

## CHAPTER ELEVEN

### Linking Habitat Selection and Brood Success in Greater Sage-Grouse

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**Abstract.** Examining links between the fitness of individual organisms and their habitat-based decisions is useful to identify key resources for conservation and management of a species, especially at multiple spatial scales because selection of habitat attributes may vary with spatial scale. Decisions of habitat use by brood-rearing Greater Sage-Grouse (*Centrocercus urophasianus*) may influence the survival of chicks. We conducted radiotelemetry on 38 sagegrouse broods within Mono County, California, during 2003–2005. At relocation and random sites, we measured habitat characteristics at three spatial scales using field procedures (scale, 0.03 ha) and Geographical Information System tools (scales, 7.9 ha and 226.8 ha). We then conducted three data analyses using an information-theoretic modeling approach. The purpose of these analyses was to: (1) identify habitat factors that were selected (defined as use disproportionate to availability) by sage grouse broods; (2) identify habitat factors associated with brood success (defined as  $\geq 1$  live chick at 50 days post-hatch; 24 were successful, 14 unsuccessful); and (3) evaluate brood

success as a function of habitat selection indices for brood-rearing sage grouse. At the smallest spatial scale (0.03 ha), grouse with broods selected areas with greater perennial forbs and higher richness of plant species. At larger scales (7.9 ha and 226.8 ha), areas with Utah juniper (*Juniperus osteosperma*) and singleleaf pinyon pine (*Pinus monophylla*) encroachment were avoided by grouse. Most importantly, the probability of fledging a brood increased as sage grouse females selected habitats with greater densities of perennial forbs (0.03 ha) and higher meadow edge (perimeter to edge ratio; 7.9 ha), perhaps because these areas provided a balance of food and protective cover for chicks. These results suggest that managers should discourage tree encroachment and preserve and enhance sagebrush stands interspersed with perennial forbs and a mixture of small upland meadows.

**Key Words:** brood success, *Centrocercus urophasianus*, forb, Greater Sage-Grouse, habitat, juniper, pinyon, selection, spatial scale, meadow.

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Patterns in habitat selection—the disproportionate use to availability of resources or conditions by organisms—are complex, and the study of these patterns has become a priority in conserving wildlife species (Morrison 2001, Brotons et al. 2004). Organisms are thought to use resources and occupy areas that optimize their fitness (i.e., survival and reproduction; Wiens 1989, Rosenzweig 1991). Beneficial management practices are those that preserve and improve environmental factors that are selected by an individual organism for the purpose of increasing survival and reproduction (Aldridge and Boyce 2008). However, to identify these environmental factors, it is challenging and often necessary to identify links between an organism's fitness and its habitat-based decisions (Morris et al. 2008).

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage grouse) populations are declining throughout their range (Schroeder et al. 1999, Connelly et al. 2004), and this decline is attributed in part to low survival of broods as well as other vital rates (Schroeder et al. 1999, Aldridge and Brigham 2001). Despite the importance of this life stage, factors influencing the survival of chicks and broods are not well understood (Gregg 2006; Aldridge and Boyce 2007, 2008). Numerous studies have described habitat use and selection by female sage grouse with broods (Klebenow 1969, Wallestad 1971, Drut et al. 1994a, Sveum et al. 1998), and these studies have played important roles in management guidelines (Braun et al. 1977, Connelly et al. 2000). Although these types of studies have been largely informative they did not link habitat use or selection to an aspect of grouse fitness, such as relationships between the success of fledging chicks and habitat-related decisions by females. It is generally assumed that selection of habitat attributes is related to an aspect of fitness, but these links had not been quantified and understood for many sage grouse populations. Some recent research that explored relationships between environmental attributes that were selected by grouse and their fitness indicated that understanding these relationships further will inform grouse management decisions (Chi 2004; Aldridge and Boyce 2007, 2008).

Habitat selection and fitness research on sage grouse have been largely conducted at a single spatial scale; data analyses at multiple spatial scales are more informative. Relationships between habitat and fitness are inherently scale-sensitive (Mayor

et al. 2009). Detecting informative temporal and spatial scales is essential to consider in ecological and conservation research (Allen and Hoekstra 1992), because scale can influence the strength of associations between independent and dependent variables (Boyce 2006). At relatively small spatial scales, habitat factors that are selected by brood-rearing sage grouse include forb abundance (Klebenow and Gray 1968, Drut et al. 1994a, Sveum et al. 1998), sagebrush cover (Aldridge and Brigham 2002, Thompson et al. 2006), grass cover (Thompson et al. 2006), and insect abundance (Klebenow and Gray 1968, Drut et al. 1994a, Thompson et al. 2006). Less studied are characteristics at larger spatial scales, but some authors have reported meadows and lake bottoms as important (Oakleaf 1971, Drut et al. 1994a, Aldridge and Boyce 2008). Additionally, pinyon (*Pinus* spp.) and juniper (*Juniperus* spp.) encroachment into sagebrush-steppe ecosystems is thought to negatively influence sage grouse populations (Connelly et al. 2004). However, empirical findings of large-scale effects related to this encroachment are lacking. Additionally, knowledge of specific links between habitat decisions by brood-rearing sage grouse and the success of broods at different spatial scales would benefit our understanding of sage grouse ecology and refine management strategies (Garton et al. 2005, Aldridge and Boyce 2008).

During the research design phase, the choice of scale may not be intuitive (Bowyer and Kie 2006), and a decision to choose a single scale may produce misleading conclusions (Mayor et al. 2009). For example, habitat attributes that are identified as influential to the response of an organism at one spatial scale may not be influential at another scale, or these attributes may have the reverse effect (Wiens 1989, Schneider 1994, Mahon et al. 2008). We chose to evaluate habitat attributes at multiple spatial scales to provide a more complete representation of potential habitat-related fitness associations for brood-rearing sage grouse. We employed this multiscale approach in the southwestern portion of sage grouse range because information on these geographically isolated and genetically distinct populations was limited (Benedict et al. 2003, Oyler-McCance et al. 2005). Population trends within Mono County were reported as relatively stable compared to other portions of sage grouse range (Connelly et al. 2004).

Our study consisted of three objectives. First, we examined habitat selection by females rearing

broods at three spatial scales (field, 0.03 ha; GIS, 7.9 ha and 226.8 ha). Second, we identified associations between brood success (defined here as  $\geq 1$  live chick at 50 days post-hatch) and habitat factors at these three scales. Third, we developed selection indices for sage grouse (based on objective 1) and used a quantitative method to link habitat selection indices to brood success at the same three scales. Explanatory habitat factors were chosen based on factors previously reported from studies elsewhere in sage grouse range (Schroeder et al. 1999, Connelly et al. 2004, Crawford et al. 2004). These factors included riparian zones, meadows (i.e., edge vs. area), plant species richness, sagebrush cover, grasses, and forbs. To our knowledge, this study is the first to investigate the differences in annual and perennial forbs and empirically evaluate the effects of pinyon and juniper encroachment on sage grouse brood success.

## STUDY AREA

We collected data in Mono County, California, at a site divided into five subareas (within 65 km of longitude 119°11' 1.94" W and latitude 38°6' 30.80" N): Sweetwater Mountains, Fales, Bodie Hills, Parker Meadows, and Long Valley (Fig. 11.1). The five subareas encompassed 481 km<sup>2</sup> and covered >59% of Mono County, which lies on the eastern side of the Sierra Nevada Mountains adjacent to the Nevada border. We defined the subareas as known concentrations of grouse that were not known to interchange with grouse in other subareas. We did not observe movements between subareas of the radio-collared grouse in this study.

Topography was highly variable, with several mountain ranges separating the northern and southern ends of the study area. Elevations ranged from 1,660–3,770 m and climate was characterized by hot, dry summers and cold winters with an average annual precipitation during the study of 36 cm. Temperatures ranged from -34°C to >32°C, with an average minimum monthly temperature of -14°C in January and an average maximum of 28°C in August (Western Regional Climate Center, Reno, NV). Vegetation types at all subareas were similar, dominated by mountain big sagebrush (*Artemisia tridentata vaseyana*), interspersed with areas of low sagebrush (*A. arbuscula*) and Wyoming big sagebrush (*A. t. wyomingensis*). Silver sagebrush (*A. cana*) and basin big sagebrush (*A. t. tridentata*) occurred



Figure 11.1. Study areas for Greater Sage-Grouse in Mono County, California, 2003–2005.

locally. Other common shrub species included snowberry (*Symphoricarpos* spp.), currant (*Ribes* spp.), bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), and Mormon tea (*Ephedra viridis*). Primary grass species included needlegrass (*Hesperostipa comata*), squirreltail (*Elymus elymoides*), and Indian ricegrass (*Achnatherum hymenoides*). Cheatgrass (*Bromus tectorum*) was present but uncommon. Dominant forbs included phlox (*Phlox* spp.), lupine (*Lupinus* spp.), buckwheat (*Eriogonum* spp.), and hawksbeard (*Crepis* spp.; Kolada et al., 2009). Singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) woodlands occurred at elevations of 1,850–3,000 m.

## METHODS

### Field Techniques

We captured 72 female sage grouse using spotlighting techniques at night (Giesen et al. 1982, Wakkinen et al. 1992) during spring (March–April) and fall (October–November) during 2003–2005. We fitted each grouse with a 21-g necklace-mounted radio transmitter (Advanced Telemetry Systems, Isanti, MN), which included an activity sensor (Sveum et al. 1998). We located each sage grouse four times a week during the March–June breeding season using Yagi antennas and receivers

(Advanced Telemetry Systems, Isanti, MN) to within 30 m by ground. Relocation coordinates in Universal Transverse Mercator (UTM) units (datum NAD83, UTM zone 11) were recorded using handheld Global Positioning System (GPS) devices. We assumed females were nesting when movements became localized (Connelly et al. 1993). We visually confirmed nest status but avoided flushing grouse to prevent observer-induced abandonment.

We visually checked nests every other day. We relocated 38 female sage grouse (21 adults, 17 yearlings) every 1–3 days following determination of nest fate. At relocations, we confirmed the presence or absence of chicks and then obtained microhabitat measurements at a sample of these relocations ( $n = 212$ , 38 broods). If we did not detect  $\geq 1$  live chick, microhabitat measurements were not conducted. Therefore, we obtained habitat measurements for all female sage grouse until chicks were no longer observed. We relocated all broods at 50 days post-hatch and classified a successful brood as a female with  $\geq 1$  live chick at 50 days post-hatch. In instances when no chicks were detected (unsuccessful), we conducted a second search within 1–3 days to prevent scoring false negatives.

#### Field Explanatory Variables

In the field, we employed three methods to measure habitat characteristics that were associated with brood locations using a 0.03-ha spatial scale (centered on the location), which has been used elsewhere (Drut et al. 1994a). First, we used the line-intercept method (Canfield 1941) to estimate the percent of sagebrush canopy cover (SAC) along a 20-m transect in a random direction centered at the grouse relocation point. This technique consisted of measuring distances along each transect where shrub vegetation intersected the line, then dividing the sum of these distances by the overall transect length. Small vegetation gaps (no intersecting vegetation within a 5-cm distance) were included in the measurement as shrub canopy cover (Boyd et al. 2007). Second, we estimated percent cover of understory perennial forbs (PEF), annual forbs (ANF), and live and residual grass (GRS) using five uniformly spaced  $20 \times 50$  cm plots at the vegetation point center and along the transect (Daubenmire 1959). Within the plots we counted the number of plant species to estimate species richness (SPR). Last, we recorded visual obstruction (VIO)

using a Robel pole (Robel et al. 1970) at the five uniformly spaced locations along each 20-m transect. Habitat measurement values were averaged across subplots to represent the relocation site at the 0.03-ha spatial scale.

#### GIS Explanatory Variables

We used a geographical information system (GIS) to measure multiple landscape-level covariates (ArcGIS, ESRI software, Redlands, CA). We digitized habitats into a vector coverage using digital orthophotography (1-m resolution) from the National Agriculture Imagery Program (NAIP, U. S. Department of Agriculture, Salt Lake City, UT). Mapping scale was 1:2,500 m spatial resolution. We classified landscape-level features across study areas as riparian (2.1%), meadow (7.8%), sagebrush-steppe shrubland with pinyon-juniper encroachment (5.6%), and sagebrush-steppe shrubland without pinyon-juniper (71.0%). We defined areas of pinyon-juniper encroachment by classifying areas that consisted of  $\leq 40$  pinyon or juniper trees per hectare in a sagebrush-dominated environment. These areas consisted of less than 5% tree canopy cover and were considered early succession, where the shrub layer was considered intact (Miller et al. 2005). Our objective was to investigate areas where pinyon and juniper were in the initial stages of encroaching (i.e., phase I). Therefore, we included these areas ( $\leq 40$  trees/ha) in our data analyses, but excluded areas with higher tree densities (middle and late stages of succession) because these areas are not thought to be suitable for sage grouse. We categorized moist areas as meadow or riparian. Meadow consisted of seasonally wet areas vegetated primarily by non-woody plants, including succulent forbs and grasses. These areas included upland meadows (i.e., springs) and bottomland agricultural areas (i.e., fields and pastures), where the water table is at or near the surface. We classified riparian zones as streams and hydrophilic plant communities associated with the stream margins including quaking aspen (*Populus tremuloides*), Fremont cottonwood (*Populus fremontii*), and willows (*Salix* spp.). We chose to examine these factors based on *a priori* hypotheses derived from other findings and suggestions in the literature (Dunn and Braun 1986, Connelly et al. 2004). The remaining landcover types (13.5%) consisted of ponds, lakes, mountain shrub, and open canopy pine forest.

We then mapped the brood relocation sites in a GIS. We determined the spatial scales of analyses by calculating the daily mean and maximum movements of each grouse and then averaged these values across all grouse and subareas (mean = 159 m, maximum = 850 m). We used these averages as radii to calculate surface areas (7.9 and 226.8 ha, respectively) that were centered on each bird location. We used these spatial scales because they were relevant to sage grouse within Mono County. Because the same scale was required across subareas for the model analyses, we did not calculate separate averages for each subarea. We then calculated the proportion of each habitat type occurring within each radius at bird relocation sites. We developed log-ratio covariates [i.e.,  $\log(a_i/b)$ ; Aebischer et al. 1993, Kurki et al. 1998] for each habitat type of interest, where sagebrush-steppe represented the denominator ( $b$ ) and the remaining classes separately represented the numerator ( $a$ ; i.e., ratio meadows/sagebrush = rME, ratio mountain shrub/sagebrush = rMO, and ratio pinyon-juniper encroachment/sagebrush = rPJ; Table 11.1). This method was appropriate because it remedied a lack of independence problem that may be associated with habitat proportions (Aebischer et al. 1993, Kurki et al. 1998). Furthermore, because sage grouse are sagebrush obligates (Rowland et al. 2006), it was appropriate to interpret our results as an influence of habitat attribute  $a$  relative to sagebrush  $b$  (Kurki et al. 1998, Manzer and Hannon 2005).

We examined the influence of meadow edge density on habitat selection and brood success to evaluate the hypothesis that female grouse prefer smaller patchy meadows (Dunn and Braun 1986, Aldridge and Boyce 2007) because greater edge likely leads to successfully rearing chicks. We calculated the density of meadow edge (MEE) within each spatial scale at the relocation sites. Edge density was a ratio of meadow perimeter (m) to surface area (m<sup>2</sup>) and was used to account for differences in effects between multiple small meadows (i.e., more edge) versus fewer, larger meadows (i.e., less edge) at each scale.

We used the NEAR command in ArcGIS to measure the distance between the relocation and the nearest edge of a meadow as the variable (DIM). We then reclassified meadows and riparian zones (i.e., surface water with trees) to be the same (i.e., mesic site as a meadow or riparian) and remeasured

the distance to the nearest area as another distance variable (DIMR). The variable DIMR was compared to DIM to evaluate the hypothesis that grouse prefer moist areas regardless of differences in vegetation (i.e., trees).

We employed a used-available design to evaluate habitat selection by brood-rearing sage grouse and calculated resource selection functions (RSF; Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). To characterize available habitat, we conducted the same habitat measurements at 175 random locations using the same field and GIS techniques as those conducted at used locations (Manly et al. 2002). The proportion of these samples of random locations for each subarea was based on the proportion of used locations. Time and logistical constraints in the field prevented sampling one random location for every used location. The range of points within each subarea was 12–39 (mean = 25), which we considered an appropriate number of random points to allow us to characterize available habitat by subarea. We calculated a minimum convex polygon (MCP) of the combined grouse relocations for each subarea. The MCPs were used to represent the boundaries of available habitat at the population level (subarea). Twenty-five random locations were removed from the analysis because these locations were not within the MCP boundaries. Thus, we used 150 remaining random locations for data analyses.

## Model Development

### *Analysis I, Habitat Selection*

We evaluated habitat selection using a design II approach (Manly et al. 2002), meaning habitat use was identified at the individual grouse level but availability assessed at the population level (i.e., subarea; Erickson et al. 2001). We classified the measured resource units as available or used. We developed generalized linear mixed models (GLMM) and specified the binomial distribution (Zuur et al. 2009). The advantage of using a binomial regression approach is that resource selection functions (RSF; Manly et al. 2002) are equivalent to the logistic discriminate function, which contrasts a sample of used and available resource units (Keating and Cherry 2004, Johnson et al. 2006). We included random effect terms in the binomial models. These terms were appropriate for representing spatial



TABLE 11.1  
*Explanatory variables (means ± SE) used in analyses of brood habitat use and brood survival of Greater Sage-Grouse in Mono County, California, 2003–2005.*

Measure	Abbr.	Description	Used sites		Random sites	
			Mean	SE	Mean	SE
Field <sup>a</sup>	SAC	Sagebrush cover (%)	27.79	0.936	23.10	1.173
	VIO	Visual obstruction (cm; i.e., Robel pole)	53.73	1.456	60.52	2.903
	SPR	Species richness of all plants	5.45	0.137	4.20	0.192
	GRS	Grass (%)	5.78	0.557	5.76	1.012
	PEF	Perennial forb (%)	4.43	0.408	2.69	0.507
	ANF	Annual forb (%)	1.67	0.298	1.94	0.443
GIS <sup>b</sup>	rPJ7.9	Ratio (log) pinyon-juniper encroachment to sagebrush at 7.9 ha	0.08	0.051	1.05	0.908
	rME7.9	Ratio (log) meadow to sagebrush shrub at 7.9 ha scale	0.18	0.062	0.12	0.045
	rMOS7.9	Ratio (log) mountain shrub to sagebrush shrub at 7.9 ha scale	0.03	0.005	0.01	0.004
	MEE7.9	Meadow edge as ratio of perimeter (m) to area (m <sup>2</sup> ) of meadow at 7.9 ha scale	0.01	0.002	0.03	0.008
	rPJ226.8	Ratio (log) pinyon-juniper encroachment to sagebrush shrub at 226.8 ha scale	0.06	0.007	0.22	0.052
	rME226.8	Ratio (log) meadow to sagebrush shrub at 226.8 ha scale	0.15	0.039	2.10	1.853
	rMOS226.8	Ratio (log) mountain shrub to sagebrush shrub at 226.8 ha scale	0.02	0.004	0.03	0.003
	MEE226.8	Meadow edge as perimeter (m) to area (m <sup>2</sup> ) of meadow at 226.8 ha scale	0.05	0.005	0.03	0.003
	DIM	Distance (km) of site to nearest meadows edge	0.46	0.028	0.65	0.063
	DIMR	Distance (km) of site to nearest meadow or riparian edge	0.44	0.023	0.55	0.061

<sup>a</sup>Field measurements were conducted for microhabitat covariates at 0.03 ha scale, centered on brood and random points.

<sup>b</sup>GIS measurements were conducted on landscape-level covariates at 7.9 and 226.8 ha scales, centered on brood and random points.

clustering (subarea), temporal correlation (year), and repeated measures for data that were gathered through time on the same individual grouse (Zuur et al. 2009). Random effects account for variation that may otherwise confound the fixed effects (e.g., forb abundance) and prevent pseudoreplication (Faraway 2006, Gillies et al. 2006, Koper and Manseau 2009). Because the variance estimate of year equaled zero, we removed it from the mixed effect models. To prevent multicollinearity in predictive models,

we excluded one or two variables that covaried ( $r \geq |0.65|$ ). No variance inflation factors were  $\geq 10$  (Menard 1995).

We carried out model comparisons in two steps. In step I, we developed a candidate set of models for each scale using the explanatory variables measured in the field and GIS (Table 11.1). We developed nine models using the field measurements. Three models were additive models that consisted of two covariates. One additive model included



plant species richness and perennial forbs and represented the hypothesis that grouse select habitat based on food for young. A second additive model consisted of perennial forbs and annual forbs and represented the hypothesis that grouse select both types of forbs. A third model consisted of visual obstruction and sagebrush cover and represented the hypothesis that grouse selected habitats that provided vertical and horizontal cover for young. We also developed a model with a single explanatory variable for each of the six variables (Table 11.1) to compare with each other and with the additive models. Using the GIS data, we developed four models that consisted of a single explanatory variable at each spatial scale (7.9 and 226.8 ha).

We evaluated evidence of support for models at each scale using Akaike's Information Criterion (AIC) with second-order bias correction ( $c$ ; Anderson 2008). We evaluated uncertainty among models using AIC<sub>c</sub> differences ( $\Delta\text{AIC}_c$ ). We assigned the number of effective degrees of freedom to the individual level (i.e., individual female) and not the observation level (relocation) to prevent Type I errors. We calculated model probabilities ( $w_{\text{model } i}$ ; Anderson 2008) and reported evidence ratios (ER =  $w_{\text{model } i} / w_{\text{model } j}$ ) of the most parsimonious model compared to other models in the set (Anderson 2008). Likelihood ratio tests (Anderson 2008) were used to evaluate each model fit relative to a null model (intercept and random effects only;  $\alpha = 0.05$ ).

In step II, we used an exploratory approach to identify the most influential covariates and spatial scales to provide information for management practices. Models were developed in step II using covariates from models that fulfilled two criteria from step I: (1)  $\Delta\text{AIC}$  was  $\leq 2$  and (2) the model fit the data significantly better than the null model. Because we used covariates from the most parsimonious models in step I, numerous additive effects were possible. Therefore, we developed models with combinations between covariates but did not allow  $>2$  covariates in each model. We prevented results that might be spurious by not developing more models than sampled grouse ( $n = 38$ ; Burnham and Anderson 2002).

#### *Analysis II, Brood Success*

To estimate the effects of explanatory variables on brood success, we developed GLMM and specified the binomial distribution (Zuur et al. 2009).

Broods were scored as successful or unsuccessful. The advantage of using a binomial model in this case was to interpret the influence of explanatory variables in terms of odds ratios with 95% confidence intervals. Subarea was included as a random effect to account for spatial correlations. We did not include year in models because variance estimates equaled zero. In this case, individual grouse was not included as a random effect because measurements were averaged for each grouse. Because we were interested in the relationship between habitat selection and success, the same *a priori* models (hypotheses) that were developed for brood habitat selection were developed for brood success. Also, we used the same two-step procedure as described for habitat selection to select the most parsimonious models and identify influential covariates.

#### *Analysis III, Linking Habitat Selection to Brood Success*

We conducted a separate analysis to identify links between habitat selection and brood success. In multiple steps, we developed selection indices of each habitat factor. First, field and GIS habitat measurements at random locations were averaged at the population level (i.e., subarea). This step was necessary to characterize the available habitat per subarea. Second, we calculated averages of the explanatory variables for each individual grouse. Third, we calculated an index for each individual grouse by measuring the difference ( $\Delta$ ) between each averaged explanatory variable for the grouse (individual level) by the averaged explanatory variable of available habitat (population level). Fourth, we developed a candidate GLMM set, specifying the binomial distribution, by assigning brood success as a response variable (0 = unsuccessful, 1 = successful) and the selection indices for habitat factors as explanatory variables.

Models were developed for this analysis using covariates of the most parsimonious models from step II of the habitat selection and brood success analysis (described earlier). We only considered models with  $\Delta\text{AIC}$  values that were  $<2$ . We used all combinations but did not include  $>2$  covariates per model. Although this analysis was exploratory, we based our models (hypotheses) on factors that were identified as important to habitat selection and/or success. All statistical analyses were

conducted using Program R (“lme4” package; Bates et al. 2008, R Development Core Team 2008).

## RESULTS

The most parsimonious model for brood habitat selection (analysis I) measured in the field (0.03 ha), of the nine considered, included perennial forbs and species richness of all plants within the 20-m transect (model 1, Table 11.2). Model 2, which consisted of species richness as the only fixed effect, explained the data equally well ( $\Delta\text{AIC}_c = 0.5$ ; Table 11.2). However, model 1 was 1.3 ( $w_{\text{model 1}}/w_{\text{model 2}}$ ) times more likely to be the best-approximating model than model 2 in explaining brood habitat selection. The probability that model 1 was the best of the

candidate set of models for describing brood habitat selection at this scale was 0.56 ( $w_{\text{model 1}}$ ). Using the likelihood ratio test ( $\chi^2 = 28.1$ ,  $P < 0.001$ ), we found that model fit was significantly improved by including these fixed covariates over a model that included no fixed effects. These analyses revealed that females with broods preferred sites with greater perennial forb and species richness of all plants than those that were randomly available (Table 11.1, Fig. 11.2). On average, using the estimated parameters, each additional plant species measured in the field appeared to increase the odds of use by approximately 33% (95% CI 19–49%). The 95% CIs for the estimated slope coefficient did not include zero. The average perennial forb cover at selected sites ( $4.43\% \pm 0.41$ ) was nearly

TABLE 11.2  
Mixed binomial regression models of Greater Sage-Grouse habitat selection models for Mono County, California, 2003–2005.

Step <sup>a</sup>	Analysis	No.	Model <sup>b</sup>	K	LL	$\Delta\text{AIC}_c$	$w$	ER	$\chi^2$ <sup>c</sup>
I	Field, 0.03 ha scale	1	SPR (+), PEF (+)	5	-207.5	0	0.56	—	28.1*
		2	SPR (+)	4	-209.1	0.5	0.43	1.3	24.9*
	GIS, 7.9 ha scale	3	rPJ7.9 (-)	4	-215.4	0	0.87	—	12.2*
		4	MEE7.9 (-)	4	-217.9	4.9	0.07	12.4	7.3*
		5	rMO7.9 (-)	4	-218.3	5.9	0.05	17.4	6.6*
		6	rME7.9	4	-220.3	9.7	<0.01	124.3	2.5
	GIS, 226.8 ha scale	7	rPJ226.8 (-)	4	-215.1	0	0.98	—	12.9*
		8	MEE226.8 (+)	4	-219.7	9.2	0.01	98	12.2*
	GIS, distance	9	DIM	4	-217.4	0	0.95	—	3.7*
		10	DIMR	4	-220.4	6.1	0.05	19.0	2.33
II	Combined (GIS, field)	11	SPR (+), PJ226.8 (-)	5	-203.1	0	0.77	—	36.9*
		12	SPR (+), PJ7.9 (-)	5	-204.4	2.7	0.20	3.8	34.2*
		13	SPR (+), DIM (-)	5	-207.2	8.1	0.01	57.4	28.8*
		14	SPR (+), PEF (+)	5	-207.5	8.8	<0.01	81.5	28.1*
		15	SPR (+)	4	-209.1	9.3	<0.01	106.5	24.9*

<sup>a</sup>Step I compared models within each scale (total models,  $n = 19$ ). Covariates of models that met two criteria ( $\Delta\text{AIC} \leq 2$  and fit significantly better than null model) were included in step II. Step II compared models that were developed with  $\leq 2$  covariates of all combinations of multiple scales (total models,  $n = 14$ ).

<sup>b</sup>All models consisted of study area and repeated measures on each individual grouse as random effects. In parentheses, signs denote positive (+) or negative (-) relationship of covariate with habitat use. Models with  $\Delta\text{AIC} \geq 10$  are not presented in table. PEF = perennial forb; SPR = species richness of all plants; MEE = meadow edge; rME = ratio (log) of meadow to sagebrush; rPJ = ratio (log) of pinyon-juniper encroachment to sagebrush cover; rMO = ratio (log) mountain shrub to sagebrush; DIM = distance to nearest meadow (e.g., upland springs and dry meadows); DIMR = distance to nearest meadow or riparian area (e.g. wet area).

<sup>c</sup>Asterisks (\*) listed in table had associated  $P < 0.05$ . Column abbreviations: K = number of parameters; LL = log-likelihood;  $\Delta\text{AIC}_c$  = difference between model of interest and most parsimonious model with second-order bias correction;  $w$  = model probability, ER = evidence ratio (e.g.,  $w_{\text{model 1}}/w_{\text{model 2}}$ ; Anderson 2008);  $\chi^2$  = chi-square statistic to test log ratio model fit relative to null.

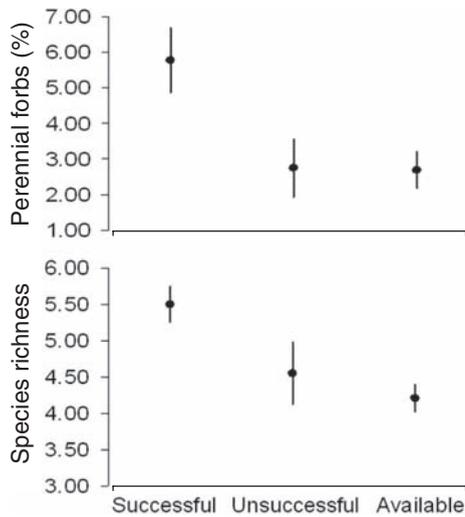


Figure 11.2. Percent perennial forb and plant species richness measured at used sites (successful and unsuccessful) of brood-rearing Greater Sage-Grouse and at random sites (available) in Mono County, California, 2003–2005.

twice as high as that of random sites ( $2.69\% \pm 0.51$ ; Table 11.1), and plant species richness at used sites ( $5.45 \pm 0.41$ ) was also greater than those at random sites ( $4.20 \pm 0.19$ ; Table 11.1).

The most parsimonious habitat selection model measured by GIS at the 7.9 ha and 226.8 ha scales consisted of the covariate pinyon–juniper encroachment (models 3 and 7; Table 11.2). Grouse avoided areas of encroachment at both spatial scales. The probabilities of pinyon–juniper models that were best for describing the data were 0.87 ( $w_{\text{model } 3}$ ) and 0.98 ( $w_{\text{model } 7}$ ) within the model sets at the 7.9-ha and 226.8-ha scales.

In a separate model set we evaluated two models; one model consisted of the covariate shortest distance to mesic sites (included meadow or riparian) and the other model consisted of a covariate distance to meadow only (no riparian). We found strong evidence for a model with meadow only covariate ( $w_{\text{model } 9} = 0.95$ ), and this model was 19 times more likely to be the best-approximating model than the model including riparian areas ( $w_{\text{model } 9}/w_{\text{model } 10}$ ). On average, using the model parameter estimates, for every kilometer away from a meadow, the odds of use were reduced by 52% (95% CI 42–66%). The 95% CIs for the estimated slope coefficient did not include zero.

Of the models considered in step II, we found that model 11 was the most parsimonious,

consisting of the covariates plant species richness (0.03 ha) and pinyon–juniper (226.8 ha), with a model probability of 0.77 ( $w_{\text{model } 11}$ ; Table 11.2). An alternative model with support included a smaller spatial scale of pinyon–juniper (7.9 ha;  $w_{\text{model } 12}$ ). Model 11 was 3.8 times more likely to be the best-approximating model than model 12 ( $w_{\text{model } 11}/w_{\text{model } 12}$ ), which indicated that grouse were 3.8 times more likely to avoid pinyon–juniper at the larger spatial scale.

Of the nine brood success models (analysis II) that included microhabitat covariates, the model with perennial forbs was the most parsimonious (model 1, Table 11.3). Twenty-four of 38 (63.1%) broods had  $\geq 1$  live chick at 50 days post-hatch. On average, using the model parameter estimates, a 1% increase in perennial forb coverage at the brood locations (0.03 ha) was associated with a 30% increase in the odds of success (odds ratio = 1.301, 95% CI = 1.004–1.680; Fig. 11.3A). The 95% CIs for the estimated slope coefficient did not include zero. Addition of a covariate of plant species richness did not improve model fit ( $w_{\text{model } 2} = 0.23$ ; Table 11.3) and showed similar support by the data than a forb-only model ( $w_{\text{model } 1} = 0.32$ ; Table 11.3). Probability of success was greater with an increase in plant species richness (Fig. 11.3B). We detected a greater average number of plant species in areas used by successful broods ( $5.5 \pm 0.2$ ) than in areas used by unsuccessful broods ( $4.5 \pm 0.4$ ). Additionally, the effect of perennial forbs alone was 3.6 ( $w_{\text{model } 1}/w_{\text{model } 4}$ ; Table 11.3) times more likely to be the best-approximating model than a model with the additive effect of perennial and annual forbs.

We found successful females were located at areas with greater meadow edge (ratio of perimeter to area,  $0.019 \pm 0.004$ ; 7.9 ha) than locations of females that were unsuccessful ( $0.004 \pm 0.001$ ; Fig. 11.3C). A model (5) that consisted of meadow edge at the 7.9-ha scale significantly improved model fit over a null model ( $\chi^2 = 4.2$ ,  $P = 0.03$ ); however, a model (9) that consisted of meadow edge at the 226.8-ha scale was not supported by the data ( $\chi^2 = 0.7$ ,  $P = 0.39$ ; Table 11.3).

In step II, the best model of the six consisted of perennial forbs (0.03 ha) and meadow edge (7.9 ha; model 15; Table 11.3). An alternative model (16) that consisted only of perennial forbs had much less support (Table 11.3). Including the additive effect of edge increased the model probability by 9.4 times ( $w_{\text{model } 15}/w_{\text{model } 16}$ ).

TABLE 11.3

Mixed-effects binomial regression models of Greater Sage-Grouse brood success ( $\geq 1$  live chick at 50 days post-hatch) for Mono County, California, 2003–2005.

Step <sup>a</sup>	Analysis	No.	Model <sup>b</sup>	<i>K</i>	LL	$\Delta AIC_c$	<i>w</i>	ER	$\chi^2c$
I	Field, 0.03 ha scale	1	PEF (+)	3	-22.0	0	0.32	—	5.1*
		2	PEF (+), SPR (+)	4	-21.0	0.7	0.23	1.4	7.1*
		3	SPR	3	-22.9	1.9	0.12	2.7	3.3
		4	PEF, ANF	4	-21.8	2.4	0.09	3.6	5.4
	GIS, 7.9 ha scale	5	MEE7.9 (+)	3	-22.5	0	0.58	—	4.2*
		6	rME7.9	3	-23.6	2.3	0.18	3.2	1.9
		7	rPJ7.9	3	-23.8	2.7	0.15	3.9	1.5
		8	rMO7.9	3	-24.3	3.7	0.09	6.4	0.5
	GIS, 226.8 ha scale	9	MEE226.8	3	-24.2	0	0.30	—	0.7
		10	rMO226.8	3	-23.6	0.2	0.27	1.1	0.6
		11	rME226.8	3	-24.5	0.6	0.23	1.3	0.2
		12	rPJ226.8	3	-24.6	0.8	0.20	1.5	<0.1
	GIS, distance-based	13	DIMR	3	-24.1	0	0.54	—	1.0
		14	DIM	3	-24.2	0.3	0.46	1.2	0.7
II	Combined (GIS, field)	15	PEF (+), MEE7.9 (+)	4	-18.4	0	0.75	—	12.3*
		16	PEF (+)	3	-22.0	4.5	0.08	9.4	5.1*
		17	PEF (+), SPR (+)	4	-21.0	5.2	0.06	13.5	7.1*
		18	MEE7.9 (+)	3	-22.5	5.4	0.05	15.2	4.1*
		19	SPR (+), MEE7.9 (+)	4	-21.3	5.8	0.04	18.2	6.5*
		20	SPR	3	-22.9	6.4	0.03	25.0	3.3

<sup>a</sup>Step I compared models within each scale (total models,  $n = 19$ ). Covariates of models that met two criteria ( $\Delta AIC \leq 2$  and fit significantly better than null model) were included in step II. Step II compared models that were developed with  $\leq 2$  covariates of all combinations of multiple scales (models,  $N = 6$ ).

<sup>b</sup>All models consisted of study area as a random effect. In parentheses, signs denote positive (+) or negative (-) relationship of covariate with habitat use. Models with AIC value exceeding the null model were not presented in table. PEF = perennial forb; SPR = species richness of all plants; ANF = annual forb; MEE = meadow edge; rME = ratio (log) of meadow to sagebrush; rPJ = ratio (log) of pinyon-juniper encroachment to sagebrush cover; rMO = ratio (log) mountain shrub to sagebrush; DIM = distance to nearest meadow (e.g., upland springs and dry meadows); DIMR = distance to nearest meadow or riparian area (e.g. wet area).

<sup>c</sup>Asterisks (\*) listed in table had associated  $P < 0.05$ . Column abbreviations: *K* = number of parameters; LL = log-likelihood;  $\Delta AIC_c$  = difference between model of interest and most parsimonious model with second-order bias correction; *w* = model probability; ER = evidence ratio (e.g.,  $w_{\text{model 1}}/w_{\text{model 2}}$ ; Anderson 2008);  $\chi^2$  = Chi-square statistic to test log ratio model fit relative to null.

In our final analysis (III) to link habitat selection indices with brood success, we considered 10 models consisting of four covariates, which were plant species richness, perennial forbs, meadow edge (7.9 ha), and pinyon–juniper encroachment (226.8 ha). The model that consisted of selection indices for perennial forbs as a covariate was the most parsimonious ( $w_{\text{model 1}} = 0.27$ ; Table 11.4), and the likelihood ratio test suggests it is significantly better

than a null model ( $\chi^2 = 4.1$ ,  $P = 0.03$ ). Perennial forbs were greater at successful brood sites than at available sites, while perennial forbs at unsuccessful and random sites did not differ (Fig. 11.2). We calculated the average selection indices (difference between used and random) in percent perennial forbs as ground cover to be  $3.3\% \pm 0.9$  for successful broods and  $0.5\% \pm 0.8$  for unsuccessful broods. The 95% CIs for the estimated slope

TABLE 11.4

Mixed-effects binomial regression models of Greater Sage-Grouse brood success ( $\geq 1$  live chick at 50 days post-hatch) as a function of indices for habitat selection in Mono County, California, 2003–2005.

No.	Model <sup>a</sup>	K	LL	$\Delta AIC_c$	$w$	ER	$\chi^{2b}$
1	$\Delta PEF$	3	-22.6	0	0.27	—	4.1*
2	$\Delta PEF, \Delta MEE7.9$	4	-21.5	0.3	0.23	1.2	6.2*
3	$\Delta PEF, \Delta rPJ226.8$	4	-22.0	1.4	0.14	2.0	5.2
4	$\Delta PEF, \Delta SPR$	4	-22.0	1.4	0.14	2.0	5.1
5	$\Delta SPR$	3	-23.9	2.7	0.07	3.9	1.3
6	$\Delta MEE7.9$	3	-24.2	3.3	0.05	5.2	0.7
7	$\Delta rPJ226.8$	3	-24.5	3.8	0.04	6.8	0.2
8	$\Delta MEE, \Delta SPR$	4	-23.7	4.9	0.02	11.4	1.7
9	$\Delta rPJ226.8, \Delta SPR$	4	-23.9	5.1	0.02	13.1	1.4
10	$\Delta rPJ226.8, \Delta MEE$	4	-24.1	5.7	0.02	16.9	0.9

<sup>a</sup> Selection indices ( $\Delta$ ) were the differences in measurements of habitat attributes between used and random location for successful and unsuccessful broods. All models are listed in the table and each one included study area as a random effect. PEF = perennial forb; SPR = species richness of all plants; MEE = meadow edge (7.9 ha); rPJ = ratio (log) of pinyon-juniper encroachment to sagebrush cover (226.8 ha).

<sup>b</sup> Asterisks (\*) listed in table had associated  $P < 0.05$ . Column abbreviations: K = number of parameters; LL = log-likelihood;  $\Delta AIC_c$  = difference between model of interest and most parsimonious model with second-order bias correction;  $w$  = model probability; ER = evidence ratio (e.g.,  $w_{\text{model 1}}/w_{\text{model 2}}$ ; Anderson 2008);  $\chi^2$  = chi-square statistic to test log ratio model fit relative to null.

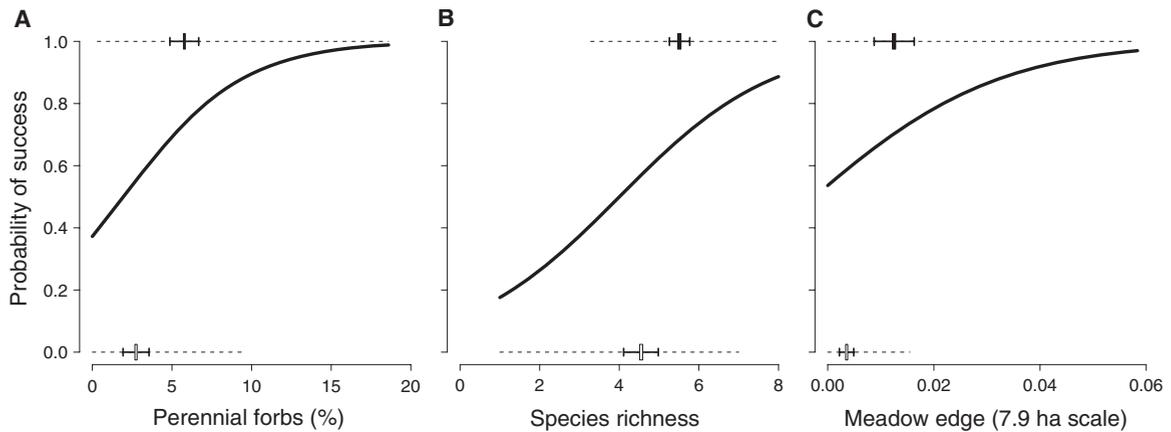


Figure 11.3. Probability of brood success in relation to (A) % perennial forb abundance (PEF), (B) species richness of all plants (SPR), and (C) meadow edge (ratio of perimeter to area) at the 7.9-ha scale (MEE) of Greater Sage-Grouse in Mono County, California, 2003–2005. Solid vertical bars represent the average of successful broods ( $n = 24$ ) and open vertical bars represent the average of unsuccessful broods ( $n = 14$ ). Solid horizontal bars represent standard error and dashed horizontal bars represent data range. Probability curves were derived from averaged parameters (intercept and slope) estimated from binomial models.

coefficient of selection indices for perennial forbs did not include zero. An alternative model with some support from the data ( $w_{\text{model 2}} = 0.23$ ; Table 11.4) consisted of an additive effect of indices for perennial forbs and meadow edge. Model 2 also fit significantly better than a null ( $\chi^2 = 6.2$ ,  $P = 0.04$ )

but did not show evidence of better fit than model 1 ( $\Delta AIC_c = 0.3$ ; Table 11.4). Model 1 was 1.2 times as likely as model 2 to be the best-approximating model. Two additional models were equally parsimonious ( $\Delta AIC_c < 2$ ) and included effects of pinyon-juniper encroachment or species richness

of all plants, but received less support than models 1 and 2 ( $w > 1.6$ ).

## DISCUSSION

The evidence in our study links maternal decision making in habitat use by brood-rearing grouse with their fecundity. The finding that brood-rearing grouse selected forb-rich environments supports results from other studies that have described similar clear, positive correlations (Klebenow 1969, Peterson 1970, Oakleaf 1971, Schoenberg 1982, Drut et al. 1994a). We also support earlier reported associations between forb abundance and brood success (Chi 2004; Gregg 2006; Aldridge and Boyce 2007, 2008). Here, we provide evidence of brood-rearing grouse that selected areas with greater perennial forbs (0.03-ha scale) and higher density of meadow edge (perimeter to area ratio; 7.9-ha scale) increased the success of fledging offspring.

Forbs are thought to provide a nutritional component to chick diet, which may be critical during initial stages of development (Drut et al. 1994b, Huwer et al. 2008). One likely explanation for this finding is that perennial forbs are associated with increased chick survival because increased forb abundance increases the growth rate of chicks (Huwer et al. 2008). Willow Ptarmigan (*Lagopus lagopus*) and Red Grouse (*L. l. scoticus*) chicks with higher growth rates are more likely to survive (Myrberget et al. 1977, Park et al. 2001). In a productive area (increased population growth rate) in Oregon, greater amounts of forbs were found in crops of sage grouse chicks than in a less productive area, where crop contents of chicks consisted primarily of sagebrush (Drut et al. 1994b). Similar to our findings, female grouse with  $\geq 1$  chick at 50 days post-hatch used sites with greater percent forbs than did females with no chicks at 50 days post-hatch on Parker Mountain, Utah (Chi 2004). Collectively, these findings and ours are consistent with the hypothesis that increased forb abundance promotes population growth by influencing survival of chicks during the brood-rearing stage (Drut et al. 1994b, Huwer 2004).

Increased density of meadow edge at the 7.9-ha scale was also related to brood success (i.e., analysis II) and decisions by females to select those sites near meadow edge appeared to influence the success of their broods (i.e., analysis III). These results support earlier research in Nevada

that indicated brood-rearing grouse often used smaller upland meadows with increased edge and surface water to feed on protein-rich forbs (Savage 1969, Oakleaf 1971). The effect of meadow edge on brood success weakened at the largest spatial scale in our study. Thus, the amount of meadow edge within a 7.9-ha area likely represented proximity of food resources that are relevant to the space use of brood-rearing sage grouse.

Meadow edge may have indirectly represented the important role of insects. For example, in sagebrush communities, increased moisture is associated with increased plant biomass (Whitford et al. 1995) and greater primary production is known to be associated with increased insect diversity (Lightfoot and Whitford 1991, Forbes et al. 2005). Particularly in the arid sagebrush ecosystems, moist areas are associated with increased insect distribution and diversity, perhaps by offering shade from plants, water sources, and humid microclimates (Wenninger and Inouye 2008). Insects supply essential nutrition for sage grouse chicks (Johnson and Boyce 1990, Drut et al. 1994b, Gregg 2006, Thompson et al. 2006) and appear to be critical for normal development, particularly during the first three weeks (Schroeder et al. 1999), in both wild (Gregg 2006) and captive settings (Johnson and Boyce 1990). Perhaps females select areas where sagebrush interfaces with mesic areas in search of Lepidoptera larvae, an order of insects that are thought to be the ultimate factor related to sage grouse chick survival in Oregon and Nevada (Gregg 2006). Moreover, insect species richness has been found to be greater in perennial plant communities compared to those of annuals (Lawton and Schröder 1977, Lawton and Strong 1981). We found greater support for a model with perennial forbs than a model with the additive effect of annual and perennial forbs.

It is possible that perennial forb abundance and meadow edge provided similar information in the observed pattern because of cross-scale correlation (i.e., correlations between predictor variables at different scales; Battin and Lawler 2006, Mahon et al. 2008). Because these variables were measured at different scales, one variable may positively reinforce the effect of the other. For example, perennial forbs may be an important component of meadow edge, which is a result of a hierarchical structure among habitat factors (Kristan and Scott 2006). However, the strong evidence of the single-variable

forb model suggested that females are choosing forbs independent of meadow edge. Furthermore, diagnostic correlations between predictor variables did not suggest multicollinearity among variables at different scales.

In evaluating habitat selection, the distinct difference between models that consisted of distance to nearest meadow versus one with distance to mesic area (including riparian) indicated that brood-rearing grouse did not prefer mesic areas that consisted of trees. We suspected that sage grouse avoided riparian areas because mammalian and avian predator densities may be greater in areas with trees. Other authors have also reported that riparian areas appear to have higher concentrations of predators (Aldridge and Boyce 2007).

The greater importance of meadow edge compared to meadow size indicated that increasing meadow size at the expense of sagebrush loss is not beneficial. Edges of small meadows provide chicks foraging areas as well as shrub for escape cover that likely reduce predation when encountering predators. Although we did not classify meadow type (i.e., upland springs vs. agriculture), these analyses clearly indicated that small, irregularly shaped meadows were more important to sage grouse broods than large areas, such as agricultural fields. Our results support similar findings in Canada (Aldridge and Boyce 2007), where brood-rearing sage grouse avoided large cultivated cropland but selected smaller meadows with patchy cover. Some evidence suggests increased vegetation provides important structure to allow chicks to avoid predation (Thompson et al. 2006). Grouse often face tradeoffs between using protective contiguous cover for survival (McNew et al., this volume, chapter 19) and relatively open areas that are productive for foraging (Aldridge and Boyce 2007). Increased heterogeneity across a landscape was associated with increased fecundity rates (including brood survival) and with reduced adult survival of Greater Prairie-Chicken (*Tympanuchus cupido*; McNew et al., this volume, chapter 19). Landscape matrices that include small upland meadows might lessen these trade-offs by providing both cover and forage. The link between selecting areas with greater edge and success of rearing broods supports management that preserves healthy sagebrush stands around the edge of small upland meadows (Dunn and Braun 1986). Because vegetation can be managed more readily than insects, we recommend practices that increase small, irregularly shaped meadows (increased perimeter to area ratio) which

interface with sagebrush habitats, as critical brood-rearing habitat.

Strong evidence indicated that brood-rearing sage grouse avoided areas of pinyon–juniper encroachment at larger spatial scales. Despite the lack of evidence of a model that explained brood success or one that identified associations between avoidance of pinyon–juniper and brood fate, these findings should still raise conservation concern. The range of pinyon and juniper woodlands expansion into the sagebrush ecosystem has increased ten-fold since the 1800s, and is thought to adversely affect sage grouse populations (Connelly et al. 2004). This expansion is causing a replacement of sagebrush and is one of the most evident changes in vegetation within the Great Basin (Miller and Tausch 2001), largely attributed to reduced occurrence of fire (Miller and Wigand 1994, Miller and Tausch 2001). These woodlands drastically reduce understory vegetation as tree density increases (Miller et al. 2005), which has been reported for Mono County (Bi-State Local Planning Group 2004). Here, the avoidance of pinyon–juniper encroachment indicated that sage grouse spatial distribution was influenced by areas that consist of  $\leq 40$  trees/ha of pinyon or juniper. A reduction in spatial distribution with encroachment may pose a significant risk to the persistence of populations.

This study was not without sampling constraints. A larger data set would have been useful in evaluating time-dependent effects in habitat selection. For example, with increased sampling, brood age categories could contain balanced data and reduce potential temporal biases. Because most unsuccessful female sage grouse retained  $\geq 1$  chick to the later stages of the 50-day brood-rearing period, and measurements for those grouse were conducted until no chicks were found, we are confident that potential time-dependent effects did not bias our results. Although our study was limited to three years, we believe these findings are representative of the fecundity of sage grouse populations in the southwestern portion of their range.

In general, it appears that the climatic and topographic factors within Mono County are favorable to sage grouse reproductive vital rates. For example, areas have relatively more mesic sites and higher annual precipitation (average = 36 cm) where sage grouse occur in Mono County than where they occur in other areas within the Great Basin (averages = 23–33 cm; Gregg 2006, Atamian 2007,

Coates and Delehanty 2008), which is in the core of sage grouse distribution (Schroeder et al. 2004). In Mono County, success of fledging chicks at 50 days post-hatch seemed high, and nest survival rates are also higher than reported for other populations range-wide (Kolada et al. 2009). Perhaps these high elevation mesic sites provide suitable conditions for successful refugia, which may partly explain the stable population growth rates observed for sage grouse in Mono County compared to the negative trends observed in other regions (Connelly et al. 2004). Furthermore, increased precipitation levels are associated with greater growth and reproduction of perennial forbs in sagebrush steppe ecosystems (Bates et al. 2006). Thus, sage grouse fecundity responses may be particularly sensitive to variation in productivity of perennial forbs and moist meadows within relatively more arid environments than those of Mono County. Additional research that investigates relationships between habitat selection and fitness in other portions of sage grouse range would be helpful. Nevertheless, management practices range-wide that preserve and enhance a landscape matrix of sagebrush stands interspersed with small upland meadows may prove to be most beneficial to sage grouse populations.

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#### LITERATURE CITED

- Aebischer, N. J., Robertson, P. A., and Kenward, R. E. 1993. Compositional analysis of habitat use from animal radiotracking data. *Ecology* 74:1313–1325.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: 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. 2001. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. *Condor* 103:537–543.
- 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.
- Allen, T. F. H., and T. W. Hoekstra. 1992. *Towards a unified ecology*. Columbia University Press, New York, NY.
- Anderson, D. R. 2008. *Model based inferences in the life sciences*. Springer Science, New York, NY.
- Atamian, M. T. 2007. Brood ecology and sex ratio of greater sage-grouse in east-central Nevada. Masters thesis, University of Nevada Reno, Reno, NV.
- Bates, D., M. Maechler, and B. Dai. 2008. lme4: linear mixed-effects models using Eigen and R package version 0.999375–27. <<http://lme4.r-forge.r-project.org/>>.
- Bates, J. D., T. Svejcar, R. F. Miller, and R. A. Angell. 2006. The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64:670–697.
- Battin, J., and J. J. Lawler. 2006. Cross-scale correlations and the design and analysis of avian habitat selection studies. *Condor* 108:59–70.
- Benedict, N. G., S. J. Oyler-McCance, S. E. Taylor, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the eastern (*Centrocercus urophasianus urophasianus*) and western (*Centrocercus urophasianus phaios*) subspecies of sage-grouse using mitochondrial control-region sequence data. *Conservation Genetics* 4:301–310.
- Bi-State Local Planning Group. 2004. Greater Sage-Grouse conservation plan for the bi-state plan area of Nevada and eastern California. 1st ed. Reno, NV.
- Boywer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions* 12:244–257.

- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269–276.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281–300.
- Boyd, C. S., J. D. Bates, and R. F. Miller. 2007. The influence of gap size on sagebrush cover estimates using line intercept technique. *Rangeland Ecology and Management* 60:199–202.
- Braun, C. L., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage grouse habitats. *Wildlife Society Bulletin* 5:99–106.
- Brotons, L., W. Thuiller, M. B. Araújo, and A. H. Hirzel. 2004. Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. *Ecography* 27:437–448.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. Springer-Verlag, New York, NY.
- Canfield, R. H. 1941. Applications of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388–394.
- Chi, R. Y. 2004. Greater Sage-Grouse reproductive ecology and tebuthiuron manipulation of dense big sagebrush on Parker Mountain. Thesis, Utah State University, Logan, UT.
- Coates, P. S., and D. J. Delehanty. 2008. Effects of environmental factors on incubation patterns of Greater Sage-Grouse. *Condor* 110:627–638.
- Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting of sage grouse in southeastern Idaho. *Condor* 95:1041–1043.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. T. Stiver. 2004. Conservation assessment of Greater Sage-Grouse and sagebrush habitats. Unpublished report. Western Association of Fish and Wildlife Agencies, Cheyenne, WY.
- 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. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2–19.
- Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:43–64.
- Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994a. Brood habitat use by sage grouse in Oregon. *Great Basin Naturalist* 54:170–176.
- Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994b. Technical note: Diets and food selection of sage grouse chicks in Oregon. *Journal of Range Management* 47:90–93.
- Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile sage grouse. *Journal of Wildlife Management* 50:228–235.
- Erickson, W. P., T. L. McDonald, K. G. Gerow, S. Howlin, and J. W. Kerr. 2001. Statistical issues in resource selection studies with radiotracked animals. Pp. 209–242 in J. J. Millspaugh and J. M. Marzluff (editors), *Radio-tracking and animal populations*. Academic Press, San Diego, CA.
- Faraway, J. J. 2006. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall, Boca Raton, FL.
- Forbes, G. S., J. W. Van Zee, W. Smith, and W. G. Whitford. 2005. Desert grassland canopy arthropod species richness: temporal patterns and effects of intense, short-duration livestock grazing. *Journal of Arid Environments* 60:627–646.
- Garton, E. O., J. T. Ratti, and J. H. Giudice. 2005. Research and experimental design. Pp. 43–71 in C. E. Braun (editor), *Techniques for wildlife investigations and management*. 6th ed. The Wildlife Society, Bethesda, MD.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224–231.
- Gillies, C., M. Hebblewhite, S. E. Nielsen, M. Krawchuk, C. Aldridge, J. Frair, C. Stevens, D. J. Saher, and C. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Gregg, M. A. 2006. Greater Sage-Grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Ph.D. dissertation, Oregon State University, Corvallis, OR.
- Huwer, S. L. 2004. Evaluating greater sage-grouse brood habitat using human-imprinted chicks. Masters thesis, Colorado State University, Fort Collins, CO.
- Huwer, S. L., D. R. Anderson, T. E. Remington, and G. C. White. 2008. Using human-imprinting chicks to evaluate the importance of forbs to sage-grouse. *Journal of Wildlife Management* 72:1622–1627.
- 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, G. D., and M. S. Boyce. 1990. Feeding trials with insects in the diet of sage grouse chicks. *Journal of Wildlife Management* 54:89–91.
- Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68:774–789.
- Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. *Journal of Wildlife Management* 33:649–662.

- Klebenow, D. A., and G. M. Gray. 1968. Food habits of juvenile sage grouse. *Journal of Range Management* 21:80–83.
- Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009. Ecological factors influencing nest survival of Greater Sage-Grouse in Mono County, California. *Journal of Wildlife Management* 73:1341–1347.
- Koper, N., and M. Manseau. 2009. Generalized estimating equations and generalized linear mixed effects models for modeling resource selection. *Journal of Applied Ecology* 46:590–599.
- Kristan, W. B., III, and J. M. Scott. 2006. Hierarchical models for avian ecologists. *Condor* 108:1–4.
- Kurki, S., A. Nikula, P. Helle, and H. Lindén. 1998. Abundance of Red Fox and Pine Marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology* 67:874–886.
- Lawton, J. H., and D. Schröder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* 265:137–140.
- Lawton, J. H., and D. R. Strong, Jr. 1981. Community patterns and competition in folivorous insects. *American Naturalist* 118:317–338.
- Lightfoot, D. C., and W. G. Whitford. 1991. Productivity of creosotebush foliage and associated canopy arthropods along a desert roadside. *American Midland Naturalist* 125:310–322.
- Mahon, C. L., K. Martin, and V. LeMay. 2008. Do cross-scale correlations confound analysis of nest site selection for Chestnut-backed Chickadees? *Condor* 110:563–568.
- Manly, 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, UK.
- Manzer, D., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. *Journal of Wildlife Management* 69:110–123.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Ecoscience* 16:238–247.
- Menard, S. 1995. Applied logistic regression analysis. Sage Publications, Thousand Oaks, CA.
- Miller, R. F., J. D. Bates, T. L. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper. Technical Bulletin 152, Agricultural Experiment Station. Oregon State University, Corvallis, OR.
- Miller, R. F., and R. J. Tausch. 2001. The role of fire in pinyon and juniper woodlands: a descriptive analysis. Tall Timbers Research Station Miscellaneous Publication No. 11:15–30.
- Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon–juniper woodlands: response to climate, fire and human activities in the US Great Basin. *BioScience* 44:465–474.
- Morris, D. W., R. Clark, and M. S. Boyce. 2008. Habitat and habitat selection: theory, tests, and implications. *Israel Journal of Ecology and Evolution* 54:287–294.
- Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management* 65:613–623.
- Myrberget, S., K. E. Erikstad, and T. K. Spidso. 1977. Variations from year to year in growth rates of willow grouse chicks. *Astarte* 10:9–14.
- Oakleaf, R. J. 1971. The relationship of sage grouse to upland meadows in Nevada. Nevada Department of Fish and Game Job Completion Report W-48-2.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the Greater Sage-Grouse across their range. *Molecular Ecology* 14:1293–1310.
- Park, K. J., P. A. Robertson, S. T. Campbell, R. Foster, Z. M. Russell, C. Newborn, and P. J. Hudson. 2001. The role of invertebrates in the diet, growth and survival of Red Grouse (*Lagopus lagopus scoticus*) chicks. *Journal of Zoology* 254:137–145.
- Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. *Journal of Wildlife Management* 34:147–155.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robel R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295–297.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *American Naturalist* 137:S5–S28.
- Rowland, M. W., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater Sage-Grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323–335.
- Savage, D. E. 1969. The relationship of sage grouse to upland meadows in Nevada. Nevada Department of Fish and Game Job Completion Report W-39-R-9.
- Schneider, D. C. 1994. Quantitative ecology: spatial and temporal scaling. Academic Press, Toronto, Ontario, Canada.
- Schoenberg, T. J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. M.S. thesis, Colorado State University, Fort Collins, CO.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. B. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobridger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363–376.

- Schroeder, M. A., J. A. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). A. Poole and F. Gill (editors), *The birds of North America* No. 425. Academy of Natural Sciences, Philadelphia, PA.
- Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998. Use and selection of brood-rearing habitat by greater sage grouse in south central Washington. *Great Basin Naturalist* 58:344–351.
- Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. *Western North American Naturalist* 66:332–342.
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20:425–426.
- Wallestad, R. O. 1971. Summer movement and habitat use by sage grouse broods in Montana. *Journal of Wildlife Management* 35:129–136.
- Wenninger, E. J., and R. S. Inouye. 2008. Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. *Journal of Arid Environments* 72:24–33.
- Whitford, W. G., G. Martinez-Turanzas, E. Martinez-Meza. 1995. Persistence of desertified ecosystems: explanations and implications. *Environmental Monitoring and Assessment* 37:1–14.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, NY.

