

Nest Site Selection by Greater Sage-Grouse in Mono County, California

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ABSTRACT Loss of nesting habitat is believed to be a factor in the decline of greater sage-grouse (*Centrocercus urophasianus*) throughout its range. Few data are available for sage-grouse in Mono County, California, USA, in the most southwestern portion of the species' range. We studied habitat selection of nesting sage-grouse in Mono County, California, from 2003 to 2005 by capturing and radiotracking females to identify nesting locations. We sampled vegetation at nest sites and randomly selected sites within 200 m of nests and within each of 5 subareas within Mono County. Nest sites were characterized by $42.4 \pm 1.3\%$ ($\bar{x} \pm SE$) shrub canopy cover, 10.5 ± 1.0 cm residual grass height, and $2.7 \pm 1.0\%$ residual grass cover. Shrub cover was the only variable found to differentiate nest sites from randomly selected sites. Unlike some other studies, we did not find understory vegetation to be important for selecting nest sites. Mean shrub cover was $38.7 \pm 1.5\%$ at random sites within 200 m of nests and $33.6 \pm 1.6\%$ at random sites at the approximate scale of home ranges, indicating that nesting females selected nesting areas that contained denser shrubs than their home range, and nest sites that contained greater shrub cover than the vicinity immediately surrounding nests. Our results suggest that managers should consider managing for greater shrub cover in Mono County than what is currently called for in other parts of sage-grouse range and that management for sage-grouse habitat may need to be tied more closely to local conditions. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):1333-1340; 2009)

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Organisms are not randomly distributed across the landscape or in habitats within the landscape (Southwood 1977). For many bird species, nest sites are chosen based on vegetation characteristics (Hines and Mitchell 1983, Martin and Roper 1988) and, for some, female experience and age may play a role (Clark and Shutler 1999). Vegetation around nest sites may produce varying degrees of concealment that could affect predation rates, which are typically the most important cause of nest loss (Ricklefs 1969). Consequently, nest success in many species of birds is related to the structure of vegetation around nest sites (Wallestad and Pyrah 1974, Hines and Mitchell 1983, Martin and Roper 1988, Gregg et al. 1994, DeLong et al. 1995). Because nest success is an important component of reproductive rates and population dynamics, selection of nest sites is potentially an important determinant of individual fitness, likely favored by natural selection (Martin and Roper 1988, Martin 1995, Clark and Shutler 1999). Potential effects of vegetation at nest sites on nest survival suggest that management of vegetation (Connelly et al. 2000) is one tool managers may use to influence dynamics of sage-grouse populations.

Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) nest in shrub steppe habitats from the western edge of the Great Basin eastward into the Dakotas and Nebraska, USA (Schroeder et al. 2004). In the sagebrush ecosystem, sage-grouse nest sites generally have greater cover of shrubs and grasses than the surrounding vegetation, which may include a mosaic of vegetation structure (Connelly et al. 2000). In Oregon, USA, cover of medium-height (40–80 cm) shrubs and tall (>18 cm)

residual grass cover was found to be greater at nest sites than in the surrounding area (Gregg et al. 1994). In Washington, USA, nests had greater shrub cover, shrub height, vertical cover height, residual cover, and litter cover than nearby random sites (Sveum et al. 1998). Holloran et al. (2005) found greater total shrub canopy cover and height at sage-grouse nest sites than at random sites in Wyoming, USA, but no difference between sites in residual grass height or cover. In contrast, no differences in vegetation, except shrub height, were found between nest sites and random sites in northern California, USA (Popham and Gutiérrez 2003).

Habitat requirements of nesting sage-grouse have not been studied in Mono County, California, the southwestern edge of sage-grouse range. Lack of local data presents problems for managers responsible for sage-grouse nesting habitat, because the vegetation community in Mono County may differ from that found in other parts of sage-grouse range (Bi-State Local Planning Group, unpublished conservation plan; hereafter Bi-state GSP). Varying amounts of herbaceous cover are present in different types of sagebrush habitats, such as mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*) and Wyoming big sagebrush (*A. tridentata* var. *wyomingensis*; Tisdale and Hironaka 1981, Hironaka et al. 1983). In addition, sagebrush biomes vary regionally between relatively xeric and mesic habitats, which can influence vegetation and complicate extrapolation of results from studies in one area to those in another (Tisdale and Hironaka 1981).

We studied habitat selection by nesting sage-grouse in Mono County, California, during 2003 to 2005. These sage-grouse are of substantial conservation concern because they are genetically distinct from all other sage-grouse

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(Oyler-McCance et al. 2005). Our objectives were to identify nest site vegetation characteristics and assess the hypothesis that females selected nesting areas and nest sites based on the vegetation structure at 2 spatial scales, the vicinity of nests and entire subareas. Based on other studies, we predicted that the cover and height of vegetation at nest sites would be greater than at random sites, which represent potential habitat available for nesting. We focused specifically on shrub cover and residual grass height and cover because ≥ 1 of these variables has been important to nesting sage-grouse in other studies (Gregg et al. 1994, Sveum et al. 1998, Holloran et al. 2005, Moynahan et al. 2007).

STUDY AREA

Within Mono County, we divided the study area into 5 subareas: Jackass Spring, Fales, Bodie Hills, Parker Meadows, and Long Valley. We defined subareas within Mono County for this study as known concentrations of birds occupying each subarea and not known to interchange regularly with sage-grouse in other subareas, based on anecdotal data from local biologists. We did not observe movements between subareas in the telemetered sample ($n = 72$) used in this study. The 5 subareas encompassed 481 km² and covered >59% of Mono County, California, which lay on the eastern side of the Sierra Nevada Mountains adjacent to the Nevada border (Fig. 1; Bi-state GSP). Approximately 84% of the county was public land, administered by United States governmental agencies, with the remaining land held by state, county, city, and private entities (Bi-state GSP). The study area was bordered by Desert Creek to the north, the Nevada state line to the east, Crowley Lake to the south, and the eastern slope of the Sierra Nevada Mountains to the west.

Topography was highly variable, with several mountain ranges separating the northern and southern ends of the study area. Elevation ranged from 1,660 m to 3,770 m; 2,790 m was the highest elevation at which we recorded nests. Climate was typical of the Basin and Range province, with hot, dry summers and cold winters (Bi-state GSP). Average annual precipitation during the study was 36 cm, with most precipitation occurring in the form of snow. Temperatures ranged from -34°C to $>32^{\circ}\text{C}$, with an average minimum temperature of -14°C in January and an average maximum of 28°C in August (Western Regional Climate Center 2005).

Vegetation was dominated by mountain big sagebrush, interspersed with areas of low sagebrush (*A. arbuscula* var. *arbuscula*) and Wyoming big sagebrush. Silver sagebrush (*A. cana*) and basin big sagebrush (*A. tridentata* var. *tridentata*) occurred locally (Bi-state GSP). 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 needle grass (*Hesperostipa comata*), squirrel tail (*Elymus elymoides*), and Indian rice grass (*Achnatherum hymenoides*). Cheat grass (*Bromus tectorum*) occurred in some isolated areas, but was generally uncommon. Dominant forbs included phlox (*Phlox* spp.), lupine

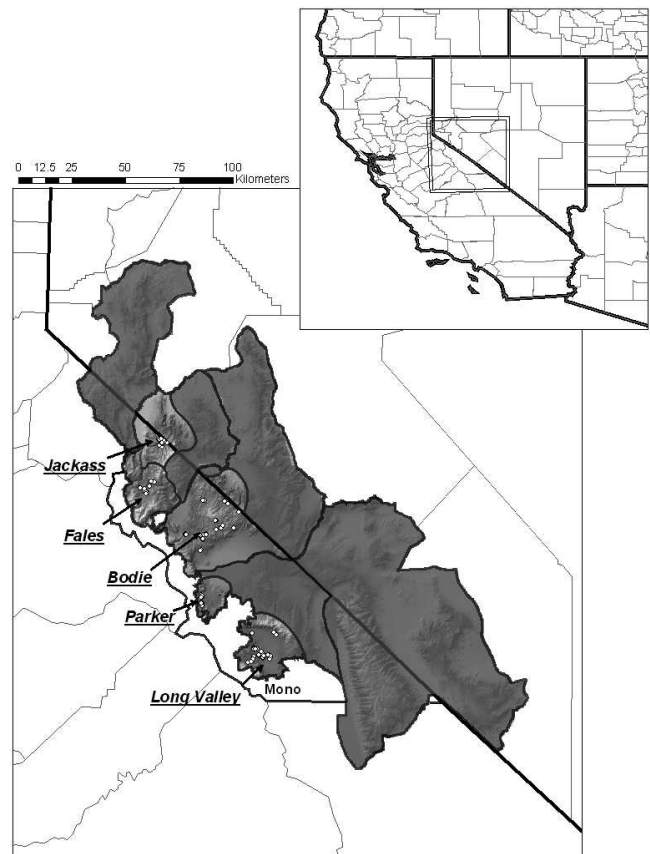


Figure 1. Location of the Mono County study area and subareas, in eastern California, USA, where we studied selection of nest sites by sage-grouse, 2003–2005. Nests indicated by white points.

(*Lupinus* spp.), buckwheat (*Eriogonum* spp.), and hawk-beard (*Crepis* spp.).

METHODS

We captured female sage-grouse by spotlighting (Giesen et al. 1982, Wakkinen et al. 1992) them on roosts surrounding lek sites in spring and near water sources in fall. We weighed each individual and determined age and sex using plumage characteristics (Beck et al. 1975). We then attached a size 14 aluminum band (National Band and Tag, Newport, KY) to females and fitted them with a 21-g necklace-mounted radiotransmitter (Advanced Telemetry Systems, Isanti, MN) with an activity sensor (Riley and Fistler 1992, Sveum et al. 1998). We released birds within 30 minutes at the point of capture and used a Global Positioning System to record all locations in Universal Transverse Mercator (UTM) units (datum NAD83, UTM zone 11).

Using a handheld yagi antenna and an Advanced Telemetry Systems receiver, we located individuals to within 30 m 4 times per week during the March–June breeding season. We assumed females were nesting when movements became localized (Connelly et al. 1993) or activity sensors indicated periods of inactivity for more than 10 minutes. This intensive tracking schedule allowed us to identify the shrub under which the nest was located using binoculars.

Table 1. Number of vegetation sites associated with sage-grouse nests sampled by each year, site type, and subarea in Mono County, California, USA, 2003–2005. Subareas include Bodie Hills (BH), Fales (FA), Jackass (JA), Long Valley (LV), and Parker (PA). Site types include nest sites (NS), nest vicinity (NV), and subarea (SAR).

Subarea	2003			2004			2005			Total
	NS	NV	SAR	NS	NV	SAR	NS	NV	SAR	
BH	4	4	4	14	14	13	9	9	4	75
FA	5	5	5	5	5	5	0	0	0	30
JA	8	7	7	7	7	5	7	7	0	55
LV	11	11	11	10	11	7	16	18	19	114
PA	2	2	1	6	4	5	3	3	2	28
Total	30	29	28	42	41	35	35	37	25	302

We recorded general vegetation and site characteristics (general stand type, slope, aspect, elevation) for each identified nest and associated random points within 2 days of the nest hatching or failing. For each nest site location (NS) sampled, we also sampled 2 random sites. One random sampling site, defined as the nest vicinity (NV) was determined by moving a random distance between 50 m and 200 m ($\bar{x} = 108$ m) from the nest in a random compass direction. Both distance and direction were determined using a random number table. The second random site was a random location within a subarea (SAR; e.g., Bodie Hills) determined using a random coordinate generator in Arcview® (Version 3.3, 2002; Environmental Systems Research Institute, Redlands, CA).

At each site, we measured live canopy cover of sagebrush and all shrubs using a 20-m transect centered at nests or random sites to be consistent with other studies of sage-grouse (Canfield 1941, Drut et al. 1994, Bureau of Land Management 1996). Transects were placed along randomly chosen compass bearings. We measured percent cover of understory perennial grasses and forbs using 4 uniformly spaced 20 × 50 cm plots along the transect and one at the nest or the center shrub at a random site (Daubenmire 1959, Bureau of Land Management 1996). We used standard cover classes, 0–5%, 6–15%, 16–25%, 26–50%, 51–75%, 76–95%, and 96–100% to characterize cover of each vegetation type (e.g., forbs or perennial grasses) within each plot. We assigned the midpoint of the appropriate class (e.g., 2.5% for the 0–5% class) as the coverage for each plot. We then averaged coverages across plots for each site to produce an estimate of percent cover for that site. We also measured visual obstruction at each site using a Robel pole (Robel et al. 1970). Because random sites did not have nests, we centered transects on the shrub nearest the random location. Otherwise, measurements at random sites were the same as at nest sites. We do not report results for Robel visual obstruction measurements because these were highly correlated ($r = 0.55$) with total live shrub cover. We focused on total live shrub cover and residual perennial grass cover and height for this paper because preliminary analyses suggested other variables did not explain nest site selection or nest success (Kolada 2007) and these variables have been the focus of management activities by federal agencies responsible for managing sage-grouse habitat.

To test the prediction that vegetation at nest sites differed from that at randomly sampled sites, we used PROC MIXED in SAS (SAS Institute 2000) to perform a multivariate analysis of variance (Wright 1998) with individual females as a random effect, site type (NS, NV, SAR), year, and subareas as fixed effects, and a vector of vegetation measures as the dependent variable. We included female as a random effect because we included more than one nest in the analysis from a subsample of marked females. We lacked vegetation data for random sites associated with a small number of nests (Table 1) but mixed-model analysis of variance does not require fully balanced designs (Searle et al. 1992). Vegetation measurements included total live shrub cover from the 20-m transects centered on the site, perennial grass residual height, and perennial grass residual cover from the 20 × 50 cm Daubenmire plots (Daubenmire 1959). We also performed 2 post hoc analyses using only sagebrush cover or forb cover as dependent variables, female as a random effect, and year, subarea, and site type as fixed effects. The most complex model included year, subarea, site type (i.e., NS, NV, SAR) and their interactions as fixed effects and vegetation measures at sites as the dependent vector. Year and subarea were used in the analysis to control for annual or large-scale spatial variation. We considered all additive and interactive combinations of fixed effects. We used the structure for multivariate mixed-models described by Wright (1998), which allowed assessment of the effects of fixed effects on each element of the response vector (residual grass cover, residual grass ht, and live shrub cover).

If vegetation at grouse nest sites differed from vegetation in the nest vicinity or the subarea, we expected models containing a site type effect to perform better than models without this effect. Secondly, we used estimates of vegetation (e.g., % shrub cover) for each site type to evaluate the scale at which nest site selection occurred (e.g., NS vs. NV or NS vs. SAR). We used an information theoretic approach to evaluate model performance and, therefore, our hypotheses (Burnham and Anderson 2002). We also report parameter estimates (e.g., percent shrub cover) and their precision, allowing us to assess the size of potential effects in the context of the estimated parameters.

To assess the distribution of nest sites across the range of available sites, we subdivided the range of vegetation measures into 2% increments for residual grass cover, 2-

Table 2. Model selection for the relationship between vegetation at sites and site type (nests, nest vicinity, or subarea) for sage-grouse in Mono County, California, USA, 2003–2005. Number of parameters (no. par.), Akaike's Information Criterion for small sample size (AIC_c) values, difference from the top AIC_c model (ΔAIC_c), and AIC_c weights (w_i) were used to rank models. Explanatory variables (fixed effects) were year (2003–2005), subarea ($n = 5$), and site type (nest site, nest vicinity, subarea). Females were included as a random effect to control for multiple nests from some females. Dependent variables were vectors including shrub cover, residual grass cover, and residual grass height. Analyses based on PROC MIXED (SAS Institute 2000).

Models ^a	No. par.	AIC_c	ΔAIC_c	w_i
Site type + yr + subarea	25	6724.4	0	1.0
Yr + subarea	19	6749.9	25.5	0
Site type + yr	13	6760.1	35.7	0
Yr*subarea	42	6761.4	37.0	0
Site type + subarea	19	6764.5	40.1	0
Site type*yr	27	6779.3	54.9	0
Yr	10	6791.0	66.6	0
Subarea	16	6797.2	72.8	0
Site type*subarea	45	6802.5	78.1	0
Site type	10	6803.1	78.7	0
Site type*yr*subarea	123	6861.1	136.7	0

^a All models allowed interaction between fixed effects and elements of the vector of dependent variables (shrub canopy cover, residual grass ht, and residual grass cover). + or * denote either an additive or interactive effect for fixed effects.

cm increments for residual grass height, and 5% increments for shrub cover. We then used a χ^2 test to compare frequencies of NSs, NVs, and SARs among increments for each vegetation measure. If female sage-grouse selected NSs differently from those available, we expected a large χ^2 statistic.

To explore the possibility that there were tradeoffs between vegetation variables when females selected nest sites based on vegetation characteristics, we examined correlations across random sites between shrub cover and residual grass height and shrub cover and residual grass cover. If females were trading off one type of cover for another (e.g., shrub cover for residual grass ht), we expected negative correlations between these variables at nest sites.

RESULTS

We captured and radiomarked 72 females in 5 subareas; 25 females produced >1 nest ($\bar{x} = 2.4$) used in the analysis. We collected data at 302 vegetation sampling sites (Table 1). We sampled 107 NSs, 107 NV sites, and 88 SAR sites. Most nests were found under mountain big sagebrush (64.5%, $n = 69$). The second most common shrub at NSs was bitterbrush (23.4%, $n = 25$). We found the remaining nests (12%, $n = 13$) under other shrubs such as snowberry, rabbitbrush, and Mormon tea.

The best model of vegetation characteristics (Akaike weight [w_i] = 0.994) contained site type, subarea, and year without interactions, indicating that vegetation characteristics not only varied among NSs, NVs and SARs, but also among years and SARs (Table 2). The second best model (difference from the top Akaike's Information Criterion model [ΔAIC_c] = 25.5, $w_i = 0.006$) was the same as the best model, except that site type was absent. The performance of the best model relative to the other models

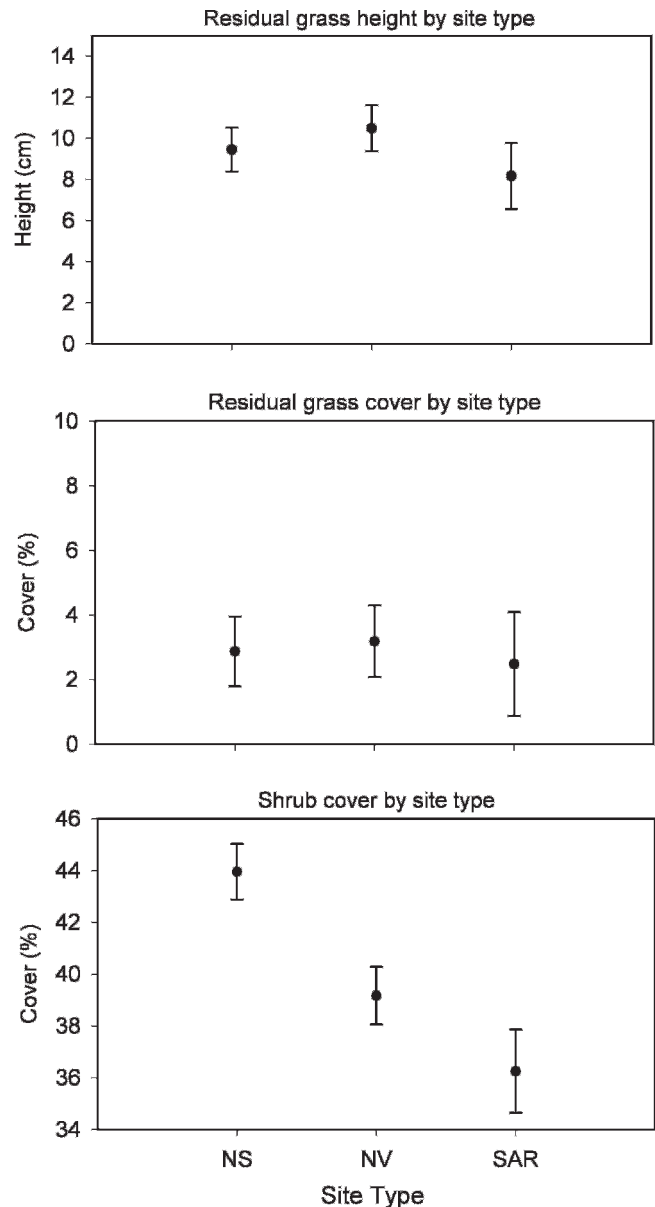


Figure 2. Least square mean estimates of residual grass height, residual grass cover, and shrub cover (\pm SE) for sage-grouse nest sites and 2 types of randomly selected sites, controlled for year and subarea effects, in Mono County, California, USA, 2003–2005. Site types denote the scale of the vegetation sampling site. These include NS (nest site), NV (nest vicinity, within 200 m of nests), and SAR (entire subarea).

provided strong support for the hypothesis that females selected NSs at both the NV and SAR scale. Residual grass height and cover did not consistently vary among site types (Fig. 2). Shrub canopy cover was the only variable that consistently varied among site types (Fig. 2). Female sage-grouse showed a consistent pattern of selecting NSs with greater shrub cover than NVs or SARs; shrub cover was greater at NSs than at NVs or SARs in 11 of 14 combinations of year and SAR categories. Females selected NVs that supported greater shrub cover than SARs in 9 of 13 combinations of year and SAR categories. Based on least squares means, controlled for effects of year and subarea, NSs had $43.9 \pm 1.1\%$ ($\bar{x} \pm$ SE) shrub canopy cover, whereas NVs and SARs had $39.2 \pm 1.1\%$ and $36.2 \pm 1.6\%$ shrub

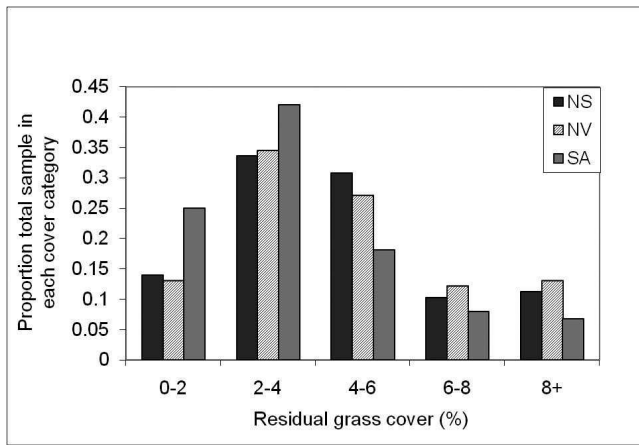


Figure 3. Proportion of sampled sites, sage-grouse nest sites (NS), nest vicinity sites (NV), and subarea sites (SAR) across 2% residual grass cover classes in Mono County, California, USA, 2003–2005. If sage-grouse chose nest sites that differed in residual grass cover from NVs or SARs, we expected frequencies of NSs to differ from frequencies of NVs or SARs for some cover classes. Because SARs were at the scale of entire subareas, a small proportion of these samples in a particular cover class represented relatively large areas supporting that cover class.

canopy cover, respectively (Fig. 2). For just sagebrush cover, NSs had $28.8 \pm 1.2\%$ sagebrush canopy cover, whereas NVs had $25.8 \pm 1.3\%$, and SARs had $24.5 \pm 1.4\%$ sagebrush canopy cover. Percent forb cover was similar among NSs, NVs, and SARs, $6.6 \pm 0.7\%$, $5.8 \pm 0.7\%$, and $7.2 \pm 1.0\%$ for the 3 site types, respectively.

Distribution of NSs among classes of residual grass cover did not differ from those for NVs ($\chi^2 = 0.63$, $df = 4$, $P = 0.96$; Fig. 3), but there was a suggestion that NSs had greater residual grass cover than SARs ($\chi^2 = 8.35$, $df = 4$, $P = 0.08$; Fig. 3), providing modest support for an effect of residual grass cover on nest site selection. The effect was weak, however, suggesting that residual grass cover was not the principal variable driving NS selection by female sage-grouse, despite the availability of sites containing greater residual grass cover than what they selected. Similarly, distribution of residual grass height at NSs did not differ from that at either NVs ($\chi^2 = 17.41$, $df = 15$, $P = 0.29$; Fig. 4) or SARs ($\chi^2 = 17.21$, $df = 15$, $P = 0.31$; Fig. 4). At the scale of subareas, substantial habitat existed, which supported greater cover or height of residual grasses than was used by sage-grouse for nest sites (Figs. 3, 4). Nest site locations differed from NVs ($\chi^2 = 29.13$, $df = 17$, $P = 0.03$; Fig. 5) and from SARs ($\chi^2 = 33.96$, $df = 17$, $P = 0.008$; Fig. 5) in percent shrub cover within 10 m of sites. Nest site locations had greater shrub cover than both classes of random sites.

The correlation coefficients for shrub cover and residual grass height ($r = 0.11$) and shrub cover and residual grass cover ($r = -0.06$) were both small, indicating very limited potential for tradeoffs between these cover types at nest sites by female sage-grouse.

DISCUSSION

Shrub cover both in NVs and SARs exceeded that reported for nests in other studies (Connelly et al. 1991, Gregg et al.

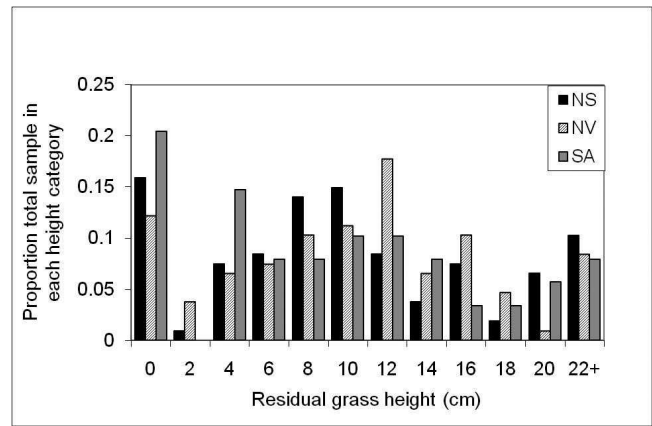


Figure 4. Proportion of sampled sites, sage-grouse nest sites (NS), nest vicinity sites (NV), and subarea sites (SAR) across 2-cm residual grass height classes in Mono County, California, USA, 2003–2005. If sage-grouse chose nest sites that differed in residual grass height from NVs or SARs, we expected frequencies of NSs to differ from frequencies of NVs or SARs for some height classes. Because SARs were at the scale of entire subareas, a small proportion of these samples in a particular height class represented relatively large areas supporting that cover class.

1994, Sveum et al. 1998, Popham and Gutiérrez 2003, Holloran et al. 2005). Shrub cover in Mono County was also greater on average than that reported for nest sites in other studies (Aldridge and Brigham 2002, Popham and Gutiérrez 2003, Holloran et al. 2005, Moynahan et al. 2007). Additionally, female sage-grouse consistently nested in NVs supporting greater shrub cover than was available on average in subareas. Our findings are consistent with the hypothesis that female sage-grouse choose nesting locations at ≥ 2 spatial scales. They choose NVs (within 200 m of nests) with greater shrub cover than available throughout their home ranges, and within these NVs, they choose nest sites with greater shrub cover than the mean for the subarea as a whole. The fact that female sage-grouse in Mono County selected nest sites with even greater shrub cover than what was available on average is consistent with the hypothesis that females were attempting to maximize concealment of their nests by shrubs. We note that both random sites and nest sites in Mono County had similar sagebrush canopy cover to that recommended by Connelly et al. (2000) for sage-grouse breeding habitat. Comparison of our findings with those of other studies, however, indicates that there is a large contribution of nonsagebrush shrubs to sage-grouse nesting habitat in Mono County, consistent with findings in some other parts of sage-grouse range (Sveum et al. 1998, Popham and Gutiérrez 2003).

Optimal shrub canopy cover reflects a balance between the importance of nest concealment (Ricklefs 1969, Gregg et al. 1994, Connelly et al. 2000) and production of forbs associated with low to moderate shrub cover (Klebenow 1969). We envision 2 mechanisms by which that balance might be achieved. First, the balance between shrub cover and forbs could be achieved by a mosaic of more open patches supporting forbs and patches of denser shrub cover where females nest. In Mono County, recent fires have created patches with high forb density used by broods within areas

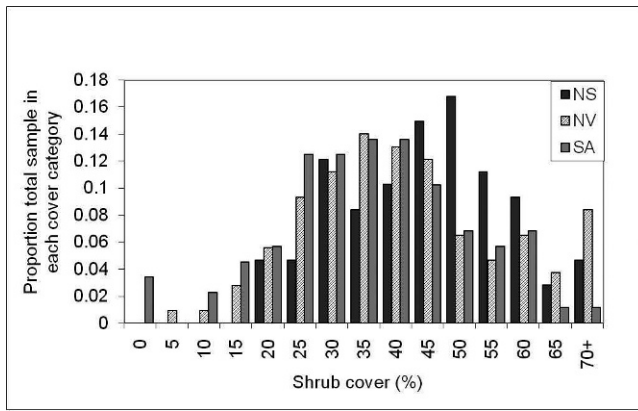


Figure 5. Proportion of sampled sites, sage-grouse nest sites (NS), nest vicinity sites (NV), and subarea sites (SAR) across 5% shrub cover classes in Mono County, California, USA, 2003–2005. If sage-grouse chose nest sites that differed in shrub cover from NVs or SARs, we expected frequencies of NSs to differ from frequencies of NVs or SARs for some cover classes. Because SARs were at the scale of entire subareas, a small proportion of these samples in a particular cover class represented relatively large areas supporting that cover class.

otherwise dominated by shrubs (E. Kolada, University of Nevada Reno, personal observation). Second, both understory vegetation and shrubs serve to conceal nests (Gregg et al. 1994, Sveum et al. 1998) and female sage-grouse could select nest sites with greater understory cover, which secondarily provided food for broods. In Mono County, understory vegetation was relatively sparse (Figs. 3, 4), and females may have selected sites with high shrub cover to compensate, although we failed to find evidence that females were trading off shrub cover against understory vegetation.

In contrast to the hypothesis that sage-grouse maximize nest concealment based on both shrub cover and understory vegetation, we found no evidence that female sage-grouse selected nest sites with greater residual grass cover or height (Figs. 3, 4), even though such sites were available. Female sage-grouse in Mono County nested in sites with substantially less residual grass cover (2.7%) or residual grass height (10.5 cm) than in other geographic locations (Gregg et al. 1994, Popham and Gutiérrez 2003, Lane 2005). Differences between our results and those of other studies suggest complexity in habitat selection by nesting sage-grouse. Nest success has been associated with vegetation at nest sites in several other studies (Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995, Holloran et al. 2005, Moynahan et al. 2007). Differences in apparent selection for specific vegetation features of nest sites in this study versus others could reflect 1) compensation by one variable (e.g., shrub cover) for another (e.g., residual grass ht) in nest concealment, 2) variation in the importance of particular predators and associated importance of certain kinds of concealment, or 3) differences in selection of specific nest site vegetation between female sage-grouse in Mono County and those in other areas. We found no evidence for compensation of one variable for another. We know that the predator community in Mono County consists of species such as coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and

ravens (*Corvus corax*), although it is difficult to assign specific predators to specific predation events (Larivière 1999). Our results are best explained by differences in selection of nest site characteristics between females in Mono County and those elsewhere. Comparison of nest success among studies is one mechanism to improve our understanding of the importance of vegetation characteristics at nest sites across the range of sage-grouse.

Comparison of nest success among sage-grouse studies is complicated by the fact that apparent nest success has been reported by most other studies (Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998). Estimates of apparent nest success are strongly influenced by visitation schedules and daily nest survival rate (Mayfield 1975, Rotella et al. 2004, Moynahan et al. 2007) and are biased high because nests that fail before they are found are not included in the sample. Because the bias is a function of both visitation schedule and external nest mortality factors, bias is unknown, making it difficult to compare studies. Nevertheless, 95% confidence intervals for our estimates of nest success (Kolada et al. 2009) overlap point estimates for other studies. Thus, nest success in Mono County appears to be comparable to, or greater than, that in other regions with somewhat different vegetation at nest sites.

One additional complication in interpreting the relationship between vegetation at nest sites and nest success is the role of female experience or quality. If more experienced females select vegetation with certain characteristics (e.g., a particular shrub canopy cover) and also experience high nest success, this will establish a relationship between vegetation characteristics and nest success that does not necessarily reflect a causal relationship between the two. It is, thus, possible that the association between nest success and vegetation at nests is an artifact of the associations between female experience and both nest site vegetation and nest success, making it impossible in our study to fully separate the direct effects of vegetation itself from that of female quality.

Overall, we interpret our results and those of other studies to indicate substantial variation in vegetation that supports nesting sage-grouse. Clearly, because sage-grouse depend on sagebrush for food, they depend on sagebrush-dominated landscapes. Our study and others (Sveum et al. 1998, Popham and Gutiérrez 2003), however, demonstrate that within such landscapes a variety of shrubs may provide suitable nest sites for sage-grouse. It is certainly possible that regional climate, through its effect on vegetation structure or community composition, governs the range of habitats available to nesting sage-grouse. Mono County sage-grouse use higher elevation sites on average than those found in other portions of their range (Connelly et al. 1988, Gregg et al. 1994, Aldridge and Brigham 2002). Additionally, Mono County receives more precipitation on average (mostly in the form of snow) than in some other portions of sage-grouse range (Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998, Western Regional Climate Center 2005). Our results, combined with those from other studies, suggest that habitat management should be influenced by local

climate conditions and that managers should consider regional variation in habitat suitable for sage-grouse.

MANAGEMENT IMPLICATIONS

Vegetation variables related to nest site selection were also associated with nest success (Kolada et al. 2009), indicating that these vegetation variables had implications for local population dynamics. Our study, combined with others, suggests that female sage-grouse use a complex suite of vegetation cover variables to select nest sites and that these variables may vary among geographic regions. Guidelines for management of sage-grouse habitat (Connelly et al. 2000) provide a first approximation of goals for sage-grouse habitat management, but our results indicate that, when possible, local variation in habitat and responses by sage-grouse to such variation should be accounted for when implementing habitat management for sage-grouse. For Mono County it may be wise to provide a greater mosaic of shrubs and greater shrub cover than currently called for in published range-wide guidelines (Connelly et al. 2000). Because Mono County supports relatively open areas with good forb production for broods in close proximity to patches containing dense shrubs (E. Kolada, personal observation), management for shrubs in nesting patches may not need to be based on the nutritional requirements of females or chicks.

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