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Habitat Relations

Crucial Nesting Habitat for Gunnison Sage-Grouse: A Spatially Explicit Hierarchical Approach

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ABSTRACT Gunnison sage-grouse (*Centrocercus minimus*) is a species of special concern and is currently considered a candidate species under Endangered Species Act. Careful management is therefore required to ensure that suitable habitat is maintained, particularly because much of the species' current distribution is faced with exurban development pressures. We assessed hierarchical nest site selection patterns of Gunnison sage-grouse inhabiting the western portion of the Gunnison Basin, Colorado, USA, at multiple spatial scales, using logistic regression-based resource selection functions. Models were selected using Akaike Information Criterion corrected for small sample sizes (AIC_c) and predictive surfaces were generated using model averaged relative probabilities. Landscape-scale factors that had the most influence on nest site selection included the proportion of sagebrush cover >5%, mean productivity, and density of 2 wheel-drive roads. The landscape-scale predictive surface captured 97% of known Gunnison sage-grouse nests within the top 5 of 10 prediction bins, implicating 57% of the basin as crucial nesting habitat. Crucial habitat identified by the landscape model was used to define the extent for patch-scale modeling efforts. Patch-scale variables that had the greatest influence on nest site selection were the proportion of big sagebrush cover >10%, distance to residential development, distance to high volume paved roads, and mean productivity. This model accurately predicted independent nest locations. The unique hierarchical structure of our models more accurately captures the nested nature of habitat selection, and allowed for increased discrimination within larger landscapes of suitable habitat. We extrapolated the landscape-scale model to the entire Gunnison Basin because of conservation concerns for this species. We believe this predictive surface is a valuable tool which can be incorporated into land use and conservation planning as well the assessment of future land-use scenarios. © 2011 The Wildlife Society.

KEY WORDS *Centrocercus minimus*, Colorado, extrapolation, Gunnison sage-grouse, habitat, hierarchical model, nesting, resource selection, sagebrush.

To properly manage habitats for wildlife species of concern, knowledge about resource requirements is necessary. This information can inform management activities, lead to the provision of suitable habitat across life stages, and ensure long-term persistence for the species (Boyce and McDonald 1999, Morrison 2001, Aldridge and Boyce 2007). Although the abundance of high quality habitats is essential for species persistence, increasingly, the spatial distribution of those resources and continued disturbance from anthropogenic developments have been recognized as important drivers affecting habitat quality (Bock and Jones 2004, Doherty et al. 2008), animal fitness (Aldridge and Boyce 2007), and population persistence (Akcakaya et al. 2004, Haines et al. 2006). Characterizing the response of animals to anthropogenic disturbances (i.e., behavioral avoidance), and resultant effects (direct or indirect) on fitness components within a spatial framework, ultimately affords one the ability to model and map critical habitat requirements (see Aldridge and Boyce 2007). Maps based on models developed from empirical data assessing wildlife-habitat associations can provide managers with the tools necessary to make informed management decisions about where and what types of

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management actions (i.e., protection, enhancement, or rehabilitation) might be required (Haines et al. 2006, Aldridge and Boyce 2007).

Capturing the correct spatial and temporal scales at which organisms operate has been recognized as one of the fundamental problems in ecology (Johnson 1980, Morris 1987, Levin 1992). The need to embrace and understand the influence of spatial scale (grain and extent) on habitat selection is central to understanding habitat requirements for species (Wiens 1989; Orians and Wittenberger 1991; Boyce 2006; Aldridge and Boyce 2007, 2008). Intuitively, selection is hierarchical (Rettie and Messier 2000), as originally proposed by Johnson (1980), when he described the concepts of nested orders of selection. Here, we define hierarchical selection as the processes where finer-scale (referring to extent only) habitat selection (i.e., nest or den site selection) occurs within the context of a priori selection for landscape-scale resources (i.e., annual or lifetime home range selection). Although hierarchical selection has rarely been assessed (but see Harvey and Weatherhead 2006), it is recognized as a potentially important constraint that should be considered with habitat selection assessments (Johnson 1980, Rettie and Messier 2000, Mayor et al. 2009).

Gunnison sage-grouse (*Centrocercus minimus*) is considered a species of special concern in Colorado and a sensitive species in Utah, the only 2 states where the species occurs. The International Union for Conservation of Nature (IUCN) includes the Gunnison sage-grouse on their Red List, considering the species endangered (IUCN 2010). Approximately 4,023 birds remain across 7 populations, with approximately 87% residing within the Gunnison Basin population (Fig. 1; A. Pfister, U.S. Fish and Wildlife Service, personal communication). Continued loss and fragmentation of sagebrush habitat from urban development and associated infrastructure, as well as direct conversion of habitats, threatens populations and limits connectivity (Oyler-McCance et al. 2001, Gunnison Sage-grouse Rangewide Steering Committee [GSGRSC] 2005). Human populations within the Gunnison Basin have been increasing since 1980, with projections estimating more than a 2-fold (2.3 times) increase in the number of people in the Gunnison River Basin by 2050 (Colorado Water Conservation Board 2009). Existing and future threats coupled with small and/or declining populations of Gunnison sage-grouse (GSGRSC 2005) contributed to the species being listed in September 2010, as a candidate species under the Endangered Species Act of 1973 (ESA; 65 Federal Register 82310).

Spatial models assessing habitat selection have been developed for greater sage-grouse (*C. urophasianus*; Doherty et al. 2008, Yost et al. 2008) and several studies have evaluated and identified the importance of selection at multiple spatial scales, across various life stages (Aldridge and Boyce 2007, 2008; Aldridge et al. 2008; Kolada et al. 2009; Carpenter et al. 2010; Doherty et al. 2010). To date, however, no spatial habitat assessments have been conducted for the closely related Gunnison sage-grouse, despite concern over the species' future viability. The goal of our study was to develop spatially explicit nesting habitat models for Gunnison sage-grouse. We define crucial habitat as resources necessary for the survival and long-term viability of Gunnison sage-grouse. Specifically, our objectives were to: 1) develop landscape models that identify crucial nesting habitat across large spatial extents; 2) develop patch models that, after being constrained by landscape-scale selection (objective 1), identify crucial nesting habitat patches within larger nesting areas; 3) spatially apply both models to our study area, allowing us to map crucial nesting habitat for Gunnison sage-grouse, integrating both landscape- and patch-level selection; 4) assess the predictive capacity of these models using independent data; and 5) apply the landscape model to a broader range extent within the Gunnison Basin and evaluate model generality using lek (communal breeding grounds) data and the potential to use these models for direct management and conservation purposes for this population, and the species in general.

STUDY AREA

The Gunnison Basin is a high-elevation valley on the eastern edge of the Colorado Plateau. The study area was approximately 84,500 ha, of which, 49,200 ha (approx. 58%) were public lands. Elevation within the study area ranges from approximately 2,180 m to 3,100 m above sea level. The Gunnison Basin had an average annual temperature of 3.1° C and an average annual precipitation of 27 cm. Gunnison sage-grouse range within the Gunnison Basin was estimated at 240,000 ha, of which 70% were public lands (GSGRSC 2005). Gunnison sage-grouse nest location data were collected in the western portion of the Gunnison Basin, focused on the Curecanti National Recreation Area managed by the National Park Service (NPS), and its surrounding area (Fig. 1).

Sagebrush-steppe was prevalent throughout the basin, with big sagebrush (*Artemisia tridentata*) dominant. Intermixed within the sagebrush community were riparian areas and drainages containing Narrowleaf Cottonwood (*Populus angustifolia*), juniper (*Juniperous scopulorum*), gamble oak (*Quercus gambelii*), serviceberry (*Amelanchier alnifolia*), and wild rose (*Rosa woodsii*). Most of the valley bottoms along major drainages had been converted to hay and pastureland. Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea spp.*), and aspen (*Populus tremuloides*) forests were found at higher elevations.

METHODS

Field Sampling

We used spotlighting techniques (Giesen et al. 1982) to capture female Gunnison sage-grouse from 7 of 10 known active leks within the study area from 2000 to 2009. We fit captured hens with a necklace-style radio transmitter (RI-2BM, Holohil Systems, Carp, Ontario, Canada; A4050, Advanced Telemetry Systems, Isanti, MN) and tracked the hens throughout the breeding season using radio telemetry to identify nesting locations. We estimated nest

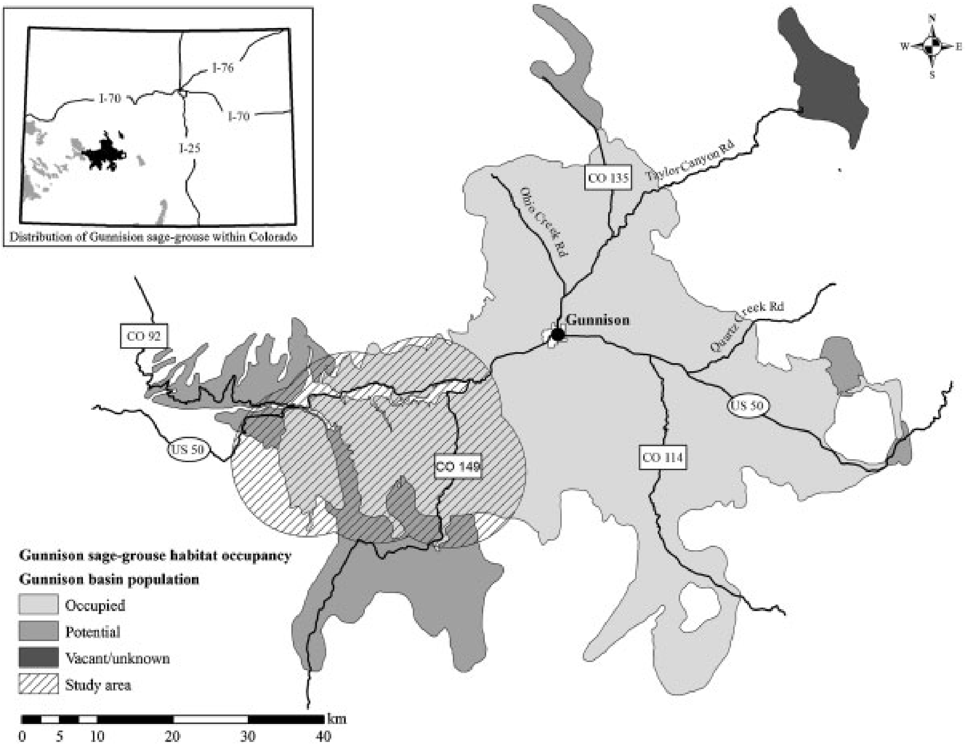

Figure 1. Study area located in the western portion of the Gunnison Basin, Colorado. Inset figure shows the distribution of Gunnison sage-grouse within Colorado as of 2005, with the Gunnison Basin population highlighted (black).

locations using triangulation vectors processed using LOCATE II (Locate II Version 1.82, http://nsac.ca/envsci/staff/vnams/Locate.htm, accessed 14 Feb 2001). We checked nest status regularly (minimum twice per week) via telemetry from an inconspicuously marked location (rock cairn or similar natural marker) ≥20 m from the estimated nest location. Once the nest was vacated, we recorded the Global Position System (GPS) coordinates of the nest site. We post-processed locations using Trimble Pathfinder Office software (Trimble Navigation Limited, Sunnyvale, CA) to increase spatial location accuracy (approx. 0.5 m). All animal handling methods and protocols were approved by the U.S. Geological Survey (USGS) Fort Collins Science Center's Institutional Animal Care and Use Committee.

Spatial Predictor Variables

We developed spatial variables thought to be important predictors of Gunnison sage-grouse nest site selection, based on resource selection studies for greater sage-grouse, and to a lesser extent, for Gunnison sage-grouse. We grouped these variables into 8 categories, 1) shrub, 2) other vegetation, 3) conifer, 4) terrain, 5) residential, 6) roads, 7) water, and 8) vegetation indices, which are detailed below. Greater sage-grouse select habitat across spatial scales (Aldridge and Boyce 2007, 2008; Doherty et al. 2008, 2010) and recent research has shown that anthropogenic disturbances can affect greater sage-grouse habitat selection (Aldridge and Boyce 2007; Doherty et al. 2008, 2010), lek dynamics (Walker et al. 2007, Holloran and Anderson 2005, Harju et al. 2010), individual movements and nesting activities (Lyon and Anderson 2003, Holloran et al. 2010), and fitness components (Aldridge and Boyce 2007, Holloran et al. 2010), all of which occur at varying spatial extents. Thus, we evaluated spatial variables affecting Gunnison sage-grouse nest site selection over 6 different spatial circular moving window sizes, all of which had some support within the sage-grouse literature. Landscape scales included the window extents of 1-km, 1.5-km, 3-km, and 6.4-km radii (see Table S1, available online at www.onlinelibrary.wiley.com). For patch models, we assessed metrics across 2 window extents; 0.045-km and 0.564-km radii, as well as at the pixel level for some variables (30 m; Table S1). In this case, a moving window is a geospatial calculation where the value of a given pixel is generated based on the values of all surrounding pixels within a specified spatial extent.

We derived shrub variables from recently developed spatial products estimating the percent cover of shrubs (all species), sagebrush (*Artemisia* spp.; all species combined), all big sagebrush (all subspecies combined), and Wyoming sagebrush (*A. t. wyomingensis*; see Homer et al. 2008, 2012). Importantly, these cover estimates are not directly proportional to typical vegetation cover estimates measured at much smaller spatial scales using quadrats or measuring tapes on the ground (see Homer et al. 2008, 2012). From these products, we calculated the mean estimated percent cover and the standard deviation (SD) over all window extents. We used SD as a surrogate for habitat heterogeneity. We also calculated the proportion of each window that was estimated to have 1–5%, 6–10%, 11–15%, 16–20%, and 21–25% cover, as well as greater than 5%, 10%, 15%, or 20% cover for each shrub variable. The category break points align with the estimated error associated with the original mapping products (approx. 5%; Homer et al. 2008, 2012). We also calculated the mean estimated percent cover and associated SD of bare ground, herbaceous vegetation, litter, and shrub height (Homer et al. 2008, 2012) over all window extents (Table S1).

We also calculated the mean and associated SDs across window scales for some terrain and vegetation indices variables. Terrain variables included Compound Topographic Index (CTI) and Terrain Ruggedness Index (TRI). The CTI is a function of both slope and upstream contributing area and can be used as a surrogate for soil moisture and vegetation productivity (Gessler et al. 1995). We based our TRI on the vector ruggedness measure (VRM) developed by Sappington et al. (2007). Low ruggedness values indicate flat areas (low slope), moderate values reflect steep but even terrain (high slope, low ruggedness), and high ruggedness values indentify areas that are steep and uneven (high ruggedness). Computational complexities prevented generation of these variables at some larger scales (see Table S1). We only assessed SD (heterogeneity) for CTI, given that TRI directly models terrain heterogeneity. We assessed vegetation indices over all scales including brightness, greenness, wetness, and Normalized Difference Vegetation Index (NDVI) indices using a tasseled cap transformation (see Table S1).

We calculated density and distance metrics for a number of potentially important drivers of Gunnison sage-grouse habitat use. We used Landfire products (Landfire 2006, Version LF_1.1.0, http://www.landfire.gov/, accessed 02 Oct 2009) to assess potential influence of conifer habitats on nesting habitat selection. We derived the density of conifer and conifer with pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) classed habitats over the suite of moving windows. Similarly, we developed density metrics across all scales to assess the influence of residential development on habitat selection and understand the scale of the effect. We defined residential development as all areas within the Gunnison town site boundaries, subdivisions identified by Gunnison County, any home site visible from 2005 National Agriculture Imagery Program (NAIP) imagery, or any other visible development (2005 NAIP 1-m imagery) occurring outside subdivision boundaries but where the county had recorded address locations. We modified address points manually to align with observed developments on the NAIP imagery and then buffered by 0.075 km. Finally, we developed road density (linear km/km^2) estimates across all spatial window extents (Table S1). We used a recently developed Bureau of Land Management (BLM) road classification based on 2005 NAIP, aided by local knowledge of road use. Road products were collaboratively developed by BLM, U.S. Forest Service, NPS, Gunnison County, and USGS across the Gunnison sage-grouse range within the Gunnison Basin.

We assessed selection in relation to proximity of conifer, roads, residential habitat, and water using straight line (Euclidean) distance, as well as quadratic terms and exponential decays as a function of Euclidean distance (Nielsen et al. 2009) to assess nonlinearities. We developed 5 decay variables using the form $e^{-d/\alpha}$ where d was the distance in meters from each pixel to a landscape feature, and α was set at 50, 100, 250, 500, and 1,000. This scaled each distance variable between 0 and 1, with highest values close to the feature of interest, capturing potential nonlinear responses from birds to a given landscape factor as the distance from that feature increases. We considered distance metrics in both landscape- and patch-scale models (see Table S1 for a complete list of the variables assessed).

Model Development

We assessed nest site selection hierarchically, first developing a landscape model using information from across the study area, and then assessing patch selection by restricting availability of resources using a threshold defined by the landscape model predictive surface, identifying habitats available for selection at the patch scale. We developed resource selection function (RSF; Manly et al. 2002) models using logistic regression (Hosmer and Lemeshow 2000) to characterize nesting habitat for Gunnison sage-grouse. We generated random locations across our study area at a density of 5 per km^2 ($n = 3{,}392$) to represent the variation in habitat availability, and compared these with nest locations to produce what we termed our landscape models. We did not consider the Blue Mesa Reservoir as available habitat and restricted available habitat (and thus model prediction space) to the distribution of spatial data from all sources. For instance, the sagebrush map products in this area were not developed above 3,100 m elevation (see Homer et al. 2012) and we did not consider these areas. Since models were heavily biased toward the larger sample of available resource units, we used an importance weight that gave full weighting to used resource units but down weighted available resource units proportional to the ratio of sampled points to available points (STATACORP 2007, Aldridge and Boyce 2007). Model structure followed the form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots \beta_k x_k)$$

where $w(x)$ is the relative probability of selection for the predictor variables, x_i, and β_i's are the coefficient estimate for each predictor variable ($1 \ldots k$).

We defined availability for the patch model by a threshold classification (geometric binning) from the landscape model defining crucial nesting areas for Gunnison sage-grouse. We based this classification on a threshold that maximized the inclusion of nest locations. We used a subset of the landscape-scale available points reflecting the reduction in spatial extent for patch-scale modeling. We developed landscape models first and subsequently developed patch models. We felt it was inappropriate to assess individual variables without some a priori consideration of habitat, given the species' affinity for sagebrush. Therefore, we initially assessed shrub metrics (i.e., shrub or sagebrush cover, etc.) as individual predictors of Gunnison sage-grouse nest occurrence for both landscape and patch models. When graphical inspection of data indicated a nonlinear variable form would more accurately represent the data, we assessed both linear and quadratic forms. We also evaluated whether the inclusion of the SD of the same spatial extent window explained additional variation. The most predictive metric (form and window extent) based on Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) was carried forward as the base model and was maintained throughout the assessment of other variables and candidate models at each scale.

Variable selection.—The number of variables considered for inclusion in models predicting the occurrence of Gunnison sage-grouse nests was large (see Table S1). To ensure balanced participation by variables belonging to each category, we first assessed variables within a category. We only considered the top performing variable(s) from each category for the development of the final candidate set of models. We evaluated each variable in combination with the shrub base using AIC_c. Within each category, we identified the most predictive window extent and form of each variable type (i.e., distance or density), as described above. If more than 1 variable was selected from a category, we again assessed variables for correlation (Pearson's $r > |0.7|$) to prevent multicollinearity issues (Aldridge and Boyce 2007). When correlated, variables carried forward had the lowest AIC_c score (most predictive) and intuitive biological interpretation. We compared the change in AIC_c from the base shrub model to each simple model (variable of interest plus base) to assess the relative contribution for each variable. We carried forward selected variables (extent and form) from each category to develop a final candidate set of models. Because of small sample sizes, we limited candidate models to 7 variables, or roughly 1 variable per 10 observations (Hosmer and Lemeshow 2000). All possible combinations of uncorrelated variables that met this criterion were included in the final candidate set of models. We ranked candidate models based on the difference in AIC_c values ($\Delta\ AIC_c$) and we used Akaike weights (w_i) to assess the strength of evidence that a particular model was the best of those in the candidate set. We repeated this process for patch models. We conducted all analyses in STATA 10.1 (STATACORP 2007).

Multi-model inference and spatial prediction.—At both the landscape and patch scales, we model averaged over the 90% confidence set to produce more robust spatial predictions and strengthen inference (Burnham and Anderson 2002). The estimated relative probabilities generated by individual models were scaled between 0 and 1 incorporating the estimated β_0. We re-calculated weights to sum to 1 for models within the 90% confidence set, and applied these adjusted weights to spatial predictions for each model, because model weights (w_i) apply to models as a whole, not their individual components (Candolo et al. 2003, Murray and Conner 2009). We added weighted predictions together in a Geographic Information System (GIS) to produce the final model averaged relative probability surface.

Greater sage-grouse nest-site selection is influenced by both landscape- and patch-level factors (Aldridge and Boyce 2007). To capture this for Gunnison sage-grouse, we multiplied the model averaged continuous relative probability surfaces for patch and landscape scales within the NPS study area, but also provide individual surfaces for visual assessment. We geometrically binned all surfaces for display purposes and to allow for summarization of classified habitats.

Model Assessment and Generalization

Model evaluation.—Various approaches have been suggested for evaluating RSFs (see Johnson et al. 2006 for a review), but most necessitate subjective binning of the RSF predictions. We used Kendall's *c* (Harrell et al. 1996) to describe the probability of concordance between model predictions (RSF relative probabilities) and observed data (nest and available locations; Harrell et al. 1996, Harrell 2001), preventing the need to bin data. In our case, Kendall's *c* is an assessment of a model's ability to discriminate between selected nest site locations and available habitats (Newson 2006). We consider probabilities of concordance >0.9 to be excellent, 0.8–0.9 to be good, and 0.7–0.8 to be fair. We assessed model discrimination for both training and testing nest datasets, contrasting nests against the available dataset used to build models, and did so for each modeling scale (patch and landscape). Using the geometric binning process described for the landscape model above, we summarized the proportion of nests that would be captured and the landscape that would be implicated with a given threshold. We followed a similar summary approach for the patch model.

Model generalization.—Since we did not have nest locations basin-wide, we used all known active lek locations in 2007 (Colorado Division of Wildlife, unpublished data) to evaluate the extrapolated landscape-scale model. Lek sites are centers of breeding activities, and their status and population demography are linked to proximity of high-quality nesting habitat (Holloran and Anderson 2005, Doherty et al. 2010). Lek location is strongly influenced by the amount of and proximity to quality nesting habitat (Connelly et al. 2000). If the landscape model is predictive, lek locations should have higher than average predicted nest occurrence, capturing nesting habitat surrounding the lek (landscape variables ranged in scale from 1- to 6.4-km radii windows). We used Kendall's *c* to assess how well our landscape model could predict lek locations, contrasting lek locations to a sample of available locations from across the Gunnison Basin.

Threshold response.—We assessed nesting habitat selection responses relative to changes in sagebrush habitat and key anthropogenic variables, by plotting the model averaged nest occurrence probabilities against the variable of interest. We calculated the mean probability of occurrence across intervals of the identified predictor variables to summarize predictions for all pixels in the landscape (see Hanser et al. 2011). We developed threshold response curves for landscape-scale crucial nest areas across the range of values available throughout the NPS study area, and assessed the patch-scale crucial nesting model within the modified patch-scale study extent.

Table 1. A comparison of variables that were carried forward to model the occurrence of Gunnison sage-grouse nests (2006–2009; $n = 73$) in the Gunnison Basin, Colorado at either the landscape or patch scale. We evaluated variables with the top shrub variable at each scale (landscape or patch base models). K indicates the number of parameters in the model (including the shrub base model). Δ Base indicates the change in Akaike Information Criterion corrected for small sample size (AIC_c) value from either the landscape or patch base.

Category	Variable	Definition	Variable structure	K	AIC_c	Δ Base
Landscape variables—null model $AIC_c = 204.393$						
Shrub	pg_e_sg_gt5	Proportion of pixels with >5% sagebrush cover across 1.5-km radius window	pg_e_sg_gt5	2	159.822	0.000
Other veg	bare_cm and bare_cs	Mean % bara ground (quadratic) across 1-km radius window and standard deviation	bare_cm + (bare_cm)^2 + bare_cs	5	150.391	−9.431
	herb_fm	Mean % herbaceous vegetation (quadratic) across a 6.4-km radius window	herb_fm + (herb_fm)^2	4	153.939	−5.883
	litter_fm and litter_fs	Mean % litter (quadratic) across 6.4-km radius window and standard deviation	litter_fm + (litter_fm)^2 + litter_fs	5	153.014	−6.808
NDVI[a]	ndvi_cm and ndvi_cs	Mean NDVI across 1-km radius window and standard deviation	ndvi_cm + ndvi_cs	4	152.538	−7.284
Terrain	cti_cm	Mean compound topographic index across 1-km radius window	cti_cm	3	137.001	−22.821
Roads	f_rd1_4	Linear density (km/ km^2) of roads classed 1–4 within a 6.4-km radius window. BLM[b] classification: 1 = primary paved highway, 2 = secondary paved highway, 3 = light duty road, constructed and regularly maintained, 4 = primitive road, sedan clearance, not regularly maintained	f_rd1_4	3	133.933	−25.889
	dist_rd1_2	Euclidian distance (km) to any road class 1 or 2. BLM classification: 1 = primary paved highway, 2 = secondary paved highway	dist_rd1_2	3	138.442	−21.380
Residential	dist_res	Euclidian distance (km) to residential development (quadratic)	dist_res + (dist_res)^2	4	150.682	−9.140
	p_res_e	Proportion of residential classed habitat within a 1.5-km radius window	p_res_e	3	148.489	−11.333
Conifer	cj_d100	Decay function of influence of conifer-pinyon juniper classed habitat, decay set at 100 m	cj_d100	3	146.683	−13.139
Water	dist_water	Euclidian distance (km) to water (quadratic)	dist_water + (dist_water)^2	4	152.724	−7.098
Patch variables—null model $AIC_c = 204.398$						
Shrub	pg_b_bs_gt10	Proportion of pixels with >10% big sagebrush (quadratic) across a 0.56-km radius window	pg_b_bs_gt10 + (pg_b_bs_gt10)^2	3	179.397	0.000
Other veg	bare_am	Mean % bare ground (quadratic) across a 3 × 3 30-m cells window	bare_am + (bare_am)^2	5	177.896	−1.501
	herb_bm and herb_bs	Mean % herbaceous vegetation (quadratic) across a 0.56-km radius window and standard deviation	herb_bm + (herb_bm)^2 + herb_bs	6	176.784	−2.613
	litter_am	Mean % litter across a 3 × 3 30-m cells window	litter_am	4	179.981	0.584
	shrbh_am	Mean shrub height across 3 × 3 30-m cells window	shrbh_am	4	181.458	2.061
NDVI	ndvi_am	Mean NDVI (quadratic) across a 3 × 3 30-m cells window	ndvi_am + (ndvi_am)^2	5	171.443	−7.954
Terrain	cti_bm	Mean compound topographic index value across 0.56-km radius window	cti_bm	4	168.263	−11.134
	slope	Slope in percent—spatial analyst calculation, pixel value	slope	4	178.292	−1.105
Roads	b_allrd	Linear density (km/ km^2) of all roads within 0.56-km radius window	b_allrd	4	177.235	−2.162
	dist_rd1_2	Euclidian distance (km) to any road class 1 or 2. BLM classification: 1 = primary paved highway, 2 = secondary paved highway	dist_rd1_2	4	170.328	−9.069
Residential	dist_res	Euclidian distance (km) to residential development (quadratic)	dist_res + (dist_res)^2	5	171.287	−9.110
	p_res_b	The proportion of residential classed habitat within a 564-m radius moving window	p_res_b	4	180.792	1.395
Conifer	p_cj_b	Proportion of conifer/pinyon juniper habitat across 0.56-km radius window	p_cj_b	4	176.576	−2.821
Water	dist_water	Euclidian distance (km) to water (quadratic)	dist_water + (dist_water)^2	5	175.933	−3.464

[a] Normalized difference vegetation index.

[b] Bureau of Land Management.

RESULTS

We located 102 nests from 75 different individuals between 2000 and 2009 (mean 1.35 ± 0.58 SD nests per individual; range 1–3). Sample sizes were low during the early years of study. We used nests from 2006 to 2009 to develop nest habitat selection models (total $n = 73$; $2006 = 14$; $2007 = 21$; $2008 = 14$; $2009 = 24$). This sample included repeat nests from 15 females ($12 = 2$ nests, $3 = 3$ nests, $40 = 1$ nest), which captured expected female fidelity to nesting areas. We used 29 nests located in 2000–2005 for model evaluation.

The maximum distance a radio marked female traveled from the lek of capture to a nesting site was 10.1 km. We applied 10.1-km circular buffers around all capture leks within the study area to define available nesting habitat for marked females at the landscape scale (Fig. 1).

Landscape Models

After screening variables for form, extent, and correlations, we retained 15 variables (including SDs) across all categories for modeling nesting habitat at the landscape scale (Table 1). The proportion of a 1.5 km-radius moving window that contained sagebrush cover greater than 5% (pg_e_sg_gt5) was the top shrub predictor and used as the landscape base, with a ΔAIC_c from the null model of 44.571 (Table 1). We assessed variables in the remaining categories with the inclusion of the landscape base (Table 1). All shrub height variables were correlated with the landscape base and were not considered further. The most predictive variables (largest decrease in AIC_c from base; Table 1) included linear density of roads classes 1–4 within a 6.437-km radius (f_rd1_4), mean productivity within a 1-km radius (cti_cm), and Euclidian distance to nearest road classed 1 or 2 (dist_rd1_2). In combination with the landscape shrub base, each of these simple models had a decrease in AIC_c values from the base model of 25.889, 22.821, and 21.380, respectively.

We developed 344 candidate models (all subsets where $K \leq 7$) using the selected variables and assessed at the landscape scale. All w_i were low due to the number of models in the candidate set and the nested nature of models (Table 2). Thirty-five models were included in the landscape model 90% confidence set. These models had good fit to the data (likelihood-ratio [LR] χ^2 range = 90.80–106.39, Df = 3–7, $P < 0.001$). The model averaged standard errors suggest that Gunnison sage-grouse nests in the western portion of the Gunnison Basin are found in areas with a higher proportion of sagebrush cover greater than 5% (1.5-km radius), higher mean productivity within 1 km (CTI), lower road density (classes 1–4) within 6.4 km, are a moderate distance from water (quadratic function), and are further from conifer-juniper forest (0.1-km decay function; Table 3).

Landscape Model Evaluation

The model averaged surface validated well based on Kendall's c, with excellent ($c_{\text{train}} = 0.936$, CI: 0.912–0.956) and good ($c_{\text{test}} = 0.800$, CI: 0.720–0.881) probability of concordance between model predictions and observed nest or available locations ($\text{nests}_{\text{train}} = 73$; $\text{nests}_{\text{test}} = 29$, $n_{\text{available}} = 3{,}369$; Fig. 2). Of the 102 identified nests, 99 (97%) occurred within the top 5 landscape-scale habitat class bins (bins 6–10), with the 3 omitted nests belonging to the testing group. Bins 6–10 (RSF values >0.119) encompass approximately 57% of the NPS study area (Fig. 2). We considered habitat falling within these bins as crucial nesting areas based on the landscape model.

Generality of Landscape Model

We used all active lek locations as of 2007 that fell within the predictive surface ($n = 44$) to evaluate the predictive capacity

Table 2. A comparison of the top 10 landscape-scale habitat models used to characterize Gunnison sage-grouse nest occurrence (2006–2009; $n = 73$) in the Gunnison Basin, Colorado. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. Akaike weights (w_i) indicate the likelihood of the model being the best of those evaluated ($n = 344$). K indicates the number of parameters in the model. The top 35 models were included in the 90% confidence set and incorporated in the model averaging procedure.

Model	Model structure	K	AIC_c	ΔAIC_c	w_i	Rank
LAND1	pg_e_sg_gt5[a] + cti_cm[b] + p_res_e[c] + f_rd1_4[d] + litter_fm[e] + (litter_fm)^2 + litter_fs[f]	8	113.523	0.000	0.159	1
LAND2	pg_e_sg_gt5 + dist_water[g] + (dist_water)^2 + cti_cm + p_res_e + f_rd1_4 + cj_d100[h]	8	114.049	0.526	0.122	2
LAND3	pg_e_sg_gt5 + cti_cm + f_rd1_4 + cj_d100 + litter_fm + (litter_fm)^2 + litter_fs	8	114.311	0.788	0.107	3
LAND4	pg_e_sg_gt5 + cti_cm + p_res_e + f_rd1_4 + cj_d100	6	115.364	1.841	0.063	4
LAND5	pg_e_sg_gt5 + dist_water + (dist_water)^2 + cti_cm + p_res_e + f_rd1_4	7	115.861	2.338	0.049	5
LAND6	pg_e_sg_gt5 + dist_water + (dist_water)^2 + cti_cm + f_rd1_4 + cj_d100	7	115.936	2.413	0.047	6
LAND7	pg_e_sg_gt5 + p_res_e + f_rd1_4 + cj_d100 + litter_fm + (litter_fm)^2 + litter_fs	8	116.201	2.678	0.042	7
LAND8	pg_e_sg_gt5 + cti_cm + f_rd1_4 + litter_fm + (litter_fm)^2 + litter_fs	7	116.553	3.030	0.035	8
LAND9	pg_e_sg_gt5 + cti_cm + p_res_e + f_rd1_4 + dist_rd1_2[i] + cj_d100	7	117.380	3.857	0.023	9
LAND10	pg_e_sg_gt5 + cti_cm + p_res_e + f_rd1_4	5	117.595	4.073	0.021	10

[a] Proportion of pixels with >5% sagebrush cover across 1.5-km radius window.

[b] Mean compound topographic index (productivity) across 1-km radius window.

[c] Proportion of residential classed habitat within a 1.5-km radius window.

[d] Linear density (km/ km^2) of roads classed 1–4 within a 6.4-km radius window. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway, 3 = light duty road, constructed and regularly maintained, 4 = primitive road, sedan clearance, not regularly maintained.

[e] Mean % litter across a 6.4-km radius window.

[f] Standard deviation of mean % litter across a 6.4-km radius window.

[g] Euclidian distance (km) to water.

[h] Decay function of influence of conifer/pinyon juniper classed habitat, decay set at 100 m.

[i] Euclidian distance (km) to any road classed 1 or 2. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway.

Table 3. Model averaged coefficients (β) and standard errors (SE) associated with each variable represented in the 90% confidence set ($n = 35$) of landscape-scale models used to predict Gunnison sage-grouse nest occurrence (2006–2009; $n = 73$) across the western portion of the Gunnison Basin, Colorado. Note that the shrub variable (pg_e_sg_gt5) was included in all models.

Variable	Model averaged β	Model averaged SE	Confidence intervals	
			Lower	Upper
pg_e_sg_gt5[a]	47.265	18.483	11.039	83.491
cti_cm[b]	0.001	<0.001	<0.001	0.002
p_res_e[c]	−36.784	28.503	−92.651	19.083
f_rd1_4[d]	−10.590	3.143	−16.750	−4.430
litter_fm[e]	0.715	0.741	−0.738	2.168
(litter_fm)^2	−0.024	0.021	−0.064	0.017
litter_fs[f]	0.016	0.321	−0.613	0.645
dist_water[g]	1.152	0.519	0.134	2.170
(dist_water)^2	−0.473	0.230	−0.923	−0.023
cj_d100[h]	−1.648	0.789	−3.195	−0.101
dist_rd1_2[i]	−0.002	0.015	−0.031	0.027
ndvi_cm[j]	−0.398	0.321	−1.028	0.232
ndvi_cs[k]	0.016	0.353	−0.676	0.708
dist_res[l]	0.036	0.027	−0.017	0.089
(dist_res)^2	−0.006	0.005	−0.015	0.003
herb_fm[m]	0.014	0.025	−0.035	0.064
(herb_fm)^2	−0.001	0.001	−0.003	0.001

[a] Proportion of pixels with >5% sagebrush cover across 1.5-km radius window.

[b] Mean compound topographic index (productivity) over a 1-km radius window.

[c] Proportion of residential classed habitat within a 1.5-km radius window.

[d] Linear density (km/ km^2) of roads classed 1–4 within a 6.4-km radius window. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway, 3 = light duty road, constructed and regularly maintained, 4 = primitive road, sedan clearance, not regularly maintained.

[e] Mean % litter across a 6.4-km radius window.

[f] Standard deviation of % litter across a 6.4-km radius window.

[g] Euclidian distance (km) to water.

[h] Decay function of influence of conifer/pinyon juniper classed habitat, decay set at 100 m.

[i] Euclidian distance (km) to any road classed 1 or 2. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway.

[j] Mean normalized difference vegetation index (productivity) over a 1-km radius window.

[k] Standard deviation of the mean normalized difference vegetation index over a 1-km radius window.

[l] Straight line distance (km) to residential development.

[m] Mean % herbaceous cover over a 6.4-km radius window.

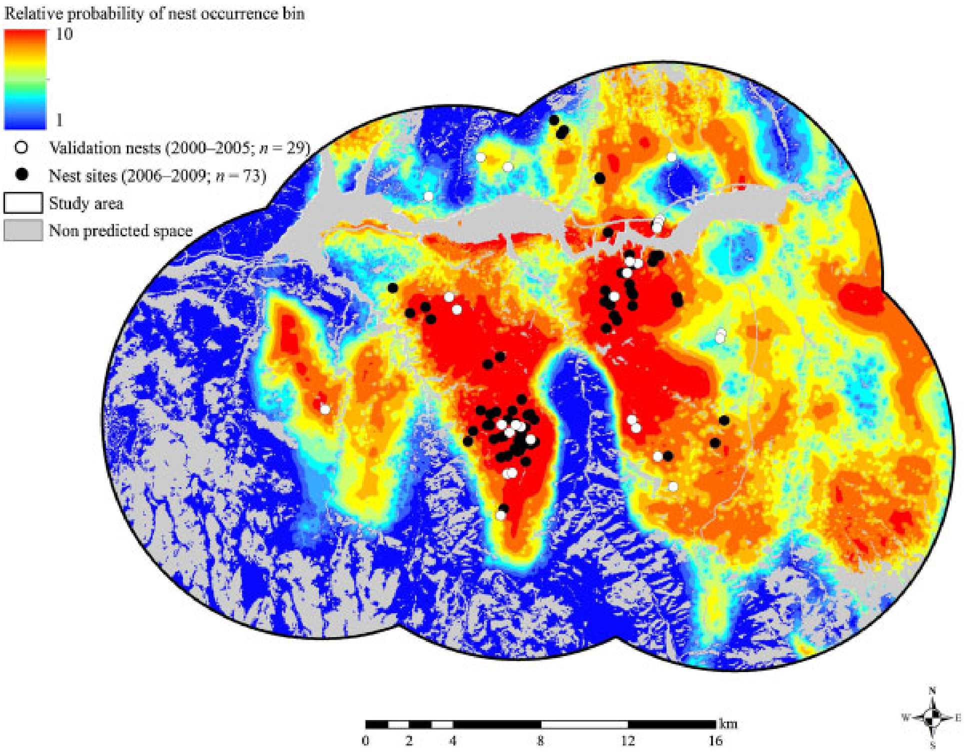

Figure 2. Model averaged relative probability surface predicting the crucial nest areas based on landscape-scale occurrence of Gunnison sage-grouse nest sites applied to the study area in the western portion of the Gunnison Basin, Colorado. We overlaid model development ($n = 73$) and model evaluation ($n = 29$) nest sites for comparison of model prediction.

of the landscape-scale model extrapolated to the entire Gunnison Basin. The model averaged surface applied across the entire basin had fair probability of concordance ($c_{\text{lek}} = 0.721$, CI: 0.642–0.800) between model predictions and observed lek or available locations ($n_{\text{leks}} = 44$; $n_{\text{available}} = 10{,}710$; Fig. 3). Of the 44 active leks identified within the basin, approximately 90% (40) occurred within bins 3–10, comprising approximately 62% of the landscape (Fig. 3).

Patch Scale Models

We defined availability for patch-scale models based on crucial nesting areas identified from the landscape-scale nesting model (bin 6 or greater). This left an area roughly half the size (approx. 36,380 ha) of the original study area considered to be available for patch models, subsequently reducing the number of available points to 1,870 for contrast against the 73 nest locations. After screening variables for form, extent, and correlations, we retained 15 variables (including SD) for patch modeling. The top AIC$_c$-selected shrub base variable was the quadratic form of the proportion of 0.564-km moving window that was classed as big sagebrush cover greater than 10%. This base model had a ΔAIC_c from the null model of -25.932. Other key predictor variables (largest decrease in AIC$_c$ from base; Table 1) considered in conjunction with the patch-scale shrub base were mean productivity over 0.564-km extent (cti_bm), Euclidean distance to residential classed habitat (dist_res, quadratic function), and Euclidian distance to nearest road classed 1 or 2 (dist_rd1_2). In combination with the patch shrub base, each of these simple models showed a decrease in AIC$_c$ values from the base model of 11.134, 9.110, and 9.069, respectively.

We evaluated 590 candidate models (all subsets $K \leq 7$) comprised of the selected variables with their forms and window scale extents maintained (Table 1; see Table 4 for the 10 most predictive models). Seventy-six models were included in the 90% confidence set and contributed to the model averaged surface. These models had good fit to the data (LR $\chi^2 = 47.65$–62.85, Df = 4–7, $P < 0.001$). The model averaged standard errors of variables contained within the patch scale models suggest that Gunnison sage-grouse nests are located in areas that have either lower or higher proportions (0.564-km moving window) of high big sagebrush cover (>10% big sagebrush cover; convex quadratic function), are a moderate distance from residential development and water sources (quadratic functions), are further from roads classed 1 or 2, and have higher vegetation productivity (ndvi_am and cti_bm; Table 5). Although the linear portion of the distance to residential development term had confidence intervals overlapping zero, a likelihood ratio test confirmed that the quadratic form of the variable was an important contributor determining Gunnison sage-grouse nest site selection (LR $\chi^2_2 = 12.87$, $P < 0.002$).

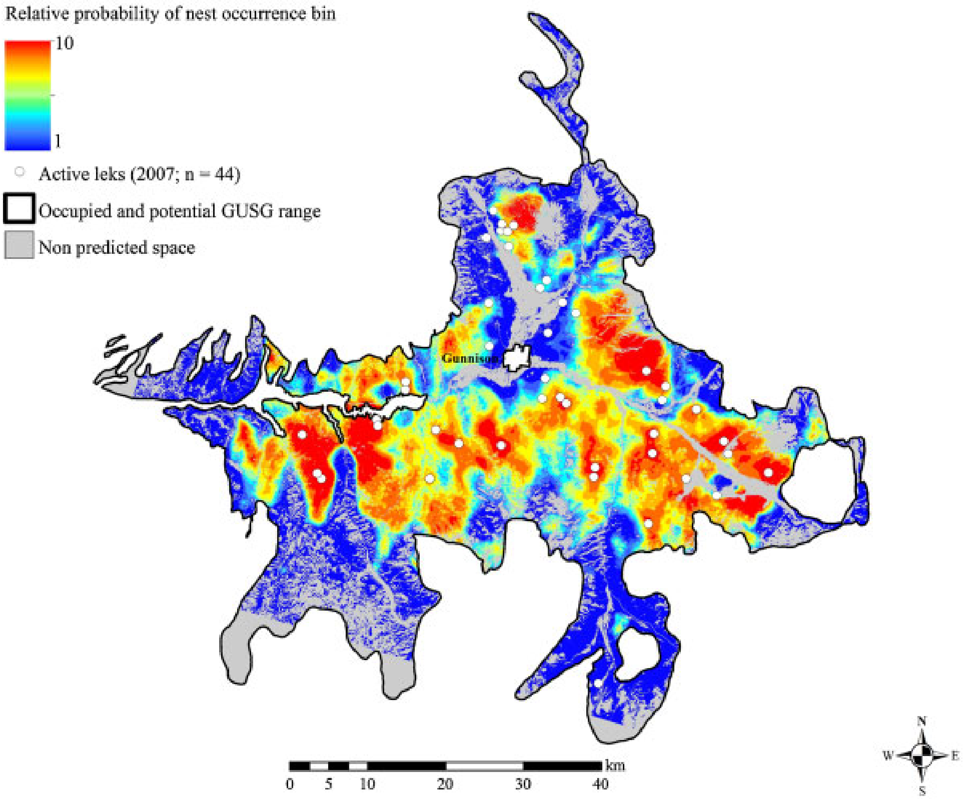

Figure 3. Relative probability of Gunnison sage-grouse (GUSG) nest occurrence predicted across all occupied and potential habitat within the Gunnison Basin. We developed the model using 73 nest locations collected from 2000 to 2005 within the western portion of the Gunnison Basin, Colorado. We used leks active in 2007 to test the generality of model predictions outside of the geographic space from where the model was developed, and show their locations for visual comparison. Non-predicted spaces are areas where model inputs were not available.

Table 4. A comparison of the top 10 patch-scale habitat models used to characterize Gunnison sage-grouse nest occurrence (2006–2009; $n = 73$) in the Gunnison Basin, Colorado. Models are ranked by the change in Akaike Information Criterion corrected for small sample size (ΔAIC_c) values. Akaike weights (w_i) indicate the likelihood of the model being the best of those evaluated ($n = 590$). K indicates the number of parameters in the model. The top 76 models were included in the 90% confidence set and were incorporated in the model averaging procedure.

Model	Model structure	K	AIC_c	ΔAIC_c	w_i	Rank
PATCH1	pg_b_bs_gt10[a] + (pg_b_bs_gt10)^2 + ndvi_am[b] + (ndvi_am)^2 + dist_res[c] + (dist_res)^2 + dist_rd1_2[d]	8	156.599	0.000	0.175	1
PATCH2	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + ndvi_am + (ndvi_am)^2 + cti_bm[e] + dist_res + (dist_res)^2	8	157.620	1.021	0.105	2
PATCH3	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + ndvi_am + (ndvi_am)^2 + cti_bm + dist_rd1_2	7	159.560	2.961	0.040	3
PATCH4	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + cti_bm + dist_res + (dist_res)^2 + dist_rd1_2	7	159.801	3.202	0.035	4
PATCH5	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + cti_bm + dist_res + (dist_res)^2 + dist_rd1_2 + p_cj_b[f]	8	159.981	3.382	0.032	5
PATCH6	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + dist_water[g] + (dist_water)^2 + ndvi_am + (ndvi_am)^2 + cti_bm	8	160.230	3.632	0.028	6
PATCH7	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + dist_res + (dist_res)^2 + dist_rd1_2 + p_cj_b	7	160.426	3.828	0.026	7
PATCH8	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + ndvi_am + (ndvi_am)^2 + cti_bm + dist_rd1_2 + p_cj_b	8	160.468	3.869	0.025	8
PATCH9	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + dist_water + (dist_water)^2 + dist_res + (dist_res)^2 + dist_rd1_2	8	161.025	4.427	0.019	9
PATCH10	pg_b_bs_gt10 + (pg_b_bs_gt10)^2 + ndvi_am + (ndvi_am)^2 + cti_bm + slope[h] + dist_rd1_2	8	161.201	4.602	0.018	10

[a] Proportion of pixels with >10% big sagebrush cover across 0.564-km radius window.

[b] Mean normalized difference vegetation index (productivity) over a 3 × 3 (30-m cells) window.

[c] Euclidian distance to residential classed habitat.

[d] Euclidian distance (km) to any road classed 1 or 2. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway.

[e] Mean compound topographic index (productivity) across a 0.564-km radius window.

[f] Proportion of pixels across a 0.564-km window classed as conifer/pinyon juniper habitat.

[g] Euclidian distance (km) to water.

[h] Slope in percent.

Patch Scale Model Evaluation

The model averaged surface validated well based on Kendall's c, with good ($c_{train} = 0.868$, CI: 0.822–0.913) and fair to good ($c_{test} = 0.794$, CI: 0.699–0.889) probability of concordance between model predictions and observed nest or available locations ($nests_{train} = 73$; $nests_{test} = 26$, $n_{available} = 1{,}870$; Fig. 4). Of the 99 nest sites contained within the patch model extent, 95 (approx. 96%) occurred in the top 6 bins (5–10), encompassing approximately 56% of the available habitat at the patch extent (previously restricted by the landscape model). Sixty-nine nests (approx. 70%) were located in the top 2 bins (approx. 13% of available habitat). Strong selection for the higher ranked predicted habitats suggests the model is predictive.

Threshold Response

Landscape models indicated that Gunnison sage-grouse selected nesting areas containing >93% (lower SD = 90%) of a 1.5-km area (radius moving window) with >5% sagebrush cover (all species; Fig. 5a). Probability of nesting approaches zero for all landscapes when the proportion of sagebrush cover >5% is less than roughly 90%. After accounting for the landscape-scale selection of sagebrush, shrubs still entered into the patch scale model, reflecting the hierarchical nature of selection. However, at the patch scale, moderate proportions of big sagebrush (all subspecies) cover >10% within 0.564-km radius patches were avoided (Fig. 5d).

At the landscape scale, Gunnison sage-grouse were more likely to nest in areas that contained less than roughly 0.55 km/km^2 of roads (class 1–4) across a 6.4-km radius landscape (Fig. 5b). Despite avoidance of areas with high road density, females also avoided nesting in close proximity to major roads (class 1–2) at the patch scale. The patch-scale threshold response curves highlight relatively low probabilities of nest occurrence until about 8 km from major roads (Fig. 5e). This pattern was similar for residential development, with threshold response curves capturing selection for large landscapes (1.5-km radii) with a low density of residential development (<1%; Fig. 5c). The patch-scale threshold curves suggest maximum probabilities of nest site selection are reached at approximately 2.5 km from any given development (Fig. 5f).

Evaluation of the Hierarchical Surface

The hierarchical model surface validated well based on Kendall's c, with good ($c_{train} = 0.898$, CI: 0.859–0.938) and fair ($c_{test} = 0.789$, CI: 0.684–0.893) probability of concordance between model predictions and observed nest or available locations ($nests_{train} = 73$, $nests_{test} = 26$, $n_{available} = 1{,}870$; Fig. 4). Ninety-three percent of all nest sites (92/99) were located within approximately 50% of the patch landscape (bins 6–10; Fig. 4). Using this as a potential threshold to further refine crucial nesting habitat to include both scales of selection (patch and landscape), we identify 18,102 ha as crucial habitat. This is a refinement of 18,301 ha over what was identified as crucial habitat using the landscape model only (36,403 ha).

Table 5. Model averaged coefficients (β) and standard errors (SE) associated with each variable represented in the 90% confidence set ($n = 76$) of patch-scale models used to predict Gunnison sage-grouse nest occurrence (2006–2009; $n = 73$) across the western portion of the Gunnison Basin, Colorado. Note that the shrub variable (pg_b_bs_gt10) was included in all models.

Variable	Model averaged β	Model averaged SE	Confidence intervals	
			Lower	Upper
pg_b_bs_gt10[a]	−19.389	5.730	−30.620	−8.158
(pg_b_bs_gt10)^2	36.724	11.262	14.651	58.798
ndvi_am[b]	118.139	48.694	22.700	213.579
(ndvi_am)^2	−226.505	94.935	−412.577	−40.433
dist_res[c]	0.821	0.509	−0.178	1.820
(dist_res)^2	−0.205	0.099	−0.399	−0.010
dist_rd1_2[d]	0.140	0.053	0.037	0.244
cti_bm[e]	0.001	<0.001	<0.001	0.001
p_cj_b[f]	−1.726	1.251	−4.179	0.726
dist_water[g]	0.168	0.083	0.005	0.331
(dist_water)^2	−0.073	0.035	−0.142	−0.004
slope[h]	<0.001	0.002	−0.003	0.004
litter_am[i]	−0.001	0.003	−0.007	0.006
b_allrd[j]	0.014	0.017	−0.019	0.047
p_res_b[k]	−0.736	1.786	−4.237	2.766
shrbht_am[l]	<0.001	0.002	−0.004	0.004
bare_am[m]	0.002	0.002	−0.001	0.006
(bare_am)^2	<−0.001	<0.001	<−0.001	<0.001
herb_bm[n]	0.002	0.003	−0.003	0.007
(herb_bm)^2	<0.001	<0.001	<−0.001	<0.001
herb_bs[o]	−0.001	0.001	−0.001	<0.001

[a] Proportion of pixels with >10% big sagebrush cover across 0.564-km radius window.
[b] Mean normalized difference vegetation index (productivity) over a 3 × 3 (30-m cells) window.
[c] Euclidian distance to residential classed habitat.
[d] Euclidian distance (km) to any road classed 1 or 2. Bureau of Land Management classification: 1 = primary paved highway, 2 = secondary paved highway.
[e] Mean compound topographic index (productivity) across a 0.564-km radius window.
[f] Proportion of pixels across a 0.564-km window classed as either conifer/pinyon juniper habitat.
[g] Euclidian distance (km) to water.
[h] Slope in percent.
[i] Mean % litter over 3 × 3 (30-m cells) window.
[j] Linear density (km/km^2) of all roads within a 0.564-km window.
[k] Proportion of pixels within a 0.564-km radius that are classed as residential habitat.
[l] Mean shrub height over a 3 × 3 (30-m cells) window.
[m] Mean % bare ground over a 3 × 3 (30-m cells) window.
[n] Mean % herbaceous cover over a 0.564-km window.
[o] Standard deviation of mean herbaceous cover over a 0.564-km window.

DISCUSSION

We identified crucial nesting habitat for Gunnison sage-grouse using a hierarchical modeling approach, and accurately predicted independent nest locations. We first developed models that captured sage-grouse selection for large areas of sagebrush habitat (1.5-km extents) with limited disturbances across larger spatial extents (up to 6.4 km; Table 4). We then redefined the availability of resources to nesting sage-grouse based on this landscape model, allowing us to hierarchically assess which patches within these landscapes are important for nesting females. Despite prior modeled selection for resources across large landscapes, we show that females are indeed making a hierarchical decision, selecting for patches of sagebrush habitat while avoiding proximity to residential developments and major roads (Table 5); a multi-scale decision process. Hierarchical selection is theorized to be an important biological construct, for which, assessment of these processes should increase understanding of resource needs for a species (Johnson 1980, Rettie and Messier 2000, Mayor et al. 2009). Harvey and Weatherhead (2006) assessed hierarchical selection for eastern massasauga rattlesnakes (*Sistrurus c. catenates*) and found that most landscape-scale selection patterns could be explained primarily by microhabitat availability within those landscapes. This was not the case for Gunnison sage-grouse, with resources at both scales affecting nest selection patterns.

Our landscape-scale results follow patterns seen with greater sage-grouse and reinforce that both species respond to landscape patterns and changes to resources when selecting nesting habitat (Aldridge and Boyce 2007, Doherty et al. 2010, Connelly et al. 2004). Sage-grouse require large expanses of contiguous sagebrush habitat across all life stages (Connelly et al. 2004). Threshold response curves allowed us to identify that large areas of sagebrush were used by Gunnison sage-grouse for nesting if roughly 95% or more of the area contained sagebrush with >5% cover (remotely estimated; Fig. 5a). Sagebrush habitat meeting these requirements is abundant within the Gunnison Basin, however much of it has been degraded due to fragmentation. Although others have found that fragmented habitats are

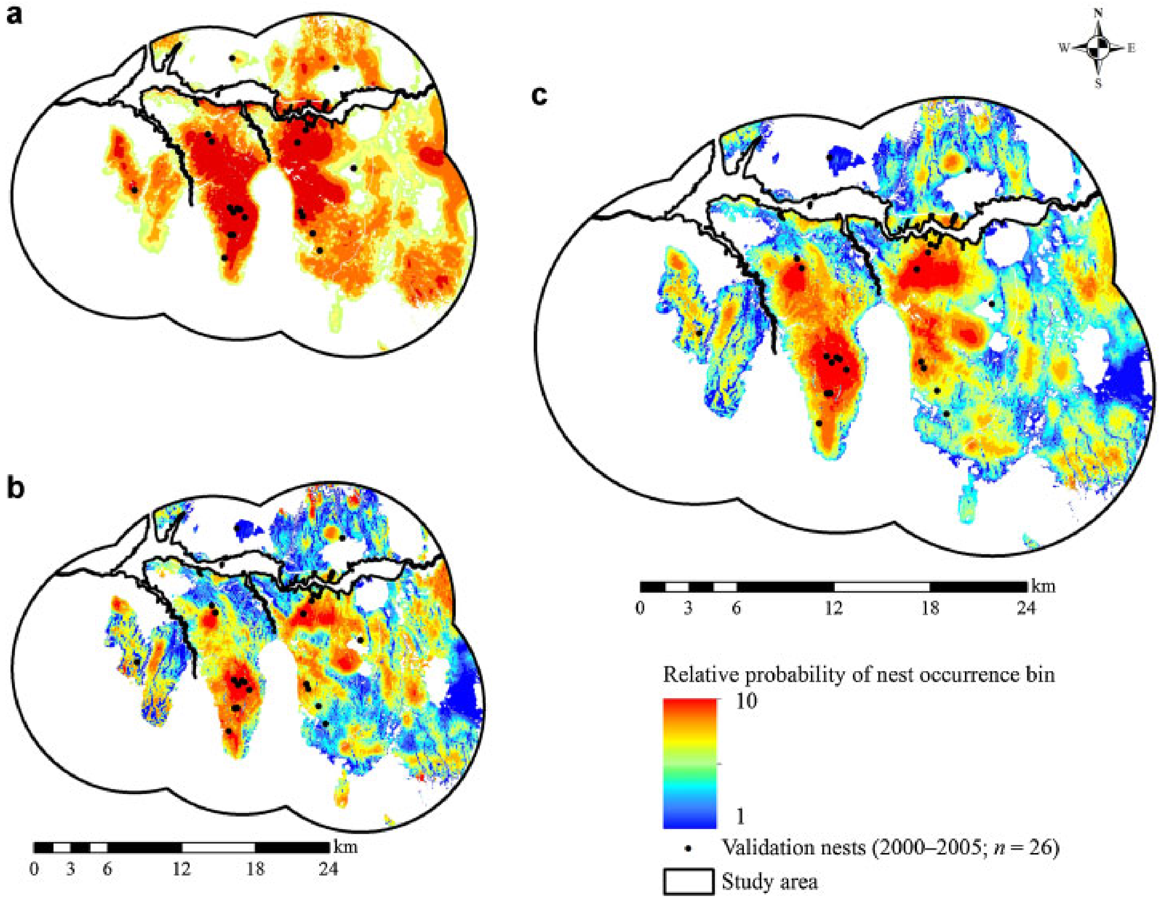

Figure 4. Crucial Gunnison sage-grouse nesting habitat within the western portion of the Gunnison Basin, Colorado. We considered crucial nesting areas the top 5 bins (6 or higher) from the landscape-scale nest occurrence model (a), and a priori refined the assessment extent of the patch-scale model (b) predicting crucial nest site habitat. We multiplied the 2 surfaces to produce a composite crucial nesting habitat surface (c) which accounts for both landscape- and patch-level habitat requirements for Gunnison sage-grouse nesting.

avoided by greater sage-grouse (Oyler-McCance et al. 2001, Lyon and Anderson 2003, Aldridge and Boyce 2007), response curves from our models identify thresholds of development, above which Gunnison sage-grouse are likely to avoid nesting. Using our landscape crucial nesting habitat cutoff probability (0.119) we can estimate that areas with road densities (roads classed 1–4) above 0.50 km/km^2 across a 6.4-km window area (Fig. 5b) are avoided. Similarly, if residential density exceeds approximately 2% of an area within a 1.5-km moving window (Fig. 5c), females avoid nesting in the area, regardless of the amount of sagebrush habitat it contains. Although the effect of residential density appears less influential (95% CIs for the coefficient overlap zero), the top landscape model (LAND1) is >3 AIC$_c$ points better than LAND8, which is the same model excluding the residential variable (Table 2). A likelihood ratio test between the 2 models (LR $\chi^2_2 = 5.27$, $P = 0.022$) also suggests residential density is an important contributor to nest-site selection.

Although increased residential and road development directly remove habitat, Gunnison sage-grouse behavioral response to these features as a result of increased human activity, noise, and changes in predator distribution and abundance, may be equally important (Forman and Alexander 1998). Similarly, it has been suggested that greater sage-grouse avoidance of forest-sagebrush interface, as we found for Gunnison sage-grouse, is a behavioral response, attempting to minimize exposure to avian predators (Doherty et al. 2008, Freese 2009, Coates and Delehanty 2010).

Although conservation interest in extrapolating our landscape-model across the entire Gunnison Basin is high, and the model had fair prediction, such extrapolations should be undertaken with caution (see Miller et al. 2004). Most importantly, these extrapolations need to be challenged with independent data to ensure predictions are valid (Miller et al. 2004). Although nest sites were not available over the entire basin, lek locations, which have previously been shown to correlate well with greater sage-grouse nest habitat models (Doherty et al. 2010), were reasonably predicted by the extrapolated model. Noted differences in available habitats (i.e., agriculture was limited in the NPS study area, but locally abundant across the basin) certainly reduced the effectiveness of model extrapolation. Despite some locally reduced fit of the model extrapolation, we argue that this landscape model could be used as an initial management tool to identify crucial nesting habitat for Gunnison sage-grouse across the basin. However, as with any spatial model, predictions should be viewed as one of many possible tools, and should not replace local knowledge when making site-

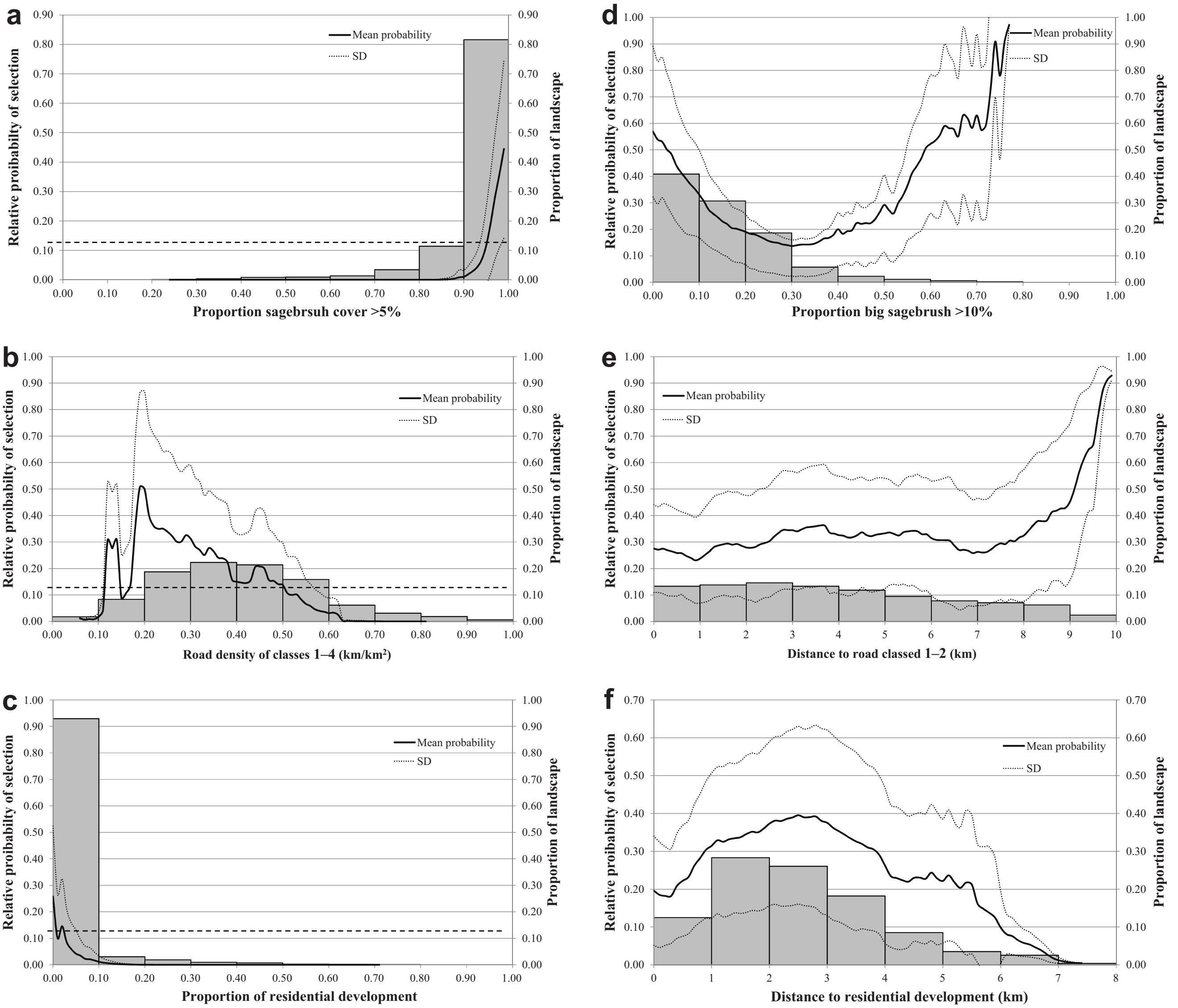

Figure 5. Gunnison sage-grouse predicted relative probability of nest occurrence plotted against key variables for both the landscape- and patch-scale model averaged predictions. We developed models using 73 nest locations collected within the western portion of the Gunnison Basin. Landscape model variables include the proportion of all sagebrush (*Artemisia* spp.) cover greater than 5% at a 1.5-km radius moving window (a), density of roads classed 1–4 at a 6.4-km radius moving window (b), and proportion of residential development within a 1.5-km moving window (c). Patch model variables include the proportion of big sagebrush (*A. tridentata* spp.) cover greater than 10% at a 0.564-km radius moving window (d), distance to roads classed 1–2 (e), and distance to residential development (f). We calculated mean relative probability of occurrence (±1 SD) values across the range of each variable. Histogram values represent the range of the Gunnison Basin landscape (right axis) occurring within a given bin value for the landscape feature of interest, for each respective model scale. The dashed line represents the threshold relative probability (0.119) above which we classified the landscape model as predicting crucial nesting habitat.

specific management decisions (Aldridge and Boyce 2007) especially when extrapolating models to novel spatial extents.

Within the framework of the landscape-scale model, we needed to decide how to classify our continuous nesting habitat surface into a binary crucial habitat classification (crucial or not). Rather than an arbitrary classification cutpoint, and given the species' high priority as a conservation species, we feel that our conservative threshold of bin 6 or higher (>0.119 relative probability), was reasonable for identification of crucial habitat within the NPS study area, given it effectively captures 97% (99/102) of known nest sites. When extrapolated across the Gunnison Basin, this would suggest approximately 50% of the landscape is crucial nesting habitat required to support >90% of known nests within the study area. Although we have mapped crucial nesting habitat, this does not preclude the need to consider other life stages, the fitness of individuals using these habitats (i.e., source vs. sink habitats), or the connectivity between habitats and across life stages, all of which might require different management actions (protection vs. enhancement; Aldridge and Boyce 2007, Aldridge et al. 2008).

We feel that our hierarchical modeling approach more closely aligns with Johnson's (1980) original perception on how animals select resources, choosing larger home ranges or areas that meet an animal's general needs (our landscape model), followed by selection to meet more specific life requirements (nest patch model). Accordingly, despite having influence at the landscape-scale, some habitat characteristics continued to affect selection at the patch scale. For instance, although more sagebrush cover above 5% was selected at the landscape scale (1.5-km radius areas; Fig. 5a) sagebrush continued to influence selection at the patch scale, but the strongest predictor was proportion big sagebrush >10% (0.564-km radius). Even though models at both scales contained similar variables, correlation between the 2 prediction surfaces was minimal (Pearson's $r = 0.411$; $n = 1{,}870$ patch-scale available points), suggesting significant additional variation is explained by the patch model.

Predicted responses to big sagebrush at the patch scale suggest selection is bimodal, with birds selecting for low or high amounts of big sagebrush above 10% cover; proportions below 0.2 or above 0.4 (Fig. 5d). However, only 3 of 73 nests used for model building were at the high end of the distribution (>0.3 in Fig. 5d), and we caution against drawing strong inferences when interpreting this part of the curve. Several factors could be contributing to this overall predicted relationship. First, although big sagebrush appeared to have a strong contribution to selection (Table 5), the low sample sizes at the high end of the distribution in conjunction with the symmetric nature of the quadratic function magnify this relationship. Second, although the patch model shows some avoidance of moderate amounts of higher estimated (>10%) big sagebrush cover, prior selection for sagebrush in our landscape model redefined availability for the patch model. Patches had already been selected with suitable sagebrush; densities in these patches were just lower than 10% big sagebrush cover. This avoidance of dense cover may subsequently reflect a need for females to seek out local habitat patches with increased lateral nest cover provided by grass, forbs, or other shrubs, which are not likely available in large areas with greater big sagebrush cover (Aldridge and Brigham 2002, Crawford et al. 2004, Hagen et al. 2007). Finally, this does not refute the well supported evidence that sage-grouse will ultimately choose to place their nests in a dense sagebrush stand (for reviews see Connelly et al. 2004, Hagen et al. 2007). Big sagebrush summarized here was at a 564-m radius moving window extent, clearly capturing different vegetation characteristics than that of an individual shrub. Current limitations of remotely-sensed vegetation models prevent our ability to capture intimate vegetation characteristics within a sagebrush stand or individual plants (<15 m; Homer et al. 2008, 2012). Despite these scalar differences, our hierarchical model predictions accurately predicted independent nest locations.

Gunnison sage-grouse also exhibit a clear avoidance of paved, high traffic volume roads (classes 1 and 2; Fig. 5e) during nesting at the patch scale, in addition to prior avoidance of higher density 2-wheel drive accessible roads at the landscape scale (6.4-km radius; classes 1–4; Fig. 5b). Landscape-level response may reflect selection for less fragmented areas (Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007, Doherty et al. 2008). However, the direct avoidance of high volume roads in patch-scale models reinforces that Gunnison sage-grouse are selecting for resources hierarchically (Rettie and Messier 2000, Mayor et al. 2009). This may be a behavioral response to disturbance (Forman and Alexander 1998) and avian predators (Knight and Kawashima 1993, Connelly et al. 2004, Bui et al. 2010) when choosing where to place a nest, despite prior selection for less fragmented habitats (landscape model). Road avoidance extends out to approximately 8 km from high volume roads, with the relative probability of nest occurrence increasing steadily beyond that point (Fig. 5e). This corresponds with a lek analysis in Wyoming and Utah which found that greater sage-grouse leks within 7.5 km of Interstate 80 appear to have declined at a much faster rate than those further away (Connelly et al. 2004). A recent analysis assessing the effects of urban development on greater sage-grouse used a 6.9-km foraging distance for mammalian and corvid predators (Knick et al. 2011). These numbers correspond with our findings of road avoidance during nesting by Gunnison sage-grouse.

Development in the Gunnison Basin is becoming increasingly exurban. This type of development results in a highly fragmented landscape as the number of roads and buildings (Theobald et al. 1996, Mitchell et al. 2002) in previously contiguous patches of sagebrush increases, clearly reducing nesting habitat quality for Gunnison sage-grouse. High density residential development was avoided at a landscape scale, and nesting females chose to place nests farther away from any single development at the patch scale. This avoidance was not linear, with a threshold at approximately 2.5 km (Fig. 5f). The joint effects of roads and residential developments within sagebrush habitats will have negative consequences on Gunnison sage-grouse nesting habitat. With future developments on the horizon for the Gunnison Basin, housing and associated road developments within 2.5 km of identified crucial habitat should be evaluated cautiously, due to the potential direct and functional loss of nesting habitat (Aldridge and Boyce 2007).

Overall, landscape models were more predictive, having higher probabilities of concordance between model predictions and independent data. This is expected, given the landscape nature of the species (Patterson 1952, Knick et al. 2003, Connelly et al. 2004), and the inability of our model inputs to characterize fine scale (<30 m) habitat characteristics known to be important for sage-grouse (Connelly et al. 2000, Hagen et al. 2007). Because of the truly nested nature of our modeling approach, some variation at the patch scale may already be captured by the landscape scale models, although this appears to be minimal. When the patch and landscape scale surfaces were multiplied to produce the hierarchical surface, evaluation was strong, and the area implicated as crucial habitat was reduced by half from considering landscape models only. We believe using the hierarchical surface, where available, will allow for better informed management decisions, particularly when sage-grouse habitat occurs on lands with multiple use mandates.

MANAGEMENT IMPLICATIONS

Our models depicting crucial nesting habitat of Gunnison sage-grouse should be seen as an initial tool to inform management and conservation across large landscapes, but does not obviate the need for local, targeted assessments and adaptive management within these areas (Aldridge et al. 2004, Aldridge and Boyce 2007). Models identify priority conservation areas for protection (i.e., high quality red areas on maps) and areas where management actions might be warranted (i.e., moderate quality yellow areas on maps), providing an initial baseline spatial accounting system (Aldridge and Boyce 2007) to track crucial nesting habitat for the species. Realistically, managers will want to know how best to threshold these continuous RSF relative probability surfaces to explicitly identify crucial habitats for protection. Given the extreme fidelity of these imperiled birds to nesting areas (Fischer et al. 1993, Connelly et al. 2004), we argue that managers should indeed strive to protect as many of these habitats as possible, and reinforce our recommendation that crucial habitat capture >90% of known nest locations. Similarly, future developments (urban or roads) should be prevented within 2.5 km of identified crucial nesting habitat, if habitats, and thus populations, are to be maintained. Finally, because input data are spatial, managers could begin to assess the impacts of future landscape scenarios, such as evaluating the potential cost and benefit for Gunnison sage-grouse nesting habitat of future urban expansion or decommissioning of roads. These models and maps could subsequently inform travel management planning, environmental impact statements, records of decisions, and development and conservation planning in general. Future work should concentrate on developing similar models for brood-rearing and winter habitat, both important life stages for sage-grouse. Ultimately, management actions must not only consider protection of crucial habitat, but also connectivity between patches, both within, and across life stages (Aldridge and Boyce 2007), if long-term persistence of the species is desired.

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LITERATURE CITED

Akcakaya, H. R., V. C. Radeloff, D. J. Mlandenoff, and H. S. He. 2004. Integrating landscape and metapopulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. Conservation Biology 18:526–537.

Aldridge, C. L., M. S. Boyce, and R. K. Baydack. 2004. Adaptive management of prairie grouse: how do we get there? Wildlife Society Bulletin 32:92–103.

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 M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology and Evolution 54:389–419.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403–410.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Bui, T.-V. D., J. M. Marzluff, and B. Bedrosian. 2010. Common raven activity in relation to land use in western Wyoming: implications for greater sage-grouse reproductive success. Condor 112:65–78.

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

Candolo, C., A. C. Davison, and C. G. B. Demétrio. 2003. A note on model uncertainty in linear regression. Statistician 52:165–177.

Carpenter, J. E., C. L. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 78:1806–1814.

Coates, P. S., and D. J. Delehanty. 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74:240–248.

Colorado Water Conservation Board (CWCB). 2009. 2050 population projections for the State of Colorado municipal and industrial water use projections. Final report prepared for Colorado Water Conservation Board, Appendix B in Colorado's water supply future: state of Colorado 2050 municipal and industrial water use projections. <http://cwcb.state.co.us/IWMD/COsWaterSupplyFuture/>. Accessed 28 May 2010.

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

Connelly, J. W., 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.

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

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.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

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

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Freese, M. T. 2009. Linking greater sage-grouse habitat use and suitability across spatioteporal scales in central Oregon. Thesis, Oregon State University, Corvalis, USA.

Gessler, P. E., I. D. Moore, N. J. McKenzie, and P. J. Ryan. 1995. Soil-landscape modeling and spatial prediction of soil attributes. International Journal of Geographical Information Science 9:421–432.

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

Gunnison Sage-Grouse Rangewide Steering Committee (GSGRSC). 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, USA.

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

Haines, A. M., M. E. Tewes, L. L. Laack, J. S. Horne, and J. H. Young. 2006. A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. Biological Conservation 132:424–436.

Hanser, S. E., C. L. Aldridge, M. Leu, and S. E. Nielsen. 2011. Dose response calculator for ArcGIS. United States Geological Survey Data Series 631. <http://pubs.usgs.gov/ds/631/>. Accessed 14 Feb 2011.

Harrell, F. E., Jr. 2001. Regression modeling strategies: with applications to linear models, logistic regression, and survival analyses. Springer-Verlag, New York, New York, USA.

Harrell, F. E., Jr., K. L. Lee, and D. B. Mark. 1996. Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measure and reducing errors. Statistics in Medicine 16:361–387.

Harju, S. M., M. R. Dzialak, R. C. Taylor, L. D. Hayden-Wing, and J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437–448.

Harvey, D. S., and P. J. Weatherhead. 2006. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). Biological Conservation 130:206–216.

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

Holloran, M. J., and S. H. Anderson. 2005. Greater sage-grouse population response to natural gas development in Western Wyoming: are regional populations affected by relatively localized disturbances? Transactions of the North American Wildlife and Natural Resources Conference 70:16–170.

Holloran, M. J. R. C., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:68–72.

Homer, C. G., C. L. Aldridge, D. K. Meyer, M. J. Coan, and Z. H. Bowen. 2008. Multiscale sagebrush rangeland habitat modeling in southwest Wyoming. Open-File Report 2008–1027. U.S. Geological Survey, Reston, Virginia, USA.

Homer, C. G., C. L. Aldridge, D. K. Meyer, and S. Schell. 2012. Multi-scale remote sensing sagebrush characterization with regression trees over Wyoming, USA; laying a foundation for monitoring. International Journal of Applied Earth Observation and Geoinformation 14:in press.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, Inc., New York, New York, USA.

International Union for Conservation of Nature (IUCN). 2010. IUCN red list of threatened species. Version 2010.1. <http://www.iucnredlist.org>. Accessed 11 Jun 2010.

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.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

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

Knick, S. E., S. E. Hanser, R. F. Miller, D. A. Pyke, M. J. Wisdom, S. P. Finn, E. T. Rinkes, and C. J. Henry. 2011. Ecological influence and pathways of land use in sagebrush. Studies in Avian Biology 38:203–251.

Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. Journal of Wildlife Management 57:266–271.

Kolada, E. J., J. S. Sedinger, and M. L. Casazza. 2009. Nest site selection by Greater sage-grouse in Mono County, California. Journal of Wildlife Management 73:1333–1340.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

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

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. Chapman and Hall, London, England.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

Miller, J. R., M. G. Turner, A. H. Smithwick, C. L. Dent, and E. H. Stanley. 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. BioScience 4:310–320.

Mitchell, J. E., R. L. Knight, and R. J. Camp. 2002. Landscape attributes of subdivided ranches. Rangelands 24:3–9.

Morris, D. W. 1987. Ecological scale and habitat. Ecology 68:362–369.

Morrison, M. L. 2001. Invited Paper: a proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613–623.

Murray, K., and M. M. Conner. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. Ecology 90:348–355.

Newson, R. 2006. Confidence intervals for rank statistics: Somers' D and extensions. The Stata Journal 6:309–334.

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.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.

Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage grouse in southwestern Colorado. Southwestern Naturalist 46:323–331.

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

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466–478.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426.

STATACORP. 2007. Stata user's guide: release 10. Stata Press, College Station, Texas, USA.

Theobald, D. M., H. Gosnell, and W. E. Riebsame. 1996. Land use and landscape change in the Colorado mountains II: a case study of the East River Valley. Mountain Research and Development 16:407–418.

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

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Yost, A. C., S. L. Petersen, M. Gregg, and R. Miller. 2008. Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using maximum entropy and a long-term dataset from southern Oregon. Ecological Informatics 3:375–386.

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