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Habitat Relations

Greater Sage-Grouse Winter Habitat Use on the Eastern Edge of Their Range

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ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*) at the western edge of the Dakotas occur in the transition zone between sagebrush and grassland communities. These mixed sagebrush (*Artemisia* sp.) and grasslands differ from those habitats that comprise the central portions of the sage-grouse range; yet, no information is available on winter habitat selection within this region of their distribution. We evaluated factors influencing greater sage-grouse winter habitat use in North Dakota during 2005–2006 and 2006–2007 and in South Dakota during 2006–2007 and 2007–2008. We captured and radio-marked 97 breeding-age females and 54 breeding-age males from 2005 to 2007 and quantified habitat selection for 98 of these birds that were alive during winter. We collected habitat measurements at 340 (177 ND, 163 SD) sage-grouse use sites and 680 random (340 each at 250 m and 500 m from locations) dependent sites. Use sites differed from random sites with greater percent sagebrush cover (14.75% use vs. 7.29% random; $P < 0.001$), percent total vegetation cover (36.76% use vs. 32.96% random; $P \leq 0.001$), and sagebrush density (2.12 plants/m^2 use vs. 0.94 plants/m^2 random; $P \leq 0.001$), but lesser percent grass cover (11.76% use vs. 16.01% random; $P \leq 0.001$) and litter cover (4.34% use vs. 5.55% random; $P = 0.001$) and lower sagebrush height (20.02 cm use vs. 21.35 cm random; $P = 0.13$) and grass height (21.47 cm use vs. 23.21 cm random; $P = 0.15$). We used conditional logistic regression to estimate winter habitat selection by sage-grouse on continuous scales. The model sagebrush cover + sagebrush height + sagebrush cover × sagebrush height ($w_i = 0.60$) was the most supported of the 13 models we considered, indicating that percent sagebrush cover strongly influenced selection. Logistic odds ratios indicated that the probability of selection by sage-grouse increased by 1.867 for every 1% increase in sagebrush cover (95% CI = 1.627–2.141) and by 1.041 for every 1 cm increase in sagebrush height (95% CI = 1.002–1.082). The interaction between percent sagebrush canopy cover and sagebrush height ($\beta = -0.01$, SE ≤ 0.01; odds ratio = 0.987 [95% CI = 0.983–0.992]) also was significant. Management could focus on avoiding additional loss of sagebrush habitat, identifying areas of critical winter habitat, and implementing management actions based on causal mechanisms (e.g., soil moisture, precipitation) that affect sagebrush community structure in this region. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Artemisia*, *Centrocercus urophasianus*, greater sage-grouse, habitat, North Dakota, resource selection, sagebrush, South Dakota.

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Knowledge of resource selection provides insight into population sustainability and the impact selected resources have in meeting species life-history requirements (Manly et al. 2002). Resource selection is based on a spatially hierarchical set of choices (Johnson 1980). Identifying scales at which resource selection is defined within this hierarchy is important for proper representation of habitat use (Alldredge and

Griswold 2006). Individuals select habitats to secure access to food or mates, reduce their vulnerability to predators, and limit their exposure to climatic stressors as a result of natural selection or prior learning (Wiens 1985). Resource agencies rely on information gained from habitat selection studies to guide their management decisions and assess the long-term needs of populations under their jurisdiction (Manly et al. 2002).

Greater sage-grouse (*Centrocercus urophasianus*) are considered a landscape-scale species because maintenance of their populations requires conservation of large areas with suitable habitat (Connelly et al. 2011); their distribution coincides with the occurrence of sagebrush habitat (*Artemisia* sp.; Schroeder et al. 2004). Sagebrush habitats have been degraded, resulting in the loss of >57 million ha (Rowland et al. 2005), and much of the loss of sagebrush habitat has been associated with agriculture, changes in fire regimes, energy development, fragmentation, grazing, pesticides, and urbanization (Braun 1998, Schroeder et al. 1999, West and Young 2000, Crawford et al. 2004). Sage-grouse populations have declined concomitantly with the sagebrush biome and are limited to 55% of their historical pre-settlement distribution (Schroeder et al. 2004).

During winter, sage-grouse depend on sagebrush for food and cover (Wallestad et al. 1975, Remington and Braun 1985); however, snow depth can severely limit available sagebrush (Hupp and Braun 1989). Winter habitat typically is located in areas providing topographical relief and accessibility to sagebrush above the snow (Beck 1977, Connelly 1982, Robertson 1991) and may be located in close proximity to leks (Connelly et al. 1988). Winter habitat tends to be limited compared to other seasonal habitats (Beck 1977, Remington and Braun 1985) and its availability influences sage-grouse distributions (Hanf et al. 1994). Maintaining connectivity between seasonal habitats is also critical for sage-grouse population persistence (Aldridge and Boyce 2007). Because sage-grouse typically use a small percentage of available sagebrush habitat during winter (Beck 1977, Swenson et al. 1987), identification of key wintering areas may help managers protect those resources and reduce the likelihood of bottlenecks between seasonal ranges or populations (Carpenter et al. 2010). Therefore, identifying region-specific winter habitat requirements may be critical because the persistence of sage-grouse populations could be disproportionately affected by degradation of winter habitat (Doherty et al. 2008). Sage-grouse winter habitat selection has been evaluated at the northern (Carpenter et al. 2010) and western fringes (Hagen et al. 2011) of its range. However, limited information on sage-grouse winter habitat selection exists because of the difficulty in accessing used sites when inundated by snow and associated inclement winter conditions that make sampling challenging.

In the Dakotas, sage-grouse occur in the transition zone between the eastern edge of the sagebrush distribution and the western edge of the prairie (Bailey 1995, Smith et al. 2006). Although species at the edge of their range can have high turnover rates (where deaths often exceed births) resulting in sink populations (Doherty et al. 2003, Aldridge and Boyce 2007), these populations may have unique local adaptations or evolutionary traits allowing them to persist when core populations undergo habitat destruction (Channell and Lomolino 2000). Also, populations at the edge of their range may use habitats differently than those in core areas because edge habitats tend to be more fragmented (Channell and Lomolino 2000). Therefore, our objective was to evaluate habitat characteristics that influence resource selection by sage-grouse during winter in North Dakota and South Dakota, the eastern terminus of their range.

STUDY AREA

We conducted our study in Bowman County, North Dakota (46°7′22.368″N, 104°0′24.318″W), Butte County, South Dakota (45°1′52.329″N, 103°44′41.196″W), and adjacent parts of Montana (Carter and Fallon counties) and Wyoming (Crook County; Fig. 1). The region was semiarid sagebrush rangeland characterized by gentle slopes to steep buttes and ridges with elevations that ranged from 640 m to 1,225 m above mean sea level (Opdahl et al. 1975, Johnson 1976). Vegetation in this region was low shrubland with short- to mid-grass prairie being dominant (Opdahl et al. 1975, Johnson 1976, Johnson and Larson 1999). Shrubs in the area were dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), but also included silver sagebrush (*Artemisia cana* ssp. *cana*), broom snakeweed (*Gutierrezia sarothrae*), rubber rabbitbrush (*Ericameria nauseosus*), and greasewood (*Sarcobatus vermiculatus*; Johnson and Larson 1999). Common perennial grasses were green needlegrass (*Nassella viridula*), Junegrass (*Koeleria macrantha*), western wheatgrass (*Pascopyrum smithii*), Kentucky bluegrass (*Poa pratensis*), Japanese brome (*Bromus japonicus*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), buffalograss (*Buchloe dactyloides*), needleandthread (*Hesperostipa comata*), and little bluestem (*Schizachrium scoparium*; Johnson and Larson 1999). Common forbs were

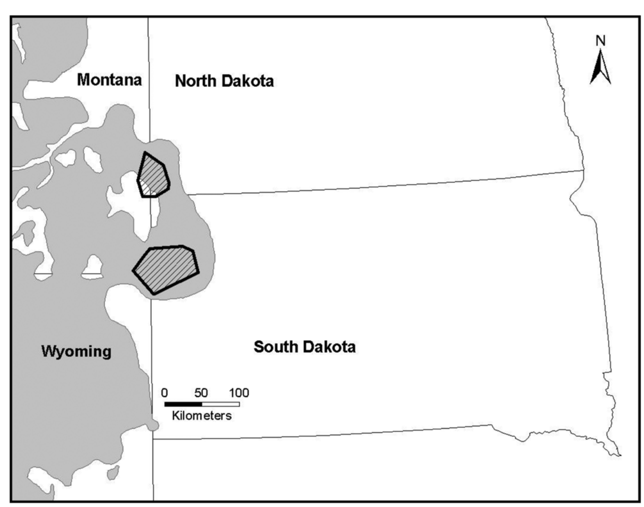

Figure 1. Study areas for sage-grouse research in North Dakota and South Dakota, 2005–2008. The shaded area encompasses known sage-grouse range (Schroeder et al. 2004) and the dashed area represents 100% minimum convex polygon of sage-grouse locations during this study.

common dandelion (*Taraxacum officinale*), textile onion (*Allium textile*), field pennycress (*Thlaspi arvense*), and western yarrow (*Achillea millefolium*; Johnson and Larson 1999). Land use was dominated by livestock grazing, 45% of Bowman County and 5% of Butte County was farmed for cultivated crops (North Dakota Agriculture Statistics Service 2011, South Dakota Agriculture Statistics Service 2011).

The climate of the region was continental with most of the precipitation occurring in late spring and early summer. Average monthly temperatures in North Dakota were -9.7° C in January and 20.8° C in July with average annual precipitation and snowfall of 39.4 cm and 122.7 cm, respectively. Average monthly temperatures in South Dakota were -4.8° C in January and 22.7° C in July with average annual precipitation and snowfall of 45.5 cm and 89.9 cm, respectively (National Climatic Data Center 2011). Winter (22 Dec–19 Mar) was considered severe in this region when cumulative snowfall approached 150 cm and minimum monthly average temperature approached -13.4° C (High Plains Regional Climate Center 2012).

METHODS

We captured breeding-age sage-grouse near active leks from late March to early May 2005–2007 using night spotlighting and a long-handled net (Giesen et al. 1982, Wakkinen et al. 1992). We classified captured birds as adults ($\geq$2 yr, second or later breeding season) and yearlings (approx. 1 yr, first breeding season) based on the length and shape of the 9th and 10th primaries (Beck et al. 1975) and assigned sex based on plumage characteristics (Bihrle 1993). We weighed all birds at the time of capture to ensure that radio-transmitters were less than 3% of the body weight at the time of attachment. We fitted females with a 21.6-g necklace-type radio transmitter (model A4060; Advanced Telemetry Systems, Isanti, MN) with an 8-hour mortality switch and an expected battery life of 434 days. We fitted males in 2006 with a backpack-type radio transmitter (model A1135; Advanced Telemetry Systems) with an 8-hour mortality switch that weighed 17.9 g and had an expected battery life of 297 days and in 2007 with a 21.6-g necklace-type radio transmitter (model A4060; Advanced Telemetry Systems) having an expected battery life of 434 days. All animal handling procedures followed guidelines approved by The Ornithological Council (Fair et al. 2010) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Approval no. 07–A032).

We located sage-grouse to document winter habitat use from 1 November through 28 February during 2005–2006 and 2006–2007 in North Dakota, and 2006–2007 and 2007–2008 in South Dakota. Similar to Hagen et al. (2011), we evaluated this period for winter habitat selection because it coincided with the formation of large flocks ($\geq$30 birds) in early November and commenced with the initiation of the breeding season (i.e., males began attending leks) in this region. We located radio-marked sage-grouse $\geq$1 time per week with a hand-held 3-element Yagi antenna or by fixed-wing aircraft when we did not detect signals from the ground. We recorded all locations using a Global Positioning System (GPS) receiver in Universal Transverse Mercator (UTM) coordinates (NAD27; UTM Zone 13).

We measured vegetation along a 100-m transect randomly positioned and centered over the location of a radio-marked sage-grouse and at 2 dependent random locations. We measured vegetation on the same day that we located the bird to avoid bias from fluctuations in snow depth. To determine habitat selection, we measured dependent random sites at 250 m and 500 m in a random cardinal direction from the location of the bird. We retained only 1 radioed bird location (per flock) for inclusion in habitat analyses to reduce the likelihood of pseudoreplication when >1 radio-marked sage-grouse was located in a flock per day (Alldredge and Ratti 1992). We measured grass height and live sagebrush density (*A. tridentata* and *A. cana*) and height at 10-m intervals along each transect using the point-centered-quarter method (Cottam and Curtis 1956). We estimated percent canopy cover of grass cover, forb cover (including plains pricklypear [*Opuntia polyacantha*], prairie sagewort [*Artemisia frigida*], and winterfat [*Krascheninnikovia lanata*]), sagebrush cover, snow cover, and litter cover using a 0.1-m^2 quadrat at 10-m intervals (Daubenmire 1959). Because snow levels fluctuated between periods of no snow and periods of accumulation during all years of the study, we only included vegetation available to grouse in vegetation canopy cover measurements (i.e., sagebrush canopy cover only included the visible portions above snow and the visible portions above bare soil or litter during periods without snow). At each 10-m interval on the transect, we placed 4 quadrats by measuring 1 m to each side of the transect and then 1 m in each perpendicular direction forming an H pattern ($n = 44$ quadrats per transect). We categorized percent canopy cover for all cover types based upon 6 cover categories (0 = no cover, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, 6 = 96–100%; Daubenmire 1959).

We summarized all measurements to a site value by recoding the category value to the midpoint of the range of percentages and averaging the matching intervals (e.g., averaged all of the measurements taken 50 m at bird and random locations). Vegetation variables for each site included sagebrush height, grass height, percent total vegetation cover, percent grass cover, percent forb cover, percent sagebrush cover, percent snow cover, and percent litter cover. We estimated sagebrush density using a distance method that produced a maximum likelihood estimate (Pollard 1971) that we summarized for the site. We modeled winter habitat selection without considering sex or age of sage-grouse because we observed large mixed flocks on multiple occasions. We used analysis of variance (ANOVA) with a liberal alpha-level of $P \leq 0.15$ to evaluate differences between use and random sites and determine variables to retain in habitat models (Hosmer and Lemeshow 2000). This allowed us to retain a comprehensive list of variables for more detailed analyses in the conditional logistic regression model and exclude variables that did not differ between use and random sites. We tested the remaining habitat variable subset for collinearity ($r \geq |0.6|$) using Pearson's correlation coefficient. If variables were correlated, we selected one variable to include in the models based upon biological importance in the literature.

We used multivariate conditional logistic regression, also called matched-case logistic regression, to compare winter habitat characteristics on continuous scales to determine habitat associations based on conditions available to the animal (Ramsey et al. 1994, Boyce 2006) using PROC MDC (SAS Institute, Inc. 2010). Because of the conditioning involved in the logit, the true value of the intercept term plays no role in determining conditional probabilities of positive outcomes; therefore, conditional models have no intercept term (Hosmer and Lemeshow 2000, Duchesne et al. 2010, SAS Institute, Inc. 2010). The conditional logistic regression model allowed us to individually compare each sage-grouse use site to the matched pair of dependent random sites. We considered 13 models using Akaike's Information Criterion (AIC) to select the most parsimonious model. We considered models differing by ≤ 2 ΔAIC from the model with the lowest AIC as potential alternative models (Burnham and Anderson 2002) and used Akaike weights (w_i) as an indication of support for each model (Burnham and Anderson 2002, Anderson 2008). We considered models ≤ 2 ΔAIC from the best model with ≥ 1 parameter more than the best model but with essentially the same maximized log-likelihood as unsupported and noncompetitive (Burnham and Anderson 2002). Consequently, we eliminated these models from consideration in our analyses. We also removed observations containing snow cover and tested 13 models to determine if habitat use differed during periods without snow. We assessed model fit using a confusion matrix to develop re-substitution misclassification estimates based on the number of correct classifications for the best model (Boyce et al. 2002).

RESULTS

We captured and radio-marked 97 breeding-age females (F) and 54 breeding-age males (M) from 2005 to 2007; 98 of which (43 F and 1 M in ND, 46 F and 8 M in SD) were alive during winter and included in the winter habitat selection analyses. In North Dakota, we monitored 19 (19 F) and 30 (29 F, 1 M) birds during the winters of 2005–2006 and 2006–2007, respectively, and monitored 30 (26 F, 4 M) and 24 (20 F, 4 M) birds during the winters of 2006–2007 and 2007–2008, respectively, in South Dakota. We quantified vegetation at 340 (177 ND; Fig. 2, 163 SD; Fig. 3) sage-grouse use sites and 680 matched random (340 each at 250 m and 500 m) sites. We quantified vegetation for each bird an average of 4.84 (range = 1–8) and 2.83 (range = 1–5) times during the winters of 2005–2006 and 2006–2007 in North Dakota, respectively, and 2.67 (range = 1–5) and 3.42 (range = 1–9) times for each bird during the winters of 2006–2007 and 2007–2008 in South Dakota, respectively. Of these, we measured 79 (39 ND, 40 SD) sites in November, 75 (35 ND, 40 SD) in December, 110 (65 ND, 45 SD) in January, and 76 (38 ND, 38 SD) in February.

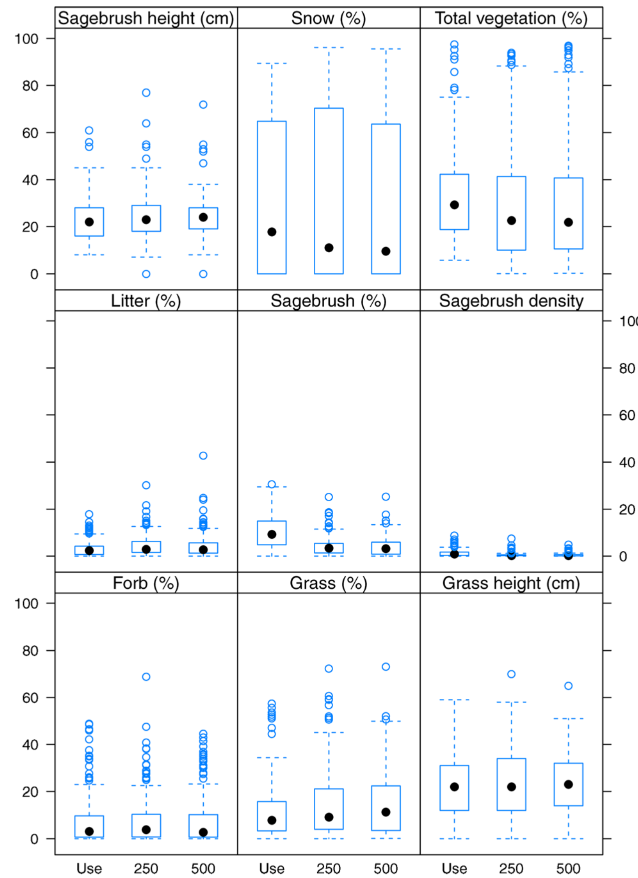

Figure 2. Vegetation characteristics of winter habitat for sage-grouse at 177 use sites and 354 random (177 each at 250 m and 500 m) dependent sites in North Dakota, 2005–2007. We quantified percent canopy cover for snow, total vegetation, litter, sagebrush, forb, and grass. We measured height for sagebrush and grass, and estimated sagebrush density as number of sagebrush plants/m^2. Variation associated with vegetation characteristics is indicated by the median (solid circles), upper and lower quartiles (box bounds), extreme values (1.5× inter-quartile range; dashed lines), and outliers (open circles). [Color figure can be seen in the online version of this article, available at http://wileyonlinelibrary.com/journal/jwmg]

All Study Sites Combined

Vegetation at sites selected by sage-grouse differed from random sites with 7.46% greater percent sagebrush cover ($F_{1,1,019} = 266.67$, $P \leq 0.001$), 3.78% greater percent total vegetation cover ($F_{1,1,019} = 8.03$, $P = 0.01$), and 1.18 more sagebrush shrubs per m^2 ($F_{1,1,019} = 179.52$, $P \leq 0.001$) at sites selected versus random sites. Conversely, selected sites had 4.24% less percent grass cover ($F_{1,1,019} = 28.20$, $P \leq 0.001$), 1.2% less litter cover ($F_{1,1,019} = 10.83$, $P \leq 0.001$), 1.33 cm lower sagebrush height ($F_{1,1,019} = 6.24$, $P = 0.01$), and 1.73 cm lower grass height ($F_{1,1,019} = 5.99$, $P = 0.02$) compared to random sites; we documented no difference between use and random sites in percent forb ($F_{1,1,019} = 0.04$, $P = 0.85$) and snow cover ($F_{1,1,019} = 0.02$, $P = 0.88$).

Uncorrelated variables used in models included percent sagebrush cover, sagebrush height, grass height, percent litter, and percent grass cover. We did not include sex as a covariate in the models because we observed mixed-sex flocks of sage-grouse on multiple occasions and use of sagebrush

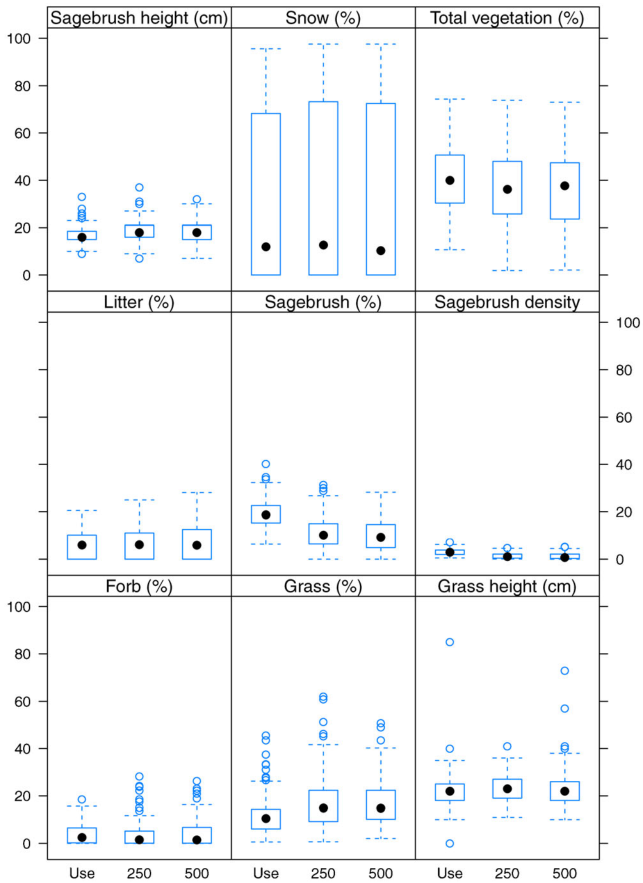

Figure 3. Vegetation characteristics of winter habitat for sage-grouse at 163 use sites and 326 random (163 each at 250 m and 500 m) dependent sites in South Dakota, 2006–2008. We quantified percent canopy cover for snow, total vegetation, litter, sagebrush, forb, and grass. We measured height for sagebrush and grass, and estimated sagebrush density as number of sagebrush plants/m^2. Variation associated with vegetation characteristics is indicated by the median (solid circles), upper and lower quartiles (box bounds), extreme values (1.5× inter-quartile range; dashed lines), and outliers (open circles). [Color figure can be seen in the online version of this article, available at http://wileyonlinelibrary.com/journal/jwmg]

cover did not differ between males ($\bar{x} = 8.63\%$, SE = 1.88 in ND; $\bar{x} = 19.38\%$, SE = 1.0 in SD) and females ($\bar{x} = 10.87\%$, SE = 0.59 in ND; $\bar{x} = 19.09\%$, SE = 0.48 in SD) in North Dakota ($t_{16} = 1.132$, $P = 0.27$) or in South Dakota ($t_{59} = 0.262$, $P = 0.79$).

Comparison Between Study Sites

Vegetation characteristics differed ($F_{1,338} \geq 13.21$, $P \leq 0.001$) at sage-grouse locations between study sites with 7.36% greater percent sagebrush cover, 6.80% greater percent total vegetation cover, 1.75 more sagebrush shrubs per m^2, and 2.47% greater litter cover on the South Dakota study site. Conversely, sagebrush height and percent forb cover were 6.08% and 3.70% greater ($F_{1,338} \geq 4.69$, $P = 0.03$), respectively, in North Dakota. We documented no difference ($F_{1,338} \leq 0.04$, $P = 0.83$) in percent grass cover, grass height, and snow cover for use sites between study sites. Vegetation characteristics at random locations showed some differences between North Dakota and South Dakota. Random locations had 2.04% greater percent grass cover, 6.50% greater sagebrush cover, 6.82% greater total vegetation cover, 2.20% greater litter cover, and 0.88 more shrubs per m^2 ($F_{1,678} \geq 4.33$, $P = 0.04$) on the South Dakota study site. Conversely, sagebrush height and forb cover were 6.20 cm and 4.14% greater ($F_{1,678} \geq 39.83$, $P \leq 0.001$), respectively, on the North Dakota study site. Grass height and snow cover were similar ($F_{1,678} \leq 0.47$, $P = 0.49$) at random locations between our study sites.

Resource Selection Models

We considered the model (sagebrush cover + sagebrush height + sagebrush cover × sagebrush height; $w_i = 0.60$) as the best approximating model for estimating sage-grouse winter habitat selection compared to 2 random scales (250 m and 500 m; Table 1). Parameter estimates (Table 2) and logistic odds ratios indicated that the probability of selection increased by 1.867 for every 1% increase in sagebrush cover (95% CI = 1.627–2.141; Fig. 4) and by 1.041 for every 1 cm increase in sagebrush height (95% CI = 1.002–1.082). The interaction between percent sagebrush canopy cover and sagebrush height ($\beta = -0.01$, SE ≤ 0.01; odds ratio = 0.987 [95% CI = 0.983–0.992]) also was significant. We did not graphically display sagebrush height because it was a weak predictor of resource selection. The top-ranked model correctly predicted presence at 84.67% (254 of 340 locations) of the sites selected by sage-grouse. We also considered the same 13 models during periods when use sites ($n = 117$) did not have snow present. The same 3 variables, sagebrush canopy cover ($\beta = 0.59$, SE = 0.11), sagebrush height ($\beta = 0.02$, SE = 0.03), and the interaction of sagebrush cover with sagebrush height ($\beta = -0.01$, SE ≤ 0.01) were in the top model ($w_i = 0.48$) predicting habitat selection for sage-grouse during periods without snow.

DISCUSSION

During our study, sage-grouse selected areas providing the greatest available sagebrush cover within 500 m of their use sites. In fact, sagebrush cover used during the winter in the Dakotas was considerably greater than during other critical periods (i.e., nesting and brood-rearing; Herman-Brunson et al. 2009; Kaczor et al. 2011*a*, *b*). Sagebrush cover was the primary factor sage-grouse selected for and was the highest ranked variable regardless of snow presence during winter. Previous studies have documented similar findings suggesting that sagebrush cover was the primary factor influencing habitat use of sage-grouse during winter (Eng and Schaldweiler 1972, Connelly et al. 2000, Doherty et al. 2008, Carpenter et al. 2010). Sagebrush cover at use sites in North Dakota (10.7%) and in South Dakota (19.2%) was less than previously reported during winter (Wallestad 1975, Autenrieth 1981, Connelly 1982, Schoenberg 1982, Robertson 1991). Those studies had >20% sagebrush cover at use sites with the exception of Robertson (1991) who documented 15% sagebrush cover in Idaho.

Sagebrush canopy cover in the Dakotas was similar to sagebrush cover used by sage-grouse in the northern (Aldridge and Brigham 2002) and western (Hagen et al. 2011) portions of the sage-grouse range (Schroeder et al. 2004). However, the sagebrush community we measured

Table 1. Conditional logistic regression models to quantify greater sage-grouse winter habitat use on the eastern edge of their range (northwestern South Dakota and southwestern North Dakota, USA), 2005–2008.

Model covariates[a]	K[b]	−2 LL	AIC[c]	ΔAIC[d]	w_i[e]
Sage + Sageht + Sage × Sageht	3	341.19	347.19	0.00	0.60
Sage + Sageht + Sage × Sageht + Grassht	4	340.68	348.67	1.54	0.28
Sage + Sageht + Sage × Sageht + Grass + Grassht	5	340.34	350.33	3.25	0.12
Sage + Sageht	2	371.18	375.17	27.94	0.00
Sage + Grassht	2	371.40	375.40	28.17	0.00
Sage + Sageht + Grass	3	369.70	375.70	28.50	0.00
Sage	1	374.58	376.58	29.33	0.00
Sage + Sageht + Grass + Grassht	4	369.36	377.36	30.22	0.00
Grass	1	685.80	687.80	340.57	0.00
Litter	1	699.16	701.16	353.90	0.00
Grassht + Sageht	2	728.96	732.97	385.74	0.00
Grassht	1	731.80	733.80	386.54	0.00
Sageht	1	734.38	736.37	389.12	0.00

[a] Sage = percent sagebrush canopy cover, Sageht = sagebrush height (cm), Grassht = grass height (cm), Grass = percent grass canopy cover, Litter = percent litter canopy cover.
[b] Number of parameters.
[c] Akaike's Information Criterion (Burnham and Anderson 2002).
[d] Difference in AIC relative to minimum AIC.
[e] Akaike weight (Burnham and Anderson 2002).

differed from those fringe areas, as 98.8% of use sites were dominated by Wyoming big sagebrush and silver sagebrush only comprised 0.32% of sagebrush cover at use sites during our study. Silver sagebrush did not occur at any use or random sites in South Dakota and occurred in <0.5% of all measured sagebrush use and random sites in North Dakota. Therefore, we were not surprised that the dominant sagebrush species used during winter in this study differed from sagebrush selected during winter in other fringe areas (i.e., silver sagebrush in Alberta, Carpenter et al. 2010; low sagebrush [*Artemisia longiloba*] in Oregon, Hagen et al. 2011) because sagebrush community structure was dissimilar. Contribution of silver sagebrush to resource selection during winter in the Dakotas was not biologically meaningful. Use of sagebrush species in fringe areas of the sage-grouse range likely reflects their preference for sagebrush species within the available sagebrush community. We acknowledge the potential for sex-specific heterogeneity in habitat selection given our low sample size of males. However, our observations of mixed sex flocks suggest that in this area of limited spatial extent of sagebrush, this bias was unlikely.

Use of conditional logistic regression models during our study was advantageous over traditional logistic models because this approach allowed us to evaluate habitat selection at finer spatial and temporal scales concomitant with the animal location instead of contrasting selection with the larger spatial domain of the study area (Compton et al. 2002, Boyce 2006). We believe that the use of 250-m and 500-m random sites accurately represented available habitat to sage-grouse because of the disconnected and patchy nature of sagebrush vegetation in this region. Also, the 250-m and 500-m random sites we selected were within known daily movement distances during winter (300 m/day; Connelly et al. 1988), which allowed us to match the scale that sage-grouse actually selected habitats within available resource units at the same time and weather conditions (Compton et al. 2002). Because weather conditions fluctuated on a daily basis (i.e., extreme cold and high winds) during our study, conditional logistic regression models accurately reflected variation in sage-grouse habitat use patterns at true presence-absence points (Duchesne et al. 2010, Dzialak et al. 2011) that could have otherwise been lost with a pooled unpaired logistic regression design. Although we lacked a detailed spatial map of sagebrush vegetation for this region, future research that uses resource selection functions (RSF; Boyce et al. 2002, Duchesne et al. 2010) to link spatial patterns of habitat and sage-grouse distribution based on conditional logistic regression models (e.g., Compton et al. 2002, Boyce et al. 2003, McDonald et al. 2006) could be valuable to resource managers in the region.

As expected, sage-grouse used dense stands of Wyoming big sagebrush to meet their requirements for food and cover. Wyoming big sagebrush is highly palatable to sage-grouse (Rosentreter 2005) and accounts for up to 90% of their diet during winter (Remington and Braun 1985). Because of the high protein and lipid content of Wyoming big sagebrush (Remington and Braun 1985, Rosentreter 2005), sage-

Table 2. Parameter estimates (β), standard errors, and significance tests from the top-ranked conditional logistic regression model to determine greater sage-grouse winter habitat selection on the eastern edge of their range (northwestern South Dakota and southwestern North Dakota, USA), 2005–2008.

Parameter[a]	β	SE	95% CI	Wald χ^2	P-value
Sage	0.62	0.07	0.487 to 0.761	79.40	<0.001
Sageht	0.04	0.02	0.002 to 0.078	4.29	0.04
Sage × Sageht	−0.01	0.002	−0.008 to −0.017	28.26	<0.001

[a] Sage, percent sagebrush canopy cover; Sageht = sagebrush height (cm).

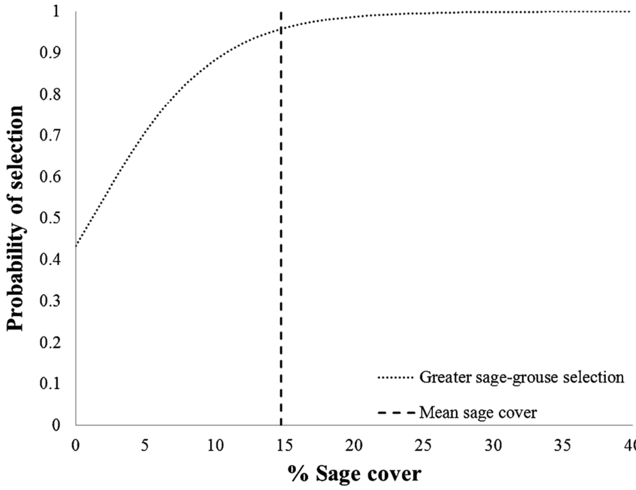

Figure 4. Mean percent sagebrush canopy cover at use sites and sage-grouse selection probability as a function of percent sagebrush canopy cover in North Dakota and South Dakota, 2005–2008.

grouse likely forage on this species to reduce expenditure of endogenous reserves that can occur when temperatures at night approach -10° C during winter (Sherfy and Perkins 1994). Furthermore, sage-grouse use of dense sagebrush cover during winter was a behavioral strategy that likely supported thermoregulation by maintaining their metabolic rate (Sherfy and Perkins 1995). Accumulation of lipids that increase body mass during winter through consumption of sagebrush also may increase fitness prior to breeding (Beck and Braun 1978). Thermoregulation, along with the security benefits that dense sagebrush provides from predators (i.e., Watters et al. 2002), may explain why sage-grouse select sagebrush habitats during winter.

Amount, timing, and type of precipitation influence sagebrush growth structure in Idaho (Dalgleish et al. 2011). We hypothesize that sagebrush structure and growth also may be effected by precipitation in the Dakotas. Overwinter (Nov–Mar) precipitation in central portions of the sage-grouse range was $\geq$10% greater than in our study area, whereas April–July rainfall was $\geq$17% greater in the Dakota sage-grouse range (National Climatic Data Center 2011). Because of the extensive and deep root system of Wyoming big sagebrush, precipitation received mainly as snow during the winter (e.g., central portions of the sage-grouse range) favor growth and development because moisture from the snow percolates deeper into the soil profile (Comstock and Ehleringer 1992, Schwinning et al. 2003). Conversely, precipitation is more likely to evaporate before infiltrating the soil in the Dakotas because most of the precipitation occurs as rain from April through July (Schwinning et al. 2003). Therefore, soil moisture conditions in the Dakotas may result in reduced sagebrush size and cover compared to similar stands of Wyoming big sagebrush in the central portion of the sage-grouse range. However, additional research is necessary to quantify the effects of precipitation on sagebrush structure in the Dakotas.

Wyoming big sagebrush is uniquely adapted to take advantage of soil moisture by retaining approximately one-third of its perennial leaves in winter and by developing ephemeral leaves early in the spring (Doescher et al. 1990, Miller and Schultz 1987). These adaptations allow Wyoming big sagebrush to begin photosynthesis and growth when soil moisture conditions are optimal (DePuit and Caldwell 1973, Miller and Schultz 1987). However, additional research is necessary to evaluate factors influencing the structure of Wyoming big sagebrush in this region. Findings from this study, and those of Herman-Brunson et al. (2009) and Kaczor et al. (2011*a*, *b*) regarding sagebrush height (20–38 cm) and sagebrush canopy cover (4.7–19.2%) suggest that sagebrush community structure may be limited by these causal mechanisms. By understanding the factors influencing sagebrush growth and structure in a region, management could focus on developing strategies that limit further degradation of sagebrush. Inadequate winter habitat could increase overwinter mortality of sage-grouse resulting in population decline and/or extinction in the Dakotas.

Sage-grouse had high survival (>90%; Swanson 2009) during 3 mild winters during our study and Kaczor et al. (2011*a*) noted that females in this region were heavier prior to nesting than those in other studies (Schroeder et al. 1999). These factors suggest that current sagebrush habitat availability allows sage-grouse to meet their physiological needs during mild winters and enter the reproductive period in good physiological condition. Unfortunately, we could not determine the effect of severe winter weather on habitat use or survival and conditions may not have been stressful enough to limit habitat availability during our study. During prolonged periods of severe winter weather, mortality could be greater (Moynahan et al. 2006) and conditions would likely force sage-grouse to move long distances into Montana and Wyoming to escape deep snow that could cause sagebrush habitat in the Dakotas to become unsuitable. However, we were unable to test for any interaction between sagebrush cover and snow depth because our random sites were located in close proximity to use sites. Additional research is needed where random sites are independent and located farther away than 500 m from use sites to quantify potential differences in snow depth during typical and severe winters.

MANAGEMENT IMPLICATIONS

Our findings indicate that sagebrush cover was the primary factor influencing habitat selection during winter by sage-grouse. Maintenance of sagebrush habitat used by sage-grouse during winter on the eastern edge of its range could be critical to the regional sustainability of sage-grouse because sage-grouse selected greater sagebrush cover than during other periods (e.g., nesting, brood-rearing; Herman-Brunson et al. 2009; Kaczor et al. 2011*a*, *b*) of their life-history. In the Dakotas, cover and height of sagebrush will likely remain below the recommendations made by Connelly et al. (2000) for winter sage-grouse habitat because of causal mechanisms affecting growth of Wyoming big sagebrush. Managers in this region could focus on providing dense sagebrush cover in areas used by sage-grouse during winter because availability of winter habitat can affect population sustainability (Moynahan et al. 2006, Anthony and Willis 2009) and protection of critical wintering sage-grouse areas could be essential to prevent further population declines (Swenson et al. 1987). Additional research is necessary to evaluate the potential impact of severe winter weather on patterns of sage-grouse habitat use, movements, and survival.

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