

MICROHABITAT SELECTION FOR NESTING AND BROOD-REARING BY THE GREATER SAGE-GROUSE IN XERIC BIG SAGEBRUSH

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Abstract. Understanding selection of breeding habitat is critical to conserving and restoring habitats for the Greater Sage-Grouse (*Centrocercus urophasianus*), particularly in xeric landscapes (≤ 25 cm annual precipitation). We monitored radio-marked female sage-grouse in south-central Wyoming in 2008 and 2009 to assess microhabitat use during nesting and brood rearing. For each model we grouped variables into three hypothesis sets on the basis of the weight of support from previous research (a priori information). We used binary logistic regression to compare habitat used by grouse to that at random locations and used an information-theoretic approach to identify the best-supported models. Selection of microhabitat for nests was more positively correlated with mountain big sagebrush (*Artemisia tridentata vaseyana*) than with Wyoming big sagebrush (*A. t. wyomingensis*) and negatively correlated with cheatgrass. Nesting hens also selected microhabitats with greater litter cover. Microhabitat for brood-rearing had more perennial grass and sagebrush cover than did random locations. Microhabitat variables most supported in the literature, such as forb cover and perennial grass cover, accounted for only 8% and 16% of the pure variation in our models for early and late brood rearing, respectively. Our findings suggest sage-grouse inhabiting xeric sagebrush habitats rely on sagebrush cover and grass structure for nesting as well as brood-rearing and that at the microhabitat scale these structural characteristics may be more important than forb availability. Therefore, in xeric sagebrush, practices designed to increase forb production by markedly reducing sagebrush cover, as a means to increase sage-grouse productivity, may not be justified.

Key words: *Centrocercus urophasianus*, brood-rearing, grass cover, biological soil crust, Greater Sage-Grouse, microhabitat selection, nest occurrence, Wyoming.

Selección de Micro Hábitat para Anidación y Cría de la Nidada por *Centrocercus urophasianus* en Ambientes Secos de *Artemisia tridentata*

Resumen. Entender la selección del hábitat reproductivo es crítico para conservar y restaurar los ambientes para *Centrocercus urophasianus*, particularmente en los paisajes secos (≤ 25 cm de precipitación anual). Marcamos con radio transmisores y monitoreamos hembras de *C. urophasianus* en el sud centro de Wyoming en 2008 y 2009 para evaluar el uso del micro hábitat durante la anidación y la cría de la nidada. Para cada modelo agrupamos las variables en tres sets de hipótesis basados en el peso de apoyo dado por estudios previos (información a priori). Usamos regresiones logísticas binarias para comparar el uso del hábitat por parte de *C. urophasianus* con localidades seleccionadas al azar y usamos un enfoque de la teoría de la información para identificar los modelos con más apoyo. La selección de micro hábitats para el nido se correlacionó más positivamente con *Artemisia tridentata vaseyana* que con *A. t. wyomingensis* y negativamente con *Bromus tectorum*. La hembra anidante también seleccionó micro hábitats con mayor cobertura de hojarasca. Los micro hábitats para la cría de los polluelos tuvo más pastos perennes y cobertura de *Artemisia* que las localidades seleccionadas al azar. Las variables de micro hábitat mas apoyadas por la literatura, como la cobertura de plantas herbáceas y pastos perennes, explicaron sólo el 8% y 16% de la variación pura en nuestros modelos para la cría temprana y tardía de los polluelos, respectivamente. Nuestros resultados sugieren que los individuos de *C. urophasianus* que habitan sitios secos de *Artemisia* dependen de la cobertura de *Artemisia* y de la estructura de los pastos para anidar lo mismo que para criar a los polluelos y que a la escala de micro hábitat estas características estructurales pueden ser más importantes que la disponibilidad de plantas herbáceas. Por lo tanto, en los sitios secos de *Artemisia*, las prácticas diseñadas para aumentar la producción de plantas herbáceas mediante la reducción marcada de la cobertura de *Artemisia*, como un medio para aumentar la productividad de *C. urophasianus*, pueden no estar justificadas.

INTRODUCTION

Over the past 60 years, researchers have documented range-wide declines in populations of the Greater Sage-Grouse (*Centrocercus urophasianus*) (Patterson 1952, Connelly and

Braun 1997, Braun 1998, Connelly et al. 2004), leading to concerns over the species' long-term viability. Sage-grouse depend on sagebrush for food and shelter throughout the year (Bent 1932, Patterson 1952, Braun et al. 1977, Swenson

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1987, Connelly et al. 2011). Extensive loss and fragmentation of big sagebrush (*Artemisia tridentata*) steppe have reduced the current distribution of sage-grouse to about one-half of its original extent (Schroeder et al. 2004). Knowing what vegetation and structural characteristics at the microhabitat scale are important to sage-grouse at each stage of their breeding cycle is critical to maintaining and restoring habitat on the remaining lands supporting sage-grouse.

Research has expanded our ecological understanding of the sage-grouse's selection of nesting habitat at the microhabitat scale (e.g., Dunn and Braun 1986, Sveum et al. 1998b, Connelly et al. 2000, Aldridge and Brigham 2002, Holloran et al. 2005, Kaczor 2008, Doherty et al. 2010). Studies have documented the importance of specific habitat features, including adequate sagebrush cover (or shrub cover) and sagebrush height (Wallestad and Pyrah 1974, Fischer 1994, Sveum et al. 1998b, Connelly et al. 2000, Braun et al. 2005, Holloran et al. 2005, Hagen et al. 2007, Kaczor 2008), as well as an herbaceous understory (Lyon 2000, Holloran et al. 2005, Hagen et al. 2007).

Microhabitats for nesting and early brood rearing often are very similar because brooding females spend their first 2–3 weeks after the eggs hatch in the vicinity of their nest (Berry and Eng 1985, Holloran and Anderson 2005). Sage-grouse chicks eat foods with high protein content (i.e., insects and actively growing forbs) almost exclusively for the first 2 weeks after hatching (Johnson and Boyce 1990); as a result, the hen likely selects habitats for early brood-rearing on the basis of abundance of insects and protein-rich forbs (Barnett and Crawford 1994, Holloran and Anderson 2004). Generally, these habitats are characterized by a well-developed sagebrush overstory and a healthy herbaceous understory (Connelly et al. 2000). Sage-grouse chicks consume fewer insects as the summer progresses, and forbs form a larger portion of their diets (Klebenow and Gray 1968, Peterson 1970). Research has suggested that late brood-rearing habitat is generally associated with more mesic sites that provide greater quantities of forbs and insects for both hens and chicks (Schroeder et al. 1999, Connelly et al. 2000). Because of the demonstrated importance of forbs to brooding hens and chicks, conservation efforts commonly focus on habitat treatments in which sagebrush is removed to increase forb production (Wroblewski and Kauffman 2003, Pyke 2011).

Habitat-selection analyses are commonly used to identify resources that are used disproportionately to their availability (Millsbaugh and Marzluff 2001), predicated on the idea that animals are making choices (i.e., habitat selection; Garshelis 2000). Thus, it reasons that these choices are influenced by habitat conditions at specific locations within a species' range. Our understanding of the sage-grouse's selection of habitat for nesting and brood rearing comes primarily from studies in habitats more mesic (e.g., Drutt 1992, Holloran 1999, Lyon 2000, Aldridge and Brigham 2002, Hausleitner 2003, Slater 2003, Aldridge 2005, Doherty et al. 2010) than those

found in our study areas, where precipitation averages 23.0 cm annually, on the basis of ≥ 21 years of data compiled from four surrounding meteorological stations (Western Regional Climate Center 2010).

Our primary objective was to explore microhabitat selection, considering both physiognomic and floristic characteristics, during nesting, early brood rearing, and late brood rearing in south-central Wyoming. We hypothesized that the microhabitat variables most predictive of selection in our drier study areas may diverge from findings in more mesic areas. We were able to gain insight into this question with sequential modeling (Arnold 2010) by defining categories of models, termed hypothesis sets, for each life stage on the basis of a priori information to select the best-supported models. On the basis of the weight of evidence in published literature on habitat selection during the reproductive period and sage-grouse biology we grouped microhabitat variables into three hypothesis sets.

METHODS

STUDY AREAS

The Atlantic Rim (AR) and Stewart Creek (SC) study areas are located in south-central Wyoming within a semi-desert grass–shrub zone characterized by expansive sagebrush steppe with low average annual precipitation (Natural Resources Conservation Service 2006). Combined, the study areas encompass approximately 1913 km² (AR = 1093 km² and SC = 820 km²) at elevations ranging from 1981 to 2529 m. The majority of land in both areas is owned and administered by the U.S. Bureau of Land Management. Grazing of cattle and domestic sheep is a major land use in both areas. The AR is also being developed for extraction of natural gas from coal beds. Both study areas are dominated by Wyoming big sagebrush (*A. t. wyomingensis*) at lower elevations and mountain big sagebrush (*A. t. vaseyana*) along foothills at higher elevations (BLM 2006b). Common forbs composing the understory include arrowleaf balsamroot (*Balsamorhiza sagittata*), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), sego lily (*Calochortus nuttallianum*), sulfur buckwheat (*Eriogonum umbellatum*), and wild onion (*Allium* spp.). Common grasses include bluebunch wheatgrass (*Pseudoroegneria spicata*), green needlegrass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), and western wheatgrass (*Pascopyrum smithii*; BLM 2006a).

RADIO-MARKING AND MONITORING SAGE-GROUSE

We captured female sage-grouse from mid-March through late April 2008 and 2009 on or near 14 leks in the AR and 5 leks in the SC by established spot-lighting and hoop-netting protocols (Giesen et al. 1982, Wakkinen et al. 1992). To ensure equal capture effort and to obtain a random sample of the population (Manly et al. 2002), we selected leks evenly distributed across both study areas. We secured VHF radio

transmitters (Model A4060; Advanced Telemetry Systems, Isanti, MN) to females with a PVC-covered wire necklace. Transmitters weighed 22 g (~1.4% of a female sage-grouse's mean body mass); had a battery with a life expectancy of 789 days, and were equipped with motion sensors (the transmitter's pulse rate increased in response to inactivity after 8 hr).

Using hand-held receivers and 3-element Yagi antennas, we located sage-grouse weekly through nesting (May–June) and brood rearing (late June–August) mainly between the hours of 08:00 and 18:00. We located the nests and broods of radio-marked birds by circling the signal's source until the surveyor saw the bird on a nest or with her brood or isolated the nest or brood to a few shrubs. After determining a female grouse was nesting, we monitored the nest biweekly until the conclusion of the nesting effort. We left nests in a meandering or zigzag pattern to reduce the potential of predators following human scent to the nest. To further minimize human-induced nest predation or nest abandonment, we monitored incubating females from a distance of ≥ 30 m by triangulating to the exact nest point or nest shrub. At each visit to a possibly brooding hen, we attempted to determine if the female was still with chicks by sighting the chicks with binoculars or by observing the brooding female's behavior (e.g., distraction displays, feigning injury, clucking, and hesitation to flush). We recorded the locations of nests and broods (± 1 m) with a hand-held 12-channel global positioning system (GPS; Garmin Etrex; Garmin International, Olathe, KS).

We established locations for random sampling by using a Geographic Information System (GIS) to generate a 1-km² grid overlaying the two study areas. We numbered, then randomized the intersection points to represent sampling locations (random locations) and employed the Northwest GAP land-cover data (2008) to constrain the random locations to sagebrush habitats while excluding areas of inappropriate habitat such as exposed rock, open water, and conifer stands.

MICROHABITAT MEASUREMENTS

We used established protocols to measure the vegetative characteristics of the microhabitat surrounding nests, broods, and random locations (Connelly et al. 2003). To sample characteristics within 5 and 10 m of each nest and brood, respectively, we measured microhabitat characteristics along two perpendicular 10-m surveyor tapes centered on nests and random locations (Gregg et al. 1994) and two perpendicular 20-m surveyor tapes centered on locations of broods and random locations (K. P. Reese, pers. comm., 2008). We recorded general habitat characteristics at nests including vegetation association after hatching in late May and June and concluded our measurements at nest and random locations in early July. At locations of broods and random locations we recorded microhabitat characteristics in July and August. We measured microhabitat characteristics at locations grouse used and at random locations concurrently. We considered the early brood period to last from hatch to 14 days (Connelly

et al. 1988, Thompson et al. 2006) and so recorded habitat characteristics for early brood rearing at one location occupied by each brood during this period. For late brood rearing we recorded habitat characteristics at one location occupied by each brood when the chicks were approximately 20 to 30 days old (Connelly et al. 1988, Connelly et al. 2011).

We determined the location of a simulated nest site (random) by selecting the closest shrub taller than or equal to 30 cm, the average height of nest shrubs in Wyoming (Patterson 1952, Holloran et al. 2005). We did not follow this convention to establish random locations for comparison with brood-rearing because hens with chicks select a variety of vegetation, including shrubs, grasses, and forbs. At each location, we measured a suite of physiognomic and floristic (Rotenberry 1985) microhabitat variables quantifying the overstory, understory, and ground cover (Table 1).

We used the line-intercept technique (Canfield 1941) to quantify shrub canopy cover by species at each location (Wambolt et al. 2006). We measured height (cm) of each sagebrush or other shrub (tallest leader, excluding inflorescences) encountered along the line and averaged these per location. The average height of sagebrush included several taxa but consisted mainly of mountain and Wyoming big sagebrush and, on occasion, basin big sagebrush (*A. t. tridentata*) and silver sagebrush (*A. cana*), but it excluded mat-forming subshrub species including fringed sagebrush (*A. frigida*) and birdfoot sagebrush (*A. pedatifida*). We quantified shrub density as the number of shrubs rooted in a belt transect 1 m wide along each line transect. To distinguish Wyoming and mountain big sagebrush accurately, we took a representative sample at each location and identified them to subspecies with a UV-light fluorescence test (Rosentreter 2005). We estimated visual obstruction with a 1-m modified Robel pole (diameter 3 cm; Robel et al. 1970, Griffith and Youtie 1988) placed in the center of each location (nest bowl or center of brood locations or random locations) and recorded measurements from each cardinal direction. We estimated the canopy or ground cover of invasive annual grasses, perennial grasses, residual perennial grasses, forb cover, food forb cover, gravel and rock, bare soil, biological soil crust, and litter within six cover classes in quadrats of 20 × 50 cm (0.1 m²; Daubenmire 1959) placed along each surveyors' tape (nest: transect intersection, 2 m, 4 m, 6 m, and 8 m; brood: transect intersection, 4 m, 6 m, 8 m, 10 m, 12 m, and 14 m) and radiating from the transect intersection. This yielded nine quadrats per location for each nest or simulated nest and 13 for each brood or simulated brood. We defined cover classes as 1 = 0–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. We grouped forbs that are known to be eaten by sage-grouse (Patterson 1952, Peterson 1970, Wallestad and Eng 1975, Barnett and Crawford 1994) as food forbs (Table 2) and others as non-food forbs. We measured the heights of residual and perennial grasses (cm) as the tallest naturally growing portion of the plant excluding flowering stalks (droop height) within 1 m

TABLE 1. Microhabitat characteristics measured at nest sites, locations of early and late brood rearing, and random locations, south-central Wyoming, 2008 and 2009.

Variable	Description	Candidate sets								
		Nest			Early-brood			Late-brood		
		I	II	III	I	II	III	I	II	III
SAGECVR	Sagebrush canopy cover (%)	×								
SHRUBDEN	Shrub density (plants m ⁻²)	×								
VOBST	Visual obstruction (horizontal cover; dm)	×				×				
FORBS	Total forb cover (%)		×		×			×		
GRSCVR	Cover of perennial and residual grasses (%)		×							
LITTER	Ground cover by litter (%)		×			×				×
ARTRW	Wyoming big sagebrush or other sagebrush			×		×				×
BIOCRUST	Biological soil crust (%)			×		×				×
CHEAT	Presence or absence of cheatgrass			×		×				×
GANDR	Gravel and rock cover (%)			×						×
PERGRS	Perennial grass cover (%)				×			×		
FOODF	Food forb cover (%)					×			×	
SAGECVR	Sagebrush canopy cover (%)					×			×	
SAGEHGHT	Average sagebrush height within location (cm)					×			×	
SHRUBDEN	Shrub density (plants m ⁻²)					×			×	
GRSHGHT	Averaged maximum perennial grass droop height (cm)					×			×	

of each Daubenmire quadrat to yield 9 or 13 height measurements for each microhabitat location.

EXPERIMENTAL DESIGN AND DATA ANALYSIS

We employed a use-versus-availability design to evaluate fourth-order habitat selection, or selection of items from a habitat patch (e.g., a nest site; Johnson 1980, Manly et al. 2002). We pooled locations individual grouse use locations to represent a population-level response (i.e., type I design of Thomas and Taylor 2006; Manly et al. 2002). Random locations were also pooled and constrained within the boundaries of each study area (Manly et al. 2002).

For statistical analyses we used SAS version 9.2 (SAS Institute 2009). We evaluated microhabitat selection with binary logistic regression modeling. For each period (nesting, early brood rearing, and late brood rearing), we determined the probability of use where used (e.g., early brood-rearing locations) and available locations (e.g., random locations) were the dependent variables (Johnson et al. 2006). We did not define random locations, representing available habitat, as unused resources because the absence of a nest or brooding female cannot be determined without error (i.e., we are not certain that the random locations were all unused). However, we excluded random locations that had evidence of nesting or brood rearing, so contamination was likely negligible (Johnson et al. 2006).

Prior to modeling, we computed a Pearson's correlation matrix to test for multicollinearity among the variables (linear dependencies among the explanatory variables) and omitted one of each correlated variables when correlation

coefficients (r) were $\geq|0.6|$. Using a correlation matrix alone is often not sufficient because, when combined, multiple variables may be highly interdependent but not be detected by the matrix procedure (Allison 2009). Consequently, we further examined multicollinearity by estimating the global model (e.g., containing all variables) in PROC REG and specified the collinearity-tolerance option. Low tolerance, approximately ($t \leq 0.40$, suggests multicollinearity (Allison 2009, SAS Institute 2009), which we used as a basis for omitting correlated variables. When omitting correlated variables we relied on the variable's importance as established in the literature and the variable we believed were most biologically relevant to sage-grouse. Finally, we checked for the stability and consistency of estimates of the regression coefficient when variables were moderately correlated ($|0.3| \leq r \leq |0.6|$). Undetected correlations between variables can cause instability in the signs of coefficients and also result in inflated standard errors (Doherty 2008). We did not permit variables to compete in the same model at any level of model selection when the variables' interactions in the same model caused the signs of coefficients to switch. Of the correlated variables causing instability in the model, we retained those that had the greatest effect on model fit. To avoid pseudoreplication, we excluded replacement nests from our analyses.

To control for spatial and temporal variability, we included site-year combinations in each candidate model as fixed effects (dummy variables; Manly et al. 2002). Thus, because we standardized site and year in each model, differences

TABLE 2. Forbs occurring in south-central Wyoming and likely consumed by Greater Sage-Grouse.

Common name	Scientific name	Status
Agoseris	<i>Agoseris</i> spp.	Native
Alfalfa	<i>Medicago sativa</i>	Introduced
Aster	<i>Symphotrichum</i> spp.	Native
Balsamroot	<i>Balsamorhiza</i> spp.	Native
Bluebells	<i>Mertensia</i> spp.	Native
Broomrape	<i>Orobanche</i> spp.	Native
Buckwheat	<i>Eriogonum</i> spp.	Native
Clover	<i>Trifolium</i> spp.	Native/introduced
Common pepperweed	<i>Lepidium densiflorum</i>	Native
Common dandelion	<i>Taraxacum officinale</i>	Native/introduced
Curlycup gumweed	<i>Grindelia squarrosa</i>	Native
Death camas	<i>Zigadenus</i> spp.	Native
Desert parsley/ biscuitroot	<i>Lomatium</i> spp.	Native/introduced
Flax	<i>Linum</i> spp.	Native/introduced
Fleabane	<i>Erigeron</i> spp.	Native
Globe mallow	<i>Sphaeralcea</i> spp.	Native
Goatsbeard	<i>Tragopogon</i> spp.	Introduced
Hawksbeard	<i>Crepis</i> spp.	Native/introduced
Indian paintbrush	<i>Castilleja</i> spp.	Native
Lupine	<i>Lupinus</i> spp.	Native
Milkvetch	<i>Astragalus</i> spp.	Native
Monkeyflower	<i>Mimulus</i> spp.	Native
Northern sweetvetch	<i>Hedysarum boreale</i>	Native
Penstemon	<i>Penstemon</i> spp.	Native
Phlox	<i>Phlox</i> spp.	Native
Prickly lettuce	<i>Lactuca serriola</i>	Introduced
Prairie clover	<i>Dalea</i> spp.	Native
Microseris	<i>Microseris</i> spp.	Native
Pussytoes	<i>Antennaria</i> spp.	Native
Sego lily	<i>Calochortus nuttallii</i>	Native
Shooting star	<i>Dodecatheon</i> spp.	Native
Slender phlox	<i>Microsteris gracilis</i>	Native
Small burnet	<i>Sanguisorba minor</i>	Introduced
Vetch	<i>Vicia</i> spp.	Native/introduced
Wild onion	<i>Allium</i> spp.	Native
Yarrow	<i>Achillea millefolium</i>	Native
Yellow sweetclover	<i>Melilotus officinalis</i>	Introduced

between models were due to the explanatory power of the microhabitat variables (Holloran et al. 2005, Ludwig et al. 2010). To make results more interpretable, we do not report site and year responses though we do report statistically significant ($P \leq 0.05$) site or year effects.

We used second-order Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) to rank candidate models by degrees of support. AIC_c penalizes a model according to its number of parameters, providing an unbiased estimate of the support of a particular candidate model. The candidate model with the lowest AIC_c value has the most support from the data, but models within $2 \Delta AIC_c$ points are competitive with that model

(Burnham and Anderson 2002:70, 131). Consequently, we considered models within $2 \Delta AIC_c$ points of the top model to be plausible. We computed cumulative Akaike weights (w_i) for all candidate models to provide weights of evidence in support of each model being the most parsimonious, in comparison to the other models being considered (Burnham and Anderson 2002:451, Rushton et al. 2004). Furthermore, we quantified the relative importance (RI) of each microhabitat variable by summing the Akaike weights of each variable across all of the models in which it appeared (Burnham and Anderson 2002). We considered parameters having 95% confidence intervals with odds ratios that included 1 to be uninformative (Hosmer and Lemeshow 1989:100).

We used the area under the receiver operator curve (ROC) to measure the predictive accuracy of the models. ROC is derived from plotting the true positives against the false positive fractions for a range of thresholds in a prediction probability (e.g., how good our best model was at discriminating between nests and random locations; Rushton et al. 2004).

Our objective was to find the most parsimonious model and the most informative microhabitat variables for each of the three periods we defined. Consequently, we used a sequential procedure (Arnold 2010) consisting of two steps. First, we grouped the models by three categories of hypothesis sets each for nesting, early brood-rearing, and late brood rearing (Table 3). The three hypothesis sets for each life stage were organized as follows: set 1 was restricted to variables described in the literature as the most supported variables for sage-grouse microhabitat selection, primarily on the basis of the meta-analysis by Hagen et al. (2007), set 2 was based on variables described in the literature as having moderate support, and set 3 contained variables that have not been verified in sage-grouse research but we believe may be biologically relevant on the basis of sage-grouse biology. To arrive at a best-fit model, we tested multiple combinations of variables (Burnham and Anderson 2002:101–102, 125) within each hypothesis set. We then compared the best model or models in each hypothesis set to the null model. If the best model was not at least $2 AIC_c$ points lower than the null model, it was not brought forward to the next level (Burnham and Anderson 2002:70, 131, Doherty et al. 2010). This design allowed us to evaluate model fit in simpler models (≤ 4 microhabitat variables) and, in turn, avoid issues with overparameterized models (Burnham and Anderson 2002:32, 131). Second, after finding the best model(s) in each hypothesis set (e.g., Nest I, Nest II, and Nest III), we allowed models to compete across sets to see if additional information produced a more parsimonious model (i.e., reduced the AIC_c value by at least 2 points; Burnham and Anderson 2002, Doherty 2008). For example, did the top model(s) from Nest I have the most support individually or did a combination of top models from Nest I and Nest II produce a model with greater support? When a single top model was not apparent from the weight of evidence (w_i), we averaged models to calculate mean coefficients and

TABLE 3. Measured variables grouped into three hypothesis sets considered in the sequential model selection analysis evaluating nesting, early brood-rearing, and late brood-rearing habitat selection in south-central Wyoming, 2008 and 2009.

Candidate sets/ variable names	Description
Nest I ^a	
SAGECVR	Sagebrush canopy cover (%)
SHRUBDEN	Shrub density (plants m ⁻²)
VOBST	Visual obstruction (horizontal cover; dm)
Nest II ^b	
FORBS	Total forb cover (%)
GRSCVR	Cover of perennial and residual grasses (%)
LITTER	Ground cover by litter (%)
Nest III ^c	
ARTRW	Wyoming big sagebrush or other sagebrush
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
GANDR	Gravel and rock cover (%)
Early-brood I ^a	
FORBS	Total forb cover (%)
PERGRS	Perennial grass cover (%)
Early-brood II ^b	
FOODF	Food forb cover (%)
SAGECVR	Sagebrush canopy cover (%)
SAGEHGHT	Average sagebrush height within location (cm)
SHRUBDEN	Shrub density (plants m ⁻²)
GRSHGHT	Averaged maximum perennial grass droop height (cm)
Early-brood III ^c	
ARTRW	Wyoming big sagebrush or other sagebrush
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
LITTER	Ground cover by litter (%)
VOBST	Visual obstruction (horizontal cover; dm)
Late-brood I ^a	
FORBS	Total forb cover (%)
PERGRS	Perennial grass cover (%)
Late-brood II ^b	
FOODF	Food forb cover (%)
GRSHGHT	Averaged maximum perennial grass droop height (cm)
SAGECVR	Sagebrush canopy cover (%)
SAGEHGHT	Average sagebrush height within location (cm)
SHRUBDEN	Shrub density (plants m ⁻²)
Late-brood III ^c	
ARTRW	Wyoming big sagebrush or other sagebrush
BIOCRUST	Biological soil crust (%)
CHEAT	Presence or absence of cheatgrass
GANDR	Gravel and rock cover (%)
LITTER	Ground cover by litter (%)

^aNest I, Early-brood I, Late-brood I hypothesis sets 1 contain the microhabitat variables that have been shown to be important in a suite of published studies of the sage-grouse's habitat selection.

^bNest II, Early-brood II, Late-brood II hypothesis sets 2 contain microhabitat variables that have been examined in published studies of the sage-grouse's habitat selection, but their importance is not well established.

^cNest III, Early-brood III, Late-brood III hypothesis sets 3 contain microhabitat variables that we theorize may be biologically relevant to the sage-grouse's habitat selection but are not prevalent in published studies.

associated standard errors and confidence intervals for each variable in the confidence set (Akaike weights within 10% of the top model; Burnham and Anderson 2002).

The meta-analysis by Hagen et al. (2007), synthesizing previous studies of nest microhabitat across the sage-grouse's range, suggests that overstory-cover variables should have the greatest support. Therefore, our Nest I hypothesis set included total sagebrush cover (SAGECVR), shrub density (SHRUBDEN), and visual obstruction (VOBST). Hypothesis set 2, for each of the three periods, was based on explanatory variables that published research has identified as being predictive of the sage-grouse's microhabitat selection (Heath et al. 1998, Sveum et al. 1998b, Holloran 1999, Lyon 2000, Aldridge and Brigham 2002, Aldridge 2005, Holloran et al. 2005, Herman-Brunson 2007, Kaczor 2008, Doherty et al. 2010) but are not ubiquitous in the literature or were not as conclusive (i.e., a lower overall effect size) in the Hagen et al. (2007) meta-analysis. Consequently, Nest II included total forb cover (FORBS), grass cover (GRSCVR = cover of live and residual perennial grasses), and litter (LITTER). For each of the three periods, hypothesis set 3 was less dependent on a priori information and more exploratory than sets 1 and 2. That is, these are variables we theorized may be related to the sage-grouse's microhabitat selection but are not omnipresent in the relevant literature. Thus Nest III included presence or absence of Wyoming big sagebrush (ARTRW), presence or absence of cheatgrass (CHEAT), biological soil crust (BIOCRUST; proxy for ecological condition), and gravel and rock (GANDR).

The definition Hagen et al. (2007) used for early and late brood rearing differed from ours, so for brood-rearing we focused on their analysis of pooled data that did not differentiate between early and late brood rearing. Following others (Berry and Eng 1985, Connelly et al. 1988, Holloran and Anderson 2005, Thompson et al. 2006), we defined early brood rearing as the first 2 weeks after hatching and late brood rearing as >2 weeks after hatching. For both periods combined, Hagen et al. (2007) demonstrated that broods selected habitats with greater herbaceous cover (forbs and grass). Therefore, Early-brood I and Late-brood I (hypothesis sets 1) contained the variables perennial grass cover (PERGRS), and FORBS. Early-brood II and Late-brood II (hypothesis sets 2), contained the variables food forbs (FOODF), SAGECVR, SHRUBDEN, sagebrush height (SAGEHGHT), and grass height (GRSHGHT). Early-brood III (hypothesis set 3) included ARTRW, CHEAT, BIOCRUST, LITTER, while VOBST and ARTRW, CHEAT, BIOCRUST, and GANDR were considered in our late-brood III hypothesis set.

When our final model was a combination of multiple subset models (e.g., top model[s] from individual hypothesis sets), we used variance decomposition to assess the relative influence of each of the subset models in our top model (Lawler and Edwards 2006, Doherty et al. 2010). Variance decomposition is a statistical approach that uses the

maximum-likelihood function to partition out the total variation into the pure variation explained by the component parts (Whittaker 1984, Lawler and Edwards 2006). For example, if our best model was a combination of subset models Nest I + Nest II + Nest III, variance decomposition enabled us to quantify the variation associated with each subset model into pure components (Lawler and Edwards 2006, Doherty et al. 2010).

RESULTS

During 2008 and 2009, we sampled microhabitat conditions at 115 nest locations, 114 random locations of simulated nests, 52 locations of early brood rearing, 52 random locations of simulated early brood rearing, 52 locations of late brood rearing, and 55 random locations of simulated late brood rearing. Of the total, 84 nests (41 in 2008, 43 in 2009) and 80 corresponding random locations (42 in 2008, 38 in 2009) were sampled in the AR and 31 nests (14 in 2008, 17 in 2009) and 34 corresponding random locations (18 in 2008, 16 in 2009) were sampled in the SC. For early brood rearing, 31 locations (18 in 2008, 13 in 2009) and 33 corresponding random locations (18 in 2008, 15 in 2009) were sampled in the AR, and 21 locations (9 in 2008, 12 in 2009) and 19 corresponding random locations (8 in 2008, 11 in 2009) were sampled in the SC. For late brood-rearing, 31 locations (18 in 2008, 13 in 2009) and 34 corresponding random locations (22 in 2008, 12 in 2009) were sampled in the AR, and 21 locations (9 in 2008, 12 in 2009) and 20 corresponding random locations (7 in 2008, 13 in 2009) were sampled in the SC. Ninety-five percent of all sage-grouse nests were located under big sagebrush (mountain big sagebrush = 45%, Wyoming big sagebrush = 33%, unidentified subspecies = 17%,).

NEST-HABITAT SELECTION

Continuous variables that were predictive in our final nest model included gravel and rock, litter, sagebrush canopy cover, total grass canopy cover, and visual obstruction (Table 4). Categorical variables that were predictive in our final nest model included presence of cheatgrass and presence of Wyoming big sagebrush. The nest-selection model with the most support in the final level of model selection was a combination of models from all hypothesis sets (Nest I, Nest II, and Nest III). Variance decomposition suggested that Nest I contained 27% of the pure variation, Nest II contained 15% of the pure variation, and Nest III contained 26% of the pure variation, whereas 32% of the variation was shared. The top model had moderate support ($w_i = 0.44$) and was 2.2 times more likely to be the best approximating model than was the second model in the set (Table 5). Because the top model lacked overwhelming support, we averaged the models within the confidence set. Three of the variables contained in the confidence set of models (BIOCRUST, FORBS, and SHRUBDEN) are ineffective predictors because the CI of the odds

ratios includes 1 (Table 6). The statistically supported variables were ARTRW, CHEAT, GANDR, GRSCVR, LITTER, SAGECVR, and VOBST, with relative importance weights from 0.6 to 1.0. Nest selection was positively related to greater grass cover, litter, sagebrush cover, and visual obstruction. For every 10% increase in sagebrush cover, the likelihood of sage-grouse nesting increased by approximately 10% (Fig. 1). When compared to available habitat, nest selection was

TABLE 4. Means (\pm SE) for all variables supported in the final AIC_c models to assess sage-grouse microhabitat selection during nesting, early brood rearing, and late brood rearing, south-central Wyoming, 2008 and 2009.

Variable category/name	Grouse locations	Random locations
	Mean \pm SE	Mean \pm SE
Nest		
Cover (%)		
Gravel and rock	2.8 \pm 0.6	7.5 \pm 1.0
Litter	45.1 \pm 1.7	31.6 \pm 1.7
Sagebrush	39.0 \pm 1.4	25.2 \pm 1.0
Total grass	17.5 \pm 1.0	16.6 \pm 1.2
Visual obstruction (dm)		
Robel pole	3.8 \pm 0.2	2.8 \pm 0.1
Early brood-rearing		
Cover (%)		
Perennial grass	14.7 \pm 1.5	9.6 \pm 0.8
Sagebrush	35.3 \pm 3.0	22.5 \pm 2.2
Height (cm)		
Perennial grass	17.7 \pm 0.8	18.5 \pm 1.1
Late brood-rearing		
Cover types (%)		
Gravel and rock	4.4 \pm 1.0	10.0 \pm 1.8
Sagebrush	37.7 \pm 2.8	21.5 \pm 1.7
Perennial grass	17.4 \pm 1.8	12.3 \pm 1.6
Biological soil crust	0.3 \pm 0.1	1.1 \pm 0.2
Density (plants/m ²)	2.3 \pm 0.14	2.5 \pm 0.3
Shrub		
Height (cm)		
Perennial grass	20.2 \pm 0.9	21.8 \pm 2.5
Sagebrush	40.8 \pm 2.6	25.9 \pm 2.3

negatively related to the presence of cheatgrass and Wyoming big sagebrush (Table 6). Cheatgrass occurred at 6% of the nest locations and 19% of the corresponding random locations. Wyoming big sagebrush occurred at 46% of our random locations but only at 35% of our nest locations. Conversely, mountain big sagebrush occurred at 32% of our random locations and 50% of our nest locations.

SELECTION OF HABITAT FOR EARLY BROOD-REARING

All of the predictive variables in our final model for early brood rearing were continuous and included canopy cover and height of perennial grasses and canopy cover of sagebrush (Table 4). No variables grouped in Early-brood III were predictive. Consequently, the final level of model selection for early brood rearing contained a combination of the top models from Early-brood I and Early-brood II. Early-brood I contained 8% and Early-brood II 37% of the pure variation. The top model had good support ($w_i = 0.61$) and was 2.4 times more likely than the second model to best explain selection of habitat for early brood-rearing (Table 7). Variables composing the top model included SAGECVR, PERGRS, and GRSHGHT, which had RI values of 1.0, 1.0, and 0.9, respectively. Early in brood-rearing, brooding hens selected habitats with greater cover of sagebrush canopy, greater cover of perennial grass, and shorter grass than in available habitat (Table 6). A 10% increase in sagebrush cover increased the odds of use for early brood rearing by approximately 20% (Fig. 1). Although the means for both food forb cover and total forb cover were slightly higher at used than at random locations ($6.7 \pm 1.3\%$ vs. $5.9 \pm 0.7\%$ and $7.5 \pm 0.9\%$ vs. 7.1 ± 0.7 , respectively), inclusion of these variables in the models was not supported.

SELECTION OF HABITAT FOR LATE BROOD-REARING

Continuous variables that were predictive in our final model for late brood rearing included biological soil crust, gravel and rock, height and canopy cover of perennial grasses, height and canopy cover of sagebrush, and shrub density (Table 4). There were no categorical variables that

TABLE 5. Top and competing ($AIC_c \leq 2.0$) models best explaining the sage-grouse's selection of nest microhabitat in south-central Wyoming, 2008 and 2009. Nest I, II, and III represent the hypothesis sets used in sequential modeling.

Model (averaged)	K^a	AIC_c^b	w_i	ROC ^c
[SAGECVR, SHRUBDEN, VOBST] _{Nest I} + [GRSCVR, LITTER] _{Nest II} + [ARTRW, CHEAT, GANDR] _{Nest III}	11	0.00	0.44	0.84
[SAGECVR, SHRUBDEN, VOBST] _{Nest I} + [LITTER] _{Nest II} + [ARTRW, CHEAT, GANDR] _{Nest III}	10	1.53	0.20	0.84
[SAGECVR, SHRUBDEN, VOBST] _{Nest I} + [GRSCVR, LITTER] _{Nest II} + [ARTRW, BIOCRUST, CHEAT, GANDR] _{Nest III}	12	1.69	0.19	0.85
Null	1	77.20	0.00	

^aNumber of parameters with site and year included in all models.

^bLowest $AIC_c = 244.84$ for nest.

^cReceiver operating curve (ROC) statistic indicating the true positive rate.

TABLE 6. Parameter estimates, values of variable importance, and odds ratios for microhabitat variables that were included in top model(s) of the sage-grouse's selection of microhabitat for nesting, early brood rearing, and late brood rearing in south-central Wyoming, 2008 and 2009.

Parameter	Estimate	95% CI		P^a	Relative ^b importance	Odds ratio	95% CI	
		Lower	Upper				Lower	Upper
Nest site ^c								
Intercept	-3.252	-4.080	-2.423	<0.001				
ARTRW	-0.737	-1.065	-0.409	0.04	1.0	0.478	0.344	0.664
BIOCRUST ^d	0.061	-0.023	0.146	0.45	0.3	1.063	0.977	1.157
CHEAT	-2.286	-2.882	-1.690	<0.001	1.0	0.102	0.056	0.185
FOODF ^d	0.001	-0.020	0.023	0.48	0.9	1.001	0.980	1.023
GANDR	-0.053	-0.080	-0.027	0.05	1.0	0.948	0.923	0.974
GRSCVR	0.028	0.014	0.041	0.05	0.6	1.028	1.014	1.042
LITTER	0.038	0.026	0.049	<0.001	1.0	1.038	1.027	1.050
SAGECVR	0.057	0.042	0.073	<0.001	1.0	1.058	1.043	1.075
SHRUBDEN ^d	0.066	-0.050	0.182	0.61	1.0	1.068	0.951	1.200
VOBST	0.143	0.005	0.282	0.32	1.0	1.154	1.005	1.325
Early brood rearing								
Intercept	-0.834	0.605	-2.272	0.73				
GRSHGHT	-0.098	-0.181	-0.015	0.02	0.9	0.907	0.834	0.986
PERGRS	0.108	0.177	0.039	0.002	1.0	1.114	1.039	1.193
SAGECVR	0.052	0.084	0.020	0.002	1.0	1.053	1.020	1.088
Late brood rearing ^c								
Intercept	-1.011	-1.965	-0.060	0.64				
ARTRW ^d	-0.549	-1.195	0.097	0.19	0.2	0.578	0.303	1.102
BIOCRUST	-0.652	-0.680	-0.624	0.07	0.8	0.521	0.507	0.536
FOODF ^d	0.009	-0.025	0.043	0.06	0.4	1.009	0.975	1.044
GANDR	-0.039	-0.076	-0.003	0.23	0.8	0.961	0.927	0.997
GRSHGHT	-0.010	-0.149	-0.050	0.05	1.0	0.905	0.861	0.951
LITTER ^d	-0.029	-0.064	0.006	0.65	0.2	0.971	0.938	1.006
PERGRS	0.107	0.067	0.147	0.009	1.0	1.113	1.069	1.158
SAGECVR	0.055	0.036	0.075	0.002	1.0	1.057	1.036	1.078
SAGEHGHT	0.052	0.029	0.075	0.03	1.0	1.053	1.029	1.078
SHRUBDEN	-0.538	-0.886	-0.189	0.10	0.3	0.584	0.412	0.828

^a P -value from combined model containing all variables in top model(s).

^bRelative importance was calculated by adding Akaike weights for all models in the candidate set containing that variable; the closer the value is to 1 the more important the variable was in the set.

^cContains model-averaged parameter estimates.

^dParameters having no predictive power, as the 95% confidence intervals of the odds ratios include 1.

were predictive in our final model for late brood rearing. A combination of models from each hypothesis set (Late-brood I, II, and III) best explained habitat selection at this stage. However, eight models in the final set were competitive ($AIC_c \leq 2$) with the top model. The top model's support did not much exceed that of the other models in the set ($w_i = 0.16$) (Table 7). Four variables, GRSHGHT, PERGRS, SAGECVR, and SAGEHGHT, were in all models in the confidence set and had relative importances of approximately 1.00. Other variables in the confidence set with some support included BIOCRUST (RI = 0.79), GANDR (RI = 0.79), and SHRUBDEN (RI = 0.31). The CI for the odds ratios around several of these variables, including ARTRW, FOODF, LITTER, overlapped 1, indicating that they were not supported

as predictive variables (Table 6). In the top model, Late-brood I explained approximately 16%, Late-brood II 58%, and Late-brood III 14% of the pure variation. Sagebrush cover, sagebrush height, and perennial grass cover were positively associated with sites of late brood rearing. Conversely, late in brood rearing grouse selected against taller grass, greater shrub density, and greater biological soil crust. The probability of use of habitat for late brood rearing increased by 3% for every 1% increase in perennial grass cover and by 1.5% for every 1% increase in sagebrush cover. Food forbs occurred in the final confidence set but had little predictive power because the CI for odds ratio included 1. As for early brood rearing, the inclusion of food forb cover and total forb cover in our models for late brood rearing had

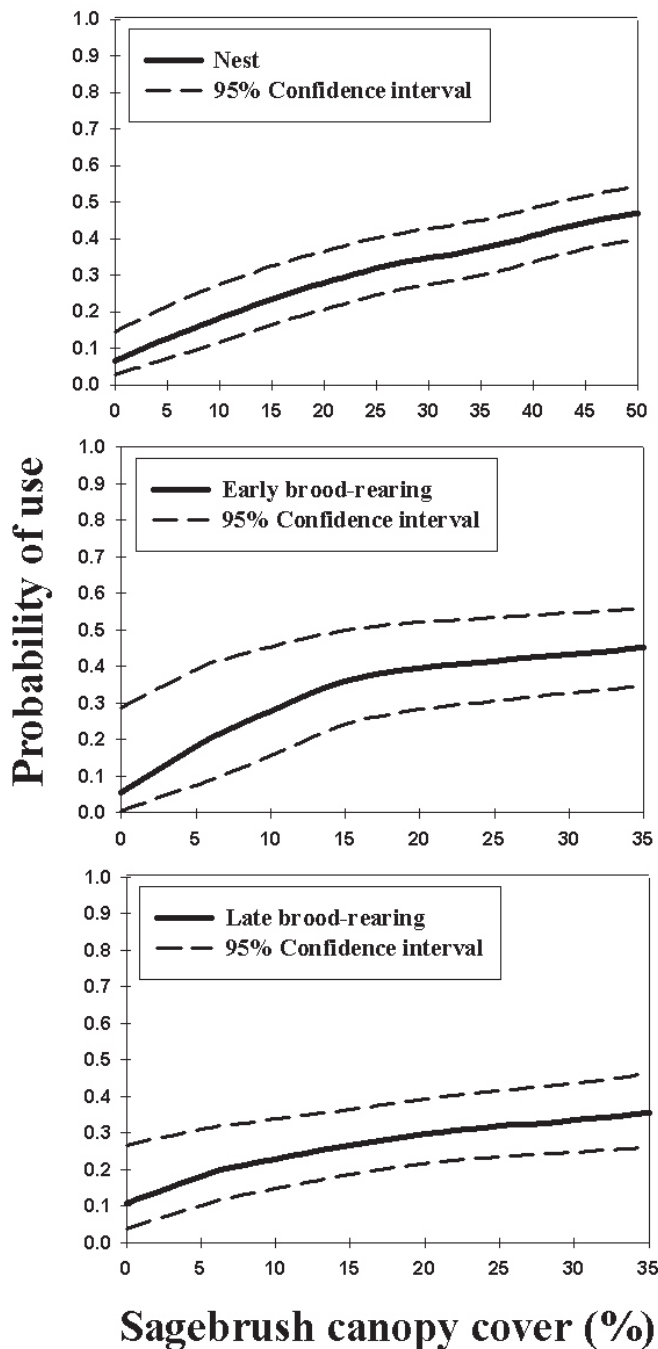


FIGURE 1. Probability of sage-grouse use of microhabitat for nesting, early brood rearing, and late brood rearing as a function of sagebrush canopy cover with 95% confidence intervals around predictions, south-central Wyoming, 2008 and 2009. Probability graphs derived from single-variable models. Sagebrush canopy cover was truncated on the basis of its median values in our data or its upper limits reported in the Hagen et al. (2007) meta-analysis.

little to no support, yet the mean values of these variables at used locations was slightly higher than at random locations ($9.5 \pm 1.1\%$ vs. $8.5 \pm 1.1\%$ and $11.0 \pm 1.1\%$ vs. $10.8 \pm 1.0\%$, respectively).

DISCUSSION

Our study design enabled us to assess the importance of several microhabitat variables in the context of a priori information derived from research on the sage-grouse's habitat selection while exploring additional microhabitat variables we theorized may be biologically relevant. By grouping variables into hypothesis sets for three stages of the breeding cycle we were able to compare selection in our study areas to predictive microhabitat variables with varying degrees of support from previous research. Variance decomposition enabled us to quantify how much information was explained by each hypothesis set and compare this to the results of previous research (e.g., Hagen et al. 2007).

In south-central Wyoming nesting sage-grouse showed strong selection for physiognomic characteristics including sagebrush cover and visual obstruction (both represented in hypothesis set Nest I). Similarly, we found that during early and late brood rearing, female grouse also preferred areas with more sagebrush cover (represented in Early-brood II and Late-brood II) than randomly available. Late in brood rearing hens used areas with taller sagebrush plants (represented in Late-brood II) than randomly available. During early and late brood rearing, females disproportionately used habitats with cover of perennial grass greater than at random locations (represented in Early-brood I and Late-brood I). Likewise, nest selection was positively associated with greater total grass cover (represented in Nest II). We did not identify a correlation between greater forb cover or food forb cover (represented in Early-brood I, Late-brood I, Early-brood II, and Late-brood II, respectively) and microhabitat selection during early or late brood-rearing.

Less studied microhabitat variables in our models proved predictive of site selection for nests and late brood rearing. Nest selection was positively correlated with greater litter and negatively correlated with cheatgrass (represented in Nest II and Nest III, respectively), and late in brood rearing hens selected microhabitats with less biological soil crust (represented in Late-brood III). Floristically, we found Mountain big sagebrush was preferred over Wyoming big sagebrush for nesting (represented in Nest III).

We predicted that the greatest amount of the pure variation in our data would be explained by hypothesis set 1, which incorporated variables with the most support in the literature (Hagen et al. 2007) for each life stage that we modeled (i.e., Nest I, Early-brood I, and Late-brood I). However, using variance decomposition, we found that this was true only for nest-site selection, where slightly more of the pure variation was explained by Nest I (27%) than by Nest III (26%). Early-brood II and Late-brood II explained the majority of the pure variation in our final brood-rearing models (37% and 58%, respectively).

The importance of sagebrush and other obstructing cover to nesting sage-grouse (Wallestad and Pyrah 1974, Connelly et al. 1991, Fischer 1994, Heath et al. 1998, Sveum

TABLE 7. Top and competing ($AIC_c \leq 2.0$) models best explaining the sage-grouse's selection of microhabitat for early and late brood rearing in south-central Wyoming, 2008 and 2009. Early-brood I, II, and III and Late-brood I, II, and III represent the hypothesis sets used in sequential modeling.

Model	K^a	AIC_c^b	w_i	ROC ^c
Early brood-rearing				
[PERGRS] _{Early-brood I} + [GRSHGHT, SAGEVCR] _{Early-brood II}	6	0.00	0.61	0.81
[PERGRS] _{Early-brood I} + [FOODF, GRSHGHT, SAGECVR] _{Early-brood II}	7	1.66	0.27	0.82
Null	1	15.35	0.00	
Late brood-rearing ^d				
[PERGRS] _{Late-brood I} + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [BIOCRUST, GANDR] _{Late-brood III}	10	0.00	0.16	0.89
[PERGRS] _{Late-brood I} + [GRSHGHT, SAGECVR, SAGEHGHT, SHRUBDEN] _{Late-brood II} + [BIOCRUST, GANDR] _{Late-brood III}	10	0.67	0.11	0.89
[PERGRS] _{Late-brood I} + [GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [BIOCRUST, GANDR] _{Late-brood III}	9	0.78	0.11	0.88
[PERGRS] _{Late-brood I} + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [BIOCRUST, GANDR] _{Late-brood III}	8	1.15	0.09	0.87
[PERGRS] _{Late-brood I} + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [ARTRW, BIOCRUST, GANDR] _{Late-brood III}	11	1.67	0.07	0.89
[PERGRS] _{Late-brood I} + [FOODF, GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [BIOCRUST, GANDR, LITTER] _{Late-brood III}	11	1.71	0.07	0.89
[PERGRS] _{Late-brood I} + [GRSHGHT, SAGECVR, SAGEHGHT] _{Late-brood II} + [BIOCRUST, GANDR, LITTER] _{Late-brood III}	7	1.93	0.06	0.86
[PERGRS] _{Late-brood I} + [GRSHGHT, SAGECVR, SAGEHGHT, SHRUBDEN] _{Late-brood II}	8	1.95	0.06	0.87
Null	1	36.14	0.00	

^aNumber of parameters (K) with site and year included in all models.

^bLowest $AIC_c = 128.05$ for early brood rearing, 110.78 for late brood rearing.

^cReceiver operating curve (ROC) statistic indicating the true positive rate.

^dModels averaged.

et al. 1998b, Popham and Gutiérrez 2003, Holloran et al. 2005, Herman-Brunson 2007, Hagen et al. 2007, Kaczor 2008, Doherty et al. 2010) and to other prairie grouse such as the Columbian Sharp-tailed Grouse (*Tympanuchus phasianellus columbianus*; Giesen and Connelly 1993), and Lesser Prairie-Chicken (*T. pallidicinctus*; Hagen et al. 2004) has been well documented. Sage-grouse selection for greater grass cover during nesting has also been reported in many studies (Heath et al. 1998, Holloran et al. 2005, Sveum et al. 1998b, Lyon 2000, Hagen et al. 2007). The total combination of these cover attributes likely provides olfactory, visual, and physical barriers to predators (Bowman and Harris 1980, Crabtree et al. 1989, Delong et al. 1995) and thermal protection (Forrester et al. 1998, Heath et al. 1998, Schroeder et al. 1999, Reese et al. 2005).

Like Sveum et al. (1998b), we found a positive relationship between sage-grouse nest selection and litter. Research on other gallinaceous species such as the Mountain Quail (*Oreortyx pictus*) also suggests an association between nest-site selection and litter (Reese et al. 2005), possibly related to hens' concealment from predators during incubation. Hens have a cryptic grayish-brown plumage (Patterson 1952, Schroeder et al. 1999) likely enabling them to conform more easily to nest sites with a high percent of litter cover that is similar in color and patterning. Further support for this suggestion comes from Kaczor (2008), who found that the

percentage of litter cover at successful sage-grouse nests in South Dakota was higher than at unsuccessful nests.

Sagebrush communities in our study areas were dominated by nearly equal distributions of Wyoming and mountain big sagebrush (BLM 2006a, Rodemaker and Driese 2006). Yet our results indicated that sage-grouse preferred nesting in mountain over Wyoming big sagebrush. When compared to Wyoming big sagebrush, mountain big sagebrush often occurs at higher elevations in areas with lower mean temperatures, greater precipitation, increased vegetation-production potential, and a more developed herbaceous understory (Goodrich 2005, Davies and Bates 2010). In addition, food forbs in close proximity to cover may be more available in mountain big sagebrush than in Wyoming big sagebrush (Goodrich 2005, Rosentreter 2005, Davies and Bates 2010). Therefore, we suspect this response is a direct result of the dry conditions in our study areas as nesting sage-grouse may be seeking out cooler and wetter microhabitats.

Cheatgrass was not widespread in either of our study areas, but when it was found it was often associated with human infrastructure. Thus female sage-grouse may avoid nesting in areas dominated by cheatgrass because cheatgrass is more prevalent in areas with anthropogenic disturbance (Pyke 2011). A likely explanation for this is that disturbance may be a mediating variable for cheatgrass, which is acting as a proxy for nest-site selection. In other words, sage-grouse may

not have directly selected against cheatgrass but may have avoided locations in our study areas with roads and infrastructure (Naugle et al. 2011) where cheatgrass was more common (Bergquist et al. 2007). The ecological mechanisms behind this finding warrant further research.

In agreement with some studies we found that for early brood-rearing female sage-grouse selected microhabitats with greater canopy cover of sagebrush (Patterson 1952, Dunn and Braun 1986, Aldridge and Brigham 2002, Thompson et al. 2006) and perennial grass (Thompson et al. 2006, Hagen et al. 2007, Kaczor 2008). Yet we found that during early and late brood rearing hens did not select areas with grass taller than at random locations, which may suggest a threshold where vertical cover is avoided. Aldridge and Boyce (2008) found that increased grass height was negatively related to chick survival. Moreover, Gregg and Crawford (2009) found that survival of sage-grouse chicks increased as the cover of short grasses (<18 cm) increased, but they found no relationship between tall grass (>18 cm) cover and chick survival. Thus brooding females may recognize the fitness consequences of using taller grass. We found cover characteristics were important in late as well as in early brood rearing. In comparison, others have identified the importance of grass cover (Hagen et al. 2007, Hermun-Brunson 2007), sagebrush cover (Dunn and Braun 1986, Aldridge and Brigham 2002, Hermun-Brunson 2007), and visual obstruction (Kaczor 2008 both early and late in brood rearing. Similarly, Hagen et al. (2005) found strong selection by brooding female Lesser Prairie-Chickens for habitats with greater visual obstruction, and Lehman et al. (2010) found that brooding female Merriam's Turkeys (*Meleagris gallopavo merriami*) preferred areas with high visual obstruction.

Contrary to our findings, several researchers have reported that brood-rearing female sage-grouse often select microhabitats with greater forb abundance (Sveum et al. 1998a, Holloran 1999, Connelly et al. 2000, Hausleitner 2003, Hagen et al. 2007) and less sagebrush cover than at random locations (Hagen et al. 2007). A likely explanation for the patterns of selection of habitat for brood rearing in our study areas is reflected in the different and sometimes contradictory findings from other studies. For example, most of the studies of brood rearing noted previously and considered by Hagen et al. (2007) did not take place in xeric (≥ 25 cm of annual precipitation; Clifton 1981, Fischer et al. 1996) sagebrush habitats (e.g., Drutt 1992, Holloran 1999, Lyon 2000, Aldridge and Brigham 2002, Hausleitner 2003, Slater 2003, Aldridge 2005, Hermun-Brunson 2007). Galliform chicks are born with poorly developed thermoregulatory systems and are vulnerable to heat stress (Forrester et al. 1998, Flanders-Wanner et al. 2004). We theorize that because the habitat available to sage-grouse in our study areas is more xeric, cover characteristics providing microclimates conducive to thermoregulation of the hen and brood may be driving microhabitat selection. Further

support for this hypothesis comes from Heath et al. (1998), whose study in xeric big sagebrush in south-central Wyoming also did not find a significant correlation between forb cover and microhabitat selection for early or late brood-rearing. Bell et al. (2010) showed the importance of shrub communities in providing thermal refugia for Lesser Prairie-Chicken broods, and Patten et al. (2005) found that Lesser Prairie-Chickens avoided microclimates that were hotter, drier, and more exposed to wind; survival increased in sheltered microhabitats with lower temperatures and higher relative humidity.

Predation is a major factor reducing rates of chick survival for the sage-grouse (Aldridge 2005, Gregg and Crawford 2009, Hagen et al. 2011) and other Galliformes (Larson et al. 2001). Thus, it reasons that refugia from avian and mammalian predators likely also contribute to selection for greater screening cover, regardless of the vegetation type, during early and late brood rearing.

Our results stress that the factors most important to sage-grouse microhabitats for nesting and brood rearing in xeric habitat in south-central Wyoming are related more to cover than to food. Additional microhabitat characteristics we identified as being predictive of use for nesting and brood rearing, such as sagebrush type, litter, biological soil crust, and the absence of cheatgrass, warrant future research. Our results concur with Hagen (2011) that the prevailing theme of the sage-grouse's seasonal habitat selection is a balance between concealment (e.g., predator avoidance) and meeting biological demands (e.g., food and thermoregulation).

On the basis of our findings managers should consider efforts to conserve sagebrush and increase cover of perennial grass and residual grass. Furthermore, management targeting habitat for nesting and brood-rearing sage-grouse in xeric sagebrush habitats should avoid practices that increase forb abundance at the expense of cover (e.g., sagebrush removal).

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