MICROHABITAT SELECTION OF BROOD-REARING SITES BY GREATER SAGE-GROUSE IN CARBON COUNTY, WYOMING

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ABSTRACT.—Declines in Greater Sage-Grouse (*Centrocercus urophasianus,* hereafter sage-grouse) populations could be attributed to low chick survival, which may be influenced by the availability of food and cover at sites used by females rearing broods. Habitat attributes important to broods may vary regionally; thus, it is necessary to understand factors affecting regional sage-grouse brood-rearing site selection, especially when estimating the impacts of development. We monitored brood-rearing female sage-grouse equipped with solar Argos Global Positioning System Platform Transmitter Terminals from 2011 to 2013 to assess microhabitat selection by broods in Carbon County, Wyoming. We measured vegetation and arthropod characteristics at diurnal sites used by broods ($n = 42$ in 2011, $n = 31$ in 2012, $n = 32$ in 2013) and at 3 paired-random sites associated with each used site ($n = 315$), located 50 m, 250 m, and 500 m from the used site. We fit conditional logistic models within an information-theoretic framework to identify vegetation and arthropod characteristics associated with microsite selection of brood-rearing sites. Sage-grouse selected brood-rearing sites with greater visual obstruction (0–45.7 cm in height), higher numbers of arthropods in the order Diptera, and lower numbers of arthropods in the order Coleoptera. There was an interaction effect between the number of arthropods in the order Hymenoptera and the canopy cover of broad-leaf forbs; the relative probability of selection increased with increasing number of Hymenoptera when there was low cover (<20%) of broad-leaf forbs, but decreased with increasing number of Hymenoptera when there was high broad-leaf forb cover (>20%). We also found a quadratic relationship between selection of brood-rearing sites and total vegetation canopy cover; the relative probability of selection increased until approximately 75% cover and then decreased with increasing cover. Sage-grouse rearing broods selected a diverse array of vegetation types, but greatest use occurred within mesic communities. Our results could be used to identify vegetation communities with high relative probabilities of use by sage-grouse rearing broods, which will help guide management decisions and provide reference conditions for future research that evaluates the effects of wind energy development on sage-grouse.

RESUMEN.—La disminución en las poblaciones de urogallo (*Centrocercus urophasianus,* en adelante urogallo) podría atribuirse a la baja supervivencia de los pollos que puede estar influenciada por la disponibilidad de alimento y de refugios en los sitios donde las hembras crían a sus nidadas. Las características del hábitat que afectan a la nidada pueden variar regionalmente; por lo tanto, es necesario entender los factores que afectan la selección de las zonas de crianza del urogallo, sobre todo al estimar el impacto que tiene el desarrollo. Desde 2001 a 2013, monitoreamos la crianza de la nidada del urogallo con un Sistema de Posicionamiento Global solar (Argos Global Positioning System Platform Transmitter Terminals) para evaluar la selección de micro-hábitats para la crianza en la zona de Carbon County, Wyoming. Medimos y tomamos las características de la vegetación y de los artrópodos en sitios diurnos utilizados por las nidadas ($n = 42$ en el 2011, $n = 31$ en el 2012, $n = 32$ en 2013) y en 3 zonas pareadas al azar asociadas a cada área utilizada ($n = 315$), ubicadas a 50 m, a 250 m y a 500 m de la zona utilizada. Ajustamos modelos logísticos condicionales dentro de un marco de información teórica para identificar características de la vegetación y de los artrópodos asociadas con la selección de micro-sitios para la crianza de las nidadas. El urogallo seleccionó sitios de crianza con obstrucción visual mayor, desde 0 cm a 45.7 cm de altura, con un número mayor de artrópodos del orden Diptera y con un menor número de artrópodos del orden Coleoptera. Encontramos una interacción entre el número de artrópodos del orden Himenóptera y la cobertura vegetal de herbáceas de hojas anchas; la probabilidad relativa de selección se incrementó con el aumento del número de himenópteros cuando la cobertura vegetal de herbáceas de hojas anchas fue menos densa (<20%), pero disminuyó con el aumento del número de himenópteros cuando la cobertura de herbáceas de hojas anchas fue más densa (>20%). Asimismo, encontramos una relación cuadrática entre la selección de áreas de crianza y la cobertura vegetal de herbáceas total. La probabilidad relativa de selección aumentó con ∼75% de cobertura vegetal y luego disminuyó con el incremento de la cobertura vegetal. Los urogallos seleccionaron una amplia gama de tipos de vegetación para la crianza de sus nidadas, pero utilizaron más el hábitat mésico. Nuestros resultados pueden ser utilizados para identificar las comunidades vegetales con probabilidades relativamente altas de ser utilizadas para la anidación del urogallo, lo que ayudará a guiar las decisiones de los gestores y proporcionar condiciones de referencia para futuras investigaciones que evalúen los efectos del desarrollo de energía eólica en el urogallo.

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Greater Sage-Grouse (*Centrocercus uro-phasianus;* hereafter, sage-grouse) populations throughout North America have declined over the past 50 years (Garton et al. 2011) due to degradation of sagebrush (*Artemisia* spp.) habitats on which they depend (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004), resulting in a "warranted but precluded" decision for listing under the Endangered Species Act (United States Fish and Wildlife Service 2010). Although adult female survival is paramount, chick survival also plays an important role in the population growth rate for sage-grouse (Dahlgren 2009, Taylor et al. 2012). Low chick survival is a potential factor in rangewide declines (Connelly and Braun 1997) and may be influenced by food and cover characteristics at diurnal foraging sites (Aldridge 2000, Gregg 2006, Thompson et al. 2006, Dahlgren 2009).

There is an important trade-off between nutrient/energy intake and predation risk (Lima 1998), which affects resource selection and ultimately demographic parameters. High-protein arthropods are a critical food source for precocial tetraonid chicks for the first several weeks post-hatch (Hill 1985, Johnson and Boyce 1990, Drut et al. 1994, Jamison et al. 2002, Hannon and Martin 2006), and forbs are important food sources for sage-grouse chicks later in the summer (Klebenow and Gray 1968, Klebenow 1969, Drut et al. 1994). Further, the horizontal and vertical protective cover that vegetation provides may be crucial to prevent predation and exposure-related chick mortality (Klebenow 1969, Wallestad 1971, Klott and Lindzey 1990, Sveum et al. 1998). Limited available habitat that offers adequate food and cover resources, especially during dry years, could result in low recruitment (Aldridge 2000).

Sage-grouse rearing broods generally select sites with less sagebrush cover, taller grasses, and more forbs (Hagen et al. 2007), but there are regional differences. Kirol et al. (2012) found that sagebrush cover and grass structure were more important to brood-rearing sage-grouse than forbs in xeric sagebrush communities (Kirol et al. 2012). Similarly, forbs were not as important to brood-rearing site selection as sagebrush in Alberta (Aldridge and Brigham 2002). Thus, it is necessary to understand factors affecting regional sage-grouse brood-rearing site selection, especially when evaluating the possible impacts of development. Our research was part of a Before-After, Control-Impact study collecting >3 years of data on sage-grouse prior to construction of a wind energy facility that will consist of 1000 turbines and produce 2000–3000 megawatts of energy (Power Company of Wyoming LLC 2009). Our objectives were to determine the food and cover resources associated with selection of microsites by female sage-grouse rearing broods, and estimate how varying resource characteristics (e.g., increasing forb cover) might affect relative probability of selection. Results from this study will provide insight on management of brood-rearing habitat and act as baseline data for future studies estimating the potential effects of wind energy development on sage-grouse selection of brood-rearing sites.

METHODS

Study Area

Our study area was located in Carbon County, Wyoming, USA, and encompassed the approximately 1295-km^2 Overland Trail Ranch and surrounding areas (Fig. 1). The area was characterized by a checkerboard private/public ownership pattern with approximately half of the land administered by the Bureau of Land Management and a small portion owned by the state of Wyoming.

Annual precipitation over the past 60 years averaged 22.8 cm in Rawlins, Wyoming, and 24.6 cm in Saratoga, Wyoming (Western Regional Climate Center 2013). Precipitation increased with elevation, which ranged from about 1890 m at the North Platte River to 2590 m near the Continental Divide. The study area was characterized topographically by a central basin that transitioned to foothills to the south, mesas to the southwest, and rocky escarpments to the north and northeast (Love and Christiansen 1985). The average monthly temperature was 0.7–12.7 °C from November to April and 15.3–28.5 °C from May to October (Western Regional Climate Center 2013).

The study area consisted of 3 ecoregions, including rolling sagebrush steppe, salt desert shrub basins, and foothill shrublands (Chapman et al. 2004). Rolling sagebrush steppe comprised approximately 66% of the study area and was characterized by Wyoming big
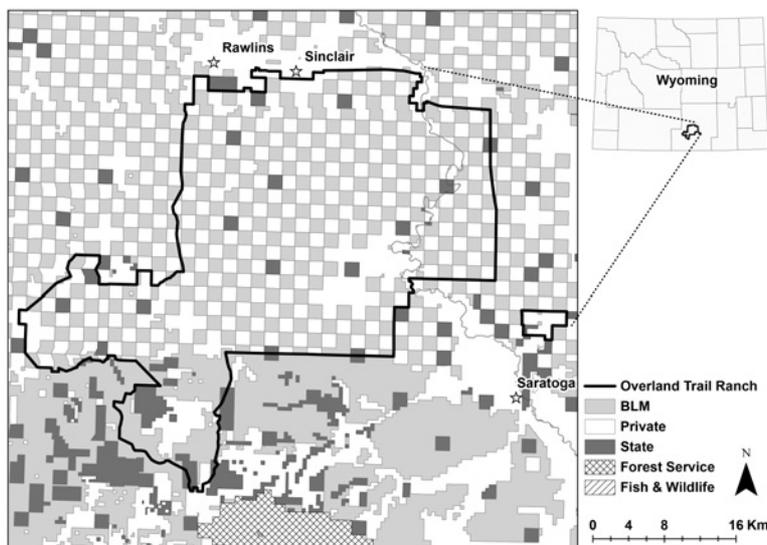
Fig. 1. Map showing the surface ownership on and near the Overland Trail Ranch, in Carbon County, Wyoming, USA, where we studied Greater Sage-Grouse selection of brood-rearing microsites from 2011 to 2013.

sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations, continuous stands of mountain big sagebrush (*A. t. vaseyana*) at higher elevations, silver sagebrush (*Artemisia cana*) in areas where the water table was within 1 m of the soil surface (Thatcher 1959), and black sagebrush (*Artemisia nova*) in exposed, rocky soils (Chapman et al. 2004). Other shrubs included rabbitbrush (*Chrysothamnus* spp. and *Ericameria nauseosa*); common forbs included phlox (*Phlox* spp.), mock goldenweed (*Stenotus* spp.), clover (*Trifolium* spp.), madwort (*Alyssum* spp.), and vetch (*Astragalus* spp.); common grasses included western wheatgrass (*Pascopyrum smithii*), bluebunch wheatgrass (*Pseudoroegneria spicata*), needle-and-thread (*Hesperostipa comata*), Idaho fescue (*Festuca idahoensis*), Sandberg bluegrass (*Poa secunda*), and prairie junegrass (*Koeleria macrantha*).

Salt desert shrub, which comprised approximately 19% of the study area, was characterized by sparse vegetation cover of Gardner's saltbush (*Atriplex gardneri*), shadscale (*Atriplex confertifolia*), and black greasewood (*Sarcobatus vermiculatus*). Sagebrush cover in this ecoregion, predominantly Wyoming big sagebrush and basin big sagebrush (*A. t. tridentata*), was sporadic and isolated to areas with topographic relief and sustained soil moisture. Forbs were scarce and usually comprised of mock goldenweed and cushion-like phlox. Grass species included alkali cordgrass (*Spartina gracilis*), Indian ricegrass (*Oryzopsis hymenoides*), blowout grass (*Redfieldia flexuosa*), alkali wildrye (*Leymus simplex*), and needle-and-thread (Chapman et al. 2004).

Montane deciduous shrublands, which comprised approximately 15% of the study area, were located at higher elevations and characterized by mountain big sagebrush, snowberry (*Symphoricarpos* spp.), serviceberry (*Amelanchier* spp.), mountain mahogany (*Cercocarpus* spp.), groves of aspen (*Populus tremuloides*), and patches of limber pine (*Pinus flexilis*). A variety of forbs and grasses were also abundant including vetch, clover, lupine (*Lupinus* spp.), prairie junegrass, bluebunch wheatgrass, and western wheatgrass (Chapman et al. 2004).

Field Methods

In spring 2010–2013, we used spotlighting techniques to capture female sage-grouse (Giesen et al. 1982). Each was fitted with a 30-g rump-mounted (Rappole and Tipton 1991) solar Argos Global Positioning System Platform Transmitter Terminal (GPS PTT; Microwave Telemetry, Inc., Columbia, MD). Capture and handling protocols were approved by the University of Missouri Animal Care and Use Committee, permit number 6750,

and Wyoming Game and Fish Department Chapter 33 Permit, permit number 752.

GPS PTTs recorded 6–8 locations per day during the brood-rearing season and we downloaded location data from Argos satellites every 3–5 days. GPS PTTs also transmitted ultra high frequency signals for approximately 8 h per day to facilitate ground-tracking. We investigated potential nest sites when we witnessed multiple locations of a female <50 m apart over a 48-h period; nests were visually confirmed from a distance >10 m to avoid disturbing the female. We utilized GPS location data to determine dates of nest abandonment (success or failure), evidenced by >3 diurnal GPS locations >50 m from the nest. When the female ceased incubating, we investigated the nest bowl to determine the fate of the nest. If the hen incubated >25 days and at least 1 eggshell had a detached membrane (Girard 1939), signifying a hatched egg, we assumed the nest was successful. After a nest successfully hatched, we verified that the female had chicks by spotlighting the brood (Dahlgren et al. 2010) ≤4 days before selecting a site for measurements. We characterized the vegetation and arthropod community at GPS locations of the female rearing a brood to assess selection of brood-rearing sites. For each brooding female, we selected and measured resources at ≥1 location during the first 7 d post-hatch, ≥1 location during 8–14 d post-hatch, and ≥1 location approximately every 14 d until the chicks were absent or reached 70 d of age, representing independence (e.g., Beck et al. 2006, Thompson 2012). All locations selected for measurements were diurnal locations from the previous 4 days.

We measured vegetation characteristics and arthropod abundance at used sites and 3 paired-random sites located 50 m, 250 m, and 500 m from the used site to quantify resource availability at different scales (e.g., Swanson et al. 2013). At each used and paired-random site, we measured vegetation characteristics along 20-m transects radiating in each cardinal direction. We completed our field measurements at the paired-random sites within 2 days of measuring the used site to ensure comparable conditions. We recorded all vegetation data on Allegro CX and MX data loggers (Juniper Systems, Logan, UT).

We measured the height of visual obstruction using a modified Robel pole (Robel et al.

1970, Benkobi et al. 2000) as a cover board at 5-m increments along each transect, ($n = 20$ measurements/site). The modified Robel pole consisted of seventy-two 1.27-cm segments divided into four 18-segment sections. At a distance of 4 m from the pole and at a height of 1 m, we recorded the number of segments with >50% obstruction in each section and averaged values to estimate visual obstruction. We used the point-centered quarter method (Cottam and Curtis 1956) to estimate density of all sagebrush and sagebrush >20 cm in height, excluding birdfoot sagebrush (*Artemisia pedatifida*) and fringed sagebrush (*Artemisia frigida*). We measured the distance to the nearest sagebrush in each of 4 quadrants surrounding the plot center, the 10-m increment, and the 20-m increment along each transect ($n = 36$ measurements per site). Equations in Pollard (1971) were used to estimate sagebrush density at each site.

While the line intercept method is more commonly used to estimate shrub cover (e.g., Connelly et al. 2003), quadrat methods (Daubenmire 1959) are more efficient, produce similar estimates to the line intercept method (Hanley 1978), and accurately estimate canopy cover (Booth et al. 2006). Thus, we estimated foliar canopy cover using a 0.1-m^2 quadrat (Daubenmire 1959) at 2.5-m increments out to 20 m along each transect ($n = 36$ measurements per site). We estimated foliar canopy cover of sagebrush, non-sagebrush shrubs, forbs, grasses, and all vegetation combined, excluding litter (total vegetation cover). We further divided forbs and grasses into broad-leaf forbs, cushion forbs, bunchgrasses, and rhizomatous grasses to separate growth forms (e.g., Cagney et al. 2010). Broad-leaf forbs generally grew in a vertical pattern with broad leaves (e.g., lupine, clover, dandelion [*Taraxacum* spp.]); cushion forbs grew in a mat-forming pattern (e.g., phlox, goldenweed, pussytoes [*Antennaria* spp.]); bunchgrasses grew in a "clumped" pattern (e.g., bluebunch wheatgrass, prairie junegrass); and rhizomatous grasses grew from rhizomes (e.g., western wheatgrass, Kentucky bluegrass [*Poa pratensis*]). We measured all vegetation types within the quadrat, even if they were covered by other species. We categorized vegetation using 6 cover classes (Daubenmire 1959): 0 (no cover), 1 (trace–5% cover), 2 (5.1%–25% cover), 3 (25.1%–50% cover), 4 (50.1%–75%

cover), 5 (75.1%–95% cover), and 6 (95.1%–100% cover). We recoded cover classes to the midpoints (e.g., 1 = 2.5%, 2 = 15%, etc.) and averaged values to obtain estimates of foliar canopy cover for vegetation. We also measured the height of the sagebrush, non-sagebrush shrub, forb, and grass (natural droop height) nearest to the corner of the quadrat that touched the transect increment and then averaged values to estimate vegetation height.

We collected arthropods within 1-m^2 quadrats covered with 0.635-mm mesh netting using a gasoline-powered backpack aspirator with a collection bag (model 1612; John W. Hock Company, Gainesville, FL). We placed quadrats 10 m and 20 m from the plot center along transects projected 45° and 225°, and 20 m from the plot center along transects projected 135° and 315° (n = 6). We vacuumed soil and vegetation surfaces within the net for 2 min, putting equal effort into collecting ground-dwelling, vegetation-dwelling, and flying arthropods. We transferred the collected material to a labeled, resealable bag and placed the contents in a freezer. We separated all identifiable arthropods and parts from debris, then oven-dried arthropods at 55 °C for 24 h. We sorted arthropods to order, then counted and weighed samples to the nearest milligram. After the 2012 field season, we eliminated arthropod collection from our sampling protocol because collection and sorting was not within the budget.

Analytical Methods

We analyzed sage-grouse selection of brood-rearing sites in 2011–2012 and 2011–2013 separately because we did not collect arthropods in 2013. We used a multistage (e.g., Franklin et al. 2000) information-theoretic modeling approach (Burnham and Anderson 2002) to evaluate the relative importance of arthropod and vegetation characteristics on selection of brood-rearing sites. Sage-grouse rearing broods might select different site attributes during early (chicks <3 weeks old; Connelly et al. 2000) and late (chicks >3 weeks old) brood-rearing periods (e.g., Connelly et al. 2011). Thus, before modeling procedures, we performed multiresponse permutation procedure (MRPP) analyses on arthropod and vegetation characteristics at used sites to determine whether early and late

brood-rearing periods should be separated for model analysis.

Next, we developed models of factors affecting selection of brood-rearing sites and grouped these models into food and cover hypothesis sets. Coleoptera (beetles) and Hymenoptera (ants) are the arthropod orders most widely consumed by sage-grouse chicks (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994), so we included these arthropod orders in food models. Diptera (flies) were abundant on our field site and are also consumed by chicks (Klebenow and Gray 1968), so we included Diptera in food models as well. Orthoptera (grasshoppers) and Lepidoptera (caterpillars/butterflies) may also be important arthropods in sage-grouse chick diets (Peterson 1970, Gregg and Crawford 2009), but they were not abundant on our field site, so we excluded them from food models. Chicks also consume many species of broadleaf forbs, (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994) and some cushion forbs (e.g., phlox; Klebenow and Gray 1968), especially late in the brood-rearing season, so we included these forb groups in food models as well.

The horizontal and vertical protective cover that vegetation provides may be crucial to prevent predation and exposure-related chick mortality (Wallestad 1971, Sveum et al. 1998, Aldridge and Brigham 2002, Thompson et al. 2006, Kaczor et al. 2011, Kirol et al. 2012). This cover is often provided by sagebrush and grasses (e.g., Aldridge and Brigham 2002, Thompson et al. 2006, Hagen et al. 2007, Kirol et al. 2012), so we included sagebrush, grass, and total vegetation cover and height variables in cover models. Vegetation provides visual obstruction which may be positively correlated with brood-rearing site selection (Kaczor et al. 2011); therefore, we also included this variable in cover models. Finally, cheatgrass (*Bromus tectorum*) may have a negative association with selection (Kirol et al. 2012), so we incorporated this variable in cover models with the hypothesis that sage-grouse would avoid sites with cheatgrass.

We determined which form of each continuous variable, including linear, quadratic, and pseudothreshold (e.g., Franklin et al. 2000), was most supported by comparing values of Akaike's information criterion (Akaike 1973)

adjusted for small sample size (AIC_c) across variable forms. We used the nonlinear form of the variable if it was >2 AIC_c units better than the linear form; otherwise, we used the linear form. Similarly, we evaluated interactions between variables if there was sound reasoning for the interaction. We maintained the interaction term through the modeling process if the model was >2 AIC_c units better than an equivalent model without an interaction. We checked for multicollinearity between variables by calculating Pearson's correlation coefficient (r) using PROC CORR (SAS 9.3, SAS Institute, Inc., Cary, NC). If $r > 0.65$, we removed the correlated variable with the highest AIC_c value.

Finally, we ranked models within food and cover hypothesis sets and combined models with AIC_c values <2 from each set to evaluate which hypothesis, or combination of hypotheses, explained the most variation in resource selection by females rearing broods. We did not include arthropod variables in 2011–2013 models, so we did not separate food and cover hypotheses for 2011–2013 model analyses. If we noticed relationships consistent with prior knowledge of sage-grouse biology that we had not previously considered, we created post hoc models to compare against other models in the set. If model uncertainty existed in our final model set, we averaged models within 2 AIC_c units of the top model (Burnham and Anderson 2002).

We used conditional logistic regression to calculate model parameter estimates and relative selection probabilities because we assumed the probability of selecting a site was relative to other available sites unique to that individual. We fit conditional logistic models using PROC PHREG (SAS Institute, Inc., Cary, NC) and included a gamma-distributed random effect for each individual grouse to account for association among multiple sites selected by one individual along with any unobserved heterogeneity. The same random effect was used across all candidate models because our focus was to determine the best predictive model based on population-level inferences of brood-rearing site selection, instead of a focus on individual grouse. For that reason, we based model selection on the marginal AIC (Vaida and Blanchard 2005) corrected for the number of fixed-effect parameters specified in the model.

We evaluated model performance by calculating McFadden's pseudo R^2 (ρ^2), which can be interpreted as the proportion of the total variability explained by the model (McFadden 1974). We considered ρ^2 values >0.2 to represent excellent model fit (McFadden 1978). We also estimated squared semipartial correlations to determine how much each variable in the final model contributed to the explained variation (Cohen and Cohen 1975). We calculated ρ^2 for the most supported model, then calculated ρ^2 for a reduced model. The difference between ρ^2 of the full and reduced models represented the squared semipartial correlation of the variable excluded. We repeated this procedure for each variable included in the most supported model and assumed the variable with the smallest squared semipartial correlation contributed the least to the explained variation in selection of brood-rearing sites.

We evaluated the predictive ability of our top models by using a modified k-fold cross-validation, "leave one out" design (Boyce et al. 2002, Leblond et al. 2010). We successively removed 1 choice set (1 used and 3 paired-random sites; "test" data) from the data and refit the most-supported model using the remaining data ("training" data). We calculated relative selection probabilities for each site in the "test" choice set using the new parameter estimates derived from the training data and ranked sites based on relative probability of selection. We assessed model performance by examining the proportion of choice sets where the site selected by the brood-rearing female had the highest relative probability of selection, compared to the paired-random sites. Given that the choice set consisted of 4 options, we expected a predictive success of 25% due to random chance alone. To understand how well our model predicted relative selection at different scales, we also calculated the proportion of choice sets where the used site had a higher relative probability of selection compared to the individual random sites located 50 m, 250 m, and 500 m from the used site. For these comparisons, we expected a predictive success of 50% due to random chance. We expected a good predictive model to show a large proportion of used sites with higher relative probabilities of selection than random sites.

TABLE 1. Average vegetation and arthropod characteristics (standard errors within parentheses) at Greater Sage-Grouse early (chicks ≤3 weeks old) and late (chicks >3 weeks old) brood-rearing microsites and pooled random sites in Carbon County, Wyoming, USA, from 2011 to 2013. We only collected arthropods in 2011 and 2012 ($n = 44$ and 29 for early and late brood-rearing periods, respectively).

Variable	Early brood rearing ($n = 63$)		Late brood rearing ($n = 42$)	
	Brood	Random	Brood	Random
Visual obstruction[a], 0–22.9 cm	9.54 (0.59)	8.02 (0.35)	12.52 (0.66)	8.99 (0.44)
Visual obstruction, 22.9–45.7 cm	2.70 (0.45)	2.09 (0.25)	5.78 (0.70)	2.99 (0.37)
Visual obstruction, 45.7–68.6 cm	0.79 (0.19)	0.70 (0.14)	2.50 (0.51)	1.24 (0.24)
Visual obstruction, 68.6–91.4 cm	0.19 (0.09)	0.25 (0.09)	1.29 (0.32)	0.48 (0.13)
Sagebrush density (no./m^2)	1.41 (0.15)	1.45 (0.11)	0.85 (0.16)	1.39 (0.14)
Sagebrush (>20 cm tall) density (no./m^2)[b]	0.68 (0.07)	0.63 (0.05)	0.53 (0.08)	0.61 (0.06)
Total sagebrush canopy cover (%)[b]	17.73 (1.23)	16.03 (0.74)	15.78 (1.55)	15.32 (0.92)
Total non-sagebrush shrub canopy cover (%)	4.11 (0.74)	3.87 (0.53)	7.11 (1.58)	5.21 (0.85)
Broad-leaf forb canopy cover (%)	6.45 (0.75)	5.03 (0.49)	8.95 (1.97)	4.44 (0.60)
Cushion forb canopy cover (%)	6.07 (0.68)	6.04 (0.42)	4.26 (1.20)	4.90 (0.56)
Total forb canopy cover (%)	13.61 (0.97)	11.96 (0.61)	14.13 (1.94)	10.55 (0.81)
Bunchgrass canopy cover (%)	15.99 (1.40)	16.19 (0.94)	15.42 (2.61)	15.97 (1.32)
Rhizomatous grass canopy cover (%)	6.51 (1.36)	4.85 (0.63)	11.46 (2.31)	6.21 (0.96)
Cheatgrass canopy cover (%)	0.55 (0.38)	0.71 (0.30)	1.44 (0.65)	2.13 (0.72)
Total grass canopy cover (%)	26.57 (2.15)	24.78 (1.29)	34.53 (3.12)	28.26 (1.69)
Total vegetation canopy cover (%)	63.82 (1.96)	57.35 (1.36)	61.19 (2.85)	53.06 (1.82)
Sagebrush height (cm)	21.90 (1.56)	19.45 (0.84)	27.27 (2.47)	20.67 (1.14)
Non-sagebrush shrub height (cm)	14.10 (1.37)	12.34 (0.97)	23.28 (3.27)	15.72 (1.69)
Grass height (cm)[c]	12.87 (0.60)	12.09 (0.38)	15.56 (1.07)	12.63 (0.43)
Number of Coleoptera[d]	1.70 (0.28)	1.75 (0.18)	1.69 (0.44)	1.61 (0.23)
Number of Hymenoptera	17.66 (4.93)	13.48 (2.15)	24.79 (9.02)	13.36 (2.65)
Number of Diptera	9.25 (6.25)	2.89 (1.47)	5.00 (2.60)	1.21 (0.32)
Number of Orthoptera	0.84 (0.52)	0.55 (0.19)	0.34 (0.16)	0.37 (0.09)
Number of Lepidoptera	0.23 (0.08)	0.23 (0.06)	0.48 (0.26)	0.30 (0.08)
Total number of arthropods	40.27 (12.83)	25.55 (3.68)	39.83 (11.67)	28.52 (6.24)
Coleoptera biomass	28.14 (4.84)	34.41 (4.37)	13.52 (2.61)	21.17 (2.87)
Hymenoptera biomass	25.66 (9.95)	19.89 (3.87)	32.45 (14.70)	14.70 (2.61)
Diptera biomass	4.18 (2.27)	2.10 (0.56)	7.14 (3.51)	1.60 (0.52)
Total arthropod biomass	94.18 (15.46)	79.55 (7.15)	100.72 (25.57)	69.22 (7.05)

[a]Number of 1.27-cm increments (out of 18) with >50% obstruction.
[b]We measured foliar canopy cover of vegetation using a 20 × 50-cm quadrat.
[c]Natural droop height.
[d]Arthropod number and biomass values represent the number or milligrams of arthropods within six 1-m^2 quadrats.

TABLE 2. Model structure, number of parameters (K), log likelihood (LL), Akaike's information criterion for small sample sizes (AIC$_c$), difference in AIC$_c$ (ΔAIC$_c$), Akaike weight (w_i), and McFadden's pseudo R^2 (ρ^2) for food hypotheses explaining Greater Sage-Grouse selection of brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2013. We excluded arthropod variables from model analysis because arthropods were not sampled in 2013.

Model[a]	K	LL	AIC$_c$	ΔAIC$_c$	w_i	ρ^2
PT[b]_Hym + PT_Dip + Col + PT_BroadForb + PT_Hym*PT_BroadForb	6	−159.997	332.291	0.000	0.525	0.080
PT_Hym + PT_Dip + PT_BroadForb + PT_Hym*PT_BroadForb	5	−162.078	334.367	2.077	0.186	0.068
Global	8	−159.830	336.171	3.880	0.076	0.081
PT_Hym + Col + PT_BroadForb + PT_Hym*PT_BroadForb	5	−163.215	336.640	4.349	0.060	0.062
PT_Hym + PT_BroadForb + PT_Hym*PT_BroadForb	4	−164.408	336.955	4.665	0.051	0.055
PT_Dip + Col + PT_BroadForb	4	−164.851	337.842	5.551	0.033	0.052
PT_TotArt + PT_BroadForb + PT_TotArt*PT_BroadForb	4	−165.216	338.571	6.281	0.023	0.050
PT_Dip + PT_BroadForb	3	−166.508	339.100	6.809	0.017	0.043
PT_Dip + Col + PT_BroadForb + PT_CushionForb	5	−164.808	339.826	7.535	0.012	0.052
PT_BroadForb	2	−168.435	340.911	8.620	0.007	0.032
Col + PT_BroadForb	3	−167.671	341.426	9.135	0.005	0.036
PT_BroadForb + PT_CushionForb	3	−168.409	342.902	10.611	0.003	0.032
PT_TotArt + PT_CushionForb	3	−168.721	343.526	11.235	0.002	0.030
TotForb	2	−172.893	349.828	17.537	0.000	0.006
Null	1	−173.915	349.845	17.554	0.000	0.000
PT_CushionForb	2	−172.978	349.998	17.707	0.000	0.005
Col + PT_CushionForb	3	−172.959	352.002	19.711	0.000	0.005

[a]Hym = number of Hymenoptera; Dip = number of Diptera; Col = number of Coleoptera; TotArt = total number of arthropods; BroadForb = foliar canopy cover of broad-leaf forbs; CushionForb = foliar canopy cover of cushion/mat-forming forbs; TotForb = foliar canopy cover of all forbs; Global = fully parameterized model; Null = unparameterized model.
[b]PT: Pseudothreshold form of the variable.

RESULTS

We monitored 48 female sage-grouse (n = 15 yearlings) during the nesting season (15 April–15 June) in 2011, 51 females (n = 2 yearlings) in 2012, and 47 females (n = 1 yearling) in 2013. We verified 49 nests (19 successful) in 2011, 41 nests (14 successful) in 2012, and 39 nests (9 successful) in 2013. We monitored 14 broods in 2011, 14 broods in 2012, and 9 broods in 2013. We measured 105 sites (n = 42 in 2011, n = 31 in 2012, n = 32 in 2013) used by broods and 315 paired-random sites (n = 105 sites at each distance) to evaluate selection of brood-rearing sites (Table 1). We measured an average of 3–4 brood-rearing sites per female each year.

Only 5 of 25 variables we included in MRPP analyses showed significant differences between early and late brood-rearing periods. These included visual obstruction from 0 cm to 45.7 cm in height, density of sagebrush, foliar canopy cover of cushion forbs and grasses, and grass height. Thus, we grouped

early and late brood-rearing periods for model analysis.

We evaluated 17 food models and 15 cover models with the 2011–2012 data set. The most supported food model included number of Diptera and Coleoptera, and an interaction between number of Hymenoptera and broad-leaf forb cover (Table 2). The most supported cover model included total vegetation cover and visual obstruction from 0 cm to 45.7 cm in height (Table 3). The cover model explained more variation than the food model, but a combination of covariates included in food and cover models provided the best overall model for the 2011–2012 data (Table 4). There was moderate uncertainty between the top 2 combined models so we model averaged parameters to derive estimates.

We evaluated 40 combined food and cover models for the 2011–2013 data set. The vegetation variables found to be influential on selection of brood-rearing sites in 2011–2012 were also included in the most supported models from 2011 to 2013 (Table 5). Due to

TABLE 3. Model structure, number of parameters (K), log likelihood (LL), Akaike's information criterion for small sample sizes (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weight (w_i), and McFadden's pseudo R^2 (ρ^2) for cover hypotheses explaining Greater Sage-Grouse selection of brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2012.

Model[a]	K	LL	AIC_c	ΔAIC_c	w_i	ρ^2
PT[b]_SectAB + TotCover + TotCover^2	4	−157.974	324.088	0.000	0.368	0.092
PT_SectAB	2	−160.868	325.777	1.689	0.158	0.075
PT_SectAB + Bunch	3	−160.183	326.450	2.362	0.113	0.079
PT_SectAB + Rhizo	3	−160.724	327.532	3.444	0.066	0.076
PT_SectAB + TotSage	3	−160.767	327.617	3.528	0.063	0.076
PT_SectAB + TotGrass	3	−160.793	327.670	3.581	0.061	0.075
PT_SectAB + Density	3	−160.841	327.766	3.677	0.059	0.075
PT_SectAB + TotSage + Bunch	4	−160.081	328.301	4.213	0.045	0.080
PT_SectAB + TotSage + Rhizo	4	−160.473	329.085	4.997	0.030	0.077
PT_SectAB + TotGrass + TotSage	4	−160.748	329.636	5.547	0.023	0.076
Global	9	−156.301	331.243	7.155	0.010	0.101
TotCover + TotCover^2 + Bunch	4	−163.735	335.609	11.521	0.001	0.059
TotCover + TotCover^2 + TotSage	4	−163.812	335.763	11.675	0.001	0.058
TotCover + TotCover^2	3	−165.885	337.853	13.765	0.000	0.046
TotCover + TotCover^2 + GrassHt	4	−165.561	339.262	15.174	0.000	0.048
TotCover + TotCover^2 + Rhizo	4	−165.632	339.403	15.315	0.000	0.048
TotSage + GrassHt	3	−167.806	341.697	17.608	0.000	0.035
Rhizo + TotSage	3	−167.901	341.886	17.798	0.000	0.035
GrassHt	2	−170.666	345.373	21.284	0.000	0.019
Rhizo	2	−171.331	346.703	22.615	0.000	0.015
TotGrass + GrassHt	3	−170.661	347.405	23.317	0.000	0.019
TotSage	2	−171.753	347.547	23.459	0.000	0.012
Bunch	2	−172.509	349.060	24.971	0.000	0.008
Null	1	−173.915	349.845	25.756	0.000	0.000
TotGrass	2	−173.049	350.140	26.052	0.000	0.005
Cheatgrass	2	−173.307	350.656	26.567	0.000	0.003
Density	2	−173.479	350.999	26.910	0.000	0.003

[a]TotCover = foliar canopy cover of all vegetation, excluding litter; SectAB = number of obstructed 1.27-cm increments from 0 cm to 45.7 cm in height; Bunch = foliar canopy cover of bunchgrasses; Rhizo = foliar canopy cover of rhizomatous grasses; TotSage = foliar canopy cover of sagebrush (*Artemisia* spp.), excluding *A. frigida* and *A. pedatifida*; TotGrass = foliar canopy cover of grasses; Cheatgrass = foliar canopy cover of cheatgrass (*Bromus tectorum*); Density = density of sagebrush; GrassHt = natural droop height of grasses; Global = fully parameterized model; Null = unparameterized model.
[b]PT: Pseudothreshold form of the variable.

TABLE 4. Model structure, number of parameters (K), log likelihood (LL), Akaike's information criterion for small sample sizes (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weight (w_i), and McFadden's pseudo R^2 (ρ^2) for combined food and cover hypotheses explaining Greater Sage-Grouse selection of brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2012.

Model[a]	K	LL	AIC_c	ΔAIC_c	w_i	ρ^2
PT[b]_Hym + PT_Dip + Col + PT_BroadForb + PT_Hym*PT_BroadForb + TotCover + TotCover^2 + PT_SectAB	9	−150.727	320.094	0.000	0.569	0.133
PT_Hym + PT_Dip + Col + PT_BroadForb + PT_Hym*PT_BroadForb + PT_SectAB	7	−153.425	321.245	1.151	0.320	0.118
TotCover + TotCover^2 + PT_SectAB	4	−157.974	324.088	3.994	0.077	0.092
PT_SectAB	2	−160.868	325.777	5.683	0.033	0.075
PT_Hym + PT_Dip + Col + PT_BroadForb + PT_Hym*PT_BroadForb	6	−159.997	332.291	12.197	0.001	0.080
Null	1	−173.915	349.845	29.751	0.000	0.000

[a]Hym = number of Hymenoptera; Dip = number of Diptera; Col = number of Coleoptera; TotCover = foliar canopy cover of all vegetation, excluding litter; SectAB = number of obstructed 1.27-cm increments from 0 cm to 45.7 cm in height; BroadForb = foliar canopy cover of broad-leaf forbs; Null = unparameterized model.
[b]PT: Pseudothreshold form of the variable.

TABLE 5. Model structure, number of parameters (K), log likelihood (LL), Akaike's information criterion for small sample sizes (AIC_c), difference in AIC_c (ΔAIC_c), Akaike weights (w_i), and McFadden's pseudo R^2 (ρ^2) for food and cover hypotheses explaining Greater Sage-Grouse selection of brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2013. We excluded arthropod variables from model analysis because arthropods were not sampled in 2013.

Model[a]	K	LL	AIC_c	ΔAIC_c	w_i	ρ^2
PT[b]_SectAB + TotCover + TotCover^2 + PT_BroadForb	5	−220.644	451.433	0.000	0.363	0.118
PT_SectAB + TotCover + TotCover^2	4	−222.361	452.819	1.387	0.182	0.112
PT_SectAB + TotCover + TotCover^2 + PT_Bunch	5	−221.546	453.237	1.804	0.147	0.115
PT_SectAB + TotCover + TotCover^2 + PT_TotGrass	5	−221.661	453.467	2.034	0.131	0.114
PT_SectAB + TotCover + TotCover^2 + TotForb	5	−221.969	454.084	2.652	0.097	0.113
PT_SectAB + TotCover + TotCover^2 + TotSage	5	−222.280	454.705	3.272	0.071	0.112
PT_BroadForb + TotCover + TotCover^2 + PT_GrassHt	5	−224.631	459.407	7.974	0.007	0.102
Global	11	−219.774	462.197	10.765	0.002	0.122
TotCover + TotCover^2 + PT_GrassHt	4	−228.690	465.477	14.044	0.000	0.086
PT_SectAB + PT_BroadForb	3	−231.899	469.856	18.423	0.000	0.073
PT_SectAB	2	−234.169	472.367	20.934	0.000	0.064
PT_SectAB + PT_Bunch	3	−233.288	472.633	21.200	0.000	0.068
PT_SectAB + PT_TotGrass	3	−233.316	472.689	21.257	0.000	0.068
PT_SectAB + TotForb	3	−233.433	472.923	21.490	0.000	0.067
PT_SectAB + Rhizo	3	−233.628	473.314	21.882	0.000	0.067
PT_SectAB + PT_CushionForb	3	−233.738	473.533	22.101	0.000	0.066
PT_SectAB + Density	3	−233.923	473.903	22.470	0.000	0.065
PT_SectAB + TotSage	3	−234.045	474.148	22.716	0.000	0.065
PT_SectAB + TotSage + PT_Bunch	4	−233.244	474.584	23.152	0.000	0.068
PT_SectAB + PT_TotGrass + TotSage	4	−233.315	474.726	23.294	0.000	0.068
PT_SectAB + TotSage + Rhizo	4	−233.620	475.336	23.904	0.000	0.067
TotCover + TotCover^2	3	−234.699	475.457	24.024	0.000	0.062
PT_BroadForb + PT_TotGrass + TotSage	4	−236.282	480.661	29.229	0.000	0.056
PT_BroadForb	2	−238.550	481.129	29.696	0.000	0.047
PT_BroadForb + PT_CushionForb	3	−238.150	482.357	30.924	0.000	0.048
PT_BroadForb + PT_TotGrass + PT_GrassHt	4	−237.139	482.374	30.942	0.000	0.052
TotSage + PT_GrassHt	3	−241.590	489.239	37.806	0.000	0.035
PT_GrassHt	2	−242.774	489.577	38.144	0.000	0.030
TotForb + PT_TotGrass + PT_GrassHt	4	−240.772	489.641	38.208	0.000	0.038
PT_TotGrass + PT_GrassHt	3	−242.036	490.129	38.696	0.000	0.033
Rhizo + TotSage	3	−244.274	494.607	43.174	0.000	0.024
Rhizo	2	−246.227	496.483	45.050	0.000	0.016
PT_TotGrass	2	−246.268	496.566	45.133	0.000	0.016
TotForb	2	−246.328	496.685	45.253	0.000	0.016
PT_CushionForb	2	−247.428	498.885	47.452	0.000	0.011
PT_Bunch	2	−248.619	501.266	49.834	0.000	0.007
Density	2	−248.780	501.588	50.156	0.000	0.006
Null	1	−250.278	502.567	51.134	0.000	0.000
TotSage	2	−249.371	502.772	51.339	0.000	0.004
Cheatgrass	2	−249.895	503.819	52.386	0.000	0.002

[a]TotCover = foliar canopy cover of all vegetation, excluding litter; SectAB = number of obstructed 1.27-cm increments from 0 cm to 45.7 cm in height; BroadForb = foliar canopy cover of broad-leaf forbs; CushionForb = foliar canopy cover of cushion/mat-forming forbs; Bunch = foliar canopy cover of bunch-grasses; Rhizo = foliar canopy cover of rhizomatous grasses; TotGrass = foliar canopy cover of grasses; TotForb = foliar canopy cover of all forbs; TotSage = foliar canopy cover of sagebrush (*Artemisia* spp.) species, excluding *A. frigida* and *A. pedatifida*; Density = density of sagebrush; GrassHt = natural droop height of grasses; Cheatgrass = foliar canopy cover of cheatgrass (*Bromus tectorum*); Global = fully parameterized model; Null = unparameterized model.
[b]PT: Pseudothreshold form of the variable.

TABLE 6. Model-averaged parameter estimates, standard errors (SE), and 95% confidence intervals (L95% and U95%) explaining Greater Sage-Grouse selection of brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2012 and 2011 to 2013.

Years	Parameter[a]	Estimate	SE	L95%	U95%
2011–2012	PT[b]_SectAB	1.271**[c]	0.433	0.422	2.121
	TotCover	0.192**	0.090	0.015	0.369
	TotCover^2	−0.0015**	0.0007	−0.0028	−0.0001
	PT_Dip	0.436**	0.216	0.014	0.859
	PT_Hym	0.697**	0.332	0.047	1.348
	PT_BroadForb	0.761*	0.414	−0.051	1.574
	PT_Hym*PT_BroadForb	−0.294*	0.158	−0.604	0.016
	Col	−0.206**	0.097	−0.395	−0.016
2011–2013	PT_SectAB	1.004**	0.306	0.405	1.604
	TotCover	0.205**	0.067	0.074	0.336
	TotCover^2	−0.0014**	0.0005	−0.0024	−0.0003
	PT_BroadForb	0.333*	0.183	−0.025	0.691
	PT_Bunch	−0.431	0.337	−1.092	0.230

[a]Hym = number of Hymenoptera (no./6 m^2); Dip = number of Diptera (no./6 m^2); Col = number of Coleoptera (no./6 m^2); TotCover = foliar canopy cover (%) of all vegetation, excluding litter; SectAB = number of obstructed 1.27-cm increments from 0 cm to 45.7 cm in height; BroadForb = foliar canopy cover (%) of broad-leaf forbs; Bunch = foliar canopy cover (%) of bunchgrasses.
[b]PT: Pseudothreshold form of the variable.
[c] ** = 95% significance; * = 90% significance.

model uncertainty, we model averaged the top 3 models to derive separate parameter estimates for the 2011–2013 data set.

From 2011 to 2012, number of Diptera had a significant ($P < 0.05$) positive pseudothreshold association with brood-rearing site selection, whereas number of Coleoptera had a significant negative linear association (Table 6). The interaction between number of Hymenoptera and broad-leaf forb cover was insignificant at the 95% confidence level, but significant at the 90% confidence level. The relative probability of a site being selected increased logistically with increasing number of Hymenoptera, if there was low cover ($<20\%$) of broad-leaf forbs. However, relative probability of selection decreased with increasing number of Hymenoptera when there were was $>20\%$ broad-leaf forb cover at the site (Fig. 2).

The pseudothreshold form of visual obstruction from 0 cm to 45.7 cm in height and the quadratic form of total vegetation cover had significant ($P < 0.05$) relationships with brood-rearing site selection for both data sets (Table 6). Relative probability of selection increased logistically with increasing visual obstruction but peaked at approximately 75% vegetation cover (Fig. 3). Broad-leaf forb cover had a positive pseudothreshold association with brood-rearing site selection in 2011–2013, but the relationship was only significant at the 90% confidence level.

McFadden's ρ^2 values for top models suggested that our models performed marginally well, but not excellently. Squared semipartial correlations of variables in the final models indicated that number of Coleoptera explained the least variation (1.50%) in brood-rearing site selection from 2011 to 2012, whereas visual obstruction from 0 cm to 45.7 cm in height explained the most variation (2.62%). Similarly, visual obstruction explained the most variation (4.73%) in selection from 2011 to 2013 and bunchgrass cover explained the least variation (0.33%). Cross validation procedures correctly classified 46.6% of the brood-rearing sites in the 2011–2012 data set and 43.8% of the brood-rearing sites for the 2011–2013 data set. When compared individually with the 50-m, 250-m, and 500-m paired-random sites, the brood-rearing site was correctly classified, respectively, in 61.6%, 76.7%, and 71.2% of the choice sets using the 2011–2012 model, and correctly classified in 66.7%, 65.7%, and 82.9% of the choice sets using the 2011–2013 model.

DISCUSSION

Sage-grouse rearing broods often select diurnal sites with concealing cover to prevent predation and exposure-related chick mortality (Wallestad 1971, Sveum et al. 1998, Aldridge and Brigham 2002, Thompson et al. 2006, Kaczor et al. 2011, Kirol et al. 2012). The strong influence of visual obstruction from 0 cm to 45.7 cm in height on brood-rearing site selection in our study confirms that concealing
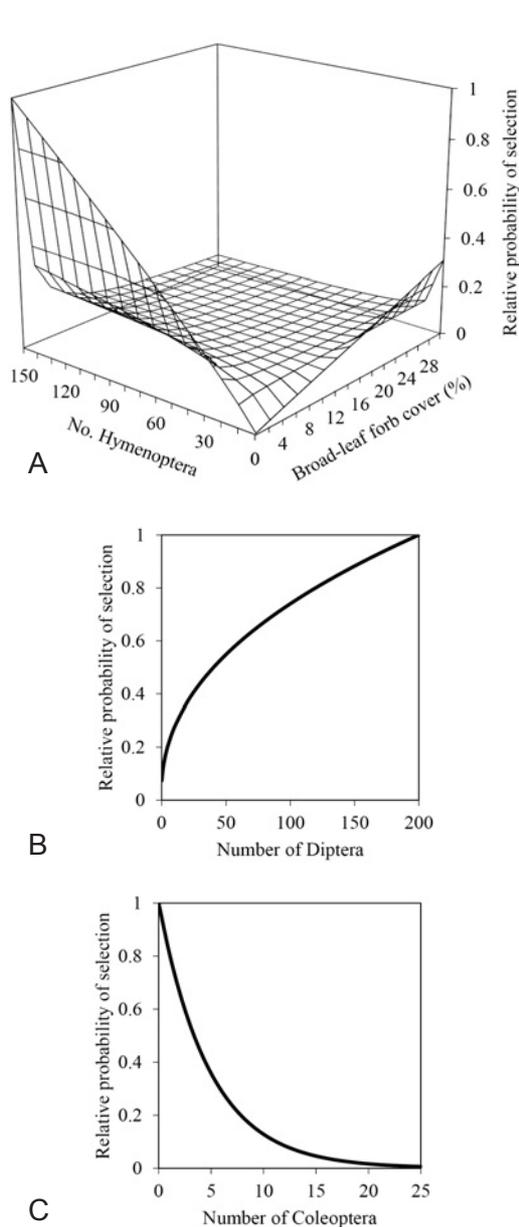
Fig. 2. Influence of (A) the interaction between number of Hymenoptera (no./6 m²) and foliar canopy cover (%) of broad-leaf forbs; (B) number of Diptera (no./6 m²); and (C) number of Coleoptera (no./6 m²) on the relative probability of Greater Sage-Grouse selecting brood-rearing microsites in Carbon County, Wyoming, USA, from 2011 to 2012. These graphs demonstrate the relative change in selection probability, rescaled from 0 to 1, not the absolute probability of a site being selected. We removed confidence intervals from figures because confidence intervals are conditional upon the choice set that is evaluated. We evaluated a hypothetical set of 256 available choices for graph A, and 25 choices for graphs B and C, each with incrementally increasing values of the variable of interest.
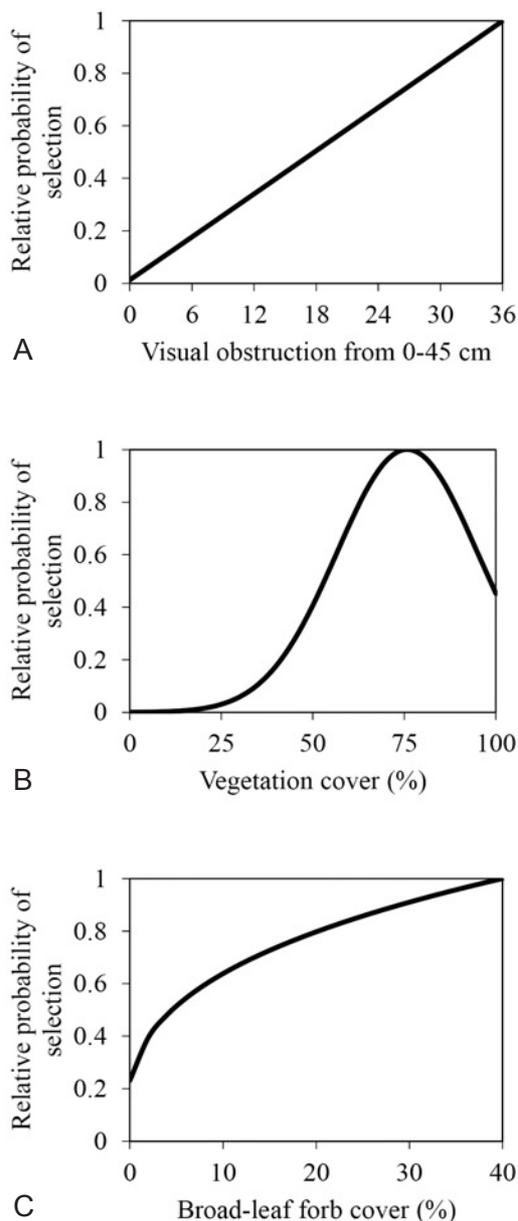
Fig. 3. Influence of (A) visual obstruction (no. of 1.27-cm increments with >50% obstruction) from 0 to 45 cm in height, (B) foliar canopy cover (%) of all vegetation species, and (C) foliar canopy cover (%) of broad-leaf forbs on Greater Sage-Grouse selection of brood-rearing sites in Carbon County, Wyoming, USA, from 2011 to 2013. These graphs demonstrate the relative change in selection probability, rescaled from 0 to 1, not the absolute probability of a site being selected. We removed confidence intervals from figures because confidence intervals are conditional upon the choice set that is evaluated. We evaluated a hypothetical set of 25 available choices, each with incrementally increasing values of the variable of interest.

cover is a high priority. Our result that relative probability of selection decreased with increasing vegetation cover >75% should not discount the importance of visual obstruction on selection of brood-rearing sites because this metric is not directly associated with concealing cover. Wambolt et al. (2002) suggested that herbaceous vegetation can become "too thick" for good brood cover. Further, Klebenow (1985) found that brood-rearing sage-grouse selected grazed meadows with average vegetation heights of 7–15 cm, whereas available vegetation averaged 10–25 cm. Thus, a mosaic of varying vegetation cover and heights that provides both foraging and escape areas might be most beneficial for broods (Klebenow 1985). Brood-rearing sage-grouse typically use cover dominated by sagebrush in late spring/early summer and then transition to mesic sites with more herbaceous cover (Connelly et al. 2011). While total vegetation cover was important for selection of brood-rearing sites, we found no influence of species-specific cover types in our analysis. This could be a result of the diversity of vegetation types used by brood-rearing sage-grouse on our study area or a dilution of effects by combining early and late brood-rearing periods.

It is well-known that arthropods are important to sage-grouse broods (e.g., Drut et al. 1994, Fischer et al. 1996, Connelly et al. 2000, Dahlgren et al. 2010) because chicks require arthropods for proper development and survival during the first few weeks post hatch (Johnson and Boyce 1990). The inclusion of arthropod covariates in our final model suggests that arthropod abundance influences brood-rearing site selection on our study site. However, not all arthropod orders included in our final model had positive influences on selection. Coleoptera were some of the most prevalent arthropods consumed by sage-grouse chicks in Idaho, Montana, and Oregon (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994), but number of Coleoptera had a significant negative correlation with selection in our study. We caution the interpretation of this finding, given that Coleoptera explained the least variation in selection of brood-rearing sites compared to other variables in the most supported model. This relationship might not be a result of brood-rearing sage-grouse actively avoiding Coleoptera, rather sage-grouse using vegetation communities that may be less attractive to some Coleoptera. Darkling beetles (Tenebrionidae), one of the most common beetles in western North America (Crawford 1981), and a food source for sage-grouse chicks (Klebenow and Gray 1968, Drut et al. 1994), are largely associated with shrub-dominated habitats (Rickard and Haverfield 1965, Parmenter et al. 1989, McIntyre 1997, Stapp 1997). Brood-rearing females in our study often selected sites in mesic areas with high herbaceous cover that may not have been attractive to darkling beetles but harbored large densities of other arthropods (Knops et al. 1999, Wenninger and Inouye 2008). Similarly, harvester ants (*Pogonomyrmex* spp.), one the most common species of Hymenoptera on our study area, are associated with sandy soils in arid environments (Kirkham and Fisser 1972), whereas broad-leaf forbs on our study site were typically associated with mesic sites. The increase in the relative probability of sage-grouse selecting sites with high numbers of Hymenoptera but low cover of broad-leaf forbs, or high broad-leaf forb cover and low number of Hymenoptera, could be a result of harvester ants not being as abundant in mesic sites. Alternatively, the interaction could be influenced by changing foraging habits, as chick diets shift from Hymenoptera (mostly ants) and beetles early in the brood-rearing season to forbs late in the season (Klebenow and Gray 1968, Peterson 1970).

Forbs are an important food source for sage-grouse chicks, especially late in the brood-rearing period (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994, Sveum et al. 1998). Though insignificant, the trends we observed suggest that broad-leaf forb cover was more influential on brood-rearing site selection than cushion forb cover. Most forbs consumed by chicks in Idaho, Montana, and Oregon were broad-leaf forbs (Klebenow and Gray 1968, Peterson 1970, Drut et al. 1994) with high crude protein content (Barnett and Crawford 1994). Sage-grouse rearing broods on our study area may have selected sites with broad-leaf forbs for their increased nutritional value. Some species of phlox are also consumed by sage-grouse chicks (Klebenow and Gray 1968, Drut et al. 1994) and might improve survival of chicks (Gregg and Crawford 2009). However, phlox and other cushion forbs such as goldenweed were primarily located in dry, rocky vegetation communities on our study

area (e.g., Gucker 2006), whereas broad-leaf forbs were often associated with mesic communities preferred by brood-rearing sage-grouse.

Similar to other studies concerning sage-grouse brood-rearing habitat, our results demonstrate that food and cover attributes are both important components of sage-grouse diurnal selection of brood-rearing sites. Most variables in our top models had pseudothreshold or quadratic forms, which suggests there is an optimum level of food and cover attributes, and a combination of these attributes is likely preferred. Sage-grouse rearing broods acquired food and cover within a diverse array of vegetation types across ecoregions on our study area but consistently selected sites within mesic communities, especially late in the brood-rearing season. High moisture in mesic communities produces visual cover from grasses and shrubs, as well as high abundance and diversity of food resources from forbs and arthropods (Jamison et al. 2002, Wenninger and Inouye 2008). The diversity of vegetation types selected within mesic communities and the increased predictive ability of our model at scales >50 m from the used site suggest that community-level food and cover characteristics may be more influential on selection of brood-rearing sites than individual attributes within the community (e.g., Harju et al. 2013). Available sites within 50 m of the used site were often in the same vegetation community, which could explain why our model did not differentiate these sites as well as it differentiated sites located 250 m or 500 m from the used site. Thus, our results could be used to identify vegetation communities with high relative probabilities of use by sage-grouse rearing broods, which will help guide management decisions and provide reference conditions for future research that evaluates the effects of wind energy development on sage-grouse.

ACKNOWLEDGMENTS

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