Sage-Grouse Habitat Selection During Winter in Alberta

Author(s): Jennifer Carpenter, Cameron Aldridge, and Mark S. Boyce

Source: Journal of Wildlife Management, 74(8):1806-1814. 2010.
Published By: The Wildlife Society-2
DOI: 10.2193/2009-368
URL: http://www.bioone.org/doi/full/10.2193/2009-368

Journal of Wildlife Management 74(8):1806–1814; 2010; DOI: 10.2193/2009-368

Management and Conservation Article

Sage-Grouse Habitat Selection During Winter in Alberta

JENNIFER CARPENTER,[1] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*
CAMERON ALDRIDGE,[2] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*
MARK S. BOYCE,[3] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada*

ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*) are dependent on sagebrush (*Artemisia* spp.) for food and shelter during winter, yet few studies have assessed winter habitat selection, particularly at scales applicable to conservation planning. Small changes to availability of winter habitats have caused drastic reductions in some sage-grouse populations. We modeled winter habitat selection by sage-grouse in Alberta, Canada, by using a resource selection function. Our purpose was to 1) generate a robust winter habitat-selection model for Alberta sage-grouse; 2) spatially depict habitat suitability in a Geographic Information System to identify areas with a high probability of selection and thus, conservation importance; and 3) assess the relative influence of human development, including oil and gas wells, in landscape models of winter habitat selection. Terrain and vegetation characteristics, sagebrush cover, anthropogenic landscape features, and energy development were important in top Akaike's Information Criterion–selected models. During winter, sage-grouse selected dense sagebrush cover and homogenous less rugged areas, and avoided energy development and 2-track truck trails. Sage-grouse avoidance of energy development highlights the need for comprehensive management strategies that maintain suitable habitats across all seasons.

KEY WORDS *Centrocercus urophasianus*, critical habitat, energy development, greater sage-grouse, resource selection functions, winter habitats.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is an endangered species in Canada (Committee on the Status of Endangered Wildlife in Canada 2004). Range-wide sage-grouse have lost approximately 44% of their presettlement range (Schroeder et al. 2004), and populations have continued to decline by 2% per year since 1965 (Connelly and Braun 1997, Connelly et al. 2004), with local declines as high as 92% (Connelly et al. 2000, Aldridge and Brigham 2003). As a result, sage-grouse are the focus of intensive research and management efforts across their range. Population declines are thought to be driven by reductions in habitat quality during 3 critical life stages: nesting, brood rearing, and wintering (Connelly et al. 2000, 2004; Moynahan et al. 2006; Aldridge and Boyce 2007; Hagen et al. 2007). Aldridge and Boyce (2007) identified and mapped critical habitats for sage-grouse nesting and brood rearing in Alberta, Canada, but Doherty et al. (2008) noted the lack information on landscape-level winter habitat needs for sage-grouse. Winter habitats are generally not considered a research priority because winter survival of sage-grouse is typically high (Connelly et al. 2004), but winter habitats may be of greater importance in declining populations. For example, in northern Colorado, USA, 80% of winter sites used by sage-grouse occurred in <7% of the total area of sagebrush (*Artemisia* spp.; Beck 1977), and small changes to the quality and availability of winter habitats have resulted in severe reductions in sage-grouse populations (Swenson et al. 1987). Furthermore, severe winters can contribute to reduced annual survival (Moynahan et al. 2006).

Most studies of sage-grouse winter habitats focused on site-specific features such as height, canopy cover, or crude protein levels in sagebrush and clearly identified the importance of moderate-to-dense sagebrush cover during winter (e.g., Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). Although important in understanding habitat use, such local studies do not present managers an understanding of habitat selection at a scale useful to identify and prioritize landscapes for conservation. An exception is in the Powder River Basin of Wyoming and Montana, USA, where a landscape approach was successfully used to determine that landscape factors, including vegetation, topography, and oil and gas development, affected sage-grouse winter habitat selection (Doherty et al. 2008).

Modeling habitat selection using resource selection functions (RSF) offers the ability to rank areas by their relative probability of selection (Manly et al. 2002). Mapping these relative probabilities in a Geographic Information System (GIS) can identify regions with high-quality habitats and can provide managers with a meaningful tool for prioritizing areas of conservation importance (Aldridge and Boyce 2007). Testing a habitat-selection model with independent data ensures inferences regarding habitat selection are robust and a competing-models framework can be used to evaluate alternative models of habitat selection (Burnham and Anderson 2002, Manly et al. 2002).

We investigated winter habitat selection by sage-grouse in southeastern Alberta. Our objectives were to 1) generate a robust winter habitat selection model for sage-grouse; 2) spatially depict habitat suitability to identify areas with a high probability of selection and thus, conservation importance; and 3) assess the relative influence of human development in landscape models, including intensive

---

[1] *Present address: Alberta Conservation Association, 1609-3 Avenue South, Lethbridge, AB T1J 2J8, Canada*

[2] *Present address: NREL, Colorado State University and United States Geological Survey, 2150 Centre Avenue, Building C, Fort Collins, CO 80526-8118, USA*

[3] *E-mail: boyce@ualberta.ca*

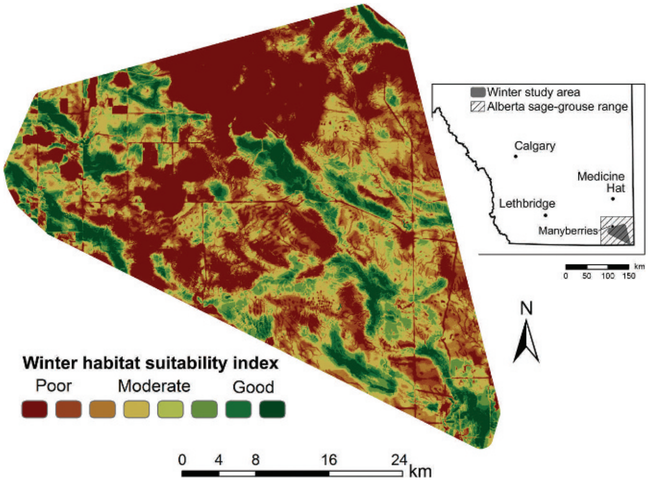

Figure 1. Winter habitat suitability for greater sage-grouse as determined by a resource selection function that incorporated terrain and vegetation, sagebrush, energy development, and anthropogenic feature variables. Good index values indicate increased probability of habitat selection by sage-grouse during winter. Inset depicts range of greater sage-grouse and location of study area within southeastern Alberta, Canada, 2002–2004.

energy development, on winter habitat selection. We hypothesized that sage-grouse select habitats containing greater abundance of sagebrush in landscapes that are free of snow throughout winter and that sage-grouse avoid landscapes with anthropogenic disturbances, such as those associated with energy development (i.e., well sites).

STUDY AREA

In the dry mixed grass prairie of southern Alberta, sage-grouse are found within an approximately 4,000-km^2 area. Cattle graze most of this area and approximately 30% of this area is influenced by oil and gas development (Aldridge and Boyce 2007). Our study area (49°24′N, 110°42′W, ∼900-m elevation) encompassed the core of the winter range (1,400 km^2; Fig. 1, inset). Snowfall between November and March averaged 73 cm, and approximately 30 days per year were $<-20^\circ$ C (Environment Canada 2009). Silver sagebrush (*Artemisia cana*) was the predominant shrub and no other species grows in this area. Grass was dominated by native grasses such as needle-and-thread grass (*Stipa comata*), June grass (*Koeleria macrantha*), and western wheatgrass (*Agropyron smithii*; Coupland 1961, Aldridge and Brigham 2003).

METHODS

We captured female sage-grouse on 5 of 8 active leks (breeding sites) in southeastern Alberta from 1999 to 2003 by using walk-in traps (Schroeder and Braun 1991). In August and September 2003, we captured additional juvenile females by on foot nightlighting of flocks containing adult females with radiocollars (Connelly et al. 2003). We fit females with 14-g necklace-style radio-transmitters (RI-2BM transmitters; Holohil Systems Ltd., Carp, ON, Canada). We located birds with a 3-element Yagi antenna and an R-1000 scanning telemetry receiver (Communications Specialists, Inc., Orange, CA). When we could not locate signals from the ground, we searched for signals from a fixed-wing aircraft. We located and flushed females approximately once per week during winter from 1 November to 15 March in 2002–2003 and 2003–2004 (hereafter winter 1 and winter 2, respectively). If a flock of birds flushed and we could not determine the exact location of the radiocollared bird, we recorded the approximate center of the flock as the use location. In this case, if we flushed multiple marked birds from the same flock, we considered a location for each bird in model development.

Geographic Information System Predictor Variables

Following Aldridge and Boyce (2007), we developed a suite of variables in a GIS that are probably important predictors of sage-grouse winter habitat selection. Following our hypotheses that sage-grouse select habitats with sagebrush and avoid landscapes with anthropogenic disturbances, we grouped variables into 4 classes: 1) terrain and vegetation; 2) sagebrush; 3) energy development; and 4) anthropogenic features, encompassing 86 variables (Table 1).

To analyze terrain and vegetation variables, we used Landsat Thematic Mapper satellite images from July 2000 to generate brightness (*brit_30*), greenness (*gren_30*), and normalized difference vegetation index (*ndvi*) by using a tasselled-cap transformation (Crist and Cicone 1984, Sellers 1985) in the program PCI Geomatica Prime 8.2 (PCI Geomatics, Richmond Hill, ON, Canada). We used a soil moisture index, referred to as compound topographic index (*cti*), that is correlated with soil moisture and nutrients and derived from a digital elevation model (Evans 2004). We also used a terrain ruggedness index (*tri*) derived from the amount of elevation difference between adjacent cells of a digital elevation model (Riley et al. 1999). We also estimated the mean of *ndvi*, *cti*, and *tri* and standard deviation of *ndvi* and *cti* values within a 1-km^2 moving window (*av_ndvi*, *sd_ndvi*, *cti_mean*, *cti_sd*, *tri_km*^{2}). We interpreted higher standard deviation values as representative of increasingly variable (heterogeneous) patches. Finally, we used a dry mixed grass plant community guide primarily based on soil types (Adams et al. 2005) to assign plant communities to ecosite categories (B. W. Adams, Alberta Sustainable Resource Development, personal communication) and estimated the proportion of each ecosite within a 1-km^2 moving window (*pec1…pec7*).

Sagebrush is an important habitat component for sage-grouse across all life stages at local scales (Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006, Hagen et al. 2007) and also across landscapes (Aldridge and Boyce 2007, Doherty et al. 2008). Following Aldridge and Boyce (2007), we estimated sagebrush cover at both the pixel (*sbcov*) and 1-km^2 moving-window (*sbmean*) by using the results of Jones et al. (2005). Because sage-grouse seem to select intermediate sagebrush cover (Aldridge and Boyce 2007), we assessed quadratic functions for all sagebrush-cover metrics to identify potential nonlinearities in selection. We developed 2 measures (*sb_patch1*, *sb_patch2*) of patchy or heterogeneous sagebrush distribution (Aldridge and Boyce 2007) based on sagebrush distribution patterns described by

Table 1. Explanatory Geographic Information System (GIS) variables used within an information-theoretic approach to model winter habitat of sage-grouse in Alberta, Canada, 2002–2004. Data are 10-m resolution except where indicated. Decay function is in the form of (−exp[dist]/decay distance), where dist is the distance to the variable and decay distance is the specified decay distance value that shapes the function.

Variable name	Description
Landscape features	
crop_dst	Distance to nearest cultivated lands in km
crop_den	Proportion of land that is cultivated within a 1-km^2 moving window
crop_dst1000/500/250/50	Decay function for distance to *crop*
urban_dst	Distance to nearest urban development in km
urban_den	Proportion of land that is urban within a 1-km^2 moving window
urban_dst1000/500/250/50	Decay function for distance to *urban*
human_dst	Distance to any human habitat (roads, wells, urban) in km
human_den	Proportion of land that is human habitats within a 1-km^2 moving window
human_dst1000/500/250/50	Decay function for distance to *human*
edge_dst	Distance to habitat that creates an anthropogenic edge (*human* and *crop*) in km
edge_den	Proportion of land that is edge habitat within 1-km^2 moving window
edge_dst1000/500/250/50	Decay function for distance to *edge*
water_dst	Distance to nearest natural water body in km
water_dst1000/500/250/50	Decay function for distance to *water*
imped_dst	Distance to nearest water impoundment (dam, dugout, canal) in km
imped_den	Count of number of water impoundments within a 1-km^2 moving window
imped_dst1000/500/250/50	Decay function for distance to water impoundment
trail_dst	Distance to nearest *trail* (non-paved or graveled 2-track truck road) in km
trail_den	Linear km per km^2 of *trail* (non-paved or graveled 2-track truck road)
trail_dst1000/500/250/50	Decay function for distance to *trail* (non-paved or graveled 2-track truck road)
road_dst	Distance to nearest *road* (paved or graveled) in km
road_den	Linear km per km^2 of *roads* (paved or graveled)
road_dst1000/500/250/50	Decay function for distance to *road*
Energy development	
well_dst	Distance to nearest standing energy well site in km
well_den	Count of energy well sites within a 1-km^2 moving window
well_dst1000/500/250/50	Decay function for distance to energy well site
Terrain and vegetation	
brit_30	Brightness generated from Landsat 7 TM satellite imagery[a]
gren_30[b]	Greenness generated from Landsat 7 TM imagery[a]
wet_30m	Wetness generated from Landsat 7 TM imagery[a]
ndvi	Normalized difference vegetation index calculated from TM[c] imagery[a]
av_ndvi[b]	Mean NDVI[d] value within a 1-km^2 moving window[a]
sd_ndvi	Standard deviation of NDVI within a 1-km^2 moving window[a]
cti[b]	Compound topographic index (CTI; high values = increased moisture)[a]
cti_mean[b]	Mean CTI values within a 1-km^2 moving window[a]
cti_sd	Standard deviation of CTI values within a 1-km^2 moving window[a]
tri_alb[b]	Terrain ruggedness index (TRI; high values = increased ruggedness)[a]
tri_km^2	Mean TRI within a 1-km^2 moving window[a]
eco1	Thin break range sites, soils vary, characterized by greater shrub cover (1,0; categorical)
eco2	Loamy upland sites with medium texture soils and needle-and-thread grass, wheatgrass (*Agropyron* spp.), and June grass (1,0; categorical)
eco3	Blowout and overflow sites, solonetzic soils; varies, but higher density of sagebrush (1,0; categorical)
eco4	Saline lowlands, swales and depression, sparse low sagebrush (1,0; categorical)
eco5	Broad, wetland, and shrubby (willow [*Salix* spp.], rose [*Rosa* spp.], snowberry [*Symphoricarpos occidentalis*]) riparian habitats (1,0; categorical)
eco6	Loamy range site with well drained soils, low sagebrush cover (1,0; categorical)
eco7	Badlands type habitats with juniper (*Juniperus horizontalis*), needle-and-thread grass, and blue grama (*Bouteloua gracilis*; 1,0; categorical)
eco8	All anthropogenic altered habitats (urban, crop, wells, roads; 1,0; categorical)
pec1, pec2, … pec7[b]	Proportion of class within a 1-km^2 moving window that is eco1, eco2, …, eco7
Sagebrush	
sbcov	Sagebrush cover (%) as identified from air photo interpretation
sbcovsq	Squared term for *sbcov*
sbmean	Mean sagebrush cover (%) within a 1-km^2 moving window
sbmeansq	Squared term for *sbmean*
sb_patch1,sb_patch2	Patchy sagebrush distribution 1 (codes 7, 8, 9) or 2 (codes 7, 8, 9, 11) from Jones et al. (2005)
sb_prop_patch1, 2	Proportion of habitat within a 1-km^2 moving window that fits within patchy sagebrush distribution 1 or 2

[a] 30-m resolution.

[b] Variables removed from model development due to correlations.

[c] Thematic Mapper.

[d] Normalized difference vegetation index.

Jones et al. (2005). We assessed the proportion of each patch class within a 1-km^2 moving-window across the landscape (*sb_prop_patch1*, *sb_prop_patch2*).

Energy developments included distance to the nearest energy well site and the number of well sites within a 1-km^2 moving window (*well_dst*, *well_den*). Anthropogenic features included distance to the nearest road (*road_dst*); 2-track truck trail (*trail_dst*); cultivated (crop) land (*crop_dst*); and urban development, including a town, farmstead, or building not at a well site (*urban_dst*). Because anthropogenic variables can change between years, we fixed these variables at their 2003 condition and incorporated them into the landscape for the sagebrush and ecosite variables by replacement where an anthropogenic feature, such as a road or well, existed in 2003. We calculated density metrics for roads and 2-track truck trails as their linear km per km^2 or as the proportion of area that was crop or urban within a 1-km^2 moving window (*road_den*, *trail_den*, *crop_den*, *urban_den*). We generated additive estimates of human (roads, energy wells, urban) and anthropogenic edge (roads, oil wells, urban, crop) metrics as both distance and density (proportion of area within a 1-km^2 moving window) variables (*human_dst*, *human_den*, *edge_dst*, *edge_den*). In addition, we included metrics measuring the distance to nearest water source (*water_dst*) and water impoundment (*imped_dst*, *imped_den*).

For all distance variables, we calculated decay variables (Nielsen et al. 2009) because the response of birds to a given landscape factor typically declines as the distance between them increases. Accordingly, we created 4 decay variables for each distance variable by using the form $e^{-\alpha/d}$, where d was the distance in meters from each pixel to a landscape feature, and we set α at 50, 250, 500, and 1,000. This scaled each distance variable between 0 and 1, with highest values close to the feature of interest.

Model Development

We used logistic regression contrasting used versus available pixels to estimate an exponential RSF to identify the relative probability of selection as a function of landscape covariates (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We generated 5,000 random locations across a 1-km buffer around a 100% minimum convex polygon surrounding 296 winter locations of 23 sage-grouse females. Annual variation can be of vital importance to understanding habitat selection if resource use varies between years (Schooley 1994). However, there was no indication of behavioral differences between winter 1 and winter 2 so to increase sample size, we included bird locations from both years in the same model. To reduce bias associated with the larger sample of available (0) resource units, we used an importance weight that gave full weighting to used resource units, but available resource units received a weighting (down) proportional to the ratio of sampled use (1) points to available points (StataCorp 2007; see Aldridge and Boyce 2007).

With limited large-scale studies on which to base a priori models (Burnham and Anderson 2002), we used a hierarchical information-theoretic method. First, we compared models or metrics and determined a best model to represent each of 4 variable classes (terrain and vegetation, sagebrush, energy developments, and anthropogenic features). Second, we allowed all combinations of the top models from each variable class to compete in an Akaike's Information Criterion (AIC) framework. At all stages, we accepted only models with a change in AIC (ΔAIC) score of $<$2, relative to the best model.

In the terrain and vegetation class, a priori models included variables for ecosite and measures of terrain. In cases of correlated predictors ($|r| > 0.7$), we chose to keep the most explanatory variable based on a univariate comparison. After removing correlated terrain variables, all models included *brit_30*, *wet_30m*, *ndvi*, *sd_ndvi*, and *cti*. We included a measure of landscape ruggedness (*tri_km*^{2}) in 2 of the models based on the importance of gentle topography in winter habitat selection by sage-grouse in Montana and Wyoming (Doherty et al. 2008). Because sagebrush and other shrubs might be important for both food and cover, we created 4 combinations of ecosite classes associated with shrub cover: higher density sagebrush (*pec1*), low sparse sagebrush (*pec4*), riparian shrubs (*pec5*), and low sagebrush cover (*pec6*).

In the sagebrush variable class, a priori models included both univariate and quadratic measures of sagebrush cover and patchiness. Based on Aldridge and Boyce (2007), we also included multi-variable models for sagebrush cover and patchiness (*sbcov*, *sbmean*, *sb_patch1*, *sb_patch2*, *sb_prop_patch1*, *sb_prop_patch2*). For the energy developments variable class, we evaluated univariate metrics for the density and distance to energy well sites by using AIC, and we selected only the best-performing metric to represent the energy variable class. We removed variables for well density and the smallest distance decay because there was no use of habitats within these buffers, causing models with the variables *well_dst50* and *well_den* to not converge. In the anthropogenic features variable class, we selected the best metric or scale for each of *road*, *trail*, *edge*, *urban*, *crop*, *water*, *imped*, and *human*. After removing correlated variables, we combined the best metrics for each of these to represent the anthropogenic variable class because we suspect these metrics all influence sage-grouse habitat selection.

After identifying a final model within each of the 4 variable classes, we allowed all 15 combinations of these top models to compete and accepted only models with a ΔAIC score $<$2 relative to the best model to represent winter sage-grouse habitat selection. At all levels of model selection, we did not allow correlated predictors ($|r| > 0.7$) in the same model. After estimating the final model, we assessed the effect size of anthropogenic features by predicting the relative probability of selection at increasing distances from the feature while holding each other variable at its mean value from the use locations.

We evaluated our top AIC-selected model by predicting it to an independent sample of 54 winter tracking locations made on birds captured between 1998 and 2001. During winters 1998–1999 and 2001–2002, 7 male (1.9 ± 0.34 locations/bird) and 25 female (1.6 ± 0.11 locations/bird)

Table 2. Akaike's Information Criterion (AIC)–selected models representing terrain and vegetation in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights (w_i) for 4 a priori candidate models.

Model[a]	LL	*K*	AIC	ΔAIC	w_i
brit_30, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km*^{2}, *pec1*, *pec2*, *pec3*, *pec4*, *pec5*, *pec6*[b]	−202.5	12	429	0	1.00
brit_30, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km*^{2}, *pec3*, *pec4*, *pec5*	−234.8	9	488	59	0.00
brit_30, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km*^{2}, *pec3*, *pec4*, *pec5*, *pec6*	−234.8	10	490	61	0.00
brit_30, *wet_30m*, *sd_ndvi*, *cti_sd*, *pec1*, *pec2*, *pec3*, *pec4*, *pec5*, *pec6*	−265.4	11	553	124	0.00

[a] Refer to Table 1 for variable descriptions.

[b] Accepted model for the terrain and vegetation class (ΔAIC < 2).

sage-grouse were flushed or located from a fixed wing aircraft. Although we used data from 9 of these females in subsequent years in model development, we believe that locations from separate years are sufficiently independent for inclusion in the evaluation of model predictive capacity. To evaluate the top AIC-selected model, we grouped the landscape by geometric means into 10 bins. Because some bins contained no data points for evaluation, we combined bins to avoid null cells, resulting in a total of 8 bins. Following Johnson et al. (2006), we converted expected and observed locations within each RSF bin into proportions and assessed the relationship between expected and observed frequencies by using linear regression testing the slope relative to 1 and evaluated overall fit using a chi-square goodness-of-fit test.

RESULTS

During the 2 winters, we obtained 296 locations for 23 females. We tracked 7 females only during winter 1, 10 only during winter 2, and 6 during both winters. There were 3 mortalities, all in February of either 2003 or 2004. Both years had close to average mean monthly temperatures. Snowfall during winter 1 (74 cm) was typical compared to the Canadian Climate Normal of 73 cm (1971–2000; Environment Canada 2009), but snowfall was greater (104 cm) during winter 2. Flock size of relocated birds was 13.5 ± 0.72 (SE; range 1–100), with many mixed sex flocks. On several occasions, radiomarked birds made long-distance movements of approximately 50 km in <2 days during winter.

Evaluation of the terrain and vegetation variable class model indicated the model combination of brightness; wetness; standard deviation of *ndvi*, *cti*; mean *tri*; and the remaining ecosite classes (*brit_30*, *wet_30m*, *sd_ndvi*, *cti_sd*, *tri_km*^{2}, *pec1 pec2*, *pec3*, *pec4*, *pec5*, *pec6*; Table 1) was the top model with greatest support, and no other models had moderate support (ΔAIC < 2.0; Table 2). The most supported model for the sagebrush variable class (ΔAIC < 2.0; Table 3) included the quadratic form of mean sagebrush cover and patchy distribution 2 (*sbmean*, *sb_prop_patch2*). Among 5 energy feature variable models, the most supported model (ΔAIC < 2.0; Table 4) was distance to well with a decay function of 250 m (*well_dst250*). For the anthropogenic features class, we removed variables for roads, urban, crop, and human (*road*, *urban*, *crop*, *human*) due to correlations with other variables. The most supported models among the impediment, water, edge, and 2-track truck trail variable groups (ΔAIC ≤ 2.0; Table 5) included impediment density (*imped_den*), distance to water (*water_dst50*), distance to edge (*edge_dst50*), and distance to 2-track truck trail (*trail_dst500*), respectively.

Combined evaluation of the best models from all 4 variable classes (Table 6) indicated the most supported model (ΔAIC < 2.0; Table 7) included the terrain and vegetation, sagebrush, energy development, and anthropogenic features. After applying this RSF model spatially to the landscape (Fig. 1), we used validation points to predict a linear regression model of the proportion of expected and observed validation location points. Model fit was high ($r^2 = 0.94$), with a slope different from zero ($P < 0.01$) and an intercept not different from zero ($\beta_0 = 0.02$, $P = 0.29$). A chi-square goodness-of-fit test ($\chi^2_8 = 5.05$, $P > 0.5$) and Spearman rank

Table 3. Akaike's Information Criterion (AIC)–selected models representing sagebrush in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights (w_i) for all 10 candidate models.

Model[a]	LL	*K*	AIC	ΔAIC	w_i
sbmean, *sbmeansq*, *sb_prop_patch2*[b]	−213	4	434	0	0.99
sbmean, *sbmeansq*	−219	3	444	10	0.01
sbmean	−235	2	474	40	0.00
sbcov, *sbcovsq*, *sb_prop_patch2*	−256	4	520	86	0.00
sbcov, *sbcovsq*	−274	3	554	120	0.00
sbcov	−284	2	572	138	0.00
sb_prop_patch2	−342	2	688	254	0.00
sb_patch2	−370	2	744	310	0.00
sb_prop_patch1	−408	2	820	386	0.00
sb_patch1	−410	2	824	390	0.00

[a] Refer to Table 1 for variable descriptions.

[b] Accepted model representing sagebrush (ΔAIC < 2).

Table 4. Akaike's Information Criterion (AIC)–selected models representing energy development in winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights (w_i) for all 4 candidate models.

Model[a]	LL	*K*	AIC	ΔAIC	w_i
well_dst250[b]	−386	2	776	0	0.95
well_dst500	−389	2	782	6	0.05
well_dst1000	−398	2	800	24	0
well_dst	−407	2	818	42	0

[a] Refer to Table 1 for variable descriptions.

[b] Accepted model representing energy development (ΔAIC < 2).

Table 5. Akaike's Information Criterion (AIC)–selected models of anthropogenic feature variables for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (K), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights (w_i) for each variable relative to similar variables at different scales. We combined the 4 accepted variables to represent the anthropogenic features variable class.

Variable[a]	LL	K	AIC	ΔAIC	w_i
water_dst50[b]	−408.0	2	820	0	0.61
water_dst250	−409.5	2	823	3	0.14
water_dst500	−409.9	2	824	4	0.09
water_dst1000	−410.0	2	824	4	0.08
water_dst	−410.0	2	824	4	0.08
trail_dst500[b]	−391.0	2	786	0	0.54
trail_den	−392.0	2	788	2	0.20
trail_dst1000	−392.0	2	788	2	0.20
trail_dst	−394.0	2	792	6	0.03
trail_dst250	−394.0	2	792	6	0.03
trail_dst50	−405.0	2	814	28	0.00
imped_den[b]	−386.0	2	776	0	0.97
imped_dst1000	−390.0	2	784	8	0.02
imped_dst500	−391.0	2	786	10	0.01
imped_dst	−392.0	2	788	12	0.00
imped_dst250	−395.0	2	794	18	0.00
imped_dst50	−408.0	2	820	44	0.00
edge_dst50[b]	−397.0	2	798	0	0.88
edge_dst	−399.0	2	802	4	0.12
edge_dst250	−407.0	2	818	20	0.00
edge_den	−409.0	2	822	24	0.00
edge_dst1000	−409.0	2	822	24	0.00
edge_dst500	−410.0	2	824	26	0.00

[a] Refer to Table 1 for variable descriptions.

[b] Accepted variables (ΔAIC < 2) included in the anthropogenic features variable class.

correlation ($r_s = 0.83$) corroborated the ability of our model to predict independent winter sage-grouse locations.

After estimating the final model, we assessed the effect size of the energy development, trail, and edge variables (*well_dst250*, *trail_dst500*, *edge_dst50*) by predicting relative probability of selection at increasing distances from the landscape feature while holding all other variables constant at their mean values (Table 8). We also added or subtracted one standard error from the coefficient of the variable of interest and held all other model variables constant at their mean, to estimate standard errors around predictions. The predicted probability of selection dropped sharply at approximately 1,900 m from energy wells and at 200 m from anthropogenic edges but for trails, the effect was less pronounced (Fig. 2).

DISCUSSION

Our habitat model was highly predictive and is useful in identifying important winter habitats for wintering sage-grouse. Consistent with findings in Wyoming and Montana (Doherty et al. 2008), and as we hypothesized, the abundance and patchy distribution of sagebrush on the landscape influenced sage-grouse winter habitat selection. Topographic metrics and measures of productivity calculated from satellite imagery also contributed to the model. Again consistent with findings of Doherty et al. (2008), sage-grouse selected less rugged areas at lower elevations. During breeding season, sage-grouse in this population showed avoidance of anthropogenic edge (Aldridge and Boyce 2007). Human impacts also were important predictors of winter habitats. During winter, sage-grouse avoided all anthropogenic edges, regardless of type, although the smallest scale we tested provided the best model fit (*edge_dst50*), and edge was pronounced in our model with no habitats selected within 100 m of edge and limited selection from 100 m to 300 m (Fig. 2).

Models that included energy development (well metrics) performed better in AIC selection than the identical competing model without wells. Furthermore, the response to energy wells was at a large scale in our model, with no habitats selected within 1,200 m and limited selection between 1,200 m and 1,900 m. Doherty et al. (2008) found that density of coal bed natural gas wells was a better measure of sage-grouse avoidance at a large scale than a more local scale. Similarly, our model for sage-grouse in Alberta

Table 6. Mean, standard deviation, and range (min. and max. values) for all covariates included in final candidate Akaike's Information Criterion models to predict greater sage-grouse winter habitat selection in Alberta, Canada, from 2002 to 2004.

Variable category	Variable name[a]	$\bar{x}$	SD	Min.	Max.
Energy	*well_dst250*	0.020	0.086	0	0.95
Sagebrush	*sbmean*	14.91	13.70	0	86.78
	sbmeansq	409.96	795.52	0	7530
	sb_prop_patch2	0.19	0.27	0	1
Terrain and vegetation	*brit_30*	217.52	20.58	54.99	360.61
	wet_30m	18.22	8.84	−8.98	86.62
	sd_ndvi	0.038	0.027	0.0091	0.19
	tri_km^2	2.37	2.63	0	18.16
	pec1	0.130	0.2630	0	1
	pec2	0.0963	0.2542	0	1
	pec3	0.355	0.4002	0	1
	pec4	0.0898	0.2412	0	1
	pec5	0.144	0.2840	0	1
	pec6	0.0834	0.1970	0	1
Anthropogenic	*imped_den*	0.42	0.66	0	5
	water_dst50	0.21	0.28	0	1
	edge_dst50	0.064	0.21	0	1
	trail_dst500	0.0032	0.048	0	1

[a] Refer to Table 1 for variable descriptions.

Table 7. Akaike's Information Criterion (AIC)–selected models for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. We report model log likelihood (LL), number of model parameters (*K*), AIC, change in AIC from lowest model (ΔAIC), and Akaike weights (w_i) for all candidate models. Variable classes include energy development (E), sagebrush (S), anthropogenic features (A), and terrain and vegetation (T).

Model[a]	LL	*K*	AIC	ΔAIC	w_i
E, S, A, T[b]	−108	20	256	0	0.98
S, A, T	−113	19	264	8	0.02
E, S, T	−119	16	270	14	<0.01
S, T	−126	15	282	26	<0.01
E, S, A	−172	9	362	106	<0.01
S, A	−182	8	380	124	<0.01
E, A, T	−180	17	393	137	<0.01
T, A	−184	16	400	144	<0.01
E, S	−202	5	414	158	<0.01
T, E	−197	13	420	164	<0.01
T	−202	12	428	172	<0.01
S	−214	4	436	180	<0.01
E, A	−337	6	686	430	<0.01
A	−354	5	718	462	<0.01
E	−386	2	776	520	<0.01

[a] Refer to Table 6 for covariates included in each variable class.

[b] Accepted model for sage-grouse winter habitat selection.

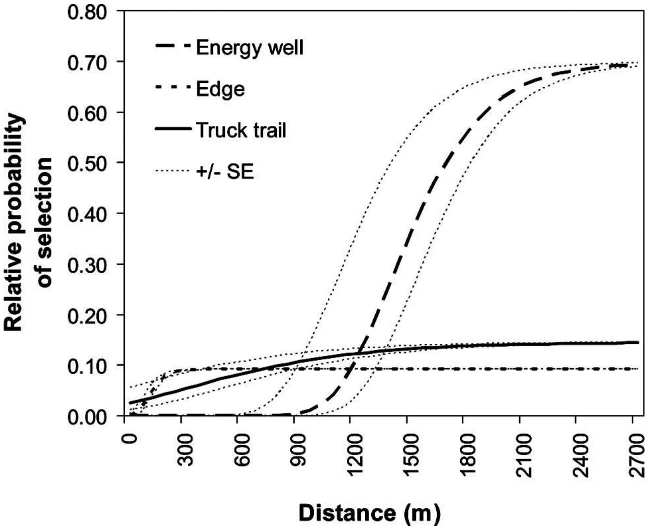

Figure 2. Predicted probability of selection by greater sage-grouse in Alberta, Canada, 2002–2004, as determined by a resource selection function. We calculated relative probabilities at different distances for 2-track truck trail, energy well, and edge (*trail_dst500*, *well_dst250*, *edge_dst50*, respectively) while holding all other model variables constant at their mean values. Faint dashed lines represent relative probabilities calculated using plus or minus a standard error to the coefficient of the variable of interest (one of *trail_dst500*, *well_dst250*, or *edge_dst50*) and recalculating the predictions.

predicted that the relative probability of selection drops sharply when habitat is within 1,900 m of an energy well (Fig. 2) and not surprisingly, the closest distance any sage-grouse was located to a well during the study was 1,293 m. Although mean distance from a well was 8,802 m (95% CI, $8{,}589 \leq \bar{x} \leq 9{,}016$), in the third of the winter study area with the highest oil and gas activity (460 km^2), mean distance to a well was 1,034 m (95% CI, $1{,}008 \leq \bar{x} \leq 1{,}060$). Thus, avoidance of energy development by sage-grouse in Alberta resulted in substantial loss of functional habitat surrounding wells, similar to other life stages (Aldridge and Boyce 2007).

Aldridge and Boyce (2007) identify the potential importance of habitat connectivity between winter and other life stages (i.e., nest and brood). Despite year-round tracking efforts, the importance of habitat connectivity was difficult to assess. Although summer and winter habitats of some birds were adjacent or overlapping, other birds made seasonal movements of 40–50 km (C. L. Aldridge, Colorado State University, unpublished data). A limited number of tracking locations suggest birds make these long movements following the topography of large valleys, potentially tracking the distribution of sagebrush. However, data collected at more frequent intervals than we obtained during

Table 8. Estimated coefficients (β), standard errors, and 95% confidence intervals of covariates included in the accepted model for winter habitat selection by greater sage-grouse in Alberta, Canada, from 2002 to 2004. To characterize habitat availability, we weighted 5,000 random points by using importance weights such that the available sample was effectively 296 points.

Variable class	Variable[a]	β	SE	95% CI	
				Lower	Upper
Energy development	*well_dst250*	−173.96	119.69	−408.54	60.62
Sagebrush	*sbmean*	0.24	0.041	0.16	0.32
	sbmeansq	−0.0019	0.0005	−0.0029	−0.0009
	sb_prop_patch2	1.74	0.82	0.14	3.34
Anthropogenic features	*edge_dst50*	−5.86	2.43	−10.62	−1.099
	water_dst50	−2.039	0.73	−3.48	−0.60
	imped_den	0.70	0.28	0.15	1.26
	trail_dst500	−1.65	0.77	−3.16	−0.14
Terrain and vegetation	*brit_30*	−0.026	0.0082	−0.042	−0.0097
	wet_30m	0.10	0.022	0.059	0.15
	sd_ndvi	15.84	7.90	0.35	31.32
	cti_sd	1.034	0.49	0.079	1.99
	tri_km^2	−1.63	0.30	−2.21	−1.035
	pec1	4.39	2.58	−0.67	9.45
	pec2	−0.72	2.69	−6.00	4.56
	pec3	−1.9664	2.4341	−6.7371	2.8043
	pec4	−2.3040	2.4912	−7.1867	2.5786
	pec5	−1.2870	2.5303	−6.2463	3.6723
	pec6	−3.9847	2.7289	−9.3332	1.3637

[a] Refer to Table 1 for variable descriptions.

our study, possibly with Global Positioning System technologies, are needed to confirm these movements and to assess how birds travel through disturbed landscapes to reach suitable winter habitats. Threats such as oil and gas development or cultivation of native habitats could reduce connectivity and disrupt migratory patterns, possibly causing bottlenecks between seasonal ranges or populations.

Sage-grouse congregate into groups of varying size during winter. We located a flock estimated at 100 birds on one occasion in 2004. This flock represented a substantial proportion of the population in one location, because the Alberta population was estimated at between 288 and 427 birds during spring 2003 (Lungle and Pruss 2008). Of the validation locations, 72% occurred in the 2 highest RSF bins, which represents just 13% of our study area. Beck (1977) also found winter habitat was limited in northern Colorado where 80% of winter sites used by sage-grouse occurred in <7% of the total area of sagebrush. Because winter habitats are limited in Alberta, comprehensive management strategies to maintain suitable habitats across all seasons are required, particularly because sage-grouse avoid energy development in otherwise suitable winter habitats.

MANAGEMENT IMPLICATIONS

Sound management planning requires an understanding of habitat selection at large scales, identifying where priority habitats are located and determining how species respond to relevant disturbances. Our model for sage-grouse winter habitats in Alberta provides one step toward meeting this management challenge. Given the endangered status of sage-grouse in Canada, any loss of crucial winter habitats could be detrimental to population persistence (Beck 1977, Swenson et al. 1987). We recommend that areas identified as crucial to meeting winter habitat needs of sage-grouse be protected from disturbance and degradation and designated as Critical Habitat under the Canadian Species at Risk Act (Species at Risk Act 2002). Moreover, we recommend a setback distance of $\geq$1,900 m for any energy development from all winter habitats identified as Critical Habitat based on our model. Mitigation of disturbances that negatively affect sage-grouse winter habitat quality (energy and anthropogenic development) could be applied in key sagebrush habitats to enhance critical winter habitats for sage-grouse.

Although much past management for prairie grouse has focused around lek sites (Aldridge and Boyce 2007), modeling approaches such as applied here permit more comprehensive conservation planning. Considering spatially explicit models for sage-grouse nest, brood, and wintering habitats, combined with knowledge of lek locations, bird movements, and habitat connectivity, provide a biological foundation for development of an effective conservation strategy for sage-grouse.

ACKNOWLEDGMENTS

We thank landowners who allowed us to conduct research on their lands. This research was supported financially, logistically, or both by Alberta Conservation Association, Alberta Sport Recreation Parks and Wildlife Foundation, Alberta Sustainable Resource Development, Cactus Communications (Medicine Hat, Alberta), Challenge Grants in Biodiversity, Endangered Species Recovery Fund (World Wildlife Fund Canada and the Canadian Wildlife Service), Esso Imperial Oil (Manyberries Alberta), Murray Chevrolet (Medicine Hat, Alberta), the North American Waterfowl Management Plan, and the University of Alberta. C. L. Aldridge was supported by Andrew Stewart Memorial Graduate Prize, Bill Shostak Wildlife Award, Dorothy J. Killam Memorial Graduate Prize, Edmonton Bird Club Scholarship, Izaak Walton Killam Memorial Scholarship, John and Patricia Schlosser Environment Scholarship, Macnaughton Conservation Scholarship, and a Natural Science and Engineering Research Council Scholarship. C. C. Nielsen and H. L. Beyer provided GIS assistance. R. Penniket, R. McNeil, B. W. Adams, L. Robinson, A. Buhlmann, and D. Eslinger assisted with data compilation and logistics. We thank P. Jones and J. Nicholson for assistance with many aspects of this project. M. Swystun, J. Sanders, and C. Peters assisted with field data collection.

LITERATURE CITED

Adams, B. W., L. Poulin-Klein, D. Moisey, and R. L. McNeil. 2005. Rangeland plant communities and range health assessment guidelines for the dry mixed grass natural subregion of Alberta. Publication Number T/040, Rangeland Management Branch, Public Lands Division, Alberta Sustainable Resource Development, Lethbridge, Alberta, Canada.

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.

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

Beck, T. D. 1977. Sage-grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18–26.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

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.

Committee on the Status of Endangered Wildlife in Canada. 2004. Canadian Species at Risk, November 2004. Committee on the Status of Endangered Wildlife in Canada. <http://www.cosewic.gc.ca/eng/sct0/sar_2004_11_e.cfm>. Accessed 1 Jun 2009.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

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. <http://sagemap.wr.usgs.gov/ConservationAssessment.aspx>. Accessed 1 Jun 2009.

Connelly, J. W., K. P. Reese, M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station; Moscow, Idaho Station Bulletin 80:1–54.

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

Coupland, R. T. 1961. A reconsideration of grassland classification in the northern Great Plains of North-America. Journal of Ecology 49:135–167.

Crawford, J. A., R. A. Olsen, 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.

Crist, E. P., and R. C. Cicone. 1984. Application of the tasselled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing 50:343–352.

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

Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. Journal of Wildlife Management 36:141–146.

Environment Canada. 2009. Climate data online. <http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html>. Accessed 1 Jun 2009.

Evans, J. 2004. Compound topographic index, AML script. ESRI Support Center Downloads. ESRI, Redlands, California, USA. <http://arcscripts.esri.com/details.asp?dbid=11863>. Accessed 1 Feb 2008.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13(Supplement 1):43–50.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Jones, P. F., R. Penniket, L. Fent, J. Nicholson, and B. Adams. 2005. Silver sagebrush community associations in southeastern Alberta, Canada. Rangeland Ecology and Management 58:400–405.

Lungle, K., and S. Pruss. 2008. Recovery strategy for the greater sage-grouse (*Centrocercus urophasianus urophasianus*) in Canada. Species at risk act recovery strategy series. Parks Canada Agency, Ottawa, Ontario, Canada.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variance in annual survival of female greater sage-grouse in north-central Montana. Ecological Applications 16:1529–1538.

Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. Journal of Conservation Planning 5:38–60.

Riley, S. J., S. D. Degloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.

Sauls, H. S. 2006. The role of selective foraging and cecal microflora in sage-grouse nutritional ecology. Thesis, University of Montana, Missoula, USA.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367–374.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnel, J. W. Connelly, P. A. Diebert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, and C. W. McCarthy. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Schroeder, M. A., and C. E. Braun. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378–385.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing 6:1335–1372.

Species at Risk Act. 2002. Statutes of Canada, Canada Gazette Part III 25:3 Chapter 29. Her Majesty the Queen in Right of Canada. <http://www.sararegistry.gc.ca/approach/act/default_e.cfm>. Accessed 1 Jun 2009.

StataCorp. 2007. Stata statistical software: release 10 user's manual. StataCrop LP, College Station, Texas, USA.

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.

Associate Editor: Twedt.