability layers can then be mapped in a Geographic Information System (GIS) to identify regions where high-quality habitat is available. Further, these models allow cross-validation and testing against independent datasets to ensure that inferences regarding habitat selection are robust (Boyce et al. 2002, Johnson et al. 2006). The relative influence of variables thought to be important in habitat selection can also be assessed in a competing-model framework (Burnham and Anderson 2002).

Previously widespread, greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have been extirpated from approximately 50% of their original range in western North America (Schroeder et al. 2004), with an estimated range-wide population decline of 45–80% and local declines of 17–92% (Connelly and Braun 1997, Connelly et al. 2000, Aldridge and Brigham 2003). Despite increased concern for their populations, little effort has gone into measuring landscape-scale winter habitat selection by greater sage-grouse. Previous winter habitat studies have focused on the importance of micro-site vegetation features such as height, canopy cover, or crude protein levels of sagebrush (e.g., Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). In winter, sage-grouse inhabit areas with moderate to dense sagebrush (Eng and Schladweiler 1972, Homer et al. 1993, Connelly et al. 2000) and typically prefer areas with gentle (<10%), south- or west-facing slopes (Beck 1977, Hupp and Braun 1989). Previous demographic studies have documented high rates of winter survival (reviewed in Connelly et al. 2004). However, Moynahan et al. (2006) demonstrated that severe winters can have substantial population-level impacts. Birds also must often move long distances to find suitable winter habitat (Patterson 1952 *in* Connelly et al. 2004; Connelly et al. 1988; Robertson 1991). Impacts to wintering habitat may have disproportionate effects on regional population size and persistence. For example, Beck (1977) found that 80% of use sites occurred in <7% of the area of sagebrush available in northern Colorado, USA, suggesting that winter habitat may be

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limited. The relationship between sagebrush and sage-grouse is arguably the closest during winter when birds switch from a diet of insects, forbs, and sagebrush to one composed of >96% sagebrush (Remington and Braun 1985, Welch et al. 1991, Connelly et al. 2000, Crawford et al. 2004). Heavy snowfall may even further reduce the amount of suitable habitat by limiting the abundance of sagebrush above the snow (Hupp and Braun 1989; Connelly et al. 2000, 2004).

Coal-bed natural gas (CBNG) development in the Powder River Basin (PRB) has caused rapid, large-scale changes to sagebrush habitats in Montana and Wyoming, USA. The sage-grouse sub-population in the PRB is a critical component of the larger Wyoming Basin population, which represents 25% of sage-grouse in the species' range (Connelly et al. 2004). The population in the PRB has a high density of active leks and serves as a link to populations in eastern Wyoming and western South Dakota, USA, and between the Wyoming Basin and central Montana, USA (Connelly et al. 2004). The CBNG field in the PRB is one of the largest developed energy fields in North America. In this region, approximately 29,000 CBNG wells have been drilled on public and private lands, and another approximately 37,000 wells are expected within a 2.4-million ha area, roughly the size of the state of New Hampshire (Bureau of Land Management 2003*a*, *b*). Drilling is typically authorized at a maximum density of 1 well per 32 ha on lands where federally owned gas reserves are extracted; however, there are no well-density restrictions placed on private or state-owned gas reserves. Wells, power lines, roads, vehicle traffic, pipelines, compressor stations, and water storage ponds within a gas field this size contribute to fragmentation of sagebrush habitats and may impact sagebrush obligates (Knick et al. 2003).

We investigated sage-grouse winter habitat use in the PRB as part of a larger study of the potential impacts of CBNG development on sage-grouse populations. Our objectives were to 1) create a robust habitat selection model for sage-grouse in winter, 2) evaluate the appropriate scale at which females select winter habitat, 3) spatially depict habitat suitability in a GIS to identify areas with a high probability of use, and 4) assess the influence of CBNG development on winter habitat selection.

STUDY AREA

Our study area in the PRB covered portions of Johnson, Sheridan, and Campbell counties in Wyoming, and Bighorn, Rosebud, and Powder River counties in Montana. Shrub-steppe habitat in the PRB was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and nonnative grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), Japanese brome (*Bromus japonicus*), cheatgrass (*B. tectorum*), and crested wheatgrass (*Agropyron cristatum*). Plains silver sagebrush (*Artemisia cana cana*) was also present in drainages but at much lower abundance. Rocky mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) were located in wooded draws and formed forests across the extreme northern extent of the study area. Conifers were largely absent from the southern half of the study area. Land use was dominated by cattle ranching; only 4% of the landscape consisted of dry land or irrigated agriculture. The PRB typically was cold and dry in January with average temperatures of −6.0° C and 16.3 cm of snowfall. Winter weather conditions in 2004 and 2005 were almost identical to historical averages. The winter of 2006 was mild; in January, temperatures were 6.5° C above normal and snowfall was 15 cm below average. The January 2007 average temperature of −5.5° C was near historical norms; however, snowfall was 60% above normal.

METHODS

Marking and Monitoring Protocols

We captured sage-grouse by rocket-netting (Giesen et al. 1982) and spotlighting (Wakkinen et al. 1992) on and around leks in 3 study areas: 1) Bighorn County, Montana, 2) Campbell County, Wyoming, and 3) Johnson County, Wyoming during March–April and August of 2003–2006. We aged and sexed grouse and fitted females with a 21.6-g necklace-style radiocollar with a 4-hour mortality switch (model A4060; Advanced Telemetry Systems, Isanti, MN). Sage-grouse in the Bighorn and Campbell county study areas were nonmigratory. In contrast, many birds in the Johnson Country study area were migratory, with distinct breeding, summer, and winter ranges. In all study sites, we obtained winter locations after birds in our migratory population had moved to wintering areas but before they had moved back to the breeding grounds. We monitored sage-grouse via aerial radiotracking during the winters of 2005–2007. We used a fixed-wing airplane with aerial telemetry antennas mounted on both wings struts and connected to a switch box. We used a Global Positioning System (GPS) receiver to record locations of used sites as we circled sage-grouse at approximately 100–200-m elevation above the ground. We radiotracked sage-grouse on foot during the winter of 2004, and recorded their positions with a GPS receiver when we obtained visual sightings of radiomarked birds. We estimated the 95% error ellipse of aerial locations by relocating a transmitter placed in rolling sagebrush cover 40 times from the air in a blind trial. We then calculated a bivariate normal home range estimator (Jennrich and Turner 1969) using these relocations to quantify our maximum resolution to estimate the location of an unknown collar (78.2-m radius). The ability of our plane to tightly circle sage-grouse was not constrained by rugged areas or conifer-dominated landscapes in the PRB because birds were not located in these habitat features; thus, our test was representative of the maximum precision of our aerial telemetry locations in rolling sagebrush habitats. We did not quantify error for ground-based locations, but we assumed error estimates were smaller than aerial-based methods. Since we treated our aerial telemetry error test as a maximum precision estimate, we conducted all analyses at scales $\geq$100 m to ensure that our inference was not confounded by location error.

Designation of Used and Available Sites

We employed a used–available design to evaluate sage-grouse habitat relationships in winter (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We defined used points as the sites where we located radiomarked sage-grouse during radiotracking. We split sage-grouse used locations into those we analyzed to build a statistical model to quantify large-scale habitat relationships and those we analyzed to test the predictive ability of our spatially explicit winter habitat model. We located birds we used to build the model during 3 flights from 2 January to 25 January 2005 ($n = 292$ locations on 106 individuals) and on 3 flights from 24 December 2005 to 1 February 2006 ($n = 241$ locations on 94 individuals). To test the model, we used 87 locations collected on the ground from 15 to 18 January 2004 ($n = 30$ locations on 28 individuals) and on 2 flights on 18 and 26 January 2007 ($n = 57$ locations on 57 individuals). Of the 85 individuals used to test the model, 57 were not included among birds marked during 2005 or 2006. We found some radiomarked birds together in flocks. To avoid the possibility of dependency in our data, we retained only one used location per flock. The final data set contained 435 locations for building the model and 74 locations for testing the model.

We selected available points within circles that had a radius to the farthest winter used point and were centered on either the lek of capture or on the lek closest to where birds were captured via spotlighting. We merged circles that overlapped within each study area to create 3 nonoverlapping polygons that corresponded with our 3 study areas. We randomly selected available points from a spatial Poisson distribution (Beyer 2004) proportional to twice the number of used points within a polygon and year to ensure a representative sample of available habitats.

GIS Habitat Classification

We acquired SPOT-5 satellite imagery (Terra Image USA, Santa Barbara, CA) for the northern portion of the study area in August 2003 and for the southern portion in August 2004 when the project expanded to encompass a larger geographic area. We ortho-rectified SPOT-5 imagery to existing digital ortho-quads of the study area. The SPOT-5 panchromatic and multi-spectral images were combined into a single panchromatic, multi-spectral file. We then used the panchromatic 25-m^2-pixel image to perform pan-sharpening to reduce the multi-spectral image pixel size from 100 m^2 to 25 m^2, greatly increasing the resolution of our analysis. We used eCognition™ 4.0 software (Definiens Imaging, Munich, Germany) to cluster the pixels into regions representing spectrally similar ground features. We exported clusters into ArcGIS 9.2 software to create a polygon database. We collected field training points ($n = 7{,}092$) that were stratified by space and landowner access to classify 5 habitat cover classes as sagebrush, conifer, grassland, riparian, and barren. Classification accuracy assessed by withholding subsamples of data (i.e., k-fold cross-validation with 10 folds; Boyce et al. 2002) was 83% for sagebrush, 77% for conifer, 76% for grassland, 70% for riparian, and 80% for barren with an overall accuracy of 78%. We removed urban areas and strip mines from analyses.

Vegetation, Topography, and Energy Development Variables

We quantified characteristics of vegetation, topography (e.g., Beck 1977, Remington and Braun 1985, Hupp and Braun 1989, Sauls 2006), and energy development around used and available points using a GIS to evaluate landscape predictors of sage-grouse winter habitat selection. We utilized used and available points to select individual 5 $\times$ 5-m raster pixels, which we then buffered by 100 m, 400 m, and 1,000 m. We quantified variables within a square centered on each used and available pixel at 3 spatial scales: 205 $\times$ 205-m (0.04-km^2), 805 $\times$ 805-m (0.65-km^2), and 2,005 $\times$ 2,005-m (4-km^2). We calculated the percent of total area covered by each of the 5 vegetation cover classes to quantify vegetation. To quantify topography, we processed a 900-m^2 resolution digital elevation model (DEM) using Spatial Analyst in ArcGIS 9.2 and used it to estimate slope and solar radiation for each pixel in the landscape. Solar radiation calculates how much sun a particular pixel receives dependent on slope and aspect. We estimated solar radiation using the hillshade command in Spatial Analyst using the angle and aspect of the sun during 15 January 2007 at 1300 hours (U.S. Navy Astronomical Applications Department 2007). We used the standard deviation of the DEM elevations within each buffer size to calculate an index to describe the roughness of the landscape. Elevation was not included as a predictor variable for GIS habitat modeling because elevational migration of sage-grouse does not occur in the PRB, and minor differences in elevation at used and available locations were biologically irrelevant. In the northern PRB, mean elevation was 1,210 m (SE = 3.8) for available locations and 1,248 m (SE = 3.9) for used locations. In the southern PRB, mean elevation was 1,363 m (SE = 4.1) for available locations and 1,378 m (SE = 3.4) for used locations. We used the density of CBNG wells as a measure of the extent of energy development. Wells are the only segment of the energy footprint accurately mapped and publicly available for the entire PRB from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, and well density within a buffer is strongly correlated with other features of CBNG development such as roads, ponds, and power lines (D. E. Naugle, University of Montana, unpublished data).

Statistical Analyses

We employed logistic regression with used and available points for model selection and RSF model parameter estimates (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We pooled used locations of individual animals and made inferences at the population level (Design I; Erickson et al. 2001, Manly et al. 2002).

We first assigned variables into one of 3 model categories: vegetation, topography, or energy development. Because no published landscape-scale studies existed upon which to base a priori models (Burnham and Anderson 2002), we tested all variables individually and removed variables with odds ratios overlapping 1.0. We tested all buffer distances for each variable and identified the scale that best represented sage-grouse habitat selection for each variable using log-likelihood values. We then allowed the best scale for each variable to compete with all possible combinations of other variables within the same category to identify the most parsimonious model. We used information-theoretic methods (Burnham and Anderson 2002) to choose between competing models by converting log-likelihood values computed in logistic regression to Akaike's Information Criterion (AIC) values. We brought models within 2 AIC points to the next hierarchy of model selection. After identifying the top model(s) within vegetation, topography, and energy development, we allowed models to compete across categories to see if the additional information increased model fit.

We did not allow correlated predictors ($r \geq |0.7|$) in the same model at any level of model selection. If variables were correlated ($r \geq |0.7|$), we chose the variable we felt had the greatest biological meaning according to known characteristics of winter sage-grouse habitat from published studies. When variables were moderately correlated (i.e., $|0.3| \leq r < |0.7|$), we checked for stability and consistency of regression coefficient estimates as we added predictor variables to models. If a regression coefficient switched signs or standard errors increased substantially when correlated variables were in the same model, we removed one variable from analysis if the other was an important predictor.

We evaluated whether sage-grouse avoided energy development in winter by using AIC values to determine if the addition of CBNG wells/km^2 to the top habitat model explained more information than habitat alone. We then examined the resulting corresponding model coefficient for CBNG wells to determine if sage-grouse avoided or were attracted to energy development and to what degree. We performed a bootstrap analysis to quantify the change in odds of use with the introduction of CBNG wells in the form of 95% confidence intervals around the odds ratios for differences in the number of wells. Because the best approximating model had a high AIC weight (w_i = 0.965), we used beta coefficients from the best approximating model for all computations (see results; Burnham and Anderson 2002). For each bootstrap data set ($n = 5{,}000$) we calculated and stored model coefficients and the mean value for all used locations for each variable. We then repeated this bootstrap analysis, varying the number of CBNG wells in a 4-km^2 area from 0 wells to 22 wells, the full range of well density we observed in our original data set. For each of the 5,000 simulations we computed the odds of use with the logistic equation. We then ordered these ratios and used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for the upper and lower 95% confidence interval bounds.

We then used the same bootstrap technique to quantify how the amount of sagebrush within a 4-km^2 area affected the odds of use in winter with and without CBNG development (12.3 wells/4 km^2 and 0.0 wells/4 km^2, respectively). We used the logistic equation to generate odds of use for each bootstrap dataset ($n = 5{,}000$) by applying stored model coefficients to mean values of parameters at used locations while systematically varying percent sagebrush within 4 km^2 from 0% to 100% at 0.0 and 12.3 wells per 4 km^2. To test if the odds of use were significantly different with the addition of CBNG we computed the difference in odds generated from each bootstrap data set with and without CBNG. Again, we ordered odds ratios with and without CBNG and their differences and used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for the upper and lower 95% confidence interval bounds.

To turn our statistical model into a spatially explicit GIS habitat model, we employed a RSF model that had the form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k), \qquad (1)$$

where $w(x)$ is the raw RSF value for each pixel in the landscape, and $x_1, x_2, \ldots x_k$ represent values for vegetation, topography, and energy development generated from a moving-window analysis for each pixel, and $\beta_1, \ldots, \beta_k$ are the model parameters estimated with logistic regression (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We applied β-coefficients from equation 1 to GIS layers in ArcView Spatial Analyst. The output was a new GIS layer that represents the RSF values generated from equation 1 for each individual 25-m^2 pixel for the entire landscape. We created each component GIS layer by moving-window analyses for key vegetation, topographic, and energy development variables identified in model selection. These analyses resulted in summary statistics for each pixel in the GIS layer at the desired scale. We resampled sagebrush to a 900-m^2 pixel size because the time required to process a 4-km^2 area for 625 million pixels exceeded our computational capacity. Sagebrush resampled well and little information was lost when evaluating the 900-m^2 resampled sagebrush layer versus the original 25-m^2 resolution sagebrush layer ($r = 0.934$). Conifer resampled poorly ($r = 0.793$) so we kept this variable at the original pixel size.

We categorized RSF values into 5 ordinal 20% quantile bins representing progressively selected habitats. We validated our spatial model with the test data set of sage-grouse locations collected during the winters of 2004 and 2007. We regressed the observed proportion of the test data set in each RSF bin against the expected proportion of use from the original RSF model to evaluate model fit (Johnson et al. 2006). A good model fit should have a high validation R^2 value, a slope not different from 1.0, and an intercept not different from zero (Johnson et al. 2006).

Table 1. Vegetation, topographic, and energy development variables that we evaluated as potential landscape predictors of sage-grouse winter habitat selection, Powder River Basin, Montana and Wyoming, USA, 2005 and 2006. We used log-likelihoods to identify best scale at which selection occurred for individual variables along with confidence intervals of odds ratios that did not overlap 1 to choose variables for model selection.

Model category	Variable	Buffer area (km^2)	Log-likelihood	Odds ratio	Upper 95% CI	Lower 95% CI
Vegetation[a]	Sagebrush	4	−799.550	1.052	1.060	1.044
	Sagebrush	0.65	−814.010	1.048	1.043	1.034
	Sagebrush	0.04	−825.694	1.030	1.035	1.024
	Grass	4	−877.583	0.972	0.980	0.964
	Grass	0.04	−878.044	0.982	0.987	0.976
	Grass	0.65	−884.551	0.980	0.987	0.973
	Conifer	0.65	−813.051	0.765	0.822	0.712
	Conifer	0.04	−833.587	0.793	0.859	0.732
	Conifer	4	−818.951	0.810	0.850	0.772
	Riparian	4	−851.246	0.843	0.882	0.805
	Riparian	0.65	−860.729	0.870	0.909	0.833
	Riparian	0.04	−889.368	0.958	0.979	0.938
	Barren	0.65	−890.643	0.897	0.940	0.856
	Barren	4	−890.197	0.866	0.919	0.816
	Barren	0.04	−898.349	0.960	0.987	0.934
Topography	Roughness	0.65[b]	−838.257	0.888	0.909	0.868
	Roughness	0.04	−844.885	0.815	0.850	0.782
	Roughness	4	−848.668	0.921	0.936	0.905
	Solar radiation	0.0009	−902.677	0.997	1.002	0.992
	Slope	0.0009	−863.384	0.879	0.907	0.852
Energy Development	Distance to nearest well		−865.638	1.000	1.002	0.997
	No. wells	4	−857.717	0.961	0.985	0.939
	No. wells	0.65	−859.699	0.833	0.943	0.736
	No. wells	0.04	−863.083	0.434	1.102	0.171

[a] We excluded grass from further habitat models because of its correlation with sagebrush ($r = -0.78$).
[b] Roughness = index calculated using the SD of a digital elevation model.

RESULTS

Sagebrush at the 4-km^2 scale was the dominant variable in univariate space (Table 1). Sagebrush and grassland accounted for >95% of the total vegetation cover at used locations, which explains their strong negative correlation ($r = -0.78$). Within a 4-km^2 area, used sites contained >75% sagebrush cover intermixed with grassland. There was 14.5% more sagebrush at used (76.0%, SE = 0.55) than at available sites (61.5%, SE = 0.61). Sage-grouse used sites averaged 19.1% (SE = 0.53) grassland cover within a 4-km^2 area.

The best model for sage-grouse vegetation use consisted of sagebrush and riparian (4-km^2 scale), as well as conifer and barren (0.65-km^2 scale; Table 2). The roughness index at a 0.65-km^2 scale and slope were both important topographic predictors of sage-grouse use (Table 2). The number of CBNG wells within a 4-km^2 area was the best model to represent energy development (Table 1).

Model fit increased when the best approximating models from vegetation, topography, and energy development were combined (Table 3). We removed barren ground from the final vegetation model because it lacked stability and

Table 2. Log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion value (AIC), change in AIC value from the top model (ΔAIC), and Akaike weight (w_i) of sage-grouse winter habitat selection for vegetation and topography models, Powder River Basin, Montana and Wyoming, USA, winters of 2005 and 2006.

Model	LL	*K*	AIC	ΔAIC	w_i
Vegetation models					
Sagebrush[a] + Conifer + Riparian + Barren	−716.337	5	1,442.674	0.000	0.998
Sagebrush + Conifer + Riparian	−723.772	4	1,455.544	12.870	0.002
Sagebrush + Conifer + Barren	−744.539	4	1,497.078	54.404	0.000
Sagebrush + Conifer	−749.355	3	1,504.710	62.036	0.000
Sagebrush + Riparian + Barren	−780.350	4	1,568.700	126.026	0.000
Sagebrush + Riparian	−787.762	3	1,581.524	138.850	0.000
Sagebrush + Barren	−799.877	3	1,605.754	163.080	0.000
Topography models					
Roughness[b] + Slope[c]	−835.881	3	1,677.762	0.000	0.798
Roughness	−838.257	2	1,680.514	2.752	0.202
Slope	−863.384	2	1,730.768	53.006	0.000

[a] Vegetation variables = % cover of each Geographic Information System vegetation category within a selected buffer distance (% sagebrush, barren and riparian within 4 km^2 + % conifer and roughness within 0.65 km^2).
[b] Roughness = index calculated using the SD of a digital elevation model (DEM).
[c] Slope = slope of pixel calculated using a DEM.

Table 3. Log-likelihood (LL), number of parameters (K), Akaike's Information Criterion value (AIC), change in AIC value from the top model (ΔAIC), and Akaike weight (w_i) of sage-grouse winter habitat model selection, Powder River Basin, Montana and Wyoming, USA, winters of 2005 and 2006.

Model[a]	LL	K	AIC	ΔAIC	w_i
Vegetation[b] + Topography[c] + CBNG[d]	−683.644	7	1,381.288	0.000	0.965
Vegetation + Topography	−687.974	6	1,387.948	6.660	0.035
Vegetation + CBNG	−718.083	5	1,446.166	64.878	0.000
Vegetation	−723.772	4	1,455.544	74.256	0.000
Topography + CBNG	−826.657	3	1,659.314	278.026	0.000
Topography	−835.881	3	1,677.762	296.474	0.000
CBNG	−857.717	2	1,719.434	338.146	0.000

[a] Models represent the AIC best combination of variables within each model category.
[b] Vegetation = % sagebrush and riparian within 4 km^2 + % conifer within 0.65 km^2.
[c] Topography = roughness of land within 0.65 km^2 + slope.
[d] CBNG = no. of coal-bed natural gas wells/4 km^2.

consistency due to its correlation with roughness ($r = 0.32$). When roughness and barren ground were in the same model, the coefficient for barren ground switched from a negative to a positive effect and its standard error increased, causing the odds ratio interval to overlap 1.0 (odds 0.96–1.06). Roughness was a more stable predictor and was unaffected by the inclusion of barren ground. The final combined model was 1.96 AIC points better when barren ground was removed.

Sage-grouse selected large expanses of sagebrush with gentle topography and avoided conifer, riparian, and energy development (Table 4). The addition of the average number of wells per 4-km^2 improved model fit by 6.66 AIC points (Table 3). An Akaike weight ($w_i = 0.965$) indicated that the model with both habitat and energy variables had overwhelming support (Table 3). The resulting model coefficients from the habitat and energy model indicate that after adjusting for sage-grouse habitat preference, birds avoid CBNG development in otherwise suitable habitat (Table 4).

Our bootstrap analysis demonstrated that current legal maximum well density on federal lands (approx. 12.3 wells/4 km^2, or 32-ha spacing) decreased the odds of sage-grouse use by 0.30 compared to the average landscape selected by our radiomarked sage-grouse (odds 0.57 vs. 0.87; Fig. 1). Sage-grouse were 1.3 times more likely to use winter habitat if CBNG development was not present. The odds of sage-grouse winter habitat use increased with greater percentage sagebrush cover within 4 km^2 (Fig. 2a). The difference in odds of use with and without CBNG development was statistically significant at all levels of sagebrush ($P < 0.05$); however, these differences were more pronounced in high-quality winter habitats dominated by sagebrush cover (Fig. 2b). Avoidance of CBNG was not relevant to winter habitat selection at low levels of sagebrush cover because sage-grouse showed strong avoidance of those areas prior to development (Fig. 2a).

The best approximating model including vegetation, topography, and energy variables accurately predicted an independent data set of 74 winter locations (validation $R^2 = 0.98$; Fig. 3). Using 6-, 7-, or 8-bin ordinal RSF models with quantile breaks did not change the strength or pattern of model validation. The slope of observed versus expected values did not differ from 1.0 (slope = 1.14, 95% CI = 0.87–1.41) and the intercept did not differ from zero (−2.85, 95% CI = −1.06–4.9). The top 2 RSF classes accounted for 86.6% of the 435 locations used to build the RSF model and 90.5% of the 74 locations used to test the winter habitat model (Fig. 3).

DISCUSSION

Our study is the first to show that abundance of sagebrush at a landscape scale influences sage-grouse habitat selection in

Table 4. Logistic regression β-coefficients (SE) and odds ratios from the best model (Akaike wt = 0.965) describing winter habitat selection and energy avoidance for sage-grouse, Powder River Basin, Montana and Wyoming, USA, 2005 and 2006.

Parameters	Estimate	SE	Odds ratio	Upper 95% CI	Lower 95% CI
Constant	−1.106	0.369			
Roughness[a]	−0.039	0.017	0.962	0.994	0.931
Slope[b]	−0.102	0.022	0.903	0.943	0.865
Conifer[c]	−0.203	0.033	0.816	0.871	0.765
Sagebrush[d]	0.028	0.004	1.028	1.037	1.020
Riparian[e]	−0.131	0.026	0.877	0.923	0.834
CBNG wells[f]	−0.035	0.014	0.966	0.992	0.940

[a] Roughness = topographic index calculated as the SD of a digital elevation model (DEM) within 0.65 km^2.
[b] Slope = slope of pixel calculated from DEM.
[c] Conifer = % conifer cover within 0.65 km^2.
[d] Sagebrush = % sagebrush cover within 4 km^2.
[e] Riparian = % riparian cover within 4 km^2.
[f] CBNG = no. of coal-bed natural gas wells within 4 km^2.

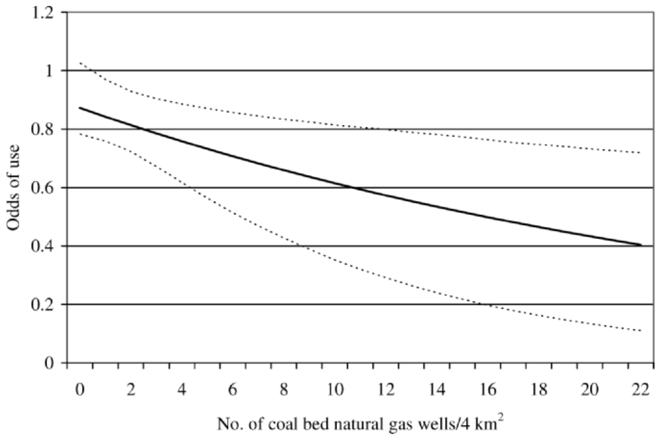

Figure 1. Reduction in the odds of sage-grouse winter habitat use versus available habitat with increasing coal-bed natural gas (CBNG) well density, Powder River Basin, Montana and Wyoming, USA, 2005–2006. Odds (solid line) and 95% confidence intervals (dashed line) are based on 5,000 bootstrap samples with densities varying between 0–22 wells per 4 km^2, the range of CBNG development we observed in our sample of used and available points.

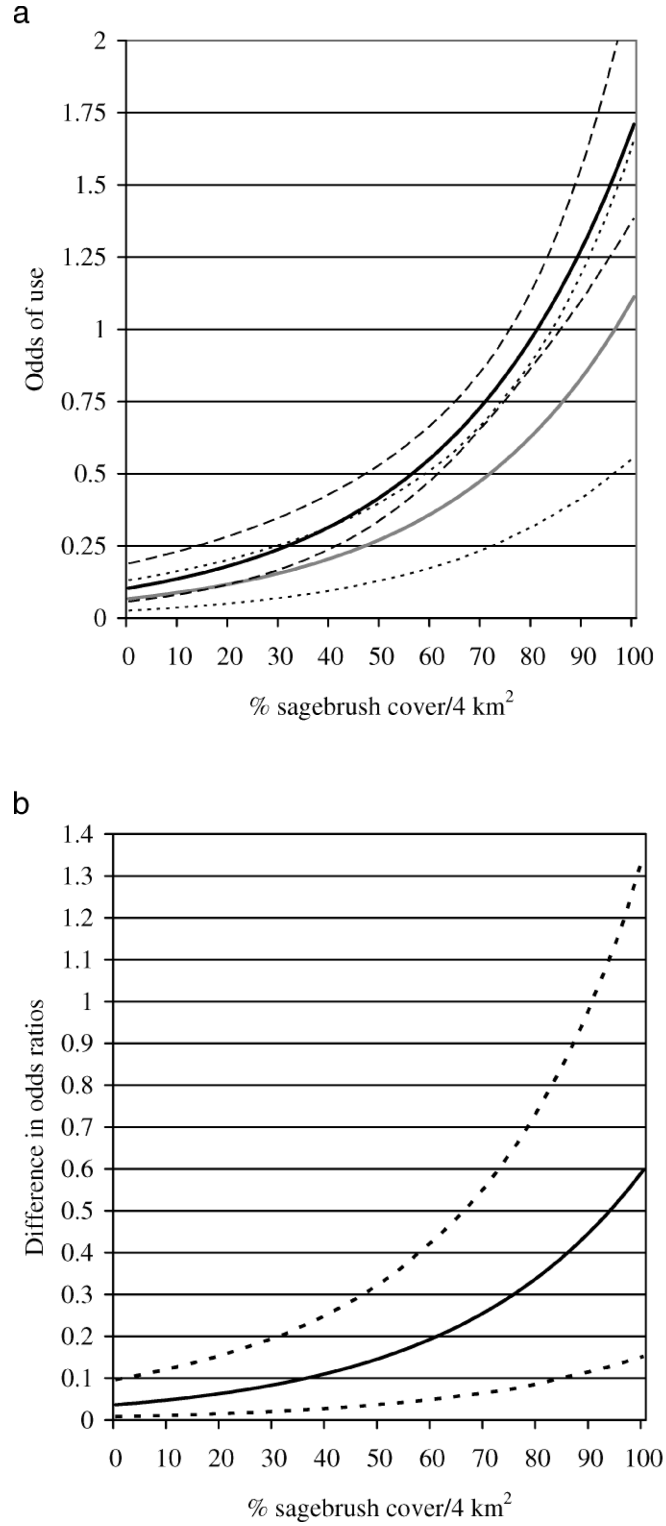

Figure 2. Odds of sage-grouse winter habitat use in relation to percent sagebrush cover per 4 km^2, Powder River Basin, Montana and Wyoming, USA, 2005–2006. Odds and 95% confidence intervals are based on 5,000 bootstrap samples with sagebrush varying from 0% to 100%, with and without coal-bed natural gas (CBNG) development. a) The gray line represents CBNG development (12.3 wells/4 km^2, 95% CI small dashed line) and the black line represents no CBNG development (0.0 wells/4 km^2, 95% CI large dashed line). b) The difference of means for odds of use with and without CBNG (black line minus grey line from part [a] above) is plotted against varying amounts of sagebrush cover per 4 km^2 (95% CI dashed line).

winter. Recent advances in RSF modeling and habitat mapping using satellite imagery enabled us to document what all major reviews on sage-grouse habitat requirements have suggested (Schroeder et al. 1999; Connelly et al. 2000, 2004; Crawford et al. 2004). At the largest scale evaluated (4 km^2), sage-grouse selected for sagebrush and grassland landscapes (>95% area) that were dominated by sagebrush (>75%) with little tolerance for other cover types. Conversion of sagebrush negatively influences sage-grouse populations (Leonard et al. 2000, Smith et al. 2005). Sage-grouse avoided riparian areas at the 4-km^2 scale and conifer habitats and rugged landscapes at a 0.65-km^2 scale, relationships that would have been less discernible at broader spatial scales. Our roughness index was a much stronger predictor than the rest of our suite of topographic variables, but slope further increased model fit. Roughness is readily calculated from available DEMs and may be applicable to other life stages for sage-grouse. In the only other sage-grouse landscape study that has evaluated habitat selection at multiple scales, birds selected large expanses (>1 km^2) of sagebrush and avoided anthropogenic edge during the breeding season (Aldridge and Boyce 2007). Our findings from winter in conjunction with those of Aldridge and Boyce (2007) highlight the need for landscape-scale research to gain further insight into sage-grouse ecology.

Our habitat model was highly predictive. We built our model using sage-grouse locations collected during mild to average winter conditions and validated it in years with average temperatures or above-average snowfall. We do not know whether we defined winter habitat broadly enough to include refugia necessary for birds to survive a 50- or 100-year winter storm event (Moynahan et al. 2006), but we believe the model is useful to identify habitat available in most winters. Extreme events may move birds into rugged landscapes as they search for exposed sagebrush, thermal

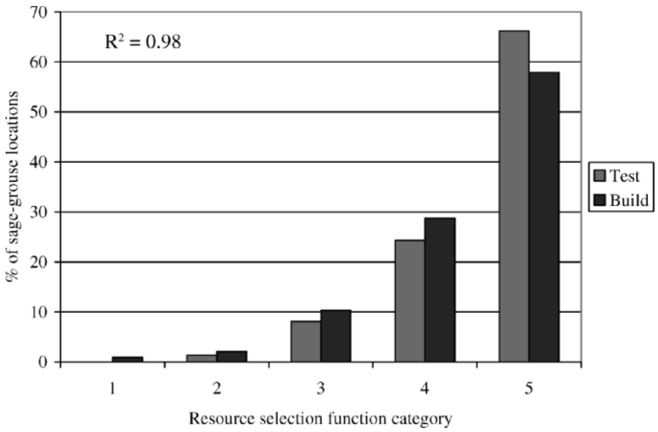

Figure 3. Percent of sage-grouse use locations in each of 5 ordinal resource-selection function bins we used to build (black bars, $n = 436$ locations from 2005 to 2006) and test (gray bars, $n = 74$ locations from 2004 and 2007) the winter habitat model, Powder River Basin, Montana and Wyoming, USA.

cover, and protection from high winds (Beck 1977, Hupp and Braun 1989, Robertson 1991, Connelly et al. 2004).

A multi-scale approach is needed to understand the relative importance of local and landscape factors influencing sage-grouse habitat selection. Local vegetation measures have been the primary focus of sage-grouse habitat research to date (Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). Ideally, local variables should compete against landscape factors in an AIC framework to predict sage-grouse habitat use. Examination of ecological processes at the landscape scale does not eliminate the need to understand habitat relationships at local scales; rather, it will likely require a combination of scales to completely understand how sage-grouse respond to their environment.

Our spatially explicit habitat model provides resource managers with a practical tool to guide conservation planning. Effective planning requires that we know which habitats are selected at landscape scales, where those habitats are located, and how species respond to disturbances. Recent advances in wildlife ecology enable biologists to develop RSF models that link resource use with changes in habitat quality and potential stressors (Manly et al. 2002, Johnson et al. 2004). Moreover, RSFs estimate the strength of selection and enable predictive equations to be linked in a GIS to depict spatial relationships across a planning region (Manly et al. 2002, Johnson et al. 2004). Spatially explicit planning tools should be used to prioritize landscapes with the highest probability of supporting populations. Once identified, local biologists provide on-site recommendations for how to best deliver on-the-ground conservation.

After adjusting for sage-grouse habitat preference, sage-grouse avoided energy development in otherwise suitable habitats in winter. Previous research has shown that breeding sage-grouse in oil and gas fields avoid development, experience higher rates of mortality, or both (Holloran 2005, Kaiser 2006, Aldridge and Boyce 2007). Accumulating evidence of the impacts of energy development in sagebrush-steppe ecosystems extends beyond that of sage-grouse. Mule deer (*Odocoileus hemionus*) avoided otherwise suitable habitats within 2.7–3.7 km of gas wells (Sawyer et al. 2006) and densities of Brewer's sparrow (*Spizella breweri*) and sage sparrow (*Amphispiza belli*) declined 36–57% within 100-m of dirt roads in gas fields (Ingelfinger and Anderson 2004). Some suitable winter habitat remains undeveloped for sage-grouse in the PRB (RSF bins 4 and 5; Fig. 3), but the anticipated addition of another 37,000 CBNG wells at 32-ha spacing has the potential to affect >1.18 million ha of land. As remaining winter habitats are developed, and sage-grouse can no longer avoid CBNG, it is unclear whether birds will be able to adapt to a disturbance of this magnitude.

MANAGEMENT IMPLICATIONS

Sage-grouse avoidance of energy development in winter shows that a comprehensive strategy is needed to maintain suitable habitats in all seasons. Identifying and setting aside areas of undeveloped, high-quality habitat within the project area should be top priority. Currently, only 0.5-km^2 (quarter-mile buffer) of land surrounding a lek is excluded from development, an area that is 8 times smaller than the scale at which individual sage-grouse selected winter habitats (i.e., 4 km^2). Timing stipulations that restrict CBNG development within 3.2 km of a lek during the breeding season (15 Mar–15 Jun) are insufficient because they do not prevent infrastructure from displacing sage-grouse in winter. An additional stipulation in Montana that restricts new drilling activities within crucial winter range (1 Dec–31 Mar) only protects sage-grouse habitat during the winter in which the drilling is scheduled. Current stipulations leave only a small fraction of the land undeveloped, place no restrictions on the location of wells in winter habitat, and allow human access to all areas throughout the life of the producing gas field. Our spatially explicit winter habitat model can be used to identify areas in the PRB that provide the best remaining habitat for sage-grouse in winter.

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