Greater sage-grouse Centrocercus urophasianus nesting success and habitat use in northeastern California

Authors: Popham, Gail P., and Gutiérrez, R. J.

Source: Wildlife Biology, 9(4) : 327-335

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.021

Greater sage-grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California

Gail P. Popham & R.J. Gutiérrez

Popham, G.P. & Gutiérrez, R.J. 2003: Greater sage-grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California. - Wildl. Biol. 9: 327-334.

From mid-March through mid-August 1998-2000, we studied greater sage-grouse *Centrocercus urophasianus* nesting habitat in northeastern California, USA. We located nest sites of 45 radio-marked hens, which had an average nest success of 40.2%. The radio-marked grouse used low sagebrush *Artemisia arbuscula* cover type less than expected; big sagebrush *A. tridentata wyomingensis* and mixed shrub cover types were used in proportion to their availability. Grouse used sites with habitat characteristics similar to random sites for nesting. However, successful nests differed from unsuccessful nests in several respects. Mean distance between nest and lek was greater for successful nests ($\bar{x}$ = 3,588 m, SE = 811 m, N = 20) than for unsuccessful nests ($\bar{x}$ = 1,964 m, SE = 386 m, N = 20). Rock cover was greater at successful nests ($\bar{x}$ = 27.7%, SE = 4.6%) than at unsuccessful nests ($\bar{x}$ = 14.49%, SE = 3.04%). Total shrub height was greater at successful nests ($\bar{x}$ = 65.5 cm, SE = 4.7) than at unsuccessful nests ($\bar{x}$ = 49.2 cm, SE = 1.7). The height of visual obstruction was greater at successful nests ($\bar{x}$ = 40.2 cm, SE = 2.6) than at unsuccessful nests ($\bar{x}$ = 32.5 cm, SE = 2.0). Our results suggest that sage-grouse use more diverse vegetation than previously reported, and we conclude that either this represents a natural behaviour for sage-grouse in this area, or we observed a selection response to a landscape altered by human activity.

Key words: Artemisia tridentata wyomingensis, California, Centrocercus urophasianus, Galliformes, greater sage-grouse, nest site selection, radio-telemetry

Gail P. Popham, Department of Wildlife, Humboldt State University, Arcata, California, USA 95521 - e-mail: gail_popham@dot.ca.gov*
R.J. Gutiérrez, Department of Wildlife, Humboldt State University, Arcata, California 95521, USA, and Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA - e-mail: gutie012@tc.umn.edu

** Present address: California Department of Transportation, 1656 Union Street, Eureka, CA 95501*

Corresponding author: R.J. Gutiérrez

Greater sage-grouse *Centrocercus urophasianus* populations have been declining throughout their range (Connelly & Braun 1997, Braun 1998). These declines have been attributed to a combination of factors, including habitat degradation caused by livestock grazing, conversion of sagebrush *Artemisia* steppe for agriculture, changes in fire frequency, drought and other human activities (Connelly & Braun 1997, Braun 1998, Beck & Mitchell 2000, Leonard, Reese & Connelly 2000).

Greater sage-grouse have been extirpated in many areas at the periphery of their range (Schroeder, Young & Braun 1999). California is on the western edge of the sage-grouse range. They now occur in the counties of Modoc and Lassen in northeastern California (Schroeder et al. 1999), but have been extirpated from the county of Siskiyou. Despite long-term declines and concern about the species' status, there are no published studies describing greater sage-grouse habitat use in northeastern California (Schroeder et al. 1999). However, nesting habitat studies have been conducted in the adjacent southeastern Oregon (Gregg 1991, DeLong, Crawford & DeLong 1995).

Because of general declines in greater sage-grouse populations, especially on the edges of its range, and increasing human development in northeastern California, we studied greater sage-grouse habitat selection in that region. Although several greater sage-grouse habitat studies have been conducted in nearby Oregon, the Sierra Nevada and Cascade ranges are adjacent to our study area and exert a strong climatic influence on the region, which may influence local grouse habitat selection patterns. Therefore, we conducted an observational study to: 1) examine greater sage-grouse selection of vegetation cover types, 2) estimate microhabitat selection, and 3) compare habitat characteristics of successful and unsuccessful nests. Knowledge of habitat selection patterns and population characteristics from studies across the species' range will be essential for the species' conservation.

Study area

Our study area encompassed 273,000 ha in the eastern part of the county of Lassen, California. The area was primarily sagebrush steppe within the Great Basin, and was characterized by volcanic substrates and faulted lava flows (Hickman 1993). Greater sage-grouse occurred in the sagebrush steppe habitat north of Honey Lake Valley and east of the Cascade Mountains.

Vegetation communities included Wyoming big sagebrush *A. tridentata wyomingensis*, low sagebrush *A. arbuscula*, silver sagebrush *A. cana*, alfalfa *Medicago sativa* fields, annual and perennial grasslands and some areas of western juniper *Juniperus occidentalis* savannah. Grazing by sheep and cattle occurred in many areas. Elevations ranged from 1,400 to 2,400 m a.s.l. Summers are hot and dry; winters and springs are cool with precipitation ($\bar{x}$ = 27.6 cm) falling as snow or rain (Western Regional Climate Center 1999). The precipitation during the study period and the year preceding the study period was near average.

Because grouse primarily use shrub-dominated habitats, we defined four types of habitat (hereafter called 'cover types'):

1) A low sagebrush cover type was dominated by low sagebrush and one-sided bluegrass *Poa secunda*, with a total shrub canopy cover ranging within 5-24%. Associated species included rubber rabbitbrush *Chrysothamnus nauseosus*, bitterbrush *Purshia tridentata*, bluebunch wheatgrass *Pseudoroegneria spicata*, squirreltail *Elymus elymoides*, Hooker's balsamroot *Balsamorhiza hookeri* and other forbs.
2) Areas with low shrub cover were in rocky, weathered basalt flow zones and were not properly classified as grassland despite the low shrub cover because shrubs were the dominant vegetation within the zone.
3) A big sagebrush cover type was dominated by Wyoming big sagebrush and cheatgrass *Bromus tectorum* with a total shrub canopy ranging within 5-40%. Associated species included rabbitbrush, Mormon tea *Ephedra viridis*, bitterbrush, little-leaf horsebrush *Tetradymia glabrata*, bluebunch wheatgrass, basin wild rye *Leymus cinereus*, silvery lupine *Lupinus argentius*, blepharapappus *Blepharapappus scaber*, perennial sunflower *Helianthus cusickii*, desert parsley *Lomatium* spp. and other forbs.
4) A mixed shrub cover type was dominated by shrub species other than sagebrush species (although sagebrush occurred in low frequency), including rabbitbrush, little-leaf horsebrush and/or bitterbrush with an under story similar to the big sagebrush cover type.

Methods

Capture

Birds were captured at night by spotlight trapping (Wakkinen, Reese, Connelly & Fischer 1992b). During March and April, we captured 20, 21 and 24 different hens in 1998, 1999, and 2000, respectively, and equipped them with 19-g battery-powered telemetry transmitters (Model 5902N, Advanced Telemetry Systems, Isanti, Minnesota, USA).

During the nesting season, we located the birds at 5-7 day intervals to estimate time of nest initiation and nest fate. We located birds with a hand-held, 2-element Yagi antenna and a Telonics TR-2 (Telonics, Mesa, Arizona, USA) receiver. We mapped nest locations using a global positioning system (Garmin GPS 12XL, GARMIN International Inc., Olathe, Kansas, USA), and avoided flushing nesting hens by circling around them at a distance of 15-20 m. To avoid nest detection by predators, we marked nests with rocks or dead shrubs placed nearby. We considered a nest successful if ≥ 1 eggshell remained that had membranes detached from the inside of the shell (Sveum 1995). If there were no eggshells remaining in the nest, we considered it an unsuccessful nest.

Habitat measurements

We used GIS software (Terrain Navigator, Maptech, Andover, Maine, USA) to estimate the distance from a nest to the nearest lek. We also classified the cover type at each grouse nest site. We randomly selected 45 sites within shrub-dominated communities to represent the available habitat. Since grouse were not selected at random from among the entire population, we sampled random sites, which were matched to nest sites (Beck & George 2000). Thus, our inferences concern the individuals sampled and not the entire population. The number of random sites was equal to the number of individual hens nesting. Thus, for each nest site we randomly selected another location within a 0.1-1 km radius of the nest because individual sage-grouse hens show fidelity to nesting areas during the breeding season (Fischer, Wakkinen, Apa, Reese & Connelly 1993, Young 1994). At the random sites, we measured the same characteristics as at nest sites, except that we measured the shrub nearest the centre of the site for comparison to the nest shrub. This centre shrub was not necessarily the same species as the nest shrub. Random locations falling in habitats that were not used by grouse (e.g. juniper savannah) were discarded and resampled.

We measured the following 12 characteristics of nest sites: distance from nest to nearest known lek, percent cover of shrubs, forbs, perennial grasses, annual grasses, litter, bare ground and rock, nest shrub species length (north-south axis of shrub) and width (east-west axis of shrub), maximum foliage height and visual obstruction. The locations of most leks were known due to access to historic air and ground surveys as well as extensive air surveys conducted during our study period. We used the line intercept method to estimate the percent cover of shrubs (Canfield 1941) and recorded canopy cover by shrub species. Along two 30-m transects oriented in the cardinal directions, with the nest at the centre of the transects, we established line intercepts. We measured the height of the closest shrub within 2 m of each 5-m mark on the transects to the nearest centimetre excluding inflorescence (Sveum 1995). If there was no shrub within 2 m, we did not record a measurement. We also measured residual grass height of the closest perennial grass within 2 m of each 5-m mark on the transects to the nearest centimetre excluding inflorescence (Sveum 1995). This potentially yielded seven shrub and grass height measurements from each of the two transects (a total of 14 shrub and grass heights) plus the height of the nest shrub, i.e. a total of ≤ 15 shrub and grass height measurements. We averaged the shrub height measurements to represent a single shrub height for the site (Klebenow 1969), and grouped all species of shrubs for this measurement. We averaged the residual perennial grass height measurements to represent the average height for each site. We used a Daubenmire frame placed at eight random, systematic locations in each vegetation survey area to measure the percent cover of perennial grasses, annual grasses, forbs, litter, bare ground and rock (Daubenmire 1959). Only rocks of > 10 cm in diameter were recorded as rock cover. We centred the Daubenmire frame lengthwise over the 1, 5, 10, 20, 25 and 30-m marks on both transects. At the 15-m mark (which was centred on the nest), we centred the Daubenmire frame lengthwise on the transect used, and placed it adjacent to the nest (or main stem of the centre shrub for random sites) on either side. We grouped all species of shrub for measuring the total shrub height, and measured the foliage height of residual perennial grasses in the same way as we measured the shrub height. To measure visual obstructions at each vegetation plot, we used a visual obstruction pole (Robel, Briggs, Dayton & Hulbert 1970) marked in 5-cm increments, placed the pole at the 7.5 and 22.5 m marks of the two transects, and viewed it from a distance of 4.5 m and, a height of 150-160 cm. When the pole was positioned in the centre of the transect, we viewed it from four randomly determined directions, and when it was positioned on the two transects, we viewed it from each of two randomly determined directions. From each of these 12 vantage points, we recorded the lowest visible obstruction height to the nearest 5 cm. This resulted in 12 visual obstruction measurements at each site, which we averaged to estimate the visual obstruction at the site in question. We sampled all nest sites in this same manner within a week after the fate (failure or hatching) of a nest was determined.

Statistical analysis

We evaluated cover type selection by comparing used to available sites (Manly, McDonald & Thomas 1993). As neither grouse nor study area was selected at random (although our study area encompassed most of the range of this grouse species in northeastern California), we matched random sites to nest sites. We only used one nest location from each hen for assessment points rather than general areas, as we did not have a complete inventory of used sites. We used logistic regression to estimate a resource selection function for nesting cover type use by omitting both the intercept and the following ratio: probability of sampling a used resource/ probability of sampling an available resource, while leaving only parameter estimates of shrub type in the model (Manly et al. 1993:129). The logistic regression model was structured so that site status (nesting = 1, or random = 0) was the response variable, while low sagebrush, mixed shrub and big sagebrush were categorical predictor variables. The general structure of our model was:

$$\text{logit}(\pi') = (\beta_1 \times \text{LOW}) + (\beta_2 \times \text{MIX}) + (\beta_3 \times \text{BIG})$$

where $\text{logit}(\pi') = \log_e[\pi'/(1-\pi')]$. In this example, π' represents the estimated probability of a site being used for nesting; β_1, β_2, and β_3 represent the parameter estimates for the three shrub-dominated cover types; LOW = 1 if the site was a low sagebrush type and 0 if it was a mixed shrub or big sagebrush type; MIXED = 1 if the site was a mixed sagebrush type and 0 if it was a low or big sagebrush type; BIG = 1 if the site was a big sagebrush type and 0 if it was a low or mixed sagebrush type. Thus, we modelled the probability of a site being used for nesting given shrub cover type. This analysis was relevant to inferences about general habitat use patterns, but not to structural components of habitats, which are probably important to sage-grouse habitat selection (see below).

To maintain independence of samples, we randomly selected one nest site for each of the radio-marked 45 hens that nested during the three years for analyses of both cover type selection and microhabitat selection. From the microhabitat analysis we excluded five nests that had been abandoned by hens because desertion may have been caused by the observers. Thus, our sample size was 40 independent nests. We first randomly selected a single successful nest without replacement for individual birds; we then randomly selected one failed nest per bird from the remaining individuals. To minimize multicollinearity and redundancy of variables, we excluded some habitat variables that were correlated. We used the variable that was most easy to interpret biologically. Thus, we used distance from nest to lek, perennial grass cover, litter cover, bare ground cover, rock cover, sagebrush cover, other shrub cover, total shrub height, residual perennial grass height and visual obstruction height for analyses. However, we omitted distance from nest to lek when comparing random and nest sites because random sites were spatially associated with the nest sites. We tested the normality of the variables by examining normal probability plot and homoscedasticity using the Modified-Levene Equal-Variance Test (Hintze 1997). We used the following transformations for variables that were not normally distributed: log transformation for distance to lek; and arcsine square root transformation for all percentage cover variables (Zar 1996). Total shrub height had unequal variance, so we transformed this variable using the reciprocal of the square root (Zar 1996). With the transformed values, we used two-factor multivariate analysis of variance (MANOVA) to test for year effects and to compare nest sites with random sites (Zar 1996). We used MANOVA rather than matched pairs logistic regression to make our results more comparable to the Oregon studies as suggested by the Western States Sage and Columbian Sharp-tailed Grouse Workshop (Schroeder et al. 1999:17). We performed another two-factor MANOVA to compare successful and unsuccessful nests and effects of year. However, we examined year effects only for 1999 and 2000 because we changed some of the vegetation sampling procedures. We resampled the 1998 nest sites in 1999 on the same date (±1 week) that we determined its fate in 1998. If the resulting Wilks' Lambda test statistic for each of the MANOVAs resulted in a P-value of 0.05, we tested each of the individual variables with an ANOVA. We also computed the descriptive statistics for characteristics of successful, unsuccessful and random sites using the statistical program NCSS 97 (NCSS Statistical Software, Kaysville, Utah, USA).

Results

Nesting activity

We radio-marked 65 different female greater sage-grouse, and monitored 20, 37 and 46 hens during March-August in 1998, 1999 and 2000, respectively. In the three years, 27, 13 and five hens (i.e. N = 45 independent grouse nests) attempted to nest, while 20 hens were not known to nest. Over the three years, we found 88 nests as some hens renested, and of these five, 14 and 16, respectively, were successful nests, resulting in an overall nest success of 39.8% (26.3, 35.9 and 45.7% for 1998, 1999 and 2000, respectively).

Cover type selection

The greater sage-grouse selected low sagebrush, big sagebrush and mixed shrub cover types for nesting. Of the 45 nest sites, 30 (67%) were in big sagebrush cover type, 13 (29%) in mixed shrub and two nests (4%) were in low sagebrush. In contrast, of the 45 random locations, 58, 13 and 29% were in big sagebrush, mixed shrub and low sagebrush cover types, respectively. The resource selection function for grouse nesting habitat was:

$$\exp[1.87\text{*LOW}) + 0.77\text{*(MIX)} + 0.14\text{*(BIG)}].$$

The 95% profile likelihood confidence intervals (CI)

Table 1. Habitat characteristics of successful (N = 20) and unsuccessful (N = 20) sage-grouse nests and random sites (N = 40) in the county of Lassen, California, during March-July 1998-2000. Numbers in parentheses are standard errors of the mean.

Variable	Successful	Unsuccessful	Random
Perennial grass cover (%)	0.14 (0.03)	0.11 (0.02)	0.11 (0.02)
Litter cover (%)	0.08 (0.02)	0.11 (0.02)	0.10 (0.01)
Bare ground cover (%)	0.23 (0.03)	0.26 (0.05)	0.29 (0.03)
Rock cover (%)	0.28 (0.05)	0.14 (0.03)	0.18 (0.03)
Sagebrush cover (%)	0.13 (0.03)	0.16 (0.03)	0.15 (0.02)
Other shrub cover (%)	0.06 (0.02)	0.05 (0.01)	0.05 (0.01)
Total shrub height (cm)	65.5 (4.7)	49.2 (1.7)	49.1 (3.0)
Perennial grass height (cm)	22.1 (2.7)	24.2 (3.1)	18.2 (1.9)
Visual obstruction height (cm)	0.2 (2.6)	32.5 (2.0)	31.9 (2.4)

indicated that grouse avoided low sagebrush (95%CI = -4.48, -0.25). In contrast, parameter estimates were positive for mixed shrub and big sagebrush, but the confidence intervals included zero (95% CI for MIX = -0.43, 2.18; BIG = -0.54, 0.84), indicating that these habitats were used as expected based on their availability within their potential breeding home range.

Microhabitat selection

There was no year effect between 1999 and 2000 ($F_{[df=9,68]} = 0.89$; $P = 0.48$), and the habitat structure between nests and random sites was similar ($F_{[df=9,68]} = 0.96$; $P = 0.54$).

There was no difference between successful and unsuccessful nests due to year for 1999 and 2000 ($F_{[df=10, 27]} = 1.55$; $P = 0.19$). However, the habitat characteristics differed between successful and unsuccessful nests ($F_{[df=10,27]} = 2.39$; $P = 0.12$). Successful grouse nests were farther (3,588 m, SE = 811 m) from the nearest lek ($F_{[df=10,27]} = 3.85$; $P = 0.06$) than unsuccessful nests (1,964 m, SE = 384 m). In addition, successful nests had greater rock cover ($F_{[df=10,27]} = 4.70$; $P = 0.04$), greater total shrub height ($F_{[df=10,27]} = 10.63$; $P < 0.01$) and greater visual obstruction height ($F_{[df=10,27]} = 5.69$; $P = 0.02$) than unsuccessful nests (Table 1).

Discussion

Most studies show that greater sage-grouse hens typically (79-95%) place nests under big sagebrush plants (e.g. Patterson 1952, Connelly, Wakkinen, Apa & Reese 1991, Gregg, Crawford, Drut & DeLong 1994, Hanf, Schmidt & Groshens 1994). Contrasting these results, we found that only 59.1% of nests were placed under big sagebrush (Table 2). Nevertheless, the nest success rates in our study were similar to the success rates in other studies (Connelly et al. 1991, Gregg 1991, Sveum 1995). Nest success was moderately higher when birds nested under other nest shrubs/vegetation (41.7%) than when they nested beneath big sagebrush (30.8%). This finding contrasts with other studies, where nest success was higher under big sagebrush (Patterson 1952, Connelly et al. 1991, Gregg 1991, Sveum 1995). Grouse avoided low sagebrush cover types for nesting in both our study and nearby southeastern Oregon (Gregg et al. 1994, Hanf et al. 1994).

Greater sage-grouse habitat studies in other states have found differences between nests and random sites (Klebenow 1969, Gregg 1991, Sveum 1995), which we did not find. Our result was unexpected because our sampling design should increase the similarity between used and available sites. Further, our findings conflicted with the findings for most of the previously published

Table 2. Plant species under which successful (N = 31) and unsuccessful (N = 57) sage-grouse nests were placed in the county of Lassen, California, during March-July 1998-2000. N gives the number of nests in each category, the outer right %-column in each category gives the percentage of nests in the respective category relative to all (88) nests located, and the other %-column gives the percentage of nests relative to the number of total successful (N = 31) or unsuccessful (N = 57) nests.

	Number of nests		Successful nests			Unsuccessful nests		
Plant species	N	%	N	%	%	N	%	%
Artemisia arbuscula	4	4.5	1	3.2	1.1	3	5.3	3.4
A. tridentata wyomingensis	52	59.1	16	51.6	18.2	36	63.2	40.9
Chrysothamnus spp.	6	6.8	1	3.2	1.1	5	8.8	5.7
Ephedra viridis	2	2.3	2	6.5	2.3	0	0.0	0.0
Purshia tridentata	4	4.5	4	12.9	4.5	0	0.0	0.0
Tetradymia glabrata	15	17.0	5	16.1	5.7	10	17.5	11.4
Leymus cinereus	2	2.3	0	0.0	0.0	2	3.5	2.3
Pseudoroegneria spicatum	3	3.4	2	6.5	2.3	1	1.8	3.2
Non - *A. tridentata* nests	36	53.4	15	48.4	17.0	21	36.8	23.9
Total number of nests	88	--	31	--	--	57	--	--

bird habitat studies, which have shown that habitat structure of used sites differs from the structure of available habitat (Block & Brennan 1993). This difference may be due to a high level of landscape heterogeneity as suggested by the variety of nest shrubs used and the habitat structure of used and random sites. Although we found no differences between nest and random sites, there were microhabitat differences between successful and unsuccessful nests.

Greater sage-grouse studies in southeastern Oregon and Washington showed that tall residual grass cover was greater at successful nests (Gregg et al. 1994, Sveum 1995). However, we found no differences as far as perennial grass cover or height was concerned. We did find greater visual obstruction at successful than at unsuccessful nest sites, which appeared to be due to higher shrub cover. Sveum (1995) reported taller visual obstruction at successful nests than at failed nests in one of two observation years. In addition, DeLong et al. (1995) found lower predation of artificial nests which had more tall grass and medium shrub cover. In contrast, Gregg (1991) found no differences in visual obstruction between successful and unsuccessful nests.

Other studies have shown that nest success was greater at nest sites that had taller shrubs (Connelly et al. 1991, Gregg 1991, DeLong et al. 1995). Similarly, we found that the mean shrub height at successful nest sites was greater than at unsuccessful nest sites. Both shrub height and visual obstruction would be biologically significant because they represent the primary vegetation concealing nesting birds from predators.

Rock, especially boulders, can be a component of mountain quail *Oreortyx pictus* cover in this region (Brennan, Block & Gutiérrez 1987). Similarly, we found that the incidence of rock cover, including boulders > 0.5 m in diameter, was greater at successful grouse nests. Other greater sage-grouse studies have not reported this variable (perhaps because lava flows and boulder fields were not present). The structural significance of rock might have been clearer if we had included rock height as a measured variable or conducted a separate analysis of characters immediately surrounding the nest. In addition, lava or boulder fields probably could impede a mammalian predator's search behaviour.

Wakkinen, Reese & Connelly (1992a) found no difference in the nest-to-lek distance between successful and unsuccessful nests. In contrast, we found that the mean distance to the nearest known lek was greater for successful nests than for unsuccessful nests. Apa, Reese & Connelly (1997) hypothesized that predators concentrate where grouse density is high and, therefore, nests far from leks are more successful. Alternatively, habitats may vary in quality over the landscape, which might result in hen movement to more suitable, distant sites. For example, leks may be situated in areas that are open (e.g. have lower shrub density), and hens may have to travel away from leks to find better nest sites. In addition, Wakkinen et al. (1992a) showed that grouse will place their nests farther from their lek of capture than the nearest available lek.

Management implications

Guidelines for managing greater sage-grouse habitats emphasize the importance of maintaining sagebrush for nest sites (Braun, Britt & Wallestad 1977, Connelly et al. 1991, Gregg 1991, Hanf et al. 1994, DeLong et al. 1995, Sveum et al. 1998, Connelly, Schroeder, Sands & Braun 2000). Further, Schroeder et al. (1999) suggest that greater sage-grouse habitat management should be directed toward specific nesting habitats. The birds in our study exhibited different habitat selection preferences at different spatial scales because they chose nest sites in cover types with taller shrubs rather than low sagebrush, and habitat structure used by successful nesting hens differed from that of unsuccessful hens. The hens in our study nested under big sagebrush less frequently than in other studies, which could be due to a lack of sagebrush habitat or a difference in selection patterns by these birds (i.e. both sagebrush and mixed shrub cover types were selected in proportion to availability).

The native shrub steppe in our study area has been degraded by excessive grazing, juniper encroachment, agriculture and anthropogenic development. Therefore, our results are equivocal regarding the following two alternative explanations for our results. First, habitat quality is lower in northeastern California because of natural conditions or human impact, and, consequently, grouse nest in areas that are not typical of other areas within the species' range. Second, grouse habitat is naturally more heterogeneous (i.e. more variable) at the edge of its range in northeastern California, and, consequently, grouse habitat selection patterns reflect this variation. Nevertheless, our results demonstrate the use of variable nesting sites. We suggest some habitat heterogeneity (i.e. structural and shrub species variability within habitats) and landscape heterogeneity (i.e. different shrub cover types) may be desirable in northeastern California. Our results show that not only sagebrush, but also a diversity of shrub species and structural variability can be important for nesting. However, we caution that continued juniper and exotic grass (e.g. *Bromus tectorum*) encroachment in this area may further degrade these shrub communities. Finally, while we attempted to make our methods comparable to other studies within our region, there is no standard methodology for examining greater sage-grouse habitat. Thus, we suggest that a meta-analysis of habitat relationships throughout the range of greater sage-grouse could be fruitful for clarifying habitat relationships of the bird and variation among studies and methods (e.g. see Anderson, Burnham, Franklin, Gutiérrez, Forsman, Anthony & Shenk 1999).

Acknowledgements - we thank the California Department of Fish and Game, the Sierra Pacific Power Company, the Marin Rod and Gun Club, the University of Minnesota and I.N. Langton for financial assistance. Personnel and volunteers from the California Department of Fish and Game captured the majority of birds. We also thank D.M. Bush, D.R. Cluck, A.B. Davis, M.E. Davis, T.L. George, F.A. Hall, B.E. Jones, D.J. Lancaster, M.W. McDonald, R.F. Miller, N.J. Nordensten, T.H. Rickman, G.D. Schoolcraft, F.W. Weckerly and G.S. Zimmerman for technical and other assistance. J.W. Connelly, T.L. George, S.M. Redpath, M.E. Seamans, F.W. Weckerly and G.S. Zimmerman read earlier drafts of the paper.

References

Anderson, D.R., Burnham, K.P., Franklin, A.B., Gutiérrez, R.J., Forsman, E.D., Anthony R.G. & Shenk, T.M. 1999: A protocol for conflict resolution in analysing empirical data related to natural resource controversies. - Wildlife Society Bulletin 27: 1050-1058.

Apa, A.D., Reese, K.P. & Connelly, J.W., Jr. 1997: An evaluation of nest placement theory using artificial and Columbian sharp-tailed grouse Tympanuchus phasianellus columbianus nests. - Wildlife Biology 3: 278.

Beck, M.J. & George, T.L. 2000: Song post and foraging site characteristics of breeding varied thrushes in northwestern California. - Condor 102: 93-103.

Beck, J.L. & Mitchell, D.L. 2000: Influences of livestock grazing on sage grouse habitat. - Wildlife Society Bulletin 28: 993-1002.

Block, W.M. & Brennan, L.A. 1993: The habitat concept in ornithology. - Current Ornithology 11: 35-83.

Braun, C.E. 1998: Sage grouse declines in western North America: what are the problems? - Proceeding of the Western Association of State Fish and Wildlife Agencies 78: 139-156.

Braun, C.E., Britt, T. & Wallestad, R.O. 1977: Guidelines for maintenance of sage grouse habitats. - Wildlife Society Bulletin 5: 99-106.

Brennan, L.A., Block, W.M. & Gutiérrez, R.J. 1987: Habitat use by mountain quail in northern California. - Condor 89: 66-74.

Canfield, R.H. 1941: Application of the line intercept method in sampling range vegetation. - Journal of Forestry 39: 386-394.

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

Connelly, J.W., Wakkinen, W.L., Apa, A.P. & Reese, K.P. 1991: Sage grouse use of nest sites in south-eastern Idaho. - Journal of Wildlife Management 55: 521-524.

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

Daubenmire, R.F. 1959: A canopy-coverage method of vegetation analysis. - Northwest Science 33: 224-227.

DeLong, A.K., Crawford, J.A. & DeLong, D.C., Jr. 1995: Relationships between vegetational structure and predation of artificial sage grouse nests. - Journal of Wildlife Management 59: 88-92.

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

Gregg, M.A. 1991: Use and selection of nesting habitat by sage grouse in Oregon. - MSc. thesis, Oregon State University, Corvallis, Oregon, USA, 45 pp.

Gregg, M.A., Crawford, J.A., Drut, M.S. & DeLong, A.K. 1994: Vegetational cover and predation of sage grouse nests in Oregon. - Journal of Wildlife Management 58: 162-166.

Hanf, J.M., Schmidt, P.A. & Groshens, E.B. 1994: Sage grouse in the high desert of central Oregon: Results of a study 1988-1993. - BLM OR/WA/PT-95/002-4120.7. US Dept. of the Interior, Bureau of Land Management, Prineville, OR, 57 pp.

Hickman, J.C. (Ed.) 1993: Jepson manual of higher plants of California. - University of California Press, Berkeley, California, USA, 1400 pp.

Hintze, J.C. 1997: NCSS 97 statistical system for windows. - NCSS, Kaysville, Utah, USA.

Klebenow, D.A. 1969: Sage grouse nesting and brood habitat in Idaho. - Journal of Wildlife Management 33: 649-662.

Leonard, K.M., Reese, K.P. & Connelly, J.M. 2000: Distribution and habitats of sage grouse Centrocercus urophasianus on the upper Snake River plain of Idaho: changes from the 1950s to the 1990s. - Wildlife Biology 6: 265-270.

Manly, B.F.J., McDonald, L.L. & Thomas, D.L. 1993: Resource selection by animals. Statistical design and analysis for field studies. - Chapman and Hall, London, UK, 200 pp.

Patterson, R.L. 1952: The sage grouse in Wyoming. - Sage Books, Inc. Denver, Colorado, USA, 341 pp.

Robel, R.J., Briggs, J.N., Dayton, A.D. & Hulbert, L.C. 1970: Relationship between visual obstruction measurements and weight of grassland vegetation. - Journal of Range Management 23: 295-297.

Schroeder, M.A., Young, J.R. & Braun, C.E. 1999: Sage Grouse (Centrocercus urophasianus). - In: Poole, A. & Gill, F. (Eds.); The Birds of North America, No. 425. The Birds of North America, Inc., Philadelphia, PA, USA, 27 pp.

Sveum, C.M. 1995: Habitat selection by sage grouse hens during the breeding season in south-central Washington. - MSc. thesis, Oregon State University, Corvallis, Oregon, USA, 86 pp.

Sveum, C.M., Edge, W.D. & Crawford, J.A. 1998: Nesting habitat selection by sage grouse in south-central Washington. - Journal of Range Management 51: 265-269.

Wakkinen, W.L., Reese, K.P. & Connelly, J.W. 1992a: Sage grouse nest locations in relation to leks. - Journal of Wildlife Management 56: 381-383.

Wakkinen, W.L., Reese, K.P., Connelly, J.W. & Fischer, R.A. 1992b: An improved spotlighting technique for capturing sage grouse. - Wildlife Society Bulletin 20: 425-426.

Western Regional Climate Center 1999: Termo 1 E, California (048873). National Climatic Data Center, Northern California Climate Summaries, http:/www.wrcc.dri.edu/, 11/15/2000.

Young, J.R. 1994: The influence of sexual selection on phenotypic and genetic divergence of Sage Grouse. - PhD thesis, Purdue University, IN, USA, 124 pp.

Zar, J.H. 1996: Biostatistical analysis. - Prentice-Hall, Upper Saddle River, New Jersey, USA, 662 pp.