



Management and Conservation Article

Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales

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ABSTRACT Considering habitat selection at multiple scales is essential to fully understand habitat requirements and management needs for wildlife species of concern. We used a hierarchical information-theoretic approach and variance decomposition techniques to analyze habitat selection using local-scale habitat variables measured in the field and landscape-scale variables derived with a Geographic Information System (GIS) for nesting greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB), Montana and Wyoming, USA, 2003–2007. We investigated relationships between habitat features that can and cannot be mapped in a GIS to provide insights into interpretation of landscape-scale-only GIS models. We produced models of habitat selection at both local and landscape scales and across scales, yet multiscale models had overwhelming statistical and biological support. Variance decomposition showed that local-scale measures explained the most pure variation (50%) in sage-grouse nesting-habitat selection. Landscape-scale features explained 20% of pure variation and shared 30% with local-scale features. Both local- and landscape-scale habitat features are important in sage-grouse nesting-habitat selection because each scale explained both pure and shared variation. Our landscape-scale model was accurate in predicting priority landscapes where sage-grouse nests would occur and is, therefore, useful in providing landscape context for management decisions. It accurately predicted locations of independent sage-grouse nests (validation $R^2 = 0.99$) and showed good discriminatory ability with >90% of nests located within only 40% of the study area. Our landscape-scale model also accurately predicted independent lek locations. We estimated twice the amount of predicted nesting habitat within 3 km of leks compared to random locations in the PRB. Likewise we estimated 1.8 times more predicted nesting habitat within 10 km of leks compared to random locations. These results support predictions of the hotspot theory of lek placement. Local-scale habitat variables that cannot currently be mapped in a GIS strongly influence sage-grouse nest-site selection, but only within priority nesting habitats defined at the landscape scale. Our results indicate that habitat treatments for nesting sage-grouse applied in areas with an unsuitable landscape context are unlikely to achieve desired conservation results.

KEY WORDS *Centrocercus urophasianus*, habitat selection, landscape, nesting, resource selection function, sagebrush, sage-grouse, scale.

The critical concept of scale in conservation research is now recognized by nearly all ecologists (e.g., O'Neill et al. 1986, Wiens 1989, Turner et al. 2001, Scott et al. 2002). Landscape-scale habitat features are known to drive ecological processes in numerous avian taxa including forest songbirds (Andren 1995, Donovan et al. 1997, Hartley and Hunter 1998), waterfowl (Stephens et al. 2003), and grouse (western capercaillie [*Tetrao urogallus*], Kurki and Linden 1995, Kurki et al. 2000; lesser prairie-chicken [*Tympanuchus pallidicinctus*], Fuhlendorf et al. 2002). Conversely, numerous ecological studies conducted at smaller scales using field-based measures provide evidence that local scales are also important in habitat selection. In many cases, amount of habitat and landscape configuration drive ecological processes at large spatial scales but become less important than finer characteristics and habitat composition at small scales (Wiens 1989, Kotliar and Wiens 1990).

The goal of research into multiscale habitat selection should not be to just pick a single scale for research or management, but rather to understand how species occurrence is influenced by contributions of habitat features

at multiple scales in the environment (Kristan and Scott 2006). Drawing conclusions about habitat selection based on observations at any one scale may misconstrue importance of variables thought to drive system behavior (Wiens 1989). Habitat relationships are known for many species at local scales that currently cannot be mapped in a Geographic Information System (GIS) because the biological detail recorded in vegetation plots often cannot be extracted from remotely sensed imagery. Questions thus arise about the relationship between habitat characteristics that cannot be mapped in a GIS, and have been historically evaluated, and those that can.

No studies have empirically evaluated the relative importance of landscape context versus local habitat for nesting sage-grouse (*Centrocercus urophasianus*). A gallinaceous species native only to western semiarid sagebrush habitats, sage-grouse were previously widespread, but loss and degradation of sagebrush habitat has resulted in extirpation of the species from almost half of its original range (Schroeder et al. 1999, 2004). Numerous studies have increased our ecological understanding of sage-grouse nesting-habitat relationships at localized scales (e.g., Hagen et al. 2007). These local-scale studies do not address landscape context or constraints in habitat selection, nor do they convey spatially explicit information about habitat at scales useful for prioritizing landscapes for sage-grouse because most of these variables cannot be mapped in a GIS.

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Only recently have studies quantified habitat variables at landscape scales (100–3,000 m) for use in modeling habitat selection by individual birds (e.g., Aldridge and Boyce 2007, Doherty et al. 2008, Yost et al. 2008).

Our objectives were to 1) create a habitat selection model for nesting sage-grouse at local scales using field-derived data, at landscape scales using GIS-derived data, and at multiple scales; 2) evaluate the relative importance and interpretation of local, landscape, and multiscale models using variance decomposition and information theoretic techniques; 3) apply a landscape-scale model to spatial data quantified in a GIS to identify specific portions of the landscape within our study region with high probability of use by nesting females; and 4) validate the best approximating models with independent nest and lek data sets to ensure appropriateness for management.

STUDY AREA

Our study area in the Powder River Basin (PRB) covered portions of Johnson, Sheridan, and Campbell counties in Northeast Wyoming, and Bighorn, Rosebud, and Powder River counties in Southeast Montana (USA). Shrub-steppe habitat was dominated by Wyoming big sagebrush (*Artemisia tridentata*) with an understory of native and nonnative grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), Japanese brome (*Bromus japonicus*), cheatgrass (*Bromus tectorum*), and crested wheatgrass (*Agropyron cristatum*). Plains silver sagebrush (*Artemisia cana*) was also present in drainages. Rocky mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) occurred in wooded draws and formed forests across the extreme northern extent of the study area. Conifers were largely absent from the southern half of the study area. Land use was dominated by cattle ranching, and only 4% of the landscape consisted of dry-land or irrigated agriculture. Doherty (2008) provides a detailed description of our study area.

METHODS

Capture and Radiotracking Sage-Grouse

We captured sage-grouse using spotlights and long-handled nets (Wakkinen et al. 1992), rocket-nets, and walk-in traps (Giesen et al. 1982) on and around leks from March to April and July to October in 2003–2007 in 3 study areas: 1) Bighorn County, Montana; 2) Johnson County, Wyoming; and 3) Campbell County, Wyoming. During our pilot year in 2003 we monitored 12 radiomarked females from 5 small leks in Campbell County for 4 months until a severe outbreak of West Nile virus resulted in extirpation of this local population (Walker et al. 2004).

We determined age and gender of captured grouse and fitted females with a 21.6-g necklace style radiocollar with a 4-hour mortality switch (model A4060; Advanced Telemetry Systems, Isanti, MN). We located sage-grouse nests by ground-based radiotracking during the breeding seasons of 2003–2007. We used hand-held Global Positioning System

(GPS) receivers to record exact locations of nests after they hatched or failed. We left no natural or artificial markers around nests, to eliminate the possibility of predators using markers to locate nests, even though effects of nest marking have varied (e.g., Picozzi 1975, Reynolds 1985, Sedinger 1990). We collected all GPS locations when estimated error was <7 m. We conducted GIS analyses at scales ≥ 100 m to ensure that inference was not confounded by GPS error.

GIS Land-Cover Habitat Classification

We acquired SPOT-5 satellite imagery (Terra Image USA, Santa Barbara, CA) for northern and southern portions of the study area in August 2003 and 2004. We rectified imagery using the National Agricultural Inventory Program (NAIP). We increased resolution of analyses from 100 m² to 25 m² by using the 25-m²-pixel panchromatic image to perform pan-sharpening. We used eCognition™ 4.06 software (Definiens Imaging, Munich, Germany) to cluster pixels into regions representing spectrally similar ground features. We created a polygon database by exporting clusters into ArcGIS 9.2 software. We manually digitized agriculture, urban, water, and strip mines visually discernible on 1-m NAIP photos and pan-sharpened SPOT-5 imagery. We collected field training points ($n = 7,092$) stratified by area and land ownership to classify polygons of spectrally similar ground features into 6 habitat cover classes: high-density sagebrush (>10% sagebrush canopy cover), sagebrush–grassland mix (<10% sagebrush canopy cover), grassland, conifer, riparian, and sparse vegetation (e.g., bare ground).

Classification was a 2-stage process. We first classified the landscape into 3 cover classes and used k-fold validation (Boyce et al. 2002) to cross-validate accuracies for prairie (93.6%), riparian (87.8%), and conifer (73.3%). We then used descriptive statistics derived from pan-sharpened SPOT-5 imagery to subdivide the prairie class into grassland, sagebrush–grassland mix, and high-density sagebrush. Accuracies within the prairie class were 97.0% for high-density sagebrush, 71.6% for grassland, and 72.3% for sagebrush–grassland mix. Misclassification rates within the prairie class between sagebrush and grassland were <3%. Full classification methods are in Doherty (2008).

Habitat Selection

We defined habitat variables quantified from field vegetation plots as local-scale habitat features. We used published protocols (Connelly et al. 2003) to quantify local vegetative features known to influence habitat selection within ≤ 15 m of nest and available points (e.g., Connelly et al. 2000, Hagen et al. 2007). Local-scale habitat variables included shrub canopy cover, shrub density, shrub height, nest shrub height, visual obstruction, and grass height (e.g., Connelly et al. 2000, Hagen et al. 2007). We collected shrub canopy cover using the line-intercept method (Canfield 1941, Connelly et al. 2003) along 2 perpendicular 30-m line transects running north–south and east–west. We centered transects on the nest bowl at nest locations and on the shrub nearest to the random point and >35 cm in height at

available locations. We counted the density of shrubs >15 cm in height within 1 m on either side of line transect (total no. of shrubs/120 m²). We also measured the average of recorded heights of the nearest shrub within 1 m at 3-m intervals along the transect line (Connelly et al. 2003). We estimated an index of visual obstruction around nests by collecting height readings (5-cm segments) at 0 m, 1 m, 3 m, and 5 m from the nest or random nest shrub in each cardinal direction 4 m from the Robel pole at a height of 1 m horizontal to the pole (Robel et al. 1970). We collected vegetative droop height of nearest and tallest grass within Daubenmire plots (Daubenmire 1959).

We defined landscape-scale features as those we quantified in a GIS. We quantified characteristics of vegetation and topography around nest and available locations in a GIS to evaluate habitat selection at 4 landscape scales (100 m, 300 m, 1,500 m, and 3,000 m). We selected the 2 largest scales to capture natural or anthropogenic processes thought to influence habitat selection, such as topography (Doherty et al. 2008), or modifications to land use that result in loss of sagebrush (Knick et al. 2003). We selected 2 intermediate scales (100 m and 350 m) as potential surrogates for mechanisms such as predation and habitat heterogeneity that affect habitat selection at extents intermediate to those at larger scales and directly at the nest (e.g., Chalfoun et al. 2002, Aldridge and Boyce 2007). We calculated percent area of grassland, high-density sagebrush, conifer, sparse vegetation, and tilled agriculture by summing the number of pixels at each scale. We used topography to calculate ruggedness of the landscape as the standard deviation of a 30-m-resolution digital elevation model (Doherty et al. 2008). We considered variables at all landscape scales because little a priori information was available to predict the scale at which variables most strongly influenced habitat selection (Boyce 2006).

We included at local and landscape scales a quadratic term for percent sagebrush habitat to further evaluate whether nesting sage-grouse select for intermediate densities of sagebrush (Aldridge and Boyce 2007). We evaluated the importance of quadratic terms in each stage of model development and against the best approximating GIS model.

We employed a used-available design to evaluate nesting habitat selection (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We identified resource use as nest locations of radiomarked females during 2003–2007. We defined available habitat randomly using a spatial Poisson distribution (Beyer 2004) proportional to the number of nests within a study area and year (Design II; Erickson et al. 2001, Manly et al. 2002). We constrained available locations to within 5 km of either the lek of capture or the lek closest to where we captured birds via spotlighting (Holloran and Anderson 2005) to avoid sampling large tracts of conifer forest. The 5-km radius encompassed 79% of all nests in our study.

We separated the 527 nest locations into 2 groups. We used 381 nests from 2004 to 2006 to build the model and 146 nest locations from 2003 and 2007 to test the model.

We tested the model by grouping the 146 test nest locations into those independent by year ($n = 146$) and nests that were independent by both individual and year ($n = 88$). We did this to avoid possible pseudo-replication caused by site fidelity of individuals to nesting areas across years (Holloran et al. 2005).

Statistical Model Selection and Variance Decomposition

We employed logistic regression with used and available locations for model selection and resource selection function (RSF) model parameter estimates (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We first tested each habitat feature at each scale individually and removed those with odds ratios whose confidence intervals overlapped 1.0. We classified remaining habitat features into 1 of 2 possible scale classes, local (field-plot based) or landscape (GIS based). We did not allow double representation for intermediate (100 m or 350 m) or large-scale variables (1,500 m or 3,000 m) of the same habitat feature and we included the variable with the lowest log-likelihood value. For example, we only allowed percent sagebrush within 100 m, rather than percent sagebrush within 350 m, to be considered in the final landscape-scale model. We disallowed double representation because variables close in scale are typically highly correlated and can compound cross-correlation issues (Lawler and Edwards 2006, Knick et al. 2008). We did not allow highly correlated variables ($r \geq 0.71$) in the same model at any level of model selection. We included the habitat feature with the greatest support for influencing nesting selection according to published studies if variables were highly correlated.

We then allowed remaining variables to compete with all variables within the same model category (local or landscape) using a backward stepwise procedure with a tolerance of 0.1. We repeated model selection to get a final model across multiple scales by adding all variables in final single-scale models into a backward stepwise procedure. Doherty (2008) arrived at the same models we presented herein but used a combination of Akaike's Information Criterion (AIC), odds ratios, and stability measures to deal with cross-scale correlations. Taking different approaches but arriving at the same results increases our confidence in the robustness of model selection.

We used a combination of competing models (Burnham and Anderson 2002, Boyce 2006) and variance decomposition techniques (Borcard et al. 1992, Cushman and McGarigal 2002, Lawler and Edwards 2006) to analyze the relative influence of local- and landscape-scale habitat features. Variance decomposition involves fitting one full and multiple subsets of models to partition out variation explained by different models (Borcard et al. 1992).

We defined our full model for variance decomposition analyses as the total set of variables that made up either our local- (Table 1) or landscape-scale (Table 2) models. We defined 2 subsets of models as groups of variables that made up either local- or landscape-scale models separately. We used variance decomposition to isolate variation explained between scales into pure and shared components (Cushman

Table 1. Best approximating local-scale habitat selection model for nesting greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA, 2004–2006.^a

Parameter ^b	Estimate	SE	P-value	Odds ratio	Upper CI	Lower CI
Constant	-2.763	0.276	<0.001			
Sagebrush cover 15 m	0.217	0.026	<0.001	1.242	1.180	1.307
Sagebrush cover ²	-0.004	0.001	<0.001	0.996	0.995	0.997
Average Robel 15 m	0.057	0.013	<0.001	1.058	1.033	1.085

^a We collected local-scale habitat measures at field vegetation plots based on 2 perpendicular 30-m line transects running N–S and E–W centered on the nest bowl at used locations and on the nearest shrub to the random point >35 cm in ht at available locations. We could not map these variables in a Geographic Information System (GIS) within our SPOT 5 GIS land-cover classification.

^b Sagebrush cover² = quadratic term of % sagebrush canopy cover within 15 m to evaluate whether birds select for intermediate canopy coverage.

and McGarigal 2002, Lawler and Edwards 2006). Shared variation is jointly explained by different models. Pure variation equates to variation independently explained by one subset model. We subtracted different components of variation using statistical deviance to isolate one shared and 2 pure components of variation. We isolated local-scale variation by subtracting the deviance explained by the landscape-scale model from the full multiscale model. We isolated the pure landscape-scale variation by subtracting the deviance explained by the local-scale model from the full multiscale model. We then isolated shared components of variation between scales by adding both pure components of variation together and subtracting their sum from the total deviance explained by the full multiscale model.

We used AIC to test the ranking of the final local (Table 1), landscape (Table 2), and multiscale models (Table 3). We computed Akaike weights (w_i), which can be interpreted as the strength of evidence of a particular model compared to other competing models on a scale of 0–1, with 1 being the highest strength of evidence (Burnham and Anderson 2002).

Creation of GIS model.—We linked our final landscape-scale model to a GIS by using the RSF:

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

Table 2. Best approximating landscape-scale habitat selection model we used to map nesting greater sage-grouse habitat in the Powder River Basin, Montana and Wyoming, USA, 2004–2006.^a

Parameter ^b	Estimate	SE	P-value	Odds ratio	Lower CI	Upper CI
Constant	0.069	0.295	0.815			
% conifer 100 m	-0.070	0.029	0.017	0.932	0.880	0.988
% grassland 100 m	-0.022	0.007	0.002	0.979	0.965	0.992
% riparian 350 m	-0.289	0.067	<0.001	0.749	0.657	0.853
% sagebrush 100 m ^c	0.026	0.010	0.012	1.026	1.006	1.047
Sagebrush ² 100 m ^d	-1.732 × 10 ⁻⁴	1.033 × 10 ⁻⁴	0.094	0.999	0.998	1.000
Roughness 100 m ^e	-0.064	0.026	0.015	0.938	0.890	0.988

^a We defined landscape-scale variables as those we quantified in a Geographic Information System (GIS) at 4 radii (100 m, 350 m, 1,500 m, and 3,000 m).

^b Agriculture 1,500 m was not included in final model for GIS predictions because of poor validation.

^c Sagebrush 100 m = % of high-density sagebrush habitat (>10% canopy cover) within 100 m.

^d Sagebrush² 100 m = quadratic term of % sagebrush within 100 m to evaluate whether birds select for intermediate canopy coverage.

^e Roughness = topographic index calculated as the SD of a 30-m resolution digital elevation model at 100-m radius.

Table 3. Best approximating combined local- and landscape-scale habitat selection model for nesting greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA, 2004–2006.^a

Parameter ^b	Estimate	SE	P-value	Odds ratio	Lower CI	Upper CI
Constant	-1.752	0.337	<0.001			
% conifer 100 m	-0.061	0.030	0.041	0.941	0.888	0.998
% grassland 100 m	-0.018	0.007	0.012	0.982	0.968	0.996
% riparian 350 m	-0.224	0.078	0.004	0.799	0.686	0.931
Sagebrush cover 15 m	0.187	0.028	<0.001	1.206	1.142	1.274
Sagebrush cover ²	-0.004	0.001	<0.001	0.996	0.995	0.998
Roughness index 100 m	-0.086	0.029	0.003	0.917	0.866	0.971
Average Robel 15 m	0.066	0.013	<0.001	1.068	1.041	1.096

^a All variables from Tables 1 and 2 were included in the multi-scale model selection analysis.

^b All habitat variables from the original within-scale habitat selection were included in the multiscale model except the quadratic terms for % high-density sagebrush habitat (>10% canopy cover) within a 100-m radius.

where $w(x)$ is the raw RSF value for each pixel in the landscape; x_1, x_2, \dots, x_k represent values for vegetation and topography generated from a moving-window analysis for each pixel; and β_1, \dots, β_k are model parameters estimated from logistic regression (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We applied β -coefficients from equation 1 to GIS layers in ArcView 9.2 Spatial Analyst. The output was a new GIS layer that represented RSF values for each individual pixel over the entire landscape. We categorized raw RSF values for each individual 25-m² pixel into quantile bins representing progressively selected habitats. Bin 1 contained the lowest 20% of raw RSF values and bin 5 contained the highest 20%. Higher predicted RSF values represent a higher likelihood of that specific area being selected by a nesting sage-grouse.

Model Validations

We validated our statistical and spatial model with an independent set of nest locations from 2003 and 2007. We tested whether logistic regression coefficients estimates had consistent positive or negative effects between nests we used

to build the model and those we used to test the model. We compared the frequency of nest locations within each RSF bin (1–5) between build and test data sets to validate our spatial model following methods outlined in Johnson et al. (2006). Resource selection function models based on presence–available data are better evaluated by withholding data (k-fold partitioning or independent data) for testing model predictions than by using usual metrics of classification success (e.g., confusion matrices, Kappa statistics, and Receiver Operating Characteristic, see Boyce et al. 2002, Johnson et al. 2006).

We first regressed the observed proportion of test nest locations in each RSF bin against the original proportion of nest locations used to build the RSF model. A good model fit leads to a high R^2 value, a slope not different from 1.0, and an intercept not different from zero when comparing build and test data sets in regression validation (Johnson et al. 2006). Secondly, we performed a chi-square test to evaluate whether nests in our test data set were located in proportion to the expected frequency of use defined by nests in the build data set. A model with good fit should show similar patterns between frequency of use for build and test data sets, resulting in nonsignificant chi-square tests.

We also validated our model using an independent lek data set within our study area (Fig. 1). The hotspot hypothesis of lek evolution suggests that leks typically become established in landscapes where females nest and, therefore, where males are most likely to encounter receptive, prenesting females (Schroeder and White 1993, Gibson 1996). Moreover, leks usually occur centrally within suitable nesting habitat (Holloran and Anderson 2005). Thus, more nesting habitat is expected to occur around leks than around random points in the landscape. We tested this prediction by quantifying the amount of area that our model classified as suitable nesting habitat (RSF bins 4 and 5) within 3 km, 5 km, 10 km, and 20 km of active leks and available locations. We used 88 leks where we counted ≥ 5 males in 2005, the midpoint of our 5-year study, reasoning that leks with ≥ 5 males were likely to have supported breeding populations during our field study. We randomly selected for comparison 88 available locations from a spatial Poisson distribution (Beyer 2004). We obtained locations and counts of displaying males from public lek databases maintained by Wyoming Game and Fish Department and Montana Fish, Wildlife and Parks.

We performed a bootstrap analysis to quantify how the change in 2 key predictor variables, sagebrush canopy cover within 15 m and percent area classified as high-density sagebrush in a GIS within a 100-m buffer, affected odds of use in 2 separate bootstrap analyses. We used the best multiscale model to estimate the odds of use for sagebrush canopy cover in the first bootstrap simulation. We used the best landscape-level GIS model to estimate odds of use as the percent area classified as high-density sagebrush in a GIS within a 100-m buffer for the second bootstrap simulation. We used the logistic equation to generate odds of use for bootstrap data sets ($n = 5,000$) by applying model coefficients to mean values of variables at nest locations

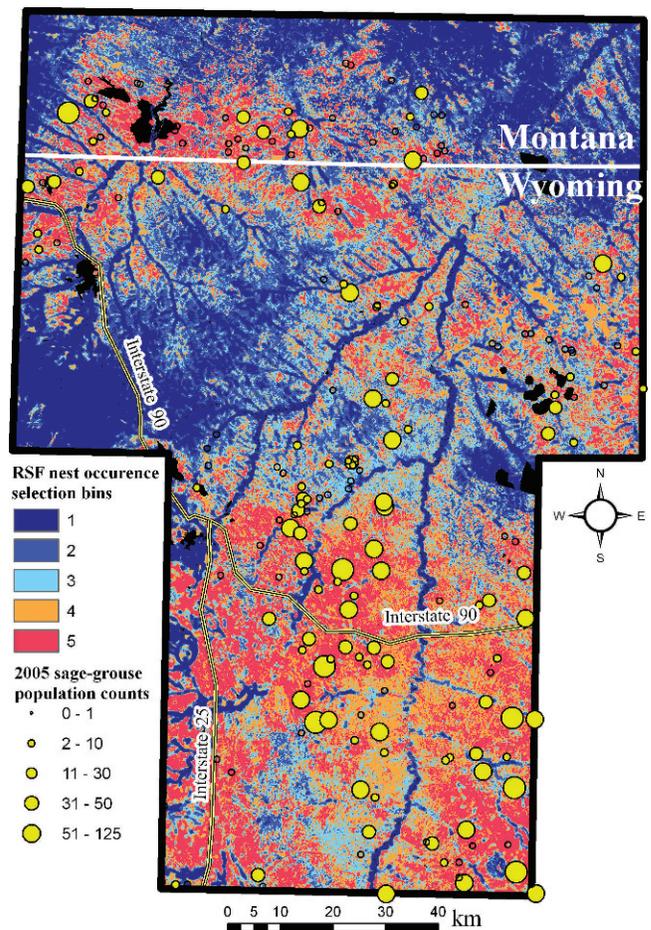


Figure 1. Nesting habitat for sage-grouse in the Powder River Basin, Montana and Wyoming, USA, 2004–2006. Color scheme from low (blue) to high (red) represents the relative probability of use of habitat by nesting females. Bins 4 and 5 (orange and red, respectively) account for $>90\%$ of nest locations used to build and test the model. Landscapes with active leks contained up to 2 times greater predicted nesting habitat than random locations. RSF = resource selection function.

while systematically varying either sagebrush canopy cover within 15 m or percent area classified as high-density sagebrush in a GIS within a 100-m buffer over their observed range of values. We computed odds of habitat use with the logistic equation for each simulation. We then ordered odds ratios and used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for upper and lower 95% confidence intervals. We gave context to these analyses by comparing odds of use with the graphical distribution of the key predictor at available locations throughout the study area.

RESULTS

Habitat Selection

Local-scale features with odds ratios that did not overlap 1.0 included sagebrush canopy cover, sagebrush density, average shrub height, and average Robel value. We excluded sagebrush density from models because it was correlated with sagebrush canopy cover ($r = 0.74$). The final local-scale model included the average Robel value and the quadratic term for sagebrush canopy cover (Table 1). Selection was

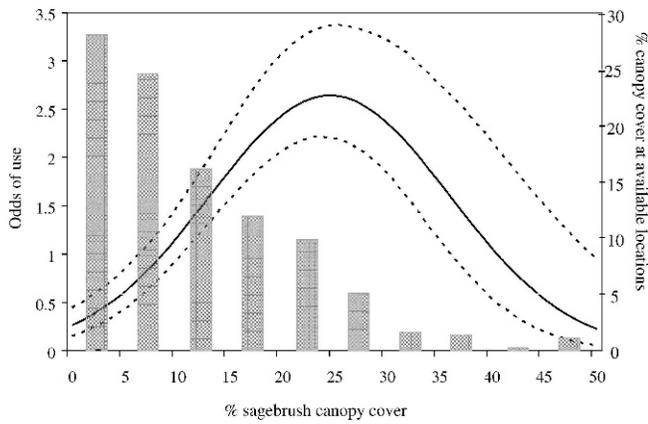


Figure 2. Odds of sage-grouse use versus available habitat with increasing sagebrush canopy cover within 15 m of the nest, Powder River Basin, Montana and Wyoming, USA, 2004–2006. We based odds (solid line) and 95% confidence intervals (dashed line) on 5,000 bootstrap samples with sagebrush canopy cover varying between 0% and 50%. Gray bars represent percent of available locations within each sagebrush canopy cover category ($n = 381$).

positively related to higher visual obstruction around the nest (15.6 cm [SE = 0.4] at nests vs. 11.7 cm [SE = 0.4] at available points). Sagebrush canopy cover averaged 19.1% (SE = 0.5) at nests compared to 11.6% (SE = 0.5) at available locations. Odds of use were highest at 25% sagebrush canopy cover and females were twice as likely to nest in stands of sagebrush when canopy cover was between 17% and 32% (Fig. 2). Sagebrush canopy cover >40% made up only 2.7% of available locations and only 1.6% of nest locations. Sagebrush canopy cover <10% occurred at 52.8% of available locations but only at 11% of nest locations.

Landscape-scale features with odds ratios that did not overlap 1.0 included terrain roughness within 100 m, percent grassland within 100 m, percent conifer within 100 m, percent area of high-density sagebrush ($\geq 10\%$ canopy cover) within 100 m, and sparse vegetation within 100 m. We evaluated percent riparian habitat within 350 m because odds ratios did not overlap 1.0. We evaluated percent riparian, percent area high-density sagebrush, percent tilled agriculture land, and percent grassland at 1,500 m. The landscape model included percent grassland within 100 m, a quadratic term for percent high-density sagebrush within 100 m, terrain roughness within 100 m, percent conifer within 100 m, percent riparian habitat within 350 m, and percent agriculture within 1,500 m (Table 2). We removed agriculture at 1,500 m from the final model because during validation the coefficient for this variable switched signs, standard errors increased, and the odds ratio overlapped 1.0. Nesting sage-grouse selected sagebrush-dominated landscapes with less riparian (0.3% [SE = 0.1] around nests vs. 1.4% [SE = 0.2] around available points; $P < 0.001$), less grassland (4.6% [SE = 0.5] vs. 11.1% [SE = 0.9]; $P = 0.002$), and less conifer (0.4% [SE = 0.1] vs. 1.2% [SE = 0.7]; $P = 0.022$). Females also selected for less rugged terrain and for high-density sagebrush habitat within 100 m (52.3% of area around nests [SE = 1.3] vs. 41.6% [SE = 1.5] available points; $P =$

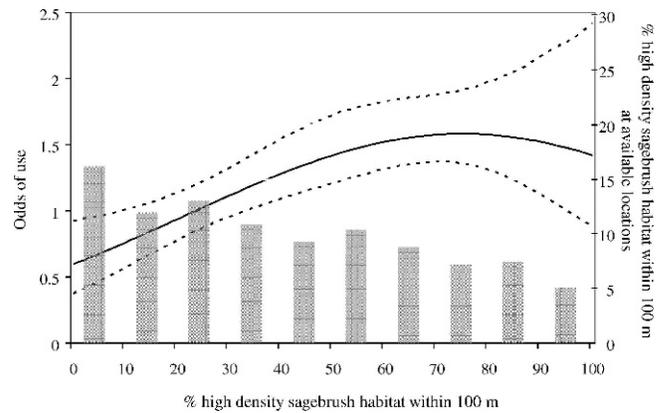


Figure 3. Odds of sage-grouse use versus available high-density sagebrush habitat (>10% canopy cover) within 100 m of nests, Powder River Basin, Montana and Wyoming, USA, 2004–2006. We based odds (solid line) and 95% confidence intervals (dashed line) on 5,000 bootstrap samples with percent high-density sagebrush within 100 m varying between 0% and 100%. Gray bars represent percent of available locations within each habitat category ($n = 381$).

0.001). Odds of use were highest when 75% of the area within 100 m of a nest had high-density sagebrush (odds = 1.58 [95% CIs = 1.36–1.91]; Fig. 3). Average odds of use remained >1.0 at 100% high-density sagebrush but dropped below 1.0 when <25% of area around the nest had high-density sagebrush (Fig. 3). Selection for high-density sagebrush habitat was inversely related to its abundance; only 14.6% of available locations had $\geq 75\%$ high-density sagebrush habitat (Fig. 3).

Multiscale Models

All variables from local- and landscape-scale models were included in the final multiscale model except the quadratic term for percent area of high-density sagebrush within 100 m (Table 3). Sage-grouse selected for less rugged topography within 100 m, for intermediate sagebrush canopy cover within 15 m (Fig. 2), against conifer and grassland within 100 m, and against riparian habitat within 350 m in the best approximating model (Table 3). The multiscale model had overwhelming statistical support ($w_i =$ approx. 1.0; Table 4) compared to either local-scale (Table 1) or landscape-scale (Table 2) models. Variance decomposition analysis quantified that local-scale variables explained 50% of pure variation, landscape-scale variables explained 20% of pure variation, and 30% was shared.

Table 4. Ranking of model strengths for local, landscape, and multiscale habitat models for greater sage-grouse nests ($n = 381$) in the Powder River Basin, Montana and Wyoming, USA, 2004–2006.^a

Model	LL ^b	K^b	AIC ^b	Δ AIC ^b	w_i^b
Local + landscape	-414.7	8	845.40	0.00	approx. 1.00
Local	-436.4	4	880.41	35.01	0.00
Landscape	-475.8	7	907.68	62.28	0.00

^a Final variables used to represent each model class (local, landscape, or local plus landscape combined) are detailed in Tables 1–3 with effect estimates and measures of precision for each variable.

^b Log-likelihood (LL), no. of parameters (K), Akaike's Information Criterion value (AIC), change in AIC value from the top model (Δ AIC), and Akaike wt (w_i).

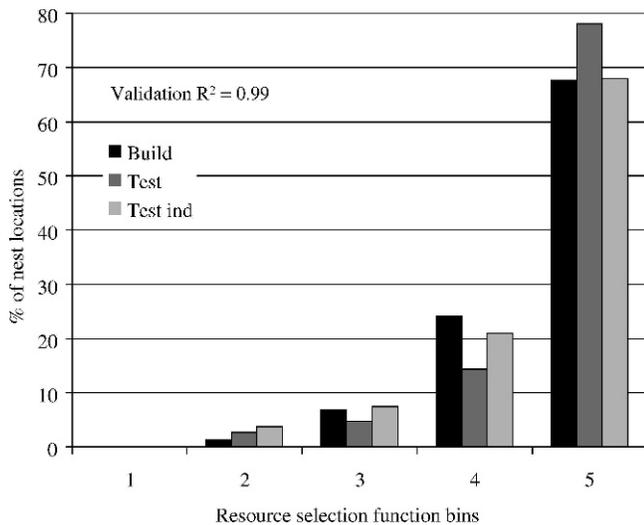


Figure 4. Percent of nest locations in 5 bins that we used to build ($n = 381$ nests from 2004 to 2006) and test ($n = 146$ nests from 2003 and 2007) the occurrence model for nesting sage-grouse, Powder River Basin, Montana and Wyoming, USA, 2003–2007. Nest locations we used to test the model were independent by year (Test $n = 146$) and by year and individual (Test ind $n = 88$). Each resource selection function category accounted for 20% of our study area. Increasing bars across build and test data sets indicate habitat selection by nesting sage-grouse.

High-density sagebrush and riparian at 1,500 m were not as strong of predictors of nest sites as high-density sagebrush at 100 m and riparian at 350 m and dropped out in model selection. Both high-density sagebrush and riparian were correlated between scales ($r = 0.61$ high-density sagebrush at 100 m and 1,500 m; $r = 0.63$ riparian at 350 m and 1,500 m) but were not correlated enough to be excluded from analyses ($r \geq 0.7$). We investigated these variables ad hoc because of the strength of correlations. Standard errors of landscape coefficients became inflated and their odds overlapped 1.0 when included with the same variable quantified at smaller landscape scales. However, percent area with high-density sagebrush within 1,500 m, and riparian within 1,500 m, were strong predictors of habitat selection when not included with high-density sagebrush at 100 m and riparian at 350 m. Selection was positively related to percent high-density sagebrush habitat (44.6% [SE = 0.8] around nests vs. 40.7% [SE 0.7] around available points; $P = 0.020$) and negatively associated with riparian habitat (0.4% [SE 0.1] vs. 1.2% [SE 0.7]; $P < 0.001$).

Model Validation

Our landscape-scale model (Table 2) accurately predicted an independent set of nest locations. Regression validations showed a high coefficient of determination value (R^2), a slope not different from 1.0, and an intercept not different from zero when comparing the percent of nests located in each RSF between build and test data sets, which is indicative of good model fit (Fig. 4). Likewise, nests in the test data set were located within RSF bins in proportion to their expected frequency of use (all χ^2 statistics > 0.05). Approximately 70% of nests used to build and test our model fell within 20% of the landscape (RSF bin 5) and

Table 5. Percent of the landscape classified as habitat for nesting sage-grouse and total sagebrush cover within 3 km, 5 km, 10 km, and 20 km of leks and random locations, Powder River Basin, Montana and Wyoming, USA, 2004–2006. Leks we used in analyses had ≥ 5 displaying males in 2005 ($n = 88$). Percent predicted nesting habitat is defined as resource selection function bins 4 and 5 (red and orange areas; Fig. 1) because these bins include $>90\%$ of nests.

% habitat	3 km	5 km	10 km	20 km
% predicted nesting habitat				
Leks	61.9	60.1	56.5	56.6
±95% CI	4.9	4.6	4.2	3.8
Random	32.1	31.4	31.3	34.7
±95% CI	5.7	5.2	4.9	4.9
% total sagebrush cover				
Leks	71.4	71.1	69.7	67.2
±95% CI	3.1	2.7	2.5	2.4
Random	54.1	53.8	54.0	54.9
±95% CI	4.0	3.7	3.4	3.0

$>90\%$ of locations were within 40% of the landscape (RSF bins 4 and 5 combined; Fig. 4).

Abundance of predicted nesting habitat corresponded with active lek locations at large spatial scales (3–20 km; Fig. 1; Table 5). In our study $>95\%$ of nests were within 10 km of leks where we captured females (54%, 79%, and 97% of nests were within 3 km, 5 km, and 10 km of a lek, respectively). Landscapes with active leks contained 1.6–2.0 times greater predicted nesting habitat (RSF bins 4 and 5) than random locations (Table 5).

DISCUSSION

Research on other species has shown that multiple spatial scales often define species–habitat relationships, and this is certainly the case for sage-grouse. We found that both local- and landscape-scale habitat features influenced nesting-habitat selection by sage-grouse individually, but multiscale models were more predictive than those containing only local- or landscape-scale features. The strength and diversity of landscape-scale features demonstrate that nesting decisions are not solely based on amount of sagebrush and visual obstruction at the nest site. Multiscale analyses increase our understanding of nesting biology with important implications for management. Sage-grouse biologists know that local-scale features influence habitat selection (e.g., Hagen et al. 2007), but variance decomposition offered new insight into the importance of landscape context (Borcard et al. 1992, Cushman and McGarigal 2002, Lawler and Edwards 2006). We identified the amount of confounding between scales by explicitly quantifying shared and pure variation between local- and landscape-scale features (Cushman and McGarigal 2002). This biological understanding could not have been accomplished by simply selecting an AIC best model (Burnham and Anderson 2002) or from research implemented at any single scale.

Our results indicate that treatments applied in areas with an unsuitable landscape context are unlikely to achieve desired conservation results. The importance of landscape context is consistent with recent analyses showing large-scale habitat features were the dominant variables structur-

ing shrub-steppe and grassland bird communities (Knick et al. 2008, Ribic et al. 2009). The documented importance of landscape context is also consistent with a recent range-wide analysis of population persistence, which concluded that maintaining large expanses of sagebrush habitat is the highest priority for conserving sage-grouse populations (Aldridge et al. 2008). State and federal guidelines (e.g., Connelly et al. 2000) should be updated to include the importance of landscape context in management of nesting habitats for sage-grouse. Additional studies sampling a wider range of variation within the sage-grouse distribution than current published models will be necessary to identify the most important features for managing sage-grouse habitats at multiple scales.

Seasonal context can be incorporated into management plans by building landscape-scale predictive models during other seasons, such as winter or brood-rearing within the same spatial area (Homer et al. 1993, Aldridge and Boyce 2007, Doherty et al. 2008). Incorporating seasonal context into landscape-scale management can ensure actions intended to enhance one season do not compromise habitat requirements in another. Habitat relationships in our study showed that sage-grouse selected for less rugged patches of sagebrush habitat with little tolerance for conifer, grassland, and riparian habitats at landscape scales. However, some riparian habitats devoid of woody vegetation, which sage-grouse avoid within 350 m during nesting, provide forbs and insects for broods in summer (Crawford et al. 2004, Dahlgren et al. 2006). Many previous works have demonstrated that context in both time and space across multiple scales is ecologically important (e.g., Rotenberry and Wiens 1980, O'Neill et al. 1986, Wiens 1989, Turner et al. 2001, Scott et al. 2002).

Context within the local scale was also important to interpretation of results. A quadratic response indicated the highest odds of nesting in stands with sagebrush canopy cover between 10% and 41% (Fig. 2). This estimate is similar to published guidelines (range = 15–25%; Connelly et al. 2000) based on descriptive studies and similar to findings from a recent meta-analysis (\bar{x} = 20–24%; range = 15–59%; Hagen et al. 2007). A common management practice is to remove dense stands of sagebrush to promote forb production and improve brood-rearing habitat. However, dense sagebrush (>40% canopy cover) was limited in the PRB (2.7% of available locations; Fig. 2), and although birds rarely nested in it, dense sagebrush can provide critical food and cover in winter after heavy snows (Beck 1977, Hupp and Braun 1989). Our findings corroborate those of Woodward (2006) and Dahlgren et al. (2006), who cautioned against managing for one life stage in one season at the expense of habitat requirements in others. Distribution of available habitat at random locations suggests a trade-off for brood habitat is unnecessary because many areas exist where brood forb plots could be placed outside of sagebrush canopy covers >10% and yet within 10 m of sagebrush stands (Dahlgren et al. 2006; Fig. 2).

Landscape-scale GIS habitat selection maps provide powerful tools for conservation planning. However, GIS

habitat models will only explain part of the variation in habitat selection for some time (50% in our study) because current technological limitations and cost of new remote-sensing platforms will preclude remote mapping at the detail of field-based habitat measures (e.g., grass ht, species-specific shrub cover). Therefore, habitat selection maps can be powerful, but they can also be misleading if underlying models are not robust. Thus, independent validations are critical in testing reliability of habitat selection maps for management (Kristan and Scott 2006). An independent set of radiomarked females showed the same pattern of habitat selection ($R^2 = 0.99$) in different years in our study. As a second and novel test, we evaluated the hotspot theory of lek placement, reasoning that our model should predict more suitable habitat around leks than random points if in fact males establish leks in landscapes where females prefer to nest (Schroeder and White 1993, Gibson 1996). Our model predicted up to twice the amount of nesting habitat (RSF bins 4 and 5) within 3–20 km of leks than at random points (Table 5). Validation with independent data sets and tests of predictions based on ecological theory provide a high degree of certainty that our landscape model is robust. Techniques such as k-fold cross-validation should be used if independent validation data sets do not exist (e.g., Boyce et al. 2002, Johnson et al. 2006).

MANAGEMENT IMPLICATIONS

New GIS-based models allow managers to increase their efficiency and effectiveness by targeting portions of the landscape where conservation actions are most likely to enhance populations. Our findings provide insights into ways of using GIS-based models to identify the best places and management actions to enhance populations at local scales. As an example, results from our landscape-scale model support the idea that juniper encroachment could displace nesting sage-grouse, as evidenced by strong avoidance of conifer within 100 m. Landscape-scale GIS models can be used to target treatment of junipers in areas that otherwise would have suitable landscape context for nesting sage-grouse. Our results also indicate that local-scale habitat variables that cannot currently be mapped in a GIS will strongly influence sage-grouse nest-site selection, but only within priority nesting habitats defined at the landscape scale. Thus, managers need to integrate landscape features into local-scale habitat management such as where to implement local-scale habitat improvements (e.g., pinyon [*Pinus* spp.]–juniper [*Juniperus* spp.] control, sagebrush planting, increasing grass ht).

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