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Source: Journal of Wildlife Management, 73(8):1341-1347. 2009.

Published By: The Wildlife Society

DOI: 10.2193/2008-339

URL: <http://www.bioone.org/doi/full/10.2193/2008-339>

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# Ecological Factors Influencing Nest Survival of Greater Sage-Grouse in Mono County, California

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**ABSTRACT** We studied nest survival of greater sage-grouse (*Centrocercus urophasianus*) in 5 subareas of Mono County, California, USA, from 2003 to 2005 to 1) evaluate the importance of key vegetation variables for nest success, and 2) to compare nest success in this population with other greater sage-grouse populations. We captured and radiotracked females ( $n = 72$ ) to identify nest sites and monitor nest survival. We measured vegetation at nest sites and within a 10-m radius around each nest to evaluate possible vegetation factors influencing nest survival. We estimated daily nest survival and the effect of explanatory variables on daily nest survival using nest-survival models in Program MARK. We assessed effects on daily nest survival of total, sagebrush (*Artemisia* spp.), and nonsagebrush live shrub-cover, Robel visual obstruction, the mean of grass residual height and grass residual cover measurements within 10 m of the nest shrub, and area of the shrub, shrub height, and shrub type at the nest site itself. Assuming a 38-day exposure period, we estimated nest survival at 43.4%, with percent cover of shrubs other than sagebrush as the variable most related to nest survival. Nest survival increased with increasing cover of shrubs other than sagebrush. Also, daily nest survival decreased with nest age, and there was considerable variation in nest survival among the 5 subareas. Our results indicate that greater shrub cover and a diversity of shrub species within sagebrush habitats may be more important to sage-grouse nest success in Mono County than has been reported elsewhere. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):1341–1347; 2009)

DOI: 10.2193/2008-339

**KEY WORDS** *Artemisia tridentata*, *Centrocercus urophasianus*, Great Basin, Greater sage-grouse, nesting, nest survival, sage-grouse.

Nest success is an important determinant of reproductive rates and, in turn, population dynamics. Population declines in greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are believed to at least be partially related to declining nesting success (Schroeder 1997, Braun 1998, Schroeder et al. 1999). Nest success also influences individual fitness, and females may select sites with particular characteristics that increase the probability that their clutches hatch (Clark and Shutler 1999). Structure of vegetation at or around nest sites is often selected by sage-grouse (Hagen et al. 2007) and is related to nesting success in many species of birds (Wallestad and Pyrah 1974, Hines and Mitchell 1983, Martin and Roper 1988, Connelly et al. 1991, Riley et al. 1992), in part because vegetation around nest sites may help conceal nests, thereby affecting probability of predation, typically the most important cause of nest loss (Ricklefs 1969).

Estimates of apparent nest success for sage-grouse have ranged from 15% to 86% (Schroeder et al. 1999). Attempts to relate nest success to local vegetation have produced variable results. Gregg et al. (1994) estimated overall nest success to be 14.5% in Oregon, USA, with successful nest sites having significantly greater cover of medium height shrubs (40–80 cm) and tall residual grasses (>18 cm). Nest success in Alberta, Canada, was estimated to be 46% (Aldridge and Brigham 2001), with increased forb cover and less grass cover at successful versus unsuccessful nest sites (Aldridge and Brigham 2002). The same study found no effect of shrub cover on nest success (Aldridge and Brigham

2002). A Wyoming, USA, study estimated nest success to be 37% and found that nest success was more strongly related to the previous year's January to June precipitation than to current vegetation (Holloran et al. 2005). Other researchers found no relationship between nest success in sage-grouse and vegetation at nest sites (Wakkinen 1990, Sveum et al. 1998, Lane 2005). Most past studies of sage-grouse estimated apparent nest success, which is known to overestimate nest survival by not accounting for lower detection rates of failed nests (Mayfield 1975, Johnson 1979). Moynahan et al. (2007) also found that the positive bias in apparent nest success estimates was highly variable, which is as great a concern as the bias itself.

We studied nest survival of sage-grouse in Mono County, California, USA, from 2003 to 2005. These sage-grouse are of conservation interest because they are genetically distinct from all other sage-grouse (Oyler-McCance et al. 2005). Additionally, Mono County's topography and geographic location mean that this area may be more mesic than many other sage-grouse habitats (Bi-State Local Planning Group, unpublished conservation plan; hereafter Bi-state GSP). Our first objective was to estimate true nest-survival rates for radiotagged sage-grouse; our second objective was to identify vegetation attributes, such as percent shrub cover at nest sites, which might influence nest success (e.g., Connelly et al. 2000). Based on previous studies, we predicted shrub cover and residual grass cover and height would be positively related to daily nest survival and true nest success. We specifically included shrub cover and residual grass height and cover because these variables have been correlated with nest success in other studies of nesting sage-grouse (Gregg

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et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005).

## STUDY AREA

The study area encompassed >59% (481,000 ha) of Mono County, California, USA, located on the eastern side of the Sierra Nevada Mountains adjacent to the Nevada, USA, state line (Bi-state GSP [Kolada et al. 2009]). 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. The study area was described in detail in Kolada et al. (2009). Vegetation was dominated by mountain big sagebrush (*Artemisia tridentata vaseyana*), interspersed with areas of low sagebrush (*A. a. arbuscula*) and Wyoming big sagebrush (*A. t. wyomingensis*). Overall, sagebrush accounted for 73% of shrub cover in the study area and 68% of shrub cover at nests (Kolada et al. 2009). Snowberry (*Symphoricarpos* spp.), currant (*Ribes* spp.), bitterbrush (*Purshia tridentata*), rabbit brush (*Chrysothamnus* spp.), and Mormon tea (*Ephedra viridis*) composed the nonsagebrush shrub community (Kolada et al. 2009). Seasonal and rotational cattle and sheep grazing was prevalent throughout the study area, with most of the federal lands included in grazing allotments (Bi-state GSP). Topographic features such as mountain ranges, valleys, or drainages divide the study area into 5 subareas: Jackass Spring, Fales, Bodie Hills, Parker Meadows, and Long Valley (Kolada et al. 2009).

## METHODS

We defined local populations for this study as known concentrations of birds occupying subareas and not known to interchange regularly with sage-grouse in other subareas, based on major topographical barriers and anecdotal data from local biologists. We detected no movement among subareas by our radiomarked sample. We captured female sage-grouse using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) and fitted them with radiotransmitters as described in Kolada et al. (2009). We weighed each individual and determined age and sex using plumage characteristics (Beck et al. 1975). Using a handheld Yagi antenna and an Advanced Telemetry Systems (ATS, Isanti, MN) receiver, we located individuals to within 30 m, 3–4 times a week during the breeding season from March to June. We assumed females were nesting when movements became localized (Connelly et al. 1993), activity sensors indicated long periods of inactivity, or both. We identified the day incubation began by tracking females approximately every other day, and located the shrub under which an individual female was nesting using binoculars. We likely, however, missed some nests that failed early in the egg-laying period. We estimated the day nests were initiated assuming a 28-day incubation period, 1.5 days/egg laid, and that incubation commenced with the laying of the last egg (Schroeder et al. 1999).

At each nest site after nest fate was determined, we used the line-intercept method to estimate live shrub canopy cover, sagebrush cover, and cover of other shrubs along a 20-

m transect in a random direction centered at the nest (Canfield 1941, Drut et al. 1994, Bureau of Land Management 1996). We estimated percent cover of understory residual grasses using 5 uniformly spaced 20-cm × 50-cm plots at the nest and along the transect (Daubenmire 1959, Bureau of Land Management 1996). We measured height of the tallest residual grass in these plots (Gregg et al. 1994, Sveum et al. 1998, Connelly et al. 2000). We also measured visual obstruction at nests with a Robel pole (Robel et al. 1970). We used nest-survival models (Rotella et al. 2004) in Program MARK (White and Burnham 1999) to estimate nest success and to test hypotheses about the relationship between vegetation variables and daily nest survival. We included total live shrub cover, live sagebrush cover, and nonsagebrush live shrub cover, and Robel obstruction from the 20-m transect centered on the nest site as covariates in models of nest survival. The means of grass residual height and grass residual cover measurements at the nest shrub did not differ from the mean of the Daubenmire plots along transects; therefore, we used the mean from Daubenmire plots as covariates in candidate models of daily nest survival. We also considered area of the nest shrub in candidate models of nest survival. The most parameterized model excluding covariates included year, subarea, and female age and allowed nest age to be fully interactive with calendar date. This model did not converge, most likely due to the large number of parameters and sparse data in some of the groups. We therefore considered models in which daily survival was constrained to contain either a linear trend or a linear plus quadratic trend as a function of nest age. We included subarea in the analysis to control for large-scale spatial variation in nest survival, and we included female age to allow for the potential that yearling females differed from older females in nest success. We also included nest initiation date in candidate models.

If sage-grouse nest survival was related to vegetation at nest sites, we expected models that included vegetation covariates to perform better than models lacking these variables. Specifically, we anticipated that residual grass height and shrub cover would be positively related to daily nest survival. Based on comments on an earlier version of the manuscript, we also considered a quadratic term for the best model including other shrub cover. Our intent here was to explore the possibility that threshold, or other nonlinear effects influenced the relationship between nest survival and other shrub cover. We restricted this structure to the other shrub cover variable because this was the only vegetation covariate that was strongly correlated to nest survival.

We considered models with only a covariate effect by themselves, but they performed poorly. Thus, we considered models in which vegetation covariates were either additive to the subarea effect or were allowed to interact with the subarea effect. To explore further if covariates explained the subarea effect, we considered models that had a mean value of a covariate for each subarea as a group covariate, which we compared against the subarea model.

**Table 1.** Number of sage-grouse nests used for analysis in Mono County, California, USA in 5 subareas from 2003 to 2005.

Subarea	2003	2004	2005	Total
Bodie Hills	4	14	9	27
Fales	4	4	0	8
Jackass	5	7	6	18
Long Valley	7	11	14	32
Parker	2	5	3	10
Total	22	41	32	95

We used data for 2 nests for each of 23 females. This practice could have produced extra binomial variation in the data if females varied in the probability of hatching their nests. There is currently no accepted method for assessing the extent of overdispersion in data used in known-fate or nest-survival models (J. J. Rotella, Montana State University, unpublished report). We compared the observed frequency of this subset of females hatching zero, one, or both of their nests to the expectation under a binomial model using a goodness-of-fit test to assess the contribution of this subset of nests to overdispersion in our data.

We used an information theoretic approach to evaluate performance of a priori models and, therefore, our hypotheses (Burnham and Anderson 2002). We report parameter estimates (e.g., percent shrub cover and daily nest-survival rates) and their 95% confidence intervals, which allowed us to assess the size of potential effects of covariates on daily nest survival.

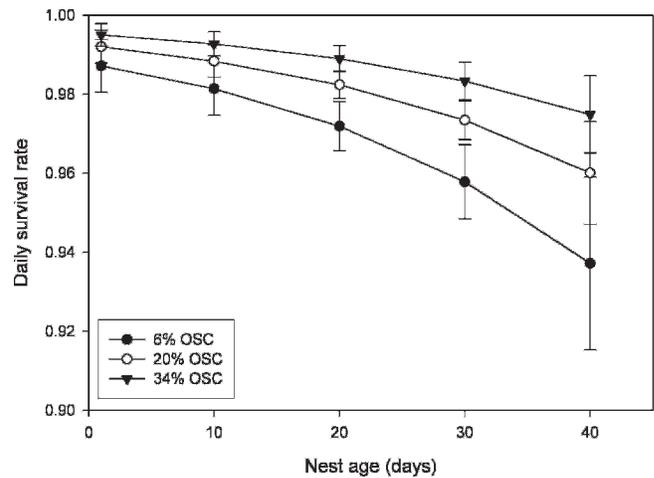
**Table 2.** Results for nest-survival models for sage-grouse nesting during 2003–2005 in Mono County, California, USA. Analyses were performed using nest-survival models in Program MARK.

Model <sup>a,b</sup>	$\Delta AIC_c^c$	Akaike wt	No. parameters	Deviance
S(AREA + T + OSC)	0.00	0.41	7	270.6
S(T + OSC)	2.63	0.11	3	281.3
S(AREA + OSC)	3.13	0.09	6	275.7
S(AREA + T + AREA × OSC)	3.19	0.08	11	265.7
S(AREA + T + NSA)	4.66	0.04	7	275.3
S(OSC)	4.94	0.04	2	285.6
S(AREA + T + SXS)	5.01	0.03	7	275.6
S(AREA + T + SC)	5.14	0.03	7	275.7
S(AREA + T + AREA × SC)	5.17	0.03	11	267.7
S(AREA + T)	5.24	0.03	6	277.9
S(AREA + T + SAC)	5.60	0.03	7	276.2
S(AREA + T + RH)	6.15	0.02	7	276.8
S(AREA + T + RC)	6.79	0.01	7	277.4
S(AREA + T + R)	6.95	0.01	7	277.6
S(AREA)	7.28	0.01	5	281.9
S(AREA + AREA × OSC)	7.39	0.01	10	271.9
S(T)	8.16	0.01	2	288.8
S(.)	9.78	0.00	1	292.4
S(AREA + AGE)	10.76	0.00	9	277.3

<sup>a</sup> AGE = age of F at nesting (juv or ad), AREA = all 5 subareas (Bodie Hills, Fales, Jackass, Long Valley, Parker), NSA = nest shrub area, OSC = other shrub cover, R = Robel, RC = residual grass cover, RH = residual grass ht, SAC = sagebrush cover, SC = shrub cover, SXS = sagebrush and other shrub interaction, T = linear trend of nest age.

<sup>b</sup> Global model did not converge.

<sup>c</sup> Difference in Akaike's Information Criterion from top model.



**Figure 1.** Model-averaged daily survival rates and the 95% confidence interval of sage-grouse nests (2003–2005) in Mono County, California, USA, at varying amounts of other shrub cover.

## RESULTS

We captured 72 females and estimated nest survival for 95 nests from 2003 to 2005 (Table 1). For the subsample of females with 2 nests, the observed frequency of females hatching zero, one, or both of their nests did not differ from the expectation under a binomial distribution ( $\chi^2 = 1.36$ , 2 df,  $P = 0.51$ ). We located 19 nests during egg laying (mean age = 7.3 days), resulting in 47 exposure days during the egg-laying period; although our early sample was limited, our results can be viewed as applying to the entire nesting period.

The best model of nest survival (wt = 0.413; Table 2) contained a subarea effect with a linear trend of nest age and other shrub cover as a covariate, indicating that there was variation in nest survival among areas, that nest survival declined with nest age, and that nest survival increased with increasing amounts of other shrub cover (Fig. 1). The second-best model (wt = 0.111; Table 2) contained a linear trend of nest age and an effect of other shrub cover on daily survival rate. Thus, the second-best model was the same as the best model, but without the subarea effect. There was a general lack of support for models that contained other variables of potential interest, such as residual grass height or cover, year, or female age effects (Table 2). Models that contained just a covariate effect on daily nest survival performed poorly. Also, models that contained interactions between vegetation covariates and subareas performed poorly. Addition of a quadratic term for other shrub cover to the best performing model only modestly improved model fit (difference in Akaike's Information Criterion from top model [ $\Delta AIC_c$ ] = 1.36,  $\beta = -0.15 \pm 0.33$  for the quadratic other shrub-cover term), indicating only modest support for a nonlinear effect of other shrub cover on nest survival. A model adding an effect of nest initiation date to the area effect was not competitive ( $\Delta AIC_c = 9.3$ ,  $\beta_{\text{initiation date}} = -0.002 \pm 0.33$ ); we did not include these

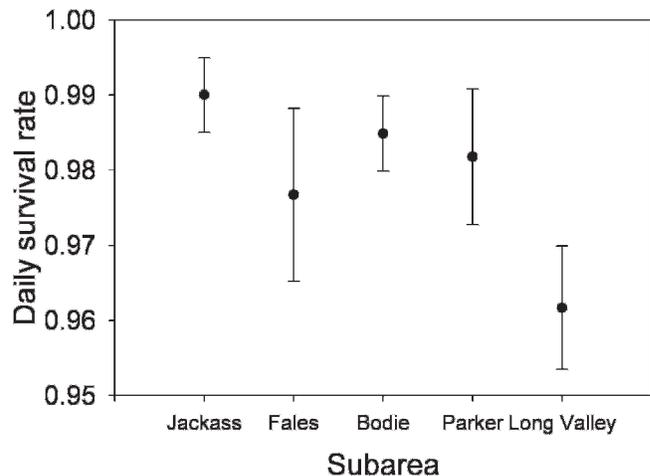
models in the model selection table to simplify comparison of effects of fixed effects and covariates.

Sum of Akaike weights for models containing nest age was 0.853, with a model equal to averaged  $\beta$  estimate for nest age of  $-0.039 \pm 0.123$ . Although the trend with nest age was relatively weak, models lacking this effect fit the data substantially more poorly. Survival decreased at 0.35% of the estimate for each day older a nest became (Fig. 1). Other shrub cover had a summed Akaike weight of 0.761, and the model-averaged  $\beta$  estimate was  $0.327 \pm 0.310$ . Daily survival increased between 0.3% and 0.4% for every 14% increase in other shrub cover within 10 m of nest sites (Fig. 1). The best model containing sagebrush cover was 5.6  $AIC_c$  units worse than the best candidate model, providing no support for an effect of sagebrush cover itself on daily nest survival in Mono County. A model containing total shrub cover performed only slightly better ( $\Delta AIC_c = 5.14$ ) than the best model containing sagebrush cover. The sum of the Akaike weights for models containing subarea was 0.845; daily nest survival was highest at Jackass, the most northerly subarea, and lowest in Long Valley, the most southerly subarea (Fig. 2). Models in which we substituted mean vegetation characteristics on subareas for a subarea effect itself performed poorly ( $\Delta AIC_c = 7.28$ ), indicating substantial spatial variation in nest survival in Mono County beyond that associated with vegetation characteristics.

## DISCUSSION

Increased cover of shrubs other than sagebrush increased nest survival of sage-grouse but we failed to find an important effect of sagebrush cover on nest success of sage-grouse in Mono County. Our results were generally consistent with findings of other studies that shrub cover is positively correlated with nest success in sage-grouse (Connelly et al. 1991, Gregg et al. 1994). Our results differed subtly from these other studies in that we failed to find a direct effect of sagebrush or total shrub cover on nest success, although the confidence interval for the total shrub-cover  $\beta$  barely overlapped zero ( $\beta = 0.27 \pm 0.36$ ). Aldridge and Boyce (2007) found that nests were at slightly greater risk of failure as sagebrush cover near the nest increased, whereas nests in heterogeneous sagebrush areas experienced greater success, which could be viewed as consistent with our result. Popham and Gutiérrez (2003) reported that shrub height was greater at successful than unsuccessful nests. Some studies found no relationship between shrub cover and nest success in sage-grouse (Wakkinen 1990, Sveum et al. 1998, Lane 2005). These studies indicate that shrub cover is important to sage-grouse nest survival, but the precise nature of the relationship appears complex.

Some studies have reported that residual grass cover (Moynahan et al. 2007) or residual grass height (Gregg et al. 1994) influenced nest success of sage-grouse. In contrast, we detected no association between residual grass height or residual grass cover and daily nest survival. The best models containing either of the grass covariates received only about 1% of the Akaike model weights. Similar to our results, Holloran et al. (2005) found that both residual grass cover



**Figure 2.** Model-averaged daily survival rates and the 95% confidence intervals for greater sage-grouse nests in each of the 5 subareas in Mono County, California, USA, during 2003–2005.

and residual grass height were similar at successful and unsuccessful nests. Taken together, these studies indicate that cover is typically positively associated with nest success, but the nature of vegetation providing cover appears to vary. The cause of such variation is currently unknown and it is unclear if this variation is a function of structure of the vegetation, variation in predator communities, or other environmental factors.

We detected substantial variation in daily nest survival among subareas, with a trend of generally decreasing nest success from the northernmost subarea, Jackass, to the southernmost subarea, Long Valley. We estimated nest success for the northernmost areas was about 3 times that of the southernmost area, 68% versus 21%. This pattern was not a result of variation in vegetation variables, because models replacing the subarea fixed effect with mean values for vegetation covariates in each subarea were not supported. Variation in composition or abundance of key predators could explain the spatial variation we observed, because predation is the principal cause of nest failure (Wallestad and Pyrah 1974, Holloran et al. 2005, Moynahan et al. 2007). There are currently no data on predator abundance in Mono County. We also note that the Long Valley subarea is closest to the Mammoth Mountain ski area, and could be influenced by increased human disturbance.

Our overall estimate of nest survival (43.4%) was higher than any of the estimates reported for an area in northern Montana by Moynahan et al. (2007), who used similar maximum likelihood methods. Moynahan et al. (2007) used an exposure period of 28 days, representing only the incubation period, whereas we included the egg-laying period (10 days) in the exposure period used to estimate nest success. Our estimate of nest success would have been even greater relative to that of Moynahan et al. (2007) had we used a comparable exposure period. Our estimate falls in the middle of the range of other studies of sage-grouse (Wakkinen 1990, Gregg et al. 1994, Schroeder 1997,

Aldridge and Brigham 2001, Holloran et al. 2005). All of these studies, however, reported apparent nest success (Wakkinen 1990, Gregg et al. 1994, Aldridge and Brigham 2001) and likely overestimated nest success. Holloran et al. (2005) used an adjustment to account for lesser detection of failed nests, which should have made their estimates more similar to maximum likelihood estimates.

Estimates of apparent nest success are strongly influenced by visitation schedules and daily nest-survival rate (Mayfield 1975) and are biased high because nests that fail before they are found are less likely to be included in the sample. Furthermore, nests found late in the nesting cycle are exposed to predation or other factors for a shorter period and are more likely to hatch for this reason alone. Because bias is a function of both visitation schedule and external nest mortality factors, bias is unknown, making it difficult to compare among studies. Nevertheless, 95% confidence interval for our estimates of nest success overlap point estimates for several other studies. Our estimate of apparent nest success (55.6%) is 28% higher than the estimate we report here. Bias in apparent nest-survival estimates ranged from 8% to 91% above maximum likelihood estimates in Moynahan et al.'s (2007) study. Variation in bias, which is unknown for other studies, makes it virtually impossible to evaluate the true extent of variation in nest survival among studies of sage-grouse. If, however, biases were similar in other studies, then sage-grouse in Mono County had among the highest nest success of populations studied to date.

Sage-grouse in Mono County selected nest sites with greater overall shrub canopy cover than what was available, both within 200 m of nests and at the subarea scale, suggesting that females attempted to maximize concealment of their nests under shrubs (Kolada et al. 2009). Selection of nest sites in areas with greater overall shrub cover would have increased the density of both sagebrush and shrubs other than sagebrush at nest sites. Nest success was strongly related to the cover of other shrubs at nests. Aldridge and Boyce (2007) also reported a complex relationship between shrub cover at nests and nest success. Although we failed to find a direct linkage between the variable females used to select nest sites (i.e., total shrub cover), and nest success, the importance of other shrub cover, a strong correlate of total shrub cover, to nest success provides a linkage between nest-site selection and factors related to nest success. We are unsure of the reason for the distinction between total shrub cover and other shrub cover, but this could suggest subtleties in predator search images or nest concealment that our methods were unable to detect.

We did not detect selection of nest sites with greater residual grass height or cover (Kolada et al. 2009), similar to results reported by Holloran et al. (2005), despite availability of sites in Mono County with greater residual grass height or cover than those that were selected. Nest success in Mono County was not related to either residual grass height or cover. In this respect our results differed from those of Gregg et al. (1994) and Moynahan et al. (2007) who detected a positive relationship between residual grass height and cover and nest success. It is possible our failure

to detect an effect of grass variables on nest success reflected relatively low levels and range of variation in grass variables in Mono County. Nevertheless, our results show a clear association between vegetation characteristics selected for nest sites and those associated with improved nest success.

We caution, however, that nest success, by itself, may not be the principal determinant of breeding population size, because nest success may not be the only limiting factor for a given sage-grouse population. Other demographic rates, such as chick survival, juvenile survival, adult survival, or movement, may be as important to sage-grouse population dynamics (Johnson and Braun 1999, Holloran et al. 2005, Aldridge and Boyce 2007). If any of these vital rates are under density-dependent control, results of increased nest success may be counterbalanced by reduction in another vital rate (e.g., chick survival). Removal of ravens (*Corvus corax*) in sage-grouse nesting areas in northeastern Nevada resulted in increased nest success, but did not improve the recruitment of individuals into the population (Coates and Delehanty 2004; Bi-state GSP). In Wyoming, nest success and chick survival did not differ between control areas and sites with coyote (*Canis latrans*) control (Slater 2003); however, coyote control could have elicited an undetected population level increase in sage-grouse.

Overall, we found other shrub cover increased sage-grouse nest success. It is unknown, however, how other shrub cover affected nest survival of sage-grouse. There was little support for other vegetation variables such as sagebrush cover and residual grass cover or height. Despite the fact that our nest success estimates are similar to, if not greater than, those in other parts of sage-grouse range, some vegetation variables identified as being important in other locations (Gregg et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005, Moynahan et al. 2007) did not influence sage-grouse nest success in Mono County. Nest success increased with the increased cover of shrubs other than sagebrush; however, sage-grouse nest success in Mono County may also be influenced by other factors, such as the composition and behavior of the local predator community.

## MANAGEMENT IMPLICATIONS

Nest survival was relatively high in Mono County, and linked to cover at nests by other shrubs. Sage-grouse selected nest sites with greater shrub cover than was available at random. Our result differs from some other parts of sage-grouse range, where sagebrush may represent >90% of shrub cover. Selection of nest sites with greater shrub cover and the positive effect of other shrub cover on nest success indicates that managers in Mono County should manage for greater cover of shrubs and greater diversity of shrubs than might be true in other portions of sage-grouse range. We caution that we are not recommending that understory vegetation be ignored, because such vegetation is important in other sage-grouse nesting areas, but we recommend that shrub cover and diversity should receive a higher priority in Mono County when managing for sage-grouse.

## ACKNOWLEDGMENTS

We thank field technicians J. Felland, R. Montano, K. Nelson, B. Barbaree, K. Gagnon, S. Alofsin, and T. Skousen for field assistance. We also thank M. Farinha for her tireless work. We thank D. Blankenship, S. Gardner, D. Racine, and the California Department of Fish and Game (CDFG), United States Forest Service, and Bureau of Land Management for support. We thank D. House and the Los Angeles Department of Water and Power. We also thank C. Overton and P. Barnes for analytical and logistical help. We extend special thanks to J. Fatooh, S. Nelson, A. Halford, and T. Taylor for providing local knowledge, help in the field, and insight into sage-grouse biology. We thank R. Haldeman and L. Fields of Quail Unlimited for financial and logistical help. We also send special thanks to the CDFG Air Services Unit in Sacramento, California. R. Morgan, W. Burnett, Jr., and R. VanBenthuyzen all provided many hours of professional air support. We thank all the students and past students of the Sedinger lab for all their help on issues ranging from theory to statistical procedures. M. Miller and J. Yee provided reviews of early versions of the manuscript. C. E. Braun and L. D. Flake reviewed an earlier draft of the manuscript. We also thank J. Connelly and T. Apa for helpful reviews of the study plan. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government.

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*Associate Editor: Burger.*