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Management and Conservation Article

Nest Predation of Greater Sage-Grouse in Relation to Microhabitat Factors and Predators

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ABSTRACT Nest predation is a natural component of greater sage-grouse (*Centrocercus urophasianus*) reproduction, but changes in nesting habitat and predator communities may adversely affect grouse populations. We used a 2-part approach to investigate sage-grouse nest predation. First, we used information criteria to compare nest survival models that included indices of common raven (*Corvus corax*) abundance with other survival models that consisted of day of incubation, grouse age, and nest microhabitat covariates using measurements from 77 of 87 sage-grouse nests. Second, we used video monitoring at a subsample of 55 of 87 nests to identify predators of depredated nests ($n = 16$) and evaluated the influence of microhabitat factors on the probability of predation by each predator species. The most parsimonious model for nest survival consisted of an interaction between day of incubation and abundance of common ravens ($w_{raven \times incubation\ day} = 0.67$). An estimated increase in one raven per 10-km transect survey was associated with a 7.4% increase in the odds of nest failure. Nest survival was relatively lower in early stages of incubation, and this effect was strengthened with increased raven numbers. Using video monitoring, we found the probability of raven predation increased with reduced shrub canopy cover. Also, we found differences in shrub canopy cover and understory visual obstruction between nests depredated by ravens and nests depredated by American badgers (*Taxidea taxus*). Increased raven numbers have negative effects on sage-grouse nest survival, especially in areas with relatively low shrub canopy cover. We encourage wildlife managers to reduce interactions between ravens and nesting sage-grouse by managing raven populations and restoring and maintaining shrub canopy cover in sage-grouse nesting areas.

KEY WORDS American badger, *Centrocercus urophasianus*, common raven, greater sage-grouse, nest predation, video monitoring.

Greater sage-grouse (*Centrocercus urophasianus*) range has declined substantially since Euro-American settlement of western North America (Schroeder et al. 2004). Many populations within the remaining range also are in decline (J. W. Connelly, Western Association of Fish and Wildlife Agencies, unpublished report). Nest survival is a natural antecedent to population recruitment and renewal. The primary source of sage-grouse nest failure is predation, accounting for an average of 94% of nest loss (Moynahan et al. 2007); hence, nest predation can be a limiting factor for population sustainability (Nelson 1955, Gregg et al. 1994, Schroeder and Baydack 2001). While predation is a natural component of game-bird reproduction, its effect on population viability may vary with habitat and predator composition (Evans 2004).

Loss of nesting habitat and increases in predator population numbers can interact and be important causal factors in nest predation of ground-nesting birds (Evans 2004). Many attributes of nesting habitat features can influence whether a nest survives, such as degree of concealment of eggs or parents from predators (Deeming 2002) or modulating thermal flux (Ar and Sidis 2002). Nest habitat features identified as important to sage-grouse include presence of sagebrush (*Artemisia* spp.; Connelly et al. 1991), canopy cover (Wallestad and Pyrah 1974, Gregg et al. 1994), grass height (Gregg et al. 1994, Holloran et al. 2005), and understory cover (Gregg et al. 1994, DeLong et al. 1995). Loss of these features can diminish rates of nest survival (Connelly et al. 1991, Gregg et al. 1994, Holloran et al. 2005). However, confirmation of the identity of sage-grouse nest predators and the effects of confirmed predators under varying microhabitat conditions is poorly documented and such knowledge might help guide management actions.

Generalist predators that reach high numbers in human-altered habitats are of great conservation concern because they can substantially reduce prey populations (Garrott et al. 1993, Schneider 2001) and these predators have been shown to continue depredating bird nests even at low prey densities (Polis et al. 1997, Sinclair et al. 1998). Common ravens (*Corvus corax*) are generalist predators that use visual cues to locate eggs and young of many animals (Boarman and Heinrich 1999), including sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001), and ravens can have substantial predatory impacts on prey populations (Andrén et al. 1985, Boarman et al. 2006). Raven numbers have increased 300% in the western United States since 1980 (Sauer et al. 2008) and remain high despite reductions in natural prey (Boarman 1993). In desert environments, population increases are thought to be caused by anthropogenic resource subsidies such as food (e.g., landfills; Webb et al. 2004) and nest substrate (e.g., transmission towers; Knight and Kawashima 1993). An understanding of the effects of raven abundance on nest predation in relation to habitat factors would aid management efforts designed to promote sage-grouse population viability, such as managing nesting habitat to reduce raven population size and reduce the chance of ravens finding and depredating nests.

We evaluated predation at sage-grouse nests in relation to microhabitat factors and raven abundance to help guide sage-grouse management plans. Our primary objective was

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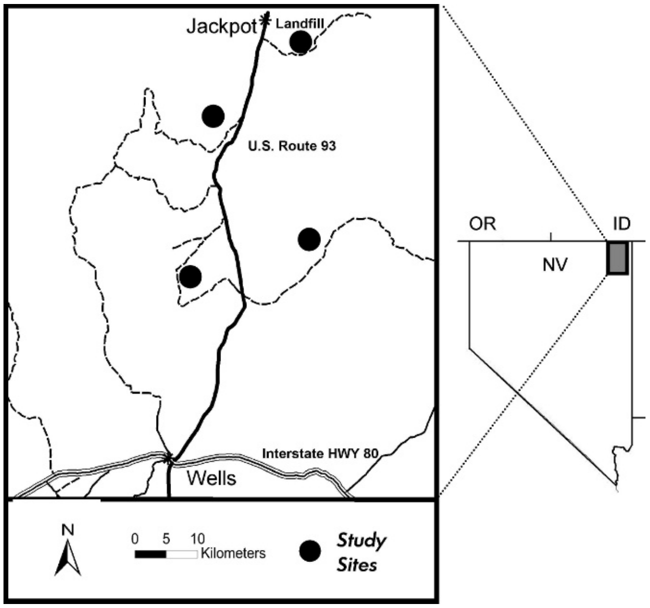

Figure 1. Greater sage-grouse study sites in northeastern Nevada, USA, during 2002–2005. Study sites were based on lek complexes and were separated by distances >20 km. United States Department of Agriculture Wildlife Services carried out raven removal activities at the southernmost study site. A public landfill was located approximately 7 km from the northernmost site.

to use information theory (Anderson 2008) to compare a priori models (hypotheses) of sage-grouse nest survival consisting of covariates supported by the literature (e.g., microhabitat variables) to models of sage-grouse nest survival that additionally included a covariate of raven abundance. We analyzed ravens, as opposed to other known sage-grouse nest predators, because ravens have been reported as a synanthropic predator (Boarman et al. 2006, Leu et al. 2008) and are thought to be detrimental to sage-grouse populations (Autenrieth 1981; J. W. Connelly, unpublished report). Our second objective was to confirm the identities of predators at depredated sage-grouse nests using around-the-clock videography and test for differences in microhabitat characteristics of depredated nests in relation to species of nest predator. In particular, we evaluated the hypothesis that nests with less surrounding vegetation are more likely to be depredated by visually cued predators like ravens and other corvids (Connelly et al. 1991).

STUDY AREA

We monitored a sample of sage-grouse nests within an area of approximately 1,430 km^2 located in Elko County, Nevada, USA (4°32′41.661″N, 82°17′42.973″E; North American Datum 1983) during 2002–2005 (Fig. 1). We captured grouse from 4 lek complexes. We defined a lek complex as an area of 1–3 breeding grounds (leks). Each of the 4 lek complexes was separated by more than 20 km. A lek within a complex was not farther than 2 km from the nearest lek.

Dominant plant communities consisted of shrub-steppe at lower elevations and mountain shrub at higher elevations across study sites. Overstory of shrub-steppe was characterized by basin big sagebrush (*Artemisia tridentata tridentata*), Wyoming big sagebrush (*A. tridentata wyomingensis*), and little sagebrush (*A. arbuscula*). Crested wheatgrass (*Agropyron cristatum*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) characterized the understory of shrub-steppe communities. Overstory of mountain shrub communities was characterized by mountain big sagebrush (*A. tridentata vaseyana*) and Saskatoon serviceberry (*Amelanchier alnifolia*) and understory was primarily native bunchgrasses. Utah Juniper (*Juniperus osteosperma*) was in peripheral areas at 2 of 4 sites.

The Nevada Department of Wildlife, in cooperation with United States Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services, manipulated raven numbers by carrying out raven removal activities at the southernmost lek complex to produce variation in the number of ravens across the study areas. Wildlife Services personnel placed 10,500 chicken egg baits treated with 3-chloro-p-toluidine hydrochloride at the southernmost lek complex throughout the sage-grouse nesting period of all study years. Raven counts were reduced significantly at this site and no reduction was detected at 3 control sites (Coates et al. 2007). A public landfill and private livestock carcass disposal area were located approximately 7 km and 3 km northeast of the northernmost lek complex in Nevada. The southernmost lek complex was approximately 55 km from the northernmost lek complex.

METHODS

We captured female sage-grouse at night by spotlighting (Giesen et al. 1982, Wakkinen et al. 1992) and determined age based on plumage (Ammann 1944) during the nesting period, 15 March–1 May 2002–2005. We equipped grouse with 17–21-g, necklace-style radiotransmitters (Advanced Telemetry Systems, Isanti, MN). We relocated grouse every 2–3 days using handheld receivers and circled around grouse at approximately 50 m. We used a handheld Global Positioning System to record Universal Transverse Mercator coordinates of grouse during relocation. We approached grouse to visually confirm nesting when we located grouse at the same coordinate as the previous location. We located nests during egg-laying or the initial days of incubation. We monitored females every 1–3 days to record their status and determine nest fate (i.e., depredated, abandoned, and hatched).

We measured microhabitat characteristics at nests 1–3 days following nest fate. We measured shrub height (cm) and understory cover (%) at 77 of 87 nests and within 25 m of each nest during 2002–2005. We measured heights of shrubs that were directly over nests. We also measured all shrub heights along 4 25-m orthogonal transects in random orientation that intersected at the nest bowl. We averaged shrub heights and did not measure shrubs at nests more than once. We used a 3-sided cover board (modified from Jones 1968) to measure understory cover at nests. We placed the cover board directly on the nest at random orientation. Each side (25 × 25 cm) of the board consisted of a checkerboard

Table 1. Means ± standard errors of explanatory variables used in analyses of nest survival of greater sage-grouse, where n = number of nests used in analyses. We collected data in northeastern Nevada, USA, during 2002–2005.

Variable	Description[a]	n	$\bar{x}$	SE
RVN	Indices of raven abundance (no. of ravens counted per 10 km) in relation to sage-grouse nests	77	2.88	0.28
NVO	Visual obstruction (%) of understory vegetation at the nest	77	76.10	0.82
50VO	Visual obstruction (%) at a 50-m scale and centered on the nest	77	56.50	0.81
HT	Ht of shrubs (cm) along 4 25-m line transects intersecting at nest bowl	77	39.32	1.40
NHT	Ht of shrub (cm) directly above nest bowl	77	66.19	2.44
TSC	Total shrub cover (%) along 4 25-m line transects measured using line intercept method	58	40.50	1.08
SBC	Sagebrush cover (%) along 4 25-m line transects measured using line intercept method	58	31.73	2.03
MFB	Dried biomass of forbs (g; 16 micro-plots placed randomly within 50 m of nest)	58	1.90	0.09
MGR	Dried biomass of grass (g; 16 micro-plots placed randomly within 50 m of nest)	58	3.08	0.38
INC	Day of incubation (no. of elapsed days between the onset of incubation and nest fate)	77	N/A	
GAGE	Grouse age (< 1 or >1 year of age)	77	N/A	
LC	Lek complex (group of leks)	77	N/A	
YR	Yr of nest (2002–2005)	77	N/A	

[a] We measured total shrub cover (TSC) and sagebrush cover (SBC) and dry biomass of forbs (MFB) and grasses (MGR) during 2004 and 2005 and included these variables in models within a restricted dataset. We excluded SBC from the models because of correlation with TSC.

pattern of 25 squares (5 × 5 cm). We randomized orientation of the board and counted the number of squares at a distance of 2 m from each side of the board that were $\leq$50% visually obstructed. We conducted measurements at 2 heights: horizontal (25 cm aboveground) and 45° above horizontal (approx. 2 m aboveground). We then averaged measurements to estimate cover obstruction across angles and cover board sides. To estimate understory cover at a 50-m scale, we used the same cover board method at 16 random points within 25 m of each nest and calculated averages.

During 2004–2005, we conducted 4 additional habitat measurements. We measured shrub canopy cover (%) of sagebrush and all shrubs and dried biomass of grass and forbs (g). We carried out these additional habitat measurements at 58 nests (restricted dataset). We estimated canopy cover (%) of sagebrush shrubs and of all shrub species at a 50-m scale using a line-intersect technique (Canfield 1941). This technique consisted of measuring distances where shrub vegetation intersected a transect line and then dividing the sum of these distances by the overall transect length. We did not classify vegetation gaps (i.e., no intersecting vegetation) that were >5 cm as shrub cover. We did not measure any section of shrub more than once. We used 4 25-m transects that intersected at the nest bowl and calculated averages. To estimate biomass of grass and forb vegetation at the 50-m scale, we clipped all live and residual grasses and forbs at ground level that were within 16 micro-plots (0.5 m^2 per plot) placed randomly within 25 m of the nest bowl, and we stored the samples from each micro-plot separately. We subsequently dried samples and weighed them in the lab. In the field we noted plots with no grasses or forbs, and we later considered these plots in averaging subsamples to estimate biomass per nest area.

We conducted strip transect surveys (Garton et al. 2005) of ravens (surveys, $n = 124$) at each sage-grouse lek complex every 3–7 days during morning (0600–1200 hr) of 20 March–1 July 2002–2005. Survey transects were 27 km during 2002–2003 and 20 km during 2004–2005 and centered on the sage-grouse lek complex. We chose a 20-km transect to encompass nearly all nests in relation to the nearest lek (Schroeder et al. 1999). We calculated the number of ravens that were observed per 10 km for each transect to avoid confounding effects associated with differences in transect lengths. We established survey points along transects every 800 m. At each survey point, we searched for a 3-minute period using binoculars and counted the number of ravens and other corvids, flying or perched, within approximately 500 m of the transect. We avoided recounting individual ravens by keeping track of ravens previously counted as we moved between survey points.

We found differences in the numbers of counted ravens during our surveys through time and found grouse initiated nests at different dates. Therefore, we calculated indices of raven abundance for each nest by averaging the numbers of counted ravens per 10 km from the affiliated survey route within the nesting dates of each individual. Our objective was to investigate how raven abundance affected nest survival of grouse, not to estimate raven population density. Because we used vehicles to move between points, we designated survey transects based on unpaved, low-use roads at the treatment and control areas.

We evaluated evidence of support for sage-grouse nest survival models using information theory (Anderson 2008). To prevent multicollinearity, we excluded 1 of 2 variables that co-varied ($r \geq 0.65$) based on variance inflation factors (VIF $\geq$ 10) and biological rationale. We reported mean (±SE) of variables that were used in the models (Table 1). We also compared models with year and site as fixed effects. To avoid pseudo-replication of individuals, we did not include renests in the analyses. We performed parameter estimation using Program R with the package RMark (R Version 2.7, www.r-project.org, accessed 13 July 2008; Laake and Rexstad 2007) that implements Program MARK (White and Burnham 1999). We included day of incubation as a time-dependent covariate in models to evaluate the hypothesis that daily survival rate (DSR) is lower in early stages of incubation because vulnerable nests are more likely to be depredated early in the incubation period (Klett and Johnson 1982). We also included an interaction between day of incubation and raven abundance in a model to better understand the effects of raven numbers as incubation advances. To calculate the day of incubation, we measured the days elapsed between the date of nest fate (i.e., depredated, abandoned, or hatched) and the date of the onset of incubation. The nest survival model in Program MARK is robust for evaluating time-dependent covariates (Dinsmore et al. 2002). We did not evaluate nest age as a covariate because of difficulty in obtaining accurate measurements of the onset of egg laying using radiotelemetry techniques. We used Akaike's Information Criterion (Akaike 1973) corrected for small sample size (AIC_c; Anderson et al. 2000) to calculate differences between models (ΔAIC_c, representing a unit of comparison across models) and to calculate model probabilities (w_i, representing estimated probability that model i was the best among those considered; Anderson 2008).

We carried out the model evaluation in 2 steps. During step 1, we compared a priori models ($n = 14$; hypotheses) from data that we measured during 2002–2005. This step allowed us to determine the most parsimonious models using the full dataset from variables measured during the study. During step 2, we restricted the dataset to include only measurements from 2004 and 2005 because we measured 4 additional variables during these years. This second set of models ($n = 12$) consisted of the 5 best fit models as determined by using the 5 greatest model probability values from the full 2002–2005 dataset and 7 additional best fit models (hypotheses) that we developed using the additional habitat characteristics measured during 2004 and 2005. We performed step 2 to determine if the additional microhabitat characteristics measured in 2004 and 2005 provided greater weight of evidence in explaining nest survival than the variables measured across all years. Restricting analyses to 2004 and 2005 for all models in step 2 was necessary because measurements of any one variable must be made at all nests when comparing models (Anderson and Burnham 2002).

To accomplish our second objective of assessing habitat features associated with species of nest predator, we identified nest predators using video-monitoring at a subsample of nests ($n = 55$; Coates et al. 2008). We chose nests for video-monitoring based on fewest estimated days of incubation. We monitored these nests with time lapse videocassette recorders and cameras equipped with infrared-emitting diodes (Fuhrman Diversified Inc., Seabrook, TX; Supercircuits, Austin, TX). To avoid abandonment (Renfrew and Ribic 2003), we deployed cameras at nests ≥7 days following the onset of incubation during morning hour while grouse were at recess from incubation, although on some occasions we unexpectedly flushed grouse from the nest. We installed fresh video tapes and batteries in video recorders every 2–3 days. To avoid deterring or attracting predators (Herranz et al. 2002), we camouflaged equipment with vegetation and vinyl photography tape that resembled shrub-steppe vegetation.

We tested the effects of microhabitat characteristics on the probability of predation by each predator classified by species (identified by video and direct observation) using exact logistic models (LogXact, Cytel Software, Cambridge, MA), a modification of the Markov chain Monte Carlo algorithm that is robust for small sample size data (Hirji et al. 1987, Forster et al. 2003). We modeled each confirmed predator species separately (e.g., raven) and for each confirmation (e.g., raven predation). We coded the unsuccessful nest as 1 and coded the successful nests as 0. We considered nests to be successful if ≥1 egg hatched (Rearden 1951). When predicting the probability of predation by ravens, we also included a model of raven abundance. We calculated means (±SE) for microhabitat characteristics of nest depredated by each species of predator. We then calculated confidence intervals (95%) of the estimated differences between means of each predator species for each habitat characteristic (Rosner 1990). These calculations allowed us to identify differences in microhabitat factors by each predator type. We only considered nest predators that were identified using video or direct observation in these analyses.

RESULTS

We monitored a total of 87 sage-grouse nests ($n = 55$ with camera and $n = 32$ with no camera). Thirty-seven nests (42.5%) were depredated, 6 (6.9%) were abandoned, and 44 (50.6%) were successful. The estimated DSR using maximum likelihood was 0.978 ± 0.003 (with camera, 0.980 ± 0.004; without camera, 0.973 ± 0.007). The calculated point estimate of nest survival was 0.44 (95% CI, 0.35–0.55) using a 37-day period (laying and incubation period). This estimate differed from the apparent nest success of 0.51.

The most parsimonious model of 14 nest survival models using the full dataset (nests, $n = 77$) included an interaction between day of incubation and raven abundance (model 1; Table 2). This model predicted 1) DSR decreased as raven abundance increased, 2) DSR was lower in early stages of incubation, and 3) this effect was strengthened with increased raven numbers (Fig. 2). No other models had a ΔAIC_c value that was ≤2. The probability that this model was best of the candidate set of models for describing nest survival was 0.67 ($w_{raven \times incubation\ day}$). The model with the second highest support from the data consisted of raven abundance (model 2; Table 2). Model 1 was 6.7 ($w_{raven \times incubation\ day}/w_{raven}$) times more likely to be best for describing nest survival than model 2 based on evidence ratios (Anderson and Burnham 2002). Raven abundance was found in each of the top 5 models. An increased index value of one observed raven (per 10 km) was associated with an approximately 7.4% increase in the odds of nest failure (odds ratio = 1.074, 95% CI = 1.034–1.114).

When comparing the 12 models of the restricted dataset (nests, $n = 58$) that included covariates of additional measurements of canopy shrub cover and biomass of forbs and grasses, we found the interaction between raven abundance and day of incubation remained the most parsimonious model (model 6; Table 2). The probability that this model was the best for describing nest survival using the restricted dataset was 51% ($w_{raven \times incubation\ day}$),

Table 2. Models that explained nest survival of greater sage-grouse. Step 1 compared models (n = 14) within the full dataset (nests, n = 77), which consisted of hypotheses derived from measurements carried out during 2002–2005. Step 2 compared models (n = 12) within a restricted dataset (nests, n = 58), which consisted of the 5 most parsimonious models of Step 1 and additional hypotheses from measurements during 2004 and 2005. The −2(log-likelihood) value is denoted by −2LL. The likelihood R^2-value (LR^2) was based on likelihood-ratio test, $1 - \exp[-2/n(\mathrm{LogL}_m - \mathrm{LogL}_o)]$, where LogL_m is the log-likelihood of the model of interest, LogL_o is the log-likelihood of the null model, and n is the number of observations (Magee 1990). $\Delta \mathrm{AIC}_c$ represents the difference between the Akaike's Information Criterion model of interest and the most parsimonious model of the model set. Akaike weight (w_i) represents the probability that the model of interest is the best predictive model of those within the model set (Anderson 2008). We collected data in northeastern Nevada, USA, during 2002–2005.

Model	Explanatory variables[a]	Parameters	−2LL	LR^2	$\Delta \mathrm{AIC}_c$	w_i
Step 1						
1	RVN × INC	4	218.3	0.21	0.0	0.67
2	RVN	2	225.9	0.13	3.7	0.10
3	RVN + INC	3	225.3	0.14	5.0	0.06
4	RVN + 50VO	3	225.4	0.14	5.1	0.05
5	RVN + NVO	3	225.9	0.13	5.7	0.04
NULL		1	236.7	N/A	12.4	0.00
Step 2						
6	RVN × INC	4	181.2	0.22	0.0	0.51
7	RVN	2	188.6	0.11	3.3	0.10
8	RVN + MFB	3	186.6	0.14	3.4	0.09
9	RVN + MGR	3	187.1	0.14	4.0	0.07
10	RVN + INC	3	187.8	0.12	4.6	0.05
NULL		1	195.6	N/A	8.4	0.01

[a] We included main effects in models with higher-order interactions. RVN = indices of raven abundance; INC = day of incubation; 50VO = visual obstruction of understory vegetation at a 50-m scale and centered on the nest; NVO = visual obstruction of understory vegetation at the nest; MFB = dried forb biomass; MGR = dried grass biomass.

and it was 5.1 times ($w_{raven \times incubation\ day}/w_{raven}$) more likely to predict nest survival than the next best model, a model of raven abundance (model 7; Table 2). A model of raven abundance and mean forb biomass (model 8; Table 2) showed similar evidence as the raven model, indicating that forb biomass did not explain any additional variation in nest survival.

Videography (n = 16) and direct (n = 1) observations of nest predation were caused by common ravens (n = 10) and American badgers (*Taxidea taxus*; n = 7; Coates et al. 2008). The probability of a nest predation by ravens increased with increasing indices of raven abundance ($\beta_1 = 0.234 \pm 0.078$; Table 3). Of predated nests, an increase of one raven (per 10 km) was associated with a 26% (95% CI = 11–51%) increase in the odds of a raven predation. The probability of a raven predation also was greater with less total shrub canopy cover ($\beta_1 = -0.078 \pm 0.031$; Table 3). A 1% decrease in shrub cover increased the odds of raven predation by 7.5% (95% CI = 2.0–15%).

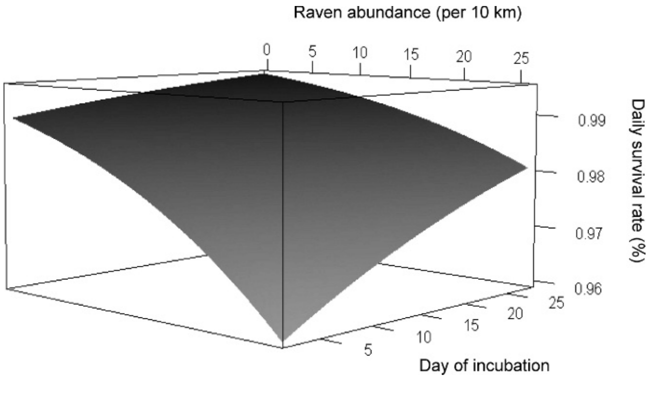

Figure 2. Effect of an interaction between the day of incubation and indices of raven abundance on daily survival rate (%) of greater sage-grouse nests in northeastern Nevada, USA, during 2002–2005. Raven abundance was the number of ravens observed during survey per 10-km transect.

We also found evidence that badger predation increased at nests with greater visual obstruction (50 m; $\beta_1 = 0.10 \pm 0.04$) and dry biomass of forbs ($\beta_1 = 0.700 \pm 0.131$) and grasses ($\beta_1 = 0.226 \pm 0.126$) in the nesting area but not directly at the nest (Table 3). When testing for differences in microhabitat characteristics between nests depredated by badgers and those that were depredated by ravens, we found differences at the 50-m scale in total shrub cover (ravens, 23.8% ± 6.3; badgers, 46.8% ± 6.9; $t_{11} = -2.46$, $P = 0.032$; 95% CI = −43.5 to −2.4) and visual obstruction at the 50-m scale (ravens, 56.9% ± 2.8; badgers, 71.2 ± 4.8; $t_9 = -2.56$, $P = 0.031$; 95% CI = −26.8 to −1.6).

DISCUSSION

Sage-grouse nest failure and observed raven predation of sage-grouse nests were associated with indices of raven abundance. Sage-grouse that nest within or near areas with unnaturally high raven numbers may be especially vulnerable to nest failure. The negative effect of indices of raven abundance on DSR of nests is consistent with the findings of authors who have described clear, positive correlations between corvid abundance and predation of both artificial and real nests of other ground nesting birds (Angelstam 1986, Johnson et al. 1989, Andrén 1992). Our findings should raise some conservation concern considering that raven abundance has increased an estimated 300% in the past 27 years in the United States (Sauer et al. 2008), including reports of 1,500% increases within an approximately 25-year period in areas of the western United States (Boarman 1993). Ravens thrive in human-altered landscapes (Luginbuhl et al. 2001, Boarman 2003) and anthropogenic resource subsidies act to increase raven reproduction and

Table 3. Effects of microhabitat factors on predation of greater sage-grouse nests by predator type (identified using videography) using exact logistic regression. We collected data in northeastern Nevada, USA, during 2002–2005.

Predator	Variable[a]	Estimate	95% CL	
			Lower	Upper
Raven	RVN	0.23	0.11	0.41*
	TSC	−0.08	−0.15	−0.02*
	MGR	0.17	−0.63	0.41
	MFB	0.16	−0.40	0.70
	50VO	0.02	−0.04	0.08
	NVO	−0.01	−0.08	0.07
	HT	0.00	−0.06	0.06
	NHT	0.00	−0.04	0.03
Badger	50VO	0.10	0.03	0.12*
	MFB	0.70	0.13	1.43*
	MGR	0.23	−0.02	0.49
	TSC	0.02	−0.02	0.06
	NHT	0.01	−0.01	0.42
	NVO	0.03	−0.02	0.11
	HT	0.0	−0.24	0.06

[a] RVN = indices of raven abundance; TSC = total shrub cover, MGR = dried grass biomass; MFB = dried forb biomass; 50VO = visual obstruction of understory vegetation at a 50-m scale; NVO = visual obstruction of understory vegetation at the nest; HT = shrub ht at the 50-m scale; NHT = shrub ht at the nest.

* Denotes a 95% confidence interval of the parameter estimate that did not include zero.

survival (Knight and Kawashima 1993, Webb et al. 2004). For example, landfills and roadkill provide unintentional food for ravens, and tall structures (e.g., power transmission towers) are selected by ravens as nesting substrate more than natural features in the environment (Knight and Kawashima 1993, Knight et al. 1995). Breeding and nonbreeding ravens have been associated with increased predation effects in desert ecosystems (Kristan and Boarman 2003). Several sensitive species in desert ecosystems are also thought to be vulnerable to high predation by ravens (Boarman and Heinrich 1999), including the California condor (*Gymnogyps californianus*; Snyder et al. 1986) and desert tortoise (*Gopherus agassizii*; Boarman 2003).

We focused on measuring indices of raven abundance and not other predators because of the growing evidence that raven populations in desert environments are increasing (Sauer et al. 2008) and pose an increased threat to nesting sage-grouse. However, badgers were responsible for nearly half the video-monitored nest predations and also have been identified as a sage-grouse nest predator elsewhere (Holloran and Anderson 2003). Although we did not estimate the effect of badger abundance on sage-grouse nest survival, limited data from Nevada suggest that the probability of predation by badgers increases with the amount of badger activity observed near nest sites (Coates 2007). The relationships that were reported were similar to those between crow and badger predation on waterfowl nests and indices of their abundances in Canada (Johnson et al. 1989).

Studies have reported an increase in nest survival of ground nesting birds as nests age (Klett and Johnson 1982, Dinsmore et al. 2002). We found evidence of a similar time-dependent effect and this effect was strengthened as raven abundance increased. This implies that the probability of nest discovery by ravens was not constant over the duration of the sage-grouse incubation period. Perhaps ravens are effective at quickly culling sage-grouse nests placed in visually exposed settings. Additionally, grouse that are not sufficiently cryptic in their behavior may be detected early by ravens. In this scenario, grouse that behave in a manner that evades predation during early incubation (e.g., less movement at the nest) also are likely to succeed during later stages, causing DSR to increase with day of incubation. Previously, we proposed that ravens find and depredate nests by detecting female grouse as they move to and from the nests in association with incubation recesses (Coates and Delehanty 2008). It is possible that the effect of day of incubation was confounded by temporal variation. Nest survival was greater at later dates in the nesting season for sage-grouse in Montana (Moynahan et al. 2007). However, this is unlikely because onset of grouse incubation occurred at different dates throughout the sage-grouse nesting period. The interaction between ravens and incubation day provides support to an earlier hypothesis that nests in risky locations are depredated more frequently during early stages of incubation (Klett and Johnson 1982).

We identified distinct differences in microhabitat factors that predicted whether a predation would likely be caused by ravens or by badgers. Sparse shrub cover appears to favor predation by ravens. Because sage-grouse typically nest under shrubs, particularly sagebrush (Connelly et al. 1991, Schroeder et al. 1999), high shrub interspace likely increases nest visibility for foraging ravens. The loss of sagebrush has led to substantial degradation of sage-grouse habitat (Braun et al. 1976, Swenson et al. 1987, Knick et al. 2003) and ravens are tolerant of degraded environments (Boarman and Heinrich 1999).

The positive relationship between badger predation and understory vegetation may have been an indirect link with the abundance of primary badger prey, similar to other findings reported from artificial sage-grouse nests (Ritchie et al. 1994). Badger diet consists primarily of ground squirrels (*Spermophilus* spp.; Messick and Hornocker 1981, Goodrich and Buskirk 1998). Forbs and bunchgrasses are positively related to ground squirrel population densities in sagebrush ecosystems (Parmenter and MacMahon 1983, Dobson and Kjelgaard 1985, Van Horne et al. 1997). Badger activity increases with ground squirrel abundance (Yensen et al. 1992), and badger home ranges often overlap in areas of high squirrel density (Messick and Hornocker 1981, Messick et al. 1981, Minta 1990). Perhaps badgers encounter and depredate sage-grouse nests in areas with greater vegetation understory because these areas are subject to greater frequency of badgers hunting ground squirrels.

Differences in habitat measurements at nests depredated by badgers and ravens may explain a general inability in the literature to identify habitat features universally associated with nest survival. For example, variables that were strongly correlated to nest predation by badgers (i.e., increased understory obstruction) differed from the predictor of nest predation by ravens (i.e., decreased canopy cover). One meaningful implication is that the relative importance of local habitat characteristics in protecting nests will vary with local predator composition. Furthermore, differences in predator communities between study areas could lead to inconsistencies among studies in the apparent relative importance of habitat variables on nest survival. Studies document that various habitat features are central to sage-grouse nest survival such as grass height (Gregg et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005), grass cover (Holloran et al. 2005, Moynahan et al. 2007), shrub height (Gregg et al. 1994, DeLong et al. 1995, Popham and Gutiérrez 2003), shrub cover (Wallestad and Pyrah 1974, Gregg et al. 1994, Watters et al. 2002), understory cover (Gregg et al. 1994, DeLong et al. 1995), rock cover (Popham and Gutiérrez 2003), and species of nesting shrub (Connelly et al. 1991). Conversely, other studies have found negative or no relationships between nest survival and grass height (Popham and Gutiérrez 2003), grass cover (Aldridge 2000), shrub height (Autenrieth 1981, Sveum et al. 1998), canopy cover (Popham and Gutiérrez 2003, Aldridge and Boyce 2007), understory cover (Aldridge and Brigham 2002), and species of nesting shrub (Autenrieth 1981, Sveum et al. 1998). Although many differences between studies or study areas could lead to discrepancies, our findings provide evidence for an expectation of discrepancies among studies, including discrepancies among studies that employ very similar techniques but likely have different predator communities.

In conclusion, elevated raven numbers pose an increased risk for nesting sage-grouse, perhaps as an unintended outcome of increased anthropogenic food and raven's nest subsidies (Boarman 1993, Boarman and Heinrich 1999, Leu et al. 2008). Sage-grouse vulnerability to nest predation varies between areas and across time, in part due to complex interactions between nest microhabitat and prevailing predator communities. Research can predict discrepancies in sage-grouse nest survival between areas and across time despite uniform habitat management prescriptions. Perhaps reducing anthropogenic resource subsidies to ravens in relation to nesting sage-grouse and other long-term management actions are ultimately needed to reduce nest predation by ravens.

MANAGEMENT IMPLICATIONS

Research that identifies the degree of overlap in distributions between ravens and nesting sage-grouse would be very beneficial, as would studies that identify key human land-use changes within sage-grouse habitat that subsidize raven populations. In areas of overlapping raven populations and sage-grouse nesting, sage-grouse nest survival would increase from well-designed raven management strategies. Furthermore, research that identifies trends in badger populations and relationships with human land-use practices in sagebrush ecosystems would be beneficial to understanding other predation risks to sage-grouse populations and would also help to inform management decisions.

Our findings augment previous calls for management actions that restore and maintain quality nesting habitat for sage-grouse, particularly intact stands of sagebrush nesting cover. Current management guidelines recommend nesting habitat with 15–25% sagebrush cover (Connelly et al. 2000) and our data suggest that sage-grouse may benefit from 20–30% sagebrush cover and $\geq$40% total shrub cover. Management that protects remaining large, robust, undeveloped stands of sagebrush shrub and herbaceous plant communities is central to stabilizing sage-grouse populations faced with growing predation threats.

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