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Original article

Nesting ecology of greater sage-grouse *Centrocercus urophasianus* at the eastern edge of their historic distribution

Katie M. Herman-Brunson, Kent C. Jensen, Nicholas W. Kaczor, Christopher C. Swanson, Mark A. Rumble & Robert W. Klaver

Greater sage-grouse *Centrocercus urophasianus* populations in North Dakota declined approximately 67% between 1965 and 2003, and the species is listed as a Priority Level 1 Species of Special Concern by the North Dakota Game and Fish Department. The habitat and ecology of the species at the eastern edge of its historical range is largely unknown. We investigated nest site selection by greater sage-grouse and nest survival in North Dakota during 2005 - 2006. Sage-grouse selected nest sites in sagebrush *Artemisia* spp. with more total vegetative cover, greater sagebrush density, and greater 1-m visual obstruction from the nest than at random sites. Height of grass and shrub (sagebrush) at nest sites were shorter than at random sites, because areas where sagebrush was common were sites in low seral condition or dense clay or clay-pan soils with low productivity. Constant survival estimates of incubated nests were 33% in 2005 and 30% in 2006. Variables that described the resource selection function for nests were not those that modeled nest survival. Nest survival was positively influenced by percentage of shrub (sagebrush) cover and grass height. Daily nest survival decreased substantially when percentage of shrub cover declined below about 9% and when grass heights were less than about 16 cm. Daily nest survival rates decreased with increased daily precipitation.

Key words: Centrocercus urophasianus, eastern range, edge of distribution, habitat, nesting, sage-grouse

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Greater sage-grouse *Centrocercus urophasianus* populations have declined by 45-80% across their range (Schroeder et al. 2004, Connelly et al. 2004). In North Dakota, greater sage-grouse (hereafter sage-grouse) declined approximately 67% from 1965 to 2003 (Connelly et al. 2004). While sage-grouse in North Dakota are genetically contiguous with populations in Montana and South Dakota (Oyler-McCance et al. 2005), they could become isolated by conversion of sagebrush into agriculture (Smith et al. 2005), and oil and gas development (Connelly et al. 2004, Walker et al. 2007). Long-term population declines in sage-grouse in North Dakota (Smith et al. 2005) have resulted in classifying sage-grouse as Priority Level 1 Species of Special Concern in North Dakota (McCarthy & Kobriger 2005). Altered habitat quality and quantity in sagebrush ecosystems (e.g. Connelly et al. 2004, Welch 2005) may result in low survival and productivity of sage-grouse (Aldridge & Brigham 2001), and declining populations. Therefore, understanding characteristics important to selection of nest sites and factors that affect nest survival is critical to the management, conservation and rehabilitation of sagebrush habitats for sage-grouse. Despite well-understood reproductive ecology in the core of the sage-grouse range, knowledge of reproductive ecology and habitat selection by sage-grouse occurring at the eastern edge of their distribution is limited. Therefore, our objective was to quantify nest habitat selection by sage-grouse in North Dakota and determine specific factors associated with survival of sage-grouse nests. These data will help in the development of management recommendations to assist state and federal agencies in managing habitats for sage-grouse.

Material and methods

Study area

Our study area included the counties of Bowman and Slope in southwestern North Dakota and Fallon in southeastern Montana. The area has flat to gently-rolling prairie, with a few buttes and intermittent streams. Annual precipitation ranges from 35.6 cm to 40.6 cm, most of which occurs during April - September. Summer temperatures range from 9.9°C to 27.5°C, and winter temperatures range from -15.6°C to 0.2°C (North Dakota Agricultural Weather Network 2006).

Vegetation communities included mixed grass prairie with perennial and annual forbs and grasses and shrub steppe comprised of silver sagebrush *Artemisia cana*, Wyoming big sagebrush *A. tridentata wyomingensis*, rubber rabbitbrush *Chrysothamnus nauseosus* and greasewood *Sarcobatus vermiculatus*. Common grasses included western wheatgrass *Pascopyrum smithii*, Kentucky bluegrass *Poa pratensis*, Japanese brome *Bromus japonicus*, needle and thread *Stipa comata* and junegrass *Koeleria macrantha*. Forbs included common dandelion *Taraxacum officinale*, common yarrow *Achillea millefodium* and textile onion *Allium textile* (Johnson & Larson 1999).

Most of the land is privately owned, and the primary land use is cattle ranching. Areas managed by the Bureau of Land Management (BLM) for grazing were stocked at 4-10 acres per animal unit month (AUM) under continuous or rotational grazing that begins in early to mid June (Mitch Iverson, Belle Fourche BLM, pers. comm.). Oil and gas development is extensive in some areas.

Capture and telemetry

We captured female sage-grouse at night on or near leks from late March through April in 2005 and 2006 (Wakkinen et al. 1992b). We recorded age (Crunden 1963) and placed a 20-g necklace radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota) with mortality sensors on each female. The transmitters were $<2\%$ of the body weight of individually marked sage-grouse. All field methods complied with the Institutional Animal Care and Use Committee (07-A032) at South Dakota State University.

We located females 2-3 times each week from the time they were captured and radio-marked, until the outcome of nesting had been determined aided with a hand-held 3-element yagi antenna. Nests were inconspicuously marked with plastic flagging >20 m south of the nest, near or at ground level to avoid making them visible except on close inspection. The nest location was recorded with a GPS. Occasionally, the interval between telemetry locations was greater than 2-3 days, because weather prohibited access to the nest area. Therefore, onset of incubation could not be accurately estimated from the behaviour of females. As a result, we flushed incubating hens and estimated nest initiation by back-dating from incubation stage estimated from egg flotation (Hays & LeCroy 1971) and adding 1.3 days for each egg laid (Patterson 1952). If the female was absent from the nest area for >3 consecutive locations, we approached the nest site to determine fate. Success or failure of nests was determined by membrane conditions of the eggs (Klebenow 1969) or observation of a brood with the radio-collared female. Nests were considered successful if ≥ 1 egg hatched.

Vegetation measurements

During May - June each year of the study, we characterized vegetation at nest sites and random sites. Most sage-grouse nest within 3.2 km of a lek (Braun et al. 1977, Aldridge & Brigham 2001), so we selected random sites from which to estimate resource selection for nesting from within a 3-km buffer surrounding leks on which we observed sage-grouse. Because nest sites are normally located beneath sagebrush (Connelly et al. 2000), we selected random sites at the nearest sagebrush plant to the random coordinates. We recorded slope and aspect at each nest and random site using a clinometer and compass.

We established four 50-m long transects that were centered over the nest or random site. We recorded species, height, length and width of sagebrush plants at the intersection of these transects. Using 10-m intervals (N = 20) along each transect, we recorded the distance to the nearest shrub (usually sagebrush) using a point-centered-quarter method (Cottam & Curtis 1956), and recorded the species, height, length and width of each shrub. We also recorded the maximum height of grass growing from beneath the sagebrush. We estimated visual obstruction (VOR) and height of grass at each nest site, and for each meter out to five meters from the nest, and then at 10-m intervals along each transect using a modified Robel pole delineated in 2.54-cm increments (Robel et al. 1970, Benkobi et al. 2000). We used the Daubenmire (1959) method to estimate canopy cover of vegetation. This method is amenable to collecting data on windy days and yields data that are similar (< 3% difference for sagebrush) to the line-intercept method (Floyd & Anderson 1987), and may provide more accurate estimates than line-intercept methods (Booth et al. 2006). We estimated canopy cover from a height of about 1 m in 24 0.1-m^2 quadrats (Daubenmire 1959). Four quadrats were placed at the intersection of the transects (over the nest) and at the four terminal ends of 1-m legs forming the pattern of an H every 10 m along each transect. We estimated percentage of canopy cover for total cover, total shrubs, total forbs, total grasses, litter, bare ground, sagebrush and dominant species of grasses and forbs using six categories (Daubenmire 1959). We obtained measures of maximum and minimum daily temperature and daily precipitation throughout the nesting season from the closest weather station in Bowman County (North Dakota Agricultural Weather Network 2006).

Data analyses

Nesting

We tested for differences in clutch size distributions between adults and yearlings using χ^2 goodness of fit test. χ^2 goodness of fit tests were used to test differences in nest initiation rates between years and among ages of females. We calculated distance from each nest to the center of nearest lek and distance from each nest to lek of capture (if the hen was captured that year) using corresponding GPS coordinates. We tested for differences in these distributions between successful and unsuccessful nests, and between adults and yearling hens using a multiple response permutation program (MRPP; Mielke & Berry 2001). Statistical significance was determined at $\alpha \leq 0.05$ for these tests.

Habitat selection

Average percentage of canopy cover was recorded for each variable at nests and random sites. We calculated VOR at the nest and at 1-m intervals out to five meters. Average VOR was also calculated for each site. We estimated sagebrush density using maximum likelihood estimates of point-centered-quarter method (Pollard 1971). We then used MRPP to test the distribution of vegetation characteristics between nests and random sites to distinguish important variables to include in models of nest survival and selection of nest sites. Statistical significance was determined with a critical value of $\alpha \leq 0.05$.

We used an information theoretic approach (Burnham & Anderson 2002) with logistic regression to estimate models depicting vegetation characteristics selected by female sage-grouse for nests. Because we had a very large number of variables from estimated canopy cover by species and collected extensive measurements, we developed 10 candidate models that included variables that exhibited differences between nest and random sites from MRPP tests (see Hosmer & Lemeshow 2000, Guthery et al. 2005, Stephens et al. 2005). These models included percent total cover, percent grass cover, percent forb cover, percent sagebrush cover and sagebrush height, site-VOR, nest VOR, 1-m VOR, grass height from the Robel pole and sagebrush density. Year was considered a design variable and was included in all candidate models. We tested the strength of the best predictive model of nest sites selected using receiver operating characteristic curves (ROC). ROC values between 0.8 and 0.9 were considered excellent discrimination, and ROC values between 0.7 and 0.8 were considered acceptable discrimination (Hosmer & Lemeshow 2000). The statistical tests described above were made using SPSS (2002) or SAS (2005).

Nest survival

We estimated daily survival rate (DSR) of nests using the nest survival model in Program MARK (White & Burnham 1999, Dinsmore et al. 2002). We established 6 May as first nest day.

Nest survival probabilities were estimated as a function of age of hen, nest age and vegetation characteristics at nests. We then modeled effects of the time-dependent variables year, maximum and minimum daily temperature, and daily precipitation using the best survival models from the previous analysis also using program MARK (White & Burnham 1999). Continuous covariates were standardized as deviations from a mean of 0. Categorical and time-dependent covariates were coded with the actual values so they would not hamper numerical optimization of likelihood (Burnham & Anderson 2002).

Results

We captured and fitted 30 hens with necklace-mounted radio-transmitters during spring 2005-2006 (21 during 2005 and 9 during 2006); 36% were adults. Of the hens captured in 2005, 11 survived and were included in our sample in 2006.

Nesting

Adults initiated nests approximately five days earlier than yearlings. Nests were 6-8 days on average into incubation when detected. There were two renests in 2005 which were initiated in mid- to late May; no renesting occurred in 2006. The renesting rate was 10%. All radio-collared hens initiated a nest in 2005. In 2006, 13 of 14 adults (93%), and five of seven yearlings (71%) incubated a nest (including those that abandoned). There was no difference in nest initiation rates between years ($P=0.11$). Nest initiation rate (including those that abandoned) for adult hens ($N=20$) was 95% and did not differ ($P=0.58$) from yearling hens (88%; $N=16$). Nest initiation averaged 92% across age groups and years.

For nests in which we could determine clutch size ($N=33$), average clutch size was 7.9 ± 0.5 eggs. There was no difference in clutch size between adults and yearlings ($P=0.86$). We eliminated four nests from further analyses because we believed that they were abandoned because of disturbance from our field crews. In 2005, three of the nests were abandoned by the hen, and five were depredated. In 2006, one nest was abandoned by the hen, and eight nests were depredated.

The average distance from nests to the lek at which a hen was captured was 4.9 km ± 4.1 ($\bar{x} \pm$ SE), and it did not differ ($P=0.67$) between successful and unsuccessful nests. The average distance from nests to the nearest lek was 2.7 km ± 2.4. Unsuccessful nests did not differ from successful nests in relation to distance to the nearest lek ($P=0.45$). Average distance to the nearest lek did not differ ($P=0.45$) between years nor ($P=0.77$) between adults or yearlings.

Nest selection

Of all nests, 85% were located under Wyoming big sagebrush ($N=29/34$). Other than sagebrush, one nest was located beneath each four-wing saltbush *Atriplex canesens*, eastern redcedar *Juniperus virginiana* and wheat stubble *Triticum* spp., and two were beneath sweet clover. Vegetation at random sites was sparse, but slightly taller than at nest sites. Sage-grouse nest sites had greater ($P \leq 0.05$) percent canopy cover of total vegetation (total cover), grass cover, forb cover, sagebrush cover and litter (Table 1). Moreover, nest sites had greater visual obstruction at the nest (nest VOR) and surprisingly even greater visual obstruction 1 m away (1-m VOR). Although vegetation was taller at random sites, VOR for nest sites was greater ($P<0.01$) than for random sites. Sagebrush density also was greater ($P<0.01$) at nest sites than at random sites (see Table 1). Intermediate wheatgrass *Thinopyrum intermedium* was the only dominant grass with greater canopy cover at random sites; otherwise canopy cover of dominant grasses was greater at nest sites. Nonetheless, grass height and shrub height were marginally taller ($P>0.07$) at random sites.

We included models with total cover, shrub density, shrub height, grass height, nest VOR and 1-m VOR in the evaluation of nest resource selection. Other variables were excluded because of correlations with these variables. Because total cover exhibited the smallest individual variable deviance, we constructed iterations of models around this variable. Of the 25 models we considered, five models were included in the set with $AIC_c<2$ (Table 2). Two models, both including total cover and shrub height, with nest VOR (highest rank), and 1-m VOR (second-highest rank) best explained the nest resource selection by female sage-grouse. Nest sites were positively associated with greater percent total cover, greater 1-m VOR and nest VOR, and negatively related to shrub height. The third ranked model included only total cover and shrub height. Models that also included grass height, although ranked in

Table 1. Average of key vegetative (±SD) characteristics from greater-sage grouse nest sites and random sites included in resource selection models from North Dakota, USA, during 2005-2006. P-values as obtained using the multiple response permutation procedure (Mielke & Berry 2001).

	Nest		Random		
Vegetative characteristic	$\bar{x}$	±SD	$\bar{x}$	±SD	P-value
Total vegetative cover (%)	70.4	15.5	54.4	20.4	>0.01
Total grass cover (%)	27.4	13.6	19.3	14.6	0.01
Total forb cover (%)	15.4	11.8	11	6.6	0.05
Shrub cover (%)	9.8	4	7.1	4.6	>0.01
Litter (%)	12.9	8.3	7.9	5	0.01
Intermediate wheatgrass (%)	1.7	2.3	2.4	2.1	0.06
Green needlegrass (%)	2.5	3.3	1.3	1.8	0.06
Western wheatgrass (%)	4.2	3.7	2.1	2.6	<0.01
Kentucky bluegrass (%)	3.3	3.7	1.9	2.7	0.05
Nest VOR (inches)	2.6	1.2	2.1	1.6	0.02
1-m VOR	3.9	2.1	2.7	2.3	>0.01
2-m VOR	3	2.1	2.73	2.3	<0.01
3-m VOR	2.5	1.4	2.2	1.8	0.12
4-m VOR	2.4	1.5	2.1	1.8	0.3
5-m VOR	2.2	1.3	2.2	2.1	0.24
Site VOR	2.6	1.2	2.1	1.6	0.02
Sagebrush density (ha)	2576.1	1833.6	1399.4	1795.1	>0.01
Grass height (inches)	10.2	3.7	11.2	3.3	0.17
Shrub height (mm)	42.1	18.4	48.4	16.7	0.07

the 'supported' set, did not improve the deviance suggesting that grass height was not really important in describing the resource selection by nesting sage-grouse. The odds ratios indicated that nest VOR was the most important of the variables in the model. An increment of 2.54 cm for nest VOR increased the predicted probability of the site to be a nest by 16% ± 1% (95%CI). Increasing total vegetative cover by 10% increased the predicted probability of the site being selected for nesting by 0.60% ± 0.3% (CI 95%). Finally, the odds ratio for shrub height indicated a 9.1% ± 1.3% decrease in the predicted probability of a nest with each 1 cm increase in shrub height. Classification accuracy of the model was acceptable with an ROC value of 0.82. Odds ratios for the second ranked model were virtually identical to the previous model, except that greater weight was placed on the 1-m VOR.

Nest survival

We included 14 hens in nest survival analyses in 2005 (eight yearlings and six adults), and 15 hens were included in nest survival analyses in 2006 (three yearlings and 12 adults). Nest survival did not differ between years ($P < 0.05$). Estimated constant nest survival was 33% in 2005 ($N = 14$) and 30% in 2006 ($N = 15$).

The best model from the nest site selection (see above) was the lowest ranked model describing nest survival of the 41 models considered (Table 3). There was virtually no support for any of the single variable models. We included precipitation, constant survival, nest age and year in the table because they are often variables of interest despite their lack of support in our models. These were the same three top models when we included only vegetation characteristics (minus precipitation). Before including pre-

Table 2. Summary of model selection of logistic regression for greater sage-grouse nests ($N = 34$) from random sites ($N = 50$) in North Dakota, USA, during 2005-2006 using the Information Theoretic approach.

Model[1]	AIC	AIC_c	AICw_i	K[2]	Deviance
Total cover + shrub height + nest VOR	95.14	0	0.23	5	84.37
Total cover + shrub height + 1-m VOR	95.52	0.39	0.18	5	84.76
Total cover + shrub height	96.17	1.03	0.13	4	87.66
Total cover + shrub height + 1-m VOR + grass height	97.113	1.97	0.08	6	84.02
Total cover + shrub height + nest VOR + grass height	97.12	1.98	0.08	6	84.03
Global model	104.48	9.34	<0.01	10	81.47

[1] A total of 25 models were considered. Model results are presented in descending order of rankings and include models with AIC values <2.0.

[2] Number of parameters includes those in model plus year and the intercept.

Table 3. Summary of model selection for greater sage-grouse nest survival considering vegetation characteristics and time-dependent variables in southwestern North Dakota, USA, during 2005-2006.

Models[1]	$\mathrm{AIC_c}$[2]	$\mathrm{AIC_c}$	$\mathrm{AIC_{w\,i}}$[3]	K[4]	Deviance
Grass height + shrub cover + nest VOR + precipitation	109.537	0	0.291 (0.376)	5	99.38
Grass height + shrub cover + total cover + nest VOR + precipitation	110.038	0.5	0.226	6	97.82
Grass height + shrub cover + nest VOR + site VOR + precipitation	111.129	1.59	0.13 (0.170)	6	105.45
Grass height + shrub cover + nest VOR	113.565	4.02	0.039	4	105.46
Precipitation	115.888	6.35	0.014	2	111.86
Constant survival	119.025	9.49	0.002	1	117.02
Nest age	120.219	10.68	0.001	2	116.19
Year	120.894	11.38	0.001	2	116.86
Best nest site selection model: total cover + shrub height + nest VOR	122.586	13.319	< 0.001	4	114.751

[1] A total of 41 models were evaluated. We evaluated vegetation characteristics first, then included precipitation and temperature. The first three models were the highest ranked models with or without precipitation.

[2] Methods and interpretation of heading are described by Burnham & Anderson (2002).

[3] $\mathrm{AIC_w}$ in parentheses are those with the second model eliminated.

[4] Number of parameters in the model includes the intercept from constant survival estimate.

cipitation, $\mathrm{AIC_w}$ for these models were 0.15, 0.14 and 0.06, respectively. Although precipitation by itself provided little insight into nest survival of sage-grouse, when included with vegetation characteristics, the three top vegetation models showed strong support, with the fourth best model including just vegetation.

Evaluation of the coefficients of the second ranked model suggested that adding total cover to the model brought in some strong variable interactions causing the intercept to be below zero. Therefore, we eliminated this model and $\mathrm{AIC_w}$ assigned to models without this are in parentheses. Unequivocally, the model with the greatest support was the model including grass height, shrub cover, nest VOR and precipitation. The addition of site VOR to the highest ranked model contributed very little reducing the deviance in the model. Therefore, we were left with the highest ranked model to interpret.

Survival of sage-grouse nests was positively associated with grass height and shrub cover, and negatively associated with precipitation and nest VOR. The relation between nest VOR and survival seemed counter-intuitive, so we examined measurements of the nest shrub and found that successful nests were indeed in shorter shrubs than unsuccessful nests. None of the 95% CIs for odds ratios included 0. Grass height and shrub cover increased the probability of nests surviving by about 1.2% for each unit increase. An increase in nest VOR of 2.5 cm decreased the chances of the nest surviving by 2%, and 1 cm of precipitation decreased the chances of a nest surviving by about 7%. Daily precipitation had a consistent negative effect on nest survival (Fig. 1), which was amplified when shrub cover was less than about 9% or when grass height was less than about 16 cm (see Fig. 1C).

Discussion

Breeding chronology and nesting

Average clutch size in southwestern North Dakota was similar to the average clutch size found throughout the range of sage-grouse (Wallestad & Pyrah 1974, Sveum 1995). Despite predictions of age-specific differences in clutch size (Wallestad & Pyrah 1974, Petersen 1980), adults and yearlings had similar clutch sizes in our study.

We interpret the earlier nesting by adults to their being physiologically more mature and ready for reproduction than yearlings (e.g. Schroeder 1997). Improved habitat (nutritional) quality was postulated to be responsible for increased production in sage-grouse in Oregon (Barnett & Crawford 1994), and Gregg et al. (2006) showed that hens with greater plasma protein were more likely to renest. The low renesting rate in our study suggests that some aspect of the habitat was lacking.

Sage-grouse do not always nest near a lek and may nest independent of lek locations (Bradbury et al. 1989, Wakkinen et al. 1992a). In Alberta Canada, less than ½ of the nests (41%) were within 3.2 km of the lek (Aldridge & Brigham 2001). However elsewhere, most nests occur within 3.2 km of leks (Braun et al. 1977). The population of sage-grouse which we studied was non-migratory, 68% of nests were within 3.2 km of a lek and 86% of nests were within 5 km of a lek. It is likely that suitable nesting habitat

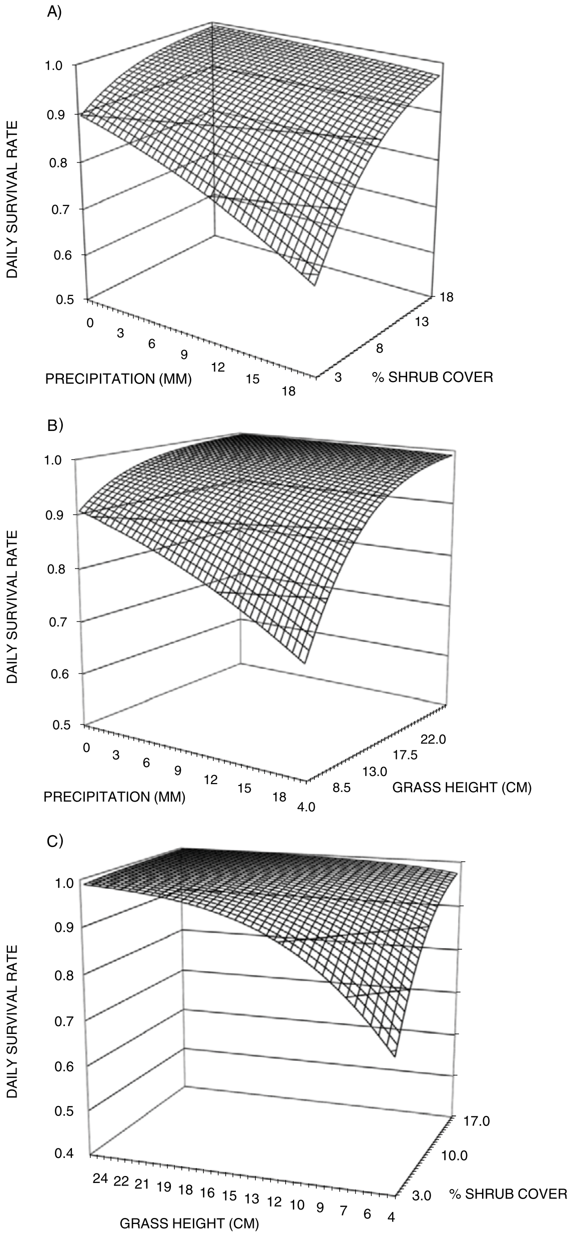

Figure 1. Daily survival as a function of precipitation and percent shrub cover with nest VOR and grass height constant at mean (A), precipitation and grass height with nest VOR and percent shrub cover held constant at the mean (B), and grass height and shrub cover with precipitation and nest VOR held constant and the mean (C).

for sage-grouse in the Dakotas, at the eastern fringe of sage-grouse range, occurs near leks. Aldridge & Brigham (2001) came to a similar conclusion for a population at the northern fringe of the sage-grouse range. While in more contiguous sagebrush of Wyoming, there was less propensity for sage-grouse to nest near the lek (Holloran & Anderson 2005).

Nest selection

Most studies describe the importance of sagebrush canopy cover and herbaceous canopy cover (Wakkinen 1990, Connelly et al. 1991, Sveum et al. 1998, Hagen et al. 2007) for sage-grouse nesting habitat. However, in southwestern North Dakota, nest resource selection may take on different characteristics than other portions of the sage-grouse range. Sage-grouse usually nest in taller sagebrush (Connelly et al. 2000) and often select the tallest sagebrush (Wakkinen 1990, Apa 1998). However, in our study, sage-grouse selected sites with greater vegetative cover and greater visual obstruction at and near the nest, but with shorter shrub height than was available in the area. Tall grass can also be an important contributor to concealment of sage-grouse nests (Connelly et al. 1991, Gregg et al. 1994), and although grass height was included in the models with marginal support, it too was shorter than at our random sites. In this area, where the sagebrush steppe transitions to mixed grass prairie, sagebrush occurs in higher densities on range sites in low seral condition and soils with low productivity. Vegetative productivity on these sites can be reduced by overgrazing by livestock (Natural Resources Conservation Service, Electronic Field Office Technical Guide, available at: http://efotg.nrcs.usda.gov/efotg_locator.aspx?map=ND; last accessed on 25 November 2008). Thus, it is not surprising that taller grass and taller shrubs (sagebrush) occurred on sites where sagebrush was less prominent. Despite the nuances of site characteristics, sage-grouse appeared to select for greater concealment at and near the nest, and other than vegetative cover nest area variables were not important to nest selection by sage-grouse in our area.

Nest survival

Across the range, sage-grouse nest survival averages just under 50% in relatively unaltered habitats and below 40% in altered habitats (Connelly et al. 2004). Nest success in stable populations generally tends to be higher (Aldridge & Brigham 2001). The population of sage-grouse which we studied would likely be considered unstable (declining) from 1951 to present (unpubl. spring sage-grouse census data; North Dakota Game and Fish Department, Bismarck, North Dakota). Most of the area has been altered by historical grazing, and oil and gas development. Nest survival in our study was typical of other altered habitats and most nests were lost to predation. While marking nests and repeat visitations to nests could attract predators, we visited nest sites only once to estimate the stage of incubation and otherwise stayed > 20 m away, and we do not believe that inconspicuous flagging on sagebrush 20 m from nests increased nest predation. Nest predation can be higher in fragmented landscapes (Herkert 1994, Sievert & Lloyd 1985). In the Powder River Basin of Wyoming, extensive large-scale modifications of sagebrush habitat, and range modification for livestock from oil and gas development were associated with significant reductions in sage-grouse populations (Walker et al. 2007).

Of the vegetative characteristics identified in the resource selection models for nests, only nest VOR was included in models of nest survival; and it had a negative relation to daily survival rates. The height of the shrubs under which nests were located was also lower at nests that survived than those that failed. We attribute these counter-intuitive relations to selection by sage-grouse for area of higher shrub/sagebrush which had a positive influence on survival of nests. Thus, our data suggested that shrub (sagebrush) cover may be more important than taller shrubs in nest survival. Areas with high shrub cover also had relative low stature sagebrush. The low stature of sagebrush in these stands likely resulted from the dense clay-pan soils or past grazing practices. Connelly et al. 2000 reviewed several studies that showed sage-grouse selecting stands with greater sagebrush cover, but also the tallest sagebrush in the stand. Tall grass improved daily survival rates and seemingly compensated to some degree for the shorter concealment by shrubs. When shrub cover was less than about 9-10% or grass height was less than about 16-18 cm nest survival declined rapidly. Although shrub cover was lower than found in most other studies, the grass height at nest sites in our study was reflective of other studies.

Predators with a keen sense of smell use olfactory cues to locate nests (Storaas 1988), and birds that are wet have been hypothesized to have stronger odour because water on the skin activates bacteria (Syrotuck 2000). Daily precipitation events decreased daily survival rates which declined in a near linear manner with increasing amounts of precipitation. Precipitation during incubation increased predation of wild turkey *Meleagris gallopavo* nests (Roberts et al. 1995, Roberts & Porter 1998, Lehman et al. 2008). However, the relation between precipitation and nest survival may be complicated by high nest attendance by the female and decreased predator activity during precipitation followed by a lag effect on subsequent days when females are away from the nest (Moynahan et al. 2007). However, the lag of precipitation was not important in our study.

Management implications

If the Bureau of Land Management (BLM) could increase its management buffer from the current 3.2 km (Resource Management Plan, Bureau of Land Management, Dickenson, North Dakota) to 5 km, this larger area would encompass 86% of nests. Currently, there are no management regulations that pertain to sage-grouse on state-owned land in North Dakota. We believe that a strategy similar to the BLM would be beneficial to sage-grouse. Our models suggest that patches of shrubs/sagebrush with > 9% canopy cover and grass taller than 16 cm improved the chances of a sage-grouse surviving to hatch. Sagebrush patches selected by nesting females were grazed and showed evidence of being in low seral condition due to past grazing or soil characteristics. There is strong evidence in the literature that if areas of sagebrush cover (> 9%) occurred with taller shrubs, sage-grouse would use them and it should improve nest survival. Tall grass is also important to sage-grouse nest survival and grazing management that provides grass heights of > 16 cm should benefit nest survival. Our results emphasize the importance of considering local conditions in the management of sage-grouse.

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