GREATER SAGE-GROUSE NEST SITE SELECTION, BROOD-REARING SITE SELECTION, AND CHICK SURVIVAL IN WYOMING

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by

LESLIE ANN SCHREIBER

Dr. Joshua J. Millspaugh, Thesis Supervisor

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

GREATER SAGE-GROUSE NEST SITE SELECTION, BROOD-REARING SITE SELECTION, AND CHICK SURVIVAL IN WYOMING

presented by Leslie A. Schreiber,

a candidate for the degree of master of sciences,

and hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Joshua J. Millspaugh

Dr. Mark A. Rumble

Dr. Frank R. Thompson, III

Dr. Bruce A. Barrett

DEDICATION

I dedicate this work to my husband, Roger Dale. Thank you for understanding why your wife chased birds all night and went to school on the other side of Nebraska. I am home for good now.

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GREATER SAGE-GROUSE NEST SITE SELECTION, BROOD-REARING SITE SELECTION, AND CHICK SURVIVAL IN WYOMING

Leslie A. Schreiber

Dr. Joshua J. Millspaugh, Thesis Supervisor

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations throughout North America were recently listed as “warranted but precluded” under the Endangered Species Act, because sage-grouse populations are declining as a result of loss and degradation of sagebrush (*Artemisia* spp.) habitat. The population growth rate of sage-grouse is sensitive to small changes in nest productivity and chick survival rates which are often mediated by the quality of sagebrush habitat associated with these life stages. Vegetation provides lateral and overhead visual obstruction which helps conceal nests from visually-cued predators, in addition to possibly creating an olfactory barrier to scent-cued predators. Vegetation also provides insulation for the incubating female resulting in a microclimate favorable to parental energy savings and less time spent away from the nest. After the eggs hatch, concealing cover is needed during the brood-rearing stage, along with specific food resources (i.e., forbs and arthropods) for growth and development of chicks. Previous research has identified high-protein arthropods as a critical food source for precocial tetraonid chicks for several weeks post-hatch. Long-term studies directly investigating potential effects of commercial wind energy development on sage-grouse do not exist. North America’s largest wind energy facility, consisting of approximately 1,000 turbines, is proposed to be built in south-central Wyoming in an area occupied by sage-grouse. Our project is part of a Before-After-Control-Impact study collecting baseline data on sage-grouse prior to construction of this wind energy facility. Our objectives were to assess sage-grouse nest-site selection (Chapter 1), evaluate resource selection patterns by female sage-grouse with broods (Chapter 2), and estimate sage-grouse nest productivity and chick survival rates (Chapter 3).

Our project was a collaborative effort among University of Missouri; U.S. Forest Service, Rocky Mountain Research Station; SWCA Environmental Consultants; Power Company of Wyoming, LLC; and Wyoming Game and Fish Department. Therefore, I use “we” when describing our methods. We monitored radio-equipped female sage-grouse (2011: $n = 44$, 2012: $n = 52$, 2013: $n = 46$) which we captured near leks associated with areas for proposed wind turbine placement and areas without proposed turbines. To evaluate nest-site selection models, we estimated vegetation canopy cover, vegetation height, lateral visual obstruction, and sagebrush density surrounding each nest (2011: $n = 37$, 2012: $n = 37$, 2013: $n = 35$) and paired available sites. To evaluate brood-rearing selection models, we collected the vegetation attributes described above in addition to estimating relative arthropod abundance at brood-rearing sites (2011: $n = 42$, 2012: $n = 31$, 2013: $n = 32$) and paired available sites. We used discrete choice modeling to evaluate nest-site selection and brood-rearing site selection. We estimated relative selection probabilities by varying explanatory variables of interest while holding other variables in the models at their mean values. We estimated net nest productivity using a weighted mean of the average brood size which is the product of the average brood size

and the rate of nest success for initial nests (2011: *n* = 16/38, 2012: *n* = 14/37, 2013: *n* = 11/37) and renests (2011: *n* = 4/10, 2012: *n* = 2/4, 2013: *n* = 1/8). We estimated chick survival by conducting repeated nocturnal spotlight surveys in which we counted the chicks associated with each radio-equipped female (2011: *n* = 14, 2012: *n* = 14, 2013: *n* = 9). We used a modified logistic-exposure method to estimate daily chick survival rates and survival over a 70-day time period while examining relationships between chick survival and weather and temporal variables.

The only covariate significant to nest-site selection was lateral visual obstruction 23−46 cm above the ground. The pseudothreshold form of lateral visual obstruction had a strong positive relationship with nest-site selection. Increasing visual obstruction from 6 cm to 15 cm almost tripled the relative probability of selection. We did not find any previous studies on sage-grouse nest-site selection where visual obstruction was found to be unimportant when it was directly considered as a covariate. Thus, the importance of lateral visual obstruction can be considered as an overriding feature of sage-grouse nesting habitat. During the brood-rearing life stage, female sage-grouse selected sites with greater lateral visual obstruction close to the ground, more sagebrush canopy cover, and greater relative abundance of arthropods compared to available sites. Our study is the first to report sage-grouse broods' selection of greater relative arthropod abundance, but not necessarily greater forb cover. Increasing sagebrush canopy cover from 15% to 33% or doubling the number of cm visually obstructed near the ground doubled the relative probability of selection by female sage-grouse with broods.

Overall, the chick to female ratios we observed of 1.5−2.8 chicks/female in early spring were similar to those observed elsewhere in the fall, suggesting that this

population of sage-grouse exhibited low recruitment that began with nesting. Chick survival rates to 70 days-post-hatch [2011: 0.120 ± 0.082 (SE), 2012: 0.031 ± 0.034 (SE), 2013: 0.157 ± 0.049 (SE)] were very low. However, these rates should be placed in the broader context of sage-grouse chick survival which exhibits high annual variation due to a variety of extrinsic factors.

The low rates of nest productivity and chick survival suggest that this area may be of marginal quality for sage-grouse. Low habitat quality could be due to inherent low capacity possibly caused by relatively arid site conditions or poor or degraded soils. Because our estimates of nest productivity and chick survival are low compared to the literature, our research highlights the importance of collecting baseline, preconstruction data when evaluating effects of wind energy development on sage-grouse. If improving sage-grouse populations is a priority, managers should consider practices aimed at enhancing nesting and brood-rearing resources. Management practices aimed at conserving vegetation that provides concealing cover, such as the native sagebrush/bunchgrass plant community, intermixed with vegetation that supports arthropods, such as numerous, small patches of wet meadows with tall grass, might help improve sage-grouse nest productivity and chick survival on our study area.

CHAPTER 1 – GREATER SAGE-GROUSE NEST SITE SELECTION IN WYOMING

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) populations have been declining across North America since at least the 1960's due to degradation of essential sagebrush (Artemisia spp.) habitat, resulting in their recent listing as "warranted but precluded" under the Endangered Species Act. These declines have been linked to measures of reproductive success which may be affected by nesting habitat. Inadequate nesting habitat may contribute to decreased nesting success; consequently, knowledge of vegetation and structural characteristics selected by nesting female sage-grouse at the microhabitat scale might promote effective conservation and management of sage-grouse habitat. We monitored radio-equipped female sage-grouse (*n* = 44 in 2011, 52 in 2012, 46 in 2013) in south-central Wyoming to assess nest-site selection prior to construction of a wind energy facility. Sage-grouse selected nest-sites with increased lateral visual obstruction 22.9−45.7 cm above the ground. Our findings are supported by previous research demonstrating that sage-grouse, and tetraonids in general, select for structural cover to conceal nests from predators and to possibly facilitate a favorable microclimate for the nest. Currently, the required structural cover is supplied by sagebrush and tall bunchgrasses. If improving sage-grouse nesting habitat is a priority, managers should consider practices aimed at enhancing plant communities composed of tall bunchgrasses and sagebrush.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations throughout North America have declined over the past 50 years due to degradation of sagebrush (*Artemisia* spp.) habitats on which they depend (Braun 1998, Connelly et al. 2004) resulting in the recent "warranted but precluded" listing under the Endangered Species Act (United States Fish and Wildlife Service 2010). Population declines in tetraonids are sometimes attributed to changes in productivity, a component of which is nest success (Blank et al. 1967, Bergerud 1988). Low quality nesting habitat may contribute to lower nesting success (Gregg et al. 1994); therefore, knowledge of vegetation and structural characteristics important to nest-site selection at the microhabitat scale is critical in managing and conserving sagebrush habitats. Furthermore, nest success varies greatly across the geographic range of sage-grouse due to environmental gradients and differences in vegetation structure among areas (Connelly et al. 2000). Thus, it is necessary to have nest habitat data which are specific to the region of interest when evaluating nesting habitat quality.

Previous research has demonstrated the importance of cover in tetraonid nest-site selection (Campbell et al. 2002, Pitman et al. 2005, Hagen et al. 2007, Goddard and Dawson 2009a, Matthews et al. 2013). Predation is the primary cause of tetraonid nest failure (Martin 1993, Schieck and Hannon 1993). Vegetation provides lateral and overhead visual obstruction which helps conceal nests from visually-cued predators, in addition to possibly creating an olfactory barrier to scent-cued predators (DeLong et al. 1995). Vegetation also provides insulation for the incubating female resulting in a microclimate favorable to parental energy savings and less time spent away from the nest (Coates 2007). Cover described above takes the form of increased sagebrush (Fischer

1994, Gregg et al. 1994, Sveum et al. 1998, Holloran et al. 2005, Hagen et al. 2007) and tall grass cover from native bunchgrasses (Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998). Cagney et al. (2010) postulated that the sagebrush/bunchgrass plant community provides excellent nesting habitat, because it provides an optimal mix of horizontal and vertical structure, and offers the most diversity of shrubs, grasses, and forbs.

Vegetation components of sage-grouse nesting habitat are often affected by site history, current management, weather, and prevailing human disturbances in the environment (Holloran 2005, Doherty 2008, Walker 2008, Naugle et al. 2011). Long-term studies directly addressing potential effects of commercial wind energy development on sage-grouse habitat do not exist (Stewart et al. 2007). North America's largest wind energy facility is proposed to be built in south-central Wyoming (Power Company of Wyoming 2009) in an area occupied by sage-grouse. Our objective was to assess nest-site selection testing our hypotheses concerning the relative importance of different plant communities, food resources, and cover types. Our study was part of a Before-After-Control-Impact study collecting baseline data on sage-grouse prior to construction of the wind energy facility.

STUDY AREA

The Power Company of Wyoming, LLC proposes to build a wind energy facility consisting of ~1,000 turbines capable of generating 2,000–3,000 megawatts on the Overland Trail Ranch (hereafter, the ranch) south of Rawlins, Wyoming, USA (Figure 1). Our study area encompassed the ranch and surrounding areas. The ranch comprises approximately 1,295 km^2 characterized by a checkerboard land ownership pattern managed as an open range yearling cattle operation. Approximately half of the study area is privately owned and approximately half is administered by the Bureau of Land Management, with a small portion owned by the State of Wyoming.

Topographically, the study area is characterized by a central basin that transitions to foothills and mesas to the south and southwest, and to rocky escarpments and rolling terrain to the north and northeast (Love and Christiansen 1985). Elevations range from 1,890 m at the North Platte River to 2,590 m near the Continental Divide in the southwestern portion of the study area (Bureau of Land Management 2012). The climate is typified by cold, moist winters and mild, dry summers (Curtis and Grimes 2004) with most precipitation occurring in the spring as snow storms or convective thunderstorms (Western Regional Climate Center 2013). Over the past 60 years, annual precipitation averaged 22.8 cm in Rawlins, WY which is 6 km north of the study area boundary and 24.6 cm in Saratoga, WY which is 14 km east of the study area boundary (Western Regional Climate Center 2013). The average monthly temperature range is 0.7–12.7 C between November and April, with the coldest temperatures occurring in January, and 15.3–28.5 C between May and October, with the warmest temperatures during July (Western Regional Climate Center 2013).

The study area lies within the rolling sagebrush steppe, salt desert shrub basins, and foothill shrublands ecoregions (Chapman et al. 2004). Rolling sagebrush steppe is the predominant ecoregion and is characterized by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations, mountain big sagebrush (*A. t. vaseyana*) at higher elevations, silver sagebrush (*A. cana*) in areas where the water table is ≤ 1 m of the soil surface (Thatcher 2006), and black sagebrush (*A. nova*) in exposed, rocky soils

(Chapman et al. 2004). Other shrubs include rabbitbrush (*Chrysothamnus* spp. and *Ericameria nauseosa*); common forbs include cushion-like phlox (*Phlox* spp.), goldenweed (*Stenotus acaulis*), clover (*Trifolium* spp.), madwort (*Alyssum* spp.), and vetch (*Astragalus* spp.); common grasses include western wheatgrass (*Elymus smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), Sandberg bluegrass (*Poa secunda*), and prairie junegrass (*Koeleria macrantha*; Bureau of Land Management 2012).

The low elevation center of the ranch is characterized by a salt desert shrub basin which comprises approximately 19% of the study area and is characterized by sparse vegetation cover of cushion-plant communities. Dominant shrub cover consists of Gardner's saltbush (*Atriplex gardneri*), shadscale (*Atriplex confertifolia*), and black greasewood (*Sarcobatus vermiculatus*; Chapman et al. 2004). Common grass species include alkali cordgrass (*Spartina gracilis*), Indian ricegrass (*Oryzopsis hymenoides*), blowout grass (*Redfieldia flexuosa*), alkali wildrye (*Leymus simplex*), and needle-and-thread (Bureau of Land Management 2012).

The higher-elevation, southwestern portion of the study area consists of montane deciduous shrublands comprising approximately 15% of the study area. Vegetation includes mountain big sagebrush, snowberry (*Symphoricarpos* spp.), serviceberry (*Amelanchier* spp.), mountain mahogany (*Cercocarpus* spp.), with groves of aspen (*Populus tremuloides*) and patches of limber pine (*Pinus flexilis*; Chapman et al. 2004). Common grasses are blue grama, prairie junegrass, and western wheatgrass (Bureau of Land Management 2012).

METHODS

Field Methods

We assessed nest-site selection by monitoring radio-equipped female sage-grouse which we captured near leks associated with areas for proposed wind turbine placement and areas without proposed turbines. We captured female sage-grouse using spotlighting techniques (Giesen et al. 1982) during March and April of 2010–2013. We fit captured females with 30-g rump-mounted (Rappole and Tipton 1991) Global Positioning System Platform Transmitter Terminals (GPS PTTs; Microwave Telemetry, Inc., Columbia, MD). Age of female sage-grouse was determined from characteristics of primary feathers on wings (Eng 1955). Capture and handling was conducted under protocols approved by the University of Missouri Animal Care and Use Committee permit number 6750.

GPS transmitters were programmed to collect 8 locations each day during the nesting season. Locations were downloaded from Argos satellites every 3−5 days. Each GPS PTT was equipped with an Ultra High Frequency (UHF) transmitter, which was operational for approximately 8 hrs/day, to facilitate ground-tracking. Multiple (>3) GPS locations within a 50 m radius over 48 hrs were investigated in the field to determine the presence of a nest or status of the female. We confirmed females on nests using telemetry and visually observed them using binoculars from >10 m from the nest to avoid disturbing the female. Starting the day before the approximate hatch date (e.g., Schroeder et al. 1999), we began visually observing the nesting female daily until the female ceased incubating. If we were unable to perform field observations due to logistical constraints, we utilized GPS location data to inform us of the exact hatch date, evidenced by >3 GPS locations >50 m from the nest.

We initiated our vegetation field measurements when a female ceased incubating. We recorded field data in Allegro CX and MX data loggers (Juniper Systems, Logan, UT). We measured the vegetative characteristics along 4 30-m transects radiating in the cardinal directions from the nest (i.e., the used site). Along each transect we measured lateral visual obstruction using a modified Robel pole (Robel et al. 1970, Benkobi et al. 2000) as a coverboard partitioned into 4 vertical sections, each with 18 1.27-cm segments. Facing the nest, we tallied the number of segments having >50% obstruction in each segment from a distance of 4 m and a height of 1 m. We measured visual obstruction at the nest bowl and at 1-m increments out to 5 m, then at 10-m increments out to 30 m along each transect.

We estimated canopy cover using a 0.1 m^2 quadrat (Daubenmire 1959) for which we estimated the cover class of each of the following categories: big sagebrush, black sagebrush, silver sagebrush, total sagebrush, greasewood, rabbitbrush, saltbush, other non-sagebrush shrubs, total non-sagebrush shrubs, phlox, goldenweed, vetch, clover, annual forb, unknown forb, total broadleaf forb, total cushion forb, total forb, bunchgrass, rhizomatous grass, sedges, cheatgrass (*Bromus tectorum*), and total grass. We measured the height of the plant closest to the corner of the quadrat nearest the transect increment for sagebrush, non-sagebrush shrub, forb, and grass. We measured canopy cover and height at the nest bowl and at 1-m increments out to 5 m, then at 5-m increments out to 30 m along each transect.

We estimated sagebrush density using the point-centered-quarter method (Cottam and Curtis 1956) at 10-m increments out to 30 m along each transect. We did not estimate density at the nest bowl, because most nests are beneath sagebrush (Patterson

1952) which would bias our sagebrush density estimate. At each increment along the transect, we measured the distance to the nearest sagebrush plant and the nearest sagebrush plant >20 cm tall in each quarter of a variable radius circular plot. All measurements were truncated at 5 m radius.

To quantify available habitat within the same patch of vegetation as the nest (i.e., the "nest patch" spatial scale), we enumerated vegetation along 4 5-m transects radiating in the cardinal directions at 3 available sites. We used a table of random numbers divided into 3 sections (0º–120º, 120º–240º, and 240º–360º) to select an azimuth to each of 3 points and a table of random numbers ($10 < x \leq 30$ m) to select the distance from the nest. Each available site was centered on the nearest sagebrush plant ≥ 20 cm tall, because sage-grouse typically nest beneath a sagebrush plant ≥ 20 cm tall (Patterson 1952). Along these transects we collected visual obstruction, canopy cover, and height measurements at the available location and at 1-m increments out to 5 m using the same techniques described above.

To quantify available habitat within the same area as the nest, but in different patches of vegetation (i.e., the "nest area" spatial scale), we measured vegetation along 4 30-m transects radiating in the cardinal directions at 2 available sites 250 m and 500 m from the nest. We used a table of random numbers (0º–360º) to select the azimuth to the 2 available sites at the nest area scale. Along each transect we collected visual obstruction measurements at the available location and at 10-m increments out to 30 m; sagebrush density was quantified at 10-m intervals out to 30 m; and canopy cover and height measurements at the available location and at 5-m intervals out to 30 m using the methods describe above. We completed our field measurements at the available sites within 2 days of measuring the used site to ensure conditions were comparable between the used and available sites.

A priori Model Development

We developed a set of *a priori* hypotheses to evaluate the relationship between sage-grouse nest-site selection and vegetation characteristics at both spatial scales. At the nest patch scale, we developed 18 candidate models (Appendix A) of which 17 assumed selection was a function of a combination of 15 covariates (Table 1), and 1 model assumed selection was random (Model 1, Appendix A). At the nest area scale, we developed 21 candidate models (Appendix B) of which 20 assumed selection was a function of a combination of 16 covariates (Table 1) and 1 model assumed selection was random (Model 1, Appendix B).

Vegetation cover and structure found around the nest provide the incubating female concealment from predators and insulation from thermal extremes (Bergerud 1988, Connelly et al. 2000, Coates 2007). Previous research demonstrated that nesting sage-grouse selected sagebrush and grass (Connelly et al. 1991, DeLong et al. 1995, Sveum et al. 1998, Holloran et al. 2005), specifically native grasses which exhibit a bunched growth form (i.e., bunchgrasses). Nesting sage-grouse may prefer the sagebrush/bunchgrass plant community over any other sagebrush/grass association (Cagney et al. 2010). Consequently, we developed models evaluating the response of selection to plant communities composed of sagebrush and total grass (Models 2−5, Appendix A; Models 2−5, Appendix B), sagebrush with bunchgrass (Models 6−7, Appendix A; Models 6, 8, Appendix B), sagebrush with rhizomatous grass (Model 8, Appendix A; Model 9, Appendix B), and sagebrush with cheatgrass (Model 9, Appendix

A; Model 10, Appendix B). Sagebrush density was measured at a larger scale making it applicable only to the nest area scale, so we created a model with this covariate and bunchgrass canopy cover (Model 7, Appendix B). In addition to canopy cover, vegetation provides lateral visual obstruction which was previously shown to be positively correlated with nest-site selection (Popham and Gutiérrez 2003, Kaczor et al. 2011, Musil 2011, Kirol et al. 2012). Therefore, we developed models incorporating lateral visual obstruction into the sagebrush/bunchgrass plant community (Model 11, Appendix A; Models 12, 14, Appendix B) and the sagebrush/rhizomatous grass plant community (Model 10, Appendix A; Models 11, 13, Appendix B).

Alternatively, nesting sage-grouse may select vegetation indicating the availability of future food resources (i.e., forbs and arthropods) for chicks (Johnson and Boyce 1990, Connelly et al. 2000), because the area surrounding the nest is often early brood-rearing habitat (Berry and Eng 1985). When females select nest-sites in the spring, most arthropods are not yet active, but previous research has shown that particular plants (e.g., rabbitbrush, forbs) were positively correlated with arthropod diversity and abundance (Thompson et al. 2006, Wenninger and Inouye 2008, Ersch 2009), therefore indicating the availability of future chick diet items. To test this hypothesis, we developed models (Models 12, 14, 16, Appendix A; Models 15, 18, 20, Appendix B) incorporating forb canopy cover and height. Wenninger and Inouye (2008) suggested that arthropod diversity and abundance in sagebrush ecosystems was positively correlated with plant diversity associated with non-sagebrush shrubs and forbs, so we included these covariates in nest-site selection models (Model 14, Appendix A; Model 17, Appendix B). Model 13 (Appendix A) and Model 16 (Appendix B) assessed the relationship between nest-sites and grass/annual forb cover which were previously found to be positively correlated with darkling beetles (Tenebrionidae; Ersch 2009). Last, Ersch (2009) found that Lepidopteron caterpillars were positively correlated with rabbitbrush cover, grass cover, and non-sagebrush shrub height (Ersch 2009) prompting us to develop models (Models 15−18, Appendix A; Models 18−21, Appendix B) incorporating these vegetation covariates. While Lepidopteron caterpillars have relatively large body sizes, they also have natural defense mechanisms including stinging hairs, glands that emit repellant chemicals, and storage of allelochemicals; thus, palatability of caterpillars for sage-grouse chicks may be influenced by presence of defense mechanisms (Ersch 2009).

Analytical Methods

We summarized the vegetation variables by calculating the average for each used and available site. Canopy cover categories were recoded to the mid-points of the range for each quadrat and averaged per site. We calculated a correlation matrix for all variables, and if Pearson's $r > |0.5|$ between a pair of variables, we selected the most biological reasonable variable that exemplified the essence of the underlying hypothesis. We fit nest-site selection models in 2 stages. First, during the screening process, we evaluated nonlinear forms of variables by fitting pseudothreshold, quadratic, and linear forms of each variable (Franklin et al. 2000). Also during the screening process, we identified the most supported measure of visual obstruction by comparing models of vertical visual obstruction at different heights and structural forms. We used the screening process to identify the most supported variable and structural form for sagebrush density (i.e., density for all sagebrush plants versus sagebrush plants ≥ 20 cm in height) and sagebrush canopy cover (i.e., canopy cover of all species of sagebrush versus canopy cover of only big sagebrush). We compared and ranked models using Akaike's Information Criterion for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002). We selected nonlinear forms if $\Delta AIC_c > 2$ above the linear form and an intuitive biological interpretation existed. We fit mixed models of explanatory variables to estimate nest-site selection that contained a random error term to account for the variability in multiple selections by the same female, within years and across years.

We used discrete choice modeling to evaluate nest-site selection at each spatial scale. Discrete choice models estimate the probability of an individual selecting a site as a function of the habitat characteristics of that site and all other available sites (Cooper and Millspaugh 1999, Cooper and Millspaugh 2001). We fit discrete choice models using the Multinomial Discrete Choice procedure in SAS 9.3 (SAS Institute, Inc., Cary, NC) to evaluate resource selection models related to our hypotheses about cover and food (Appendix A, Appendix B). We fit our *a priori* models incorporating the covariates identified by the screening process. We addressed model selection uncertainty by calculating model-averaged parameter estimates and unconditional standard errors from the 90% Akaike weight confidence set (Burnham and Anderson 2002). We estimated relative selection probabilities by varying explanatory variables of interest while holding other variables in the models at their mean values.

We calculated odds ratios and 95% confidence intervals for parameter estimates to assess which parameters in the 90% set had a stronger relationship with nest-site selection. Finally, we determined goodness-of-fit of our models by calculating the likelihood ratio index (ρ) for each model using:

$$\rho = 1 - \frac{LL(\hat{\beta})}{LL(\emptyset)}$$

where $LL(\hat{\beta})$ is the log-likelihood of the parameterized model and $LL(\emptyset)$ is the log-likelihood of the null model (Train 2003). The likelihood ratio index ranges from 0 to 1, with higher values closer to 1 signifying a better performing model compared to the null model (Train 2003).

We evaluated the predictive ability of the most supported discrete choice models at each spatial scale by using a modified *k*-fold cross-validation design (Boyce et al. 2002). The probability of a nest-site's selection is conditional on the available choice set; therefore, we randomly divided the data into 5 random subsets, each containing 20% of the choice sets. We successively removed 1 subset (testing data) and refit the model-averaged model using the remaining 80% (training data) which results in the calculation of new parameter coefficients each time. Validation was based on the testing data, where we fit selection probabilities to each option in every unique choice set and ranked them based on relative probability of use. We assessed the model performance by examining the percentage of nest-sites correctly predicted by the model. Given that we used sets of 4 choices at the nest patch scale and 3 choices at the nest area scale, we would expect predictive success of 25% and 33%, respectively, to be due to random chance alone. We anticipate a good predictive model to demonstrate a large proportion of nest-sites to be ranked as number 1.

When conducting studies at multiple spatial scales, cross-scale correlation can confound interpretation when habitat variables at different spatial scales are correlated with each other, because the habitat selection pattern associated with a given spatial scale could be the result of selection at another scale (Battin and Lawler 2006). To identify cross-scale correlations, we calculated Spearman's rank correlation coefficients for covariates from the most supported models at each spatial scale (Battin and Lawler 2006).

RESULTS

We captured, radio-marked, and monitored 44 female sage-grouse (*n* = 12 yearlings, *n* = 32 adults) in 2011, 52 female sage-grouse (*n* = 2 yearlings, *n* = 50 adults) in 2012, and 46 female sage-grouse (*n* = 1 yearlings, *n* = 45 adults) in 2013. We verified 38 initial nests (*n* = 16 successful) and 10 renests (*n* = 4 successful) in 2011; 37 initial nests (*n* = 14 successful) and 4 renests (*n* = 2 successful) in 2012; and 37 initial nests (*n* = 11 successful) and 8 renests (*n* = 1 successful) in 2013. Average hatch date in 2011 [13 June ± 12.2 days (SE)] and 2013 [10 June ± 13.0 days (SE)] was approximately 3 weeks later than in 2012 [22 May ± 8.6 days (SE)]. We calculated average sagebrush and grass canopy cover and height for used and available sites at both spatial scales (Table 2).

We included 109 sage-grouse nests (2011: *n* = 37, 2012: *n* = 37, 2013: *n* = 35) to evaluate nest-site selection models. At both spatial scales, the screening process identified lateral visual obstruction, sagebrush density, and sagebrush height as having pseudothreshold forms while identifying lateral visual obstruction 22.9−45.7 cm in height as most supported. At the nest area scale, the screening process identified the most supported sagebrush density covariate as the density of plants ≥ 20 cm tall. The screening process identified all species of sagebrush canopy cover as the most supported at the nest patch scale, but only big sagebrush canopy cover at the nest area scale.

Of the 18 models we evaluated at the nest patch spatial scale (Appendix A), model selection uncertainty existed with 2 models falling into the 90% confidence set of candidate models (Table 3); therefore, we model averaged parameter estimates and estimates of unconditional standard errors (Table 4). Both of the top models included the covariates bunchgrass canopy cover, lateral visual obstruction 22.9−45.7 cm in height, and rhizomatous grass canopy cover around the nest site (Table 3). Model averaged estimates and odds ratios demonstrated that the pseudothreshold form of lateral visual obstruction 22.9−45.7 cm in height was the only significant covariate (Table 4). The pseudothreshold form of lateral visual obstruction had a strong positive relationship with nest-site selection. Increasing the number of cm obstructed from 6 cm to 15 cm almost tripled the probability of selection (Figure 2). The 2 top models had relatively low likelihood ratio values (0.286 and 0.273; Table 3), but k-fold cross validation procedures correctly classified the actual nest-site in the test data being ranked first 59% of the time, with 25% ranked as the second-most probable, 11% third, and 5% fourth. Our nest patch scale top model predicted nest-site selection better than random chance by 34%.

Of the 21 models we evaluated at the nest area spatial scale (Appendix A), model selection uncertainty existed with 3 models falling into the 90% confidence set (Table 3); thus, we model-averaged estimates and calculated unconditional standard errors (Table 4). All of the top models included variables that provided cover around the nest. The most supported covariates included big sagebrush canopy cover, rhizomatous grass canopy cover, bunchgrass canopy cover, and pseudothreshold forms of sagebrush density and lateral visual obstruction 22.9−45.7 cm in height (Table 3). Model averaged estimates and odds ratios demonstrate that lateral visual obstruction was the only significant covariate related to nest-site selection (Table 4). Similar to the nest patch scale, visual obstruction had a strong positive relationship with nest-site selection. Increasing the number of cm obstructed from 5 to 11.5 tripled the relative probability of nest-site selection (Figure 3). The top 3 models had higher likelihood ratio values (i.e., 0.379, 0.379, and 0.375) than the nest patch scale (Table 3), and k-fold cross validation procedures correctly classified the actual nest-site in the test data being ranked as the most probable choice out of the choice set 65% of the time, with 28% ranked as the second-most probable, and 7% as third. Our model of nest area predicted nest-site selection with an improvement of 32% over random chance. Cross-scale correlation was present, as increased lateral visual obstruction occurred in the nest patch when lateral visual obstruction was selected for in the nest area ($\rho_s = 0.927$, $P < 0.0001$).

DISCUSSION

The importance of visual obstruction at tetraonid nests is well documented for sharp-tailed grouse (*Tympanuchus phasianellus*; Manzer and Hannon 2005, Goddard and Dawson 2009b), greater prairie-chickens (*Tympanuchus cupido*; Matthews et al. 2013), red grouse (*Lagopus lagopus scoticus*; Campbell et al. 2002), lesser prairie-chickens (*Tympanuchus pallidicinctus*; Pitman et al. 2005), white-tailed ptarmigan (*Lagopus leucurus*; Wiebe and Martin 1998), and willow ptarmigan (*Lagopus lagopus*; Schieck and Hannon 1993). Recent sage-grouse studies have also found that females select nest-sites with lateral visual obstruction at or around the nest bowl (Popham and Gutiérrez 2003, Kaczor et al. 2011, Musil 2011, Kirol et al. 2012). We did not find any previous studies on sage-grouse nest-site selection where visual obstruction was found to be unimportant when it was directly measured and subsequently considered as a covariate. Thus, the importance of lateral visual obstruction can be considered as an overriding feature of sage-grouse nesting habitat.

On our study area, overhead visual obstruction may offer the female the best tradeoff between lowering the risk of predation, increasing nest concealment from predators, and maintaining a favorable microclimate. Ground-nesting birds need to balance concealment of the eggs with a view of the surroundings for quick escape in the event of a predator's approach (Wiebe and Martin 1998). The probability of mortality to nesting white-tailed ptarmigan increased rapidly with increasing lateral cover at the nest-site, while the probability of the nest being depredated only declined gradually (Wiebe and Martin 1998). Increased visual obstruction less than 22.9 cm tall may inhibit the ability of the nesting female to detect approaching predators. Instead, females selected for lateral visual obstruction >22.9 cm tall. Vegetation structure selected by ground-nesting birds also provides protection from the sun and wind creating a favorable microclimate (Walsberg 1985, With and Webb 1993, Ar and Sidis 2002, Coates 2007). Considering that female sage-grouse spend 96% of their day incubating (Coates 2007), and the effects of nest insulation is less important to eggs when parents are present (Ar and Sidis 2002), nest insulation may have a stronger effect on parents than hatchability of eggs (Coates 2007). Nest insulation provided by vegetation results in parental energy-savings and decreased time foraging (Coates 2007). However, we did not study local predator communities or nest microclimates in the context of microhabitat component importance during nest-site selection (Ar and Sidis 2002, Coates and Delehanty 2010).

Overhead and lateral visual obstruction is supplied by structure from vegetation. Sage-grouse reside in ecosystems where structure is provided by varying mixtures of sagebrush and grass (Schroeder et al. 1999). Most previous sage-grouse nest-site selection research found that the composition of vegetation providing structure included sagebrush canopy cover, grass canopy cover, sagebrush height, and grass height (Fischer 1994, Gregg et al. 1994, Sveum et al. 1998, Holloran et al. 2005, Hagen et al. 2007). In our study lateral visual obstruction 22.9−45.7 cm in height was the only significant covariate related to nest-site selection. Although this result seems at odds with other sage-grouse nest-site selection studies, this discrepancy is likely a byproduct of the choice of field data, because those studies did not measure lateral visual obstruction. We did not find that vegetation composition was selected, because lateral visual obstruction explained selection better than vegetation composition. Lateral visual obstruction may be a central theme to nest-site selection by sage-grouse and tetraonids in general (Schieck and Hannon 1993, Wiebe and Martin 1998, Campbell et al. 2002, Manzer and Hannon 2005, Goddard and Dawson 2009b). In addition to lateral cover, nest-site selection tended to have a positive relationship with bunchgrass and a negative relationship with rhizomatous grass (Table 3). This general pattern lends support to the hypothesis that the native sagebrush/bunchgrass plant community provides an optimal mix of horizontal and vertical structure (Sveum et al. 1998, Cagney et al. 2010). Tall bunchgrasses supply lateral visual obstruction during the current year, but also conceal sage-grouse nests the following spring by providing residual, standing dead grass cover at the time of nest initiation. If improving sage-grouse nesting habitat is a priority, managers should consider practices aimed at enhancing plant communities composed of tall bunchgrasses and sagebrush.

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Table 1. Description for covariates used in models related to nest-site selection by Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Type	**Covariate**	**Description**
Canopy Cover	Bunchgrass	Bunchgrass canopy cover (%)[a]
	Rhizograss	Rhizomatous grass canopy cover (%)[a]
	Totgrass	Total grass canopy cover (%)[a]
	Bigsage	Big sagebrush (*Artemisia tridentata*) canopy cover (%)[a]
	Totsage	Total sagebrush (*Artemisia* spp.) canopy cover (%)[a]
	Cheatgrass	Cheatgrass (*Bromus tectorum*) canopy cover (%)[a]
	Broadforb	Broadleaf forb canopy cover (%)[a]
	Rabbitbrush	Rabbitbrush (*Chrysothamnus* spp. and *Ericameria nauseosa*) canopy cover (%)[a]
	Totshrub	Total shrub (non-sagebrush) canopy cover (%)[a]
	Totforb	Total forb canopy cover (%)[a]
	Annualforb	Annual forb canopy cover (%)[a]
Sagebrush Density	Totsagedensity	Density of sagebrush (plants/m^2)[b]
	Sagedensity	Density of sagebrush ≥ 20 cm in height (plants/m^2)[b]
Height	Grasshgt	Average grass height (cm)[c]
	Forbhgt	Average forb height (cm)[c]
	Shrubhgt	Average shrub (non-sagebrush) height (cm)[c]
	Sagehgt	Average sagebrush (*Artemisia* spp.) height (cm)[c]
Vertical Visual Obstruction	SectA	Number of cm > 50% visually obstructed from 0 cm to 22.9 cm in height[d]

	SectB	Number of cm > 50% visually obstructed from 22.9 cm to 45.7 cm in height[d]
	SectC	Number of cm > 50% visually obstructed from 45.7 cm to 68.6 cm in height[d]
	SectD	Number of cm > 50% visually obstructed from 68.6 cm to 91.5 cm in height[d]
	SectAB	Number of cm > 50% visually obstructed from 0 cm to 45.7 cm in height[d]

[a] Summarized from 96 measurements of 0.10-m^2 quadrats from 4 sites at the nest patch scale and 84 measurements from 3 sites at the nest area scale

[b] Summarized from 36 measurements from 3 sites at the nest area scale

[c] Summarized from 96 measurements from 4 sites at the nest patch scale and 84 measurements from 3 sites at the nest area scale

[d] Summarized from 96 measurements from 4 sites at the nest patch scale and 48 measurements from 3 sites at the nest area scale

Table 2. Vegetation characteristics at 109 locations used by female Greater sage-grouse for nest-sites and paired randomly available locations at 2 spatial scales on the Overland Trail Ranch, Wyoming, USA, 2011–2013. Means and standard deviation (in parentheses) are presented.

Spatial Scale	**Parameter**	**Used**	**Available**
Nest Patch	Sagebrush canopy cover (%)	30.4 (32.0)	22.8 (28.0)
	Sagebrush height (cm)	32.8 (19.5)	26.5 (17.5)
	Grass canopy cover (%)	22.5 (21.7)	23.0 (21.7)
	Grass height (cm)	13.3 (9.8)	12.7 (8.8)
Nest Area	Sagebrush canopy cover (%)	26.4 (30.8)	20.8 (26.9)
	Sagebrush height (cm)	30.2 (19.1)	22.6 (16.6)
	Grass canopy cover (%)	22.4 (21.8)	21.0 (21.6)
	Grass height (cm)	13.0 (9.6)	11.4 (7.3)

Table 3. Support for models in 90% confidence set (based on Akaike weights) explaining Greater sage-grouse nest-site selection at 2 spatial scales for 109 nests on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Spatial Scale	**Model**	**-2 LL**[a]	**K**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	w_i[e]	ρ[f]
Nest Patch	LSectB[g], Rhizograss	215.876	2	222.105	0.000	0.866	0.286
	LSectB, Bunchgrass	219.605	2	225.834	3.729	0.134	0.273
Nest Area	LSectB, Bigsage, Rhizograss	148.623	3	157.007	0.000	0.388	0.379
	LSectB, LDensity20, Rhizograss	148.686	3	157.071	0.063	0.376	0.379
	LSectB, Bigsage, Bunchgrass	149.626	3	158.010	1.003	0.235	0.375

[a] -2 LL: -2 times the log-likelihood estimate
[b] K: no. of parameters in each model
[c] AIC$_c$: Akaike's information criterion for small sample sizes
[d] ΔAIC$_c$: difference in AIC$_c$ between the model and the best performing model
[e] w_i: Akaike weights
[f] ρ: likelihood ratio index value
[g] L: pseudothreshold form (e.g., Franklin et al. 2000)

Table 4. Model-averaged parameter estimates and unconditional standard errors explaining Greater sage-grouse nest-site selection at 2 spatial scales for 109 nests on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Spatial Scale	**Parameter**	**Estimate**	**SE**	**Odds Ratio**	**Lower 95% CI**	**Upper 95% CI**
Nest Patch	Lateral visual obstruction 22.9−45.7 cm	1.166	0.161	3.210	2.341	4.402
	Rhizomatous grass	-0.021	0.021	0.979	0.940	1.020
	Bunchgrass	0.003	0.003	1.003	0.996	1.010
Nest Area	Lateral visual obstruction 22.9−45.7 cm	0.862	0.164	2.367	1.716	3.266
	Big sagebrush	0.028	0.017	1.029	1.000	1.063
	Rhizomatous grass	-0.024	0.019	0.976	0.940	1.014
	Sagebrush (>20 cm tall) density	0.231	0.185	1.260	0.877	1.810
	Bunchgrass	0.003	0.005	1.003	0.992	1.015

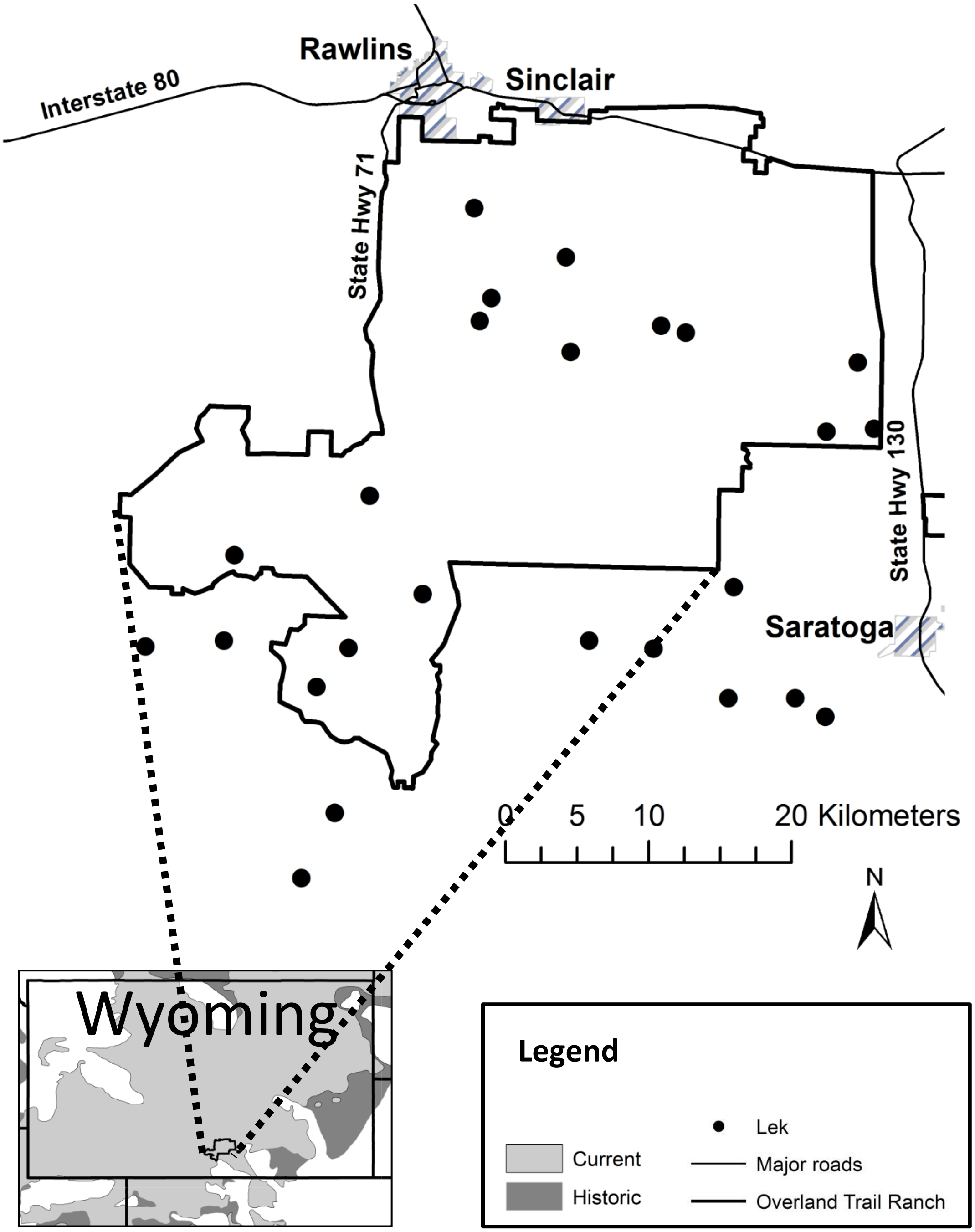

Figure 1. Map of study area showing the current and historic range of Greater sage-grouse (inset; Schroeder 2002), the Overland Trail Ranch, and locations of leks females were captured at during March and April 2010−2013 in Carbon County, Wyoming, USA.

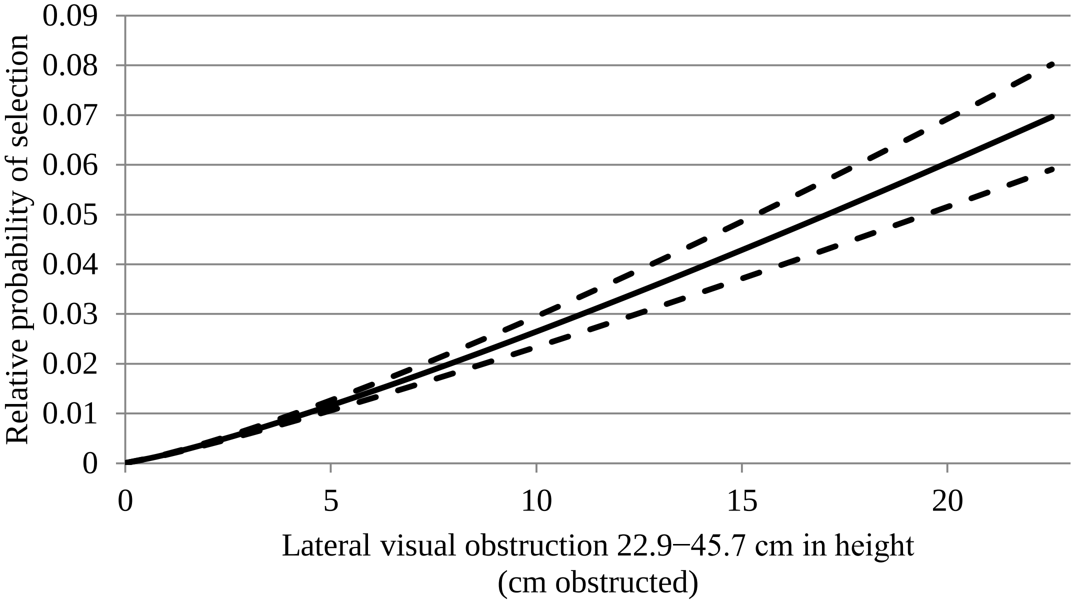

Figure 2. Influence of lateral visual obstruction 22.9−45.7 cm in height on the relative probability of nest-site selection at the nest patch scale for 109 nests on the Overland Trail Ranch, Wyoming, USA, 2011−2013. Dashed lines represent bootstrapped 95% confidence intervals.

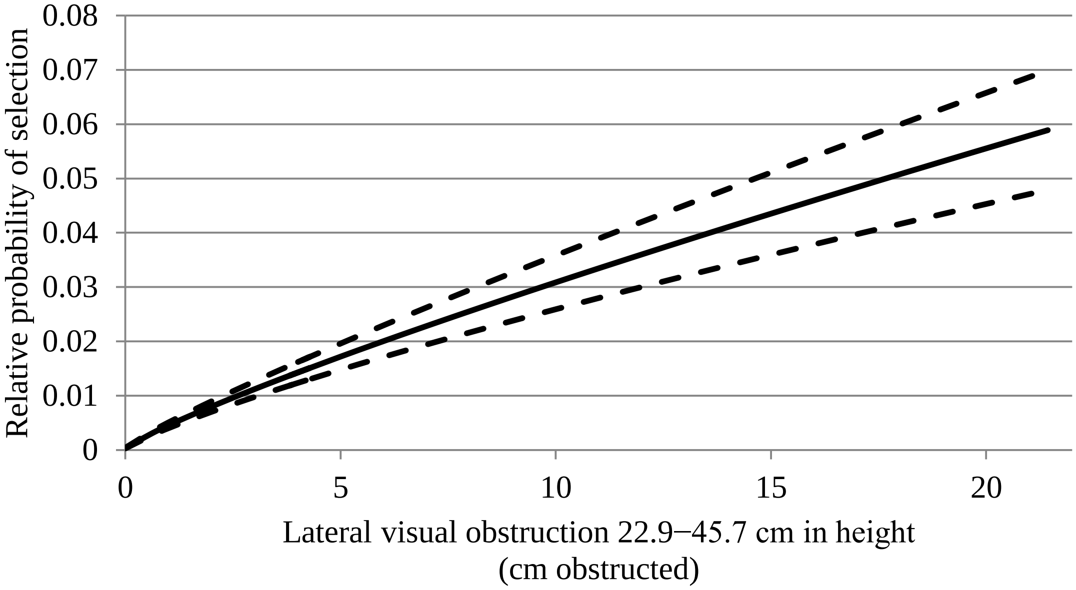

Figure 3. Influence of lateral visual obstruction 22.9−45.7 cm in height on the relative probability of nest-site selection at the nest area scale for 109 nests on the Overland Trail Ranch, Wyoming, USA, 2011−2013. Dashed lines represent bootstrapped 95% confidence intervals.

Appendix A. Models representing specific hypotheses about the influence of vegetation within 5 m on nest-site selection by female Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Model No.	Model	Model Structure	Predicted Results(s)	Units of Measurement
1	Null		Random Selection	
2	$S_{Totsage+Grasshgt}$	β_1(Totsage)+ β_2(Grasshgt)	$\beta_1>0$, $\beta_2>0$	% canopy cover^a + cm^b
3	$S_{Totgrass+Sagehgt}$	β_1(Totgrass)+β_2(Sagehgt)	$\beta_1>0$, $\beta_2>0$	% canopy cover^a + cm^b
4	$S_{Sagehgt+Grasshgt}$	β_1(Sagehgt)+β_2(Grasshgt)	$\beta_1>0$, $\beta_2>0$	cm^b + cm^b
5	$S_{Totgrass+Totsage}$	β_1(Totgrass)+β_2(Totsage)	$\beta_1>0$, $\beta_2>0$	% canopy cover^a + % canopy cover^a
6	$S_{Totsage+Bunchgrass}$	β_1(Totsage)+β_2(Bunchgrass)	$\beta_1>0$, $\beta_2>0$	% canopy cover^a + % canopy cover^a
7	$S_{Bunchgrass}$	β_1(Bunchgrass)	$\beta_1<0$	% canopy cover^a
8	$S_{Totsage+Rhizograss}$	β_1(Totsage)+β_2(Rhizograss)	$\beta_1>0$, $\beta_2<0$	% canopy cover^a + % canopy cover^a
9	$S_{Totsage+Cheatgrass}$	β_1(Totsage)+β_2(Cheatgrass)	$\beta_1>0$, $\beta_2<0$	% canopy cover^a + % canopy cover^a
10	$S_{VOR+Totsage+Rhizograss}$	β_1(VOR)+β_2(Totsage)+β_3(Rhizograss)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$	cm^c + % canopy cover^a + % canopy cover^a
11	$S_{VOR+Totsage+Bunchgrass}$	β_1(VOR)+β_2(Totsage)+β_3(Bunchgrass)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	cm^c + % canopy cover^a + % canopy cover^a

12	$S_{Broadforb+Forbhgt}$	$\beta1(\text{Broadforb})+\beta_2(\text{Forbhgt})$	$\beta_1>0, \beta_2>0$	% canopy cover[a] + cm[b]
13	$S_{Annualforb+Totgrass}$	$\beta_1(\text{Annualforb})+\beta_2(\text{Totgrass})$	$\beta_1>0, \beta_2>0$	% canopy cover[a] + % canopy cover[a]
14	$S_{Totforb+Totshrub}$	$\beta_1(\text{Totforb})+\beta_2(\text{Totshrub})$	$\beta_1>0, \beta_2>0$	% canopy cover[a] + % canopy cover[a]
15	$S_{Rabbitbrush+Forbhgt}$	$\beta_1(\text{Rabbitbrush})+\beta_2(\text{Forbhgt})$	$\beta_1>0, \beta_2>0$	% canopy cover[a] + cm[b]
16	$S_{Broadforb+Rabbitbrush}$	$\beta_1(\text{Broadforb})+\beta_2(\text{Rabbitbrush})$	$\beta_1>0, \beta_2>0$	% canopy cover[a] + % canopy cover[a]
17	$S_{Totgrass+Rabbitbrush+Shrubhgt}$	$\beta_1(\text{Totgrass})+\beta_2(\text{Rabbitbrush})+\beta_3(\text{Shrubhgt})$	$\beta_1>0, \beta_2>0, \beta_3>0$	% canopy cover[a] + % canopy cover[a] + cm[b]
18	$S_{Shrubhgt}$	$\beta_1(\text{Shrubhgt})$	$\beta_1>0$	cm[b]

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[a] Summarized from 84 measurements of 0.1-m2 quadrats from 3 30-m radius sites

[b] Summarized from 84 measurements from 3 30-m radius sites

[c] Number of cm > 50% visually obstructed among 4 22.9-cm tall sections on a Robel pole; summarized from 48 measurements at 3 30-m radius sites

Appendix B. Models representing specific hypotheses about the influence of vegetation within 30 m on nest-site selection by female Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Model No.	Model	Model Structure	Predicted Result(s)	Units of Measurement
1	Null		Random Selection	
2	$S_{Totsage+Grasshgt}$	β_1(Totsage)+ β_2(Grasshgt)	$\beta_1>0, \beta_2>0$	% canopy cover^{a} + cm^{b}
3	$S_{Totgrass+Sagehgt}$	β_1(Totgrass)+β_2(Sagehgt)	$\beta_1>0, \beta_2>0$	% canopy cover^{a} + cm^{b}
4	$S_{Sagehgt+Grasshgt}$	β_1(Sagehgt)+β_2(Grasshgt)	$\beta_1>0, \beta_2>0$	cm^{b} + cm^{b}
5	$S_{Totgrass+Totsage}$	β_1(Totgrass)+β_2(Totsage)	$\beta_1>0, \beta_2>0$	% canopy cover^{a} + % canopy cover^{a}
6	$S_{Totsage+Bunchgrass}$	β_1(Totsage)+β_2(Bunchgrass)	$\beta_1>0, \beta_2>0$	% canopy cover^{a} + % canopy cover^{a}
7	$S_{Sagedensity+Bunchgrass}$	β_1(Sagedensity)+β_2(Bunchgrass)	$\beta_1>0, \beta_2>0$	No. plants/sq. m^{c} + % canopy cover^{a}
8	$S_{Bunchgrass}$	β_1(Bunchgrass)	$\beta_1<0$	% canopy cover^{a}
9	$S_{Totsage+Rhizograss}$	β_1(Totsage)+β_2(Rhizograss)	$\beta_1>0, \beta_2<0$	% canopy cover^{a} + % canopy cover^{a}
10	$S_{Totsage+Cheatgrass}$	β_1(Totsage)+β_2(Cheatgrass)	$\beta_1>0, \beta_2<0$	% canopy cover^{a} + % canopy cover^{a}
11	$S_{VOR+Totsage+Rhizograss}$	β_1(VOR)+β_2(Totsage)+β_3(Rhizograss)	$\beta_1>0, \beta_2>0, \beta_3<0$	cm^{d} + % canopy cover^{a} + % canopy cover^{a}
12	$S_{VOR+Totsage+Bunchgrass}$	β_1(VOR)+β_2(Totsage)+β_3(Bunchgrass)	$\beta_1>0, \beta_2>0, \beta_3>0$	cm^{d} + % canopy cover^{a} + % canopy cover^{a}

13	$S_{VOR+Sagedensity+Rhizograss}$	β_1(VOR)+β_2(Sagedensity)+β_3(Rhizograss)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$	cm[d] + No. plants/sq. m[c] + % canopy cover[a]
14	$S_{VOR+Sagedensity+Bunchgrass}$	β_1(VOR)+β_2(Sagedensity)+β_3(Bunchgrass)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	cm[d] + No. plants/sq. m[c] + % canopy cover[a]
15	$S_{Broadforb+Forbhgt}$	$\beta 1$(Broadforb)+β_2(Forbhgt)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + cm[b]
16	$S_{Annualforb+Totgrass}$	β_1(Annualforb)+β_2(Totgrass)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + % canopy cover[a]
17	$S_{Totforb+Totshrub}$	β_1(Totforb)+β_2(Totshrub)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + % canopy cover[a]
18	$S_{Rabbitbrush+Forbhgt}$	β_1(Rabbitbrush)+β_2(Forbhgt)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + cm[b]
19	$S_{Broadforb+Rabbitbrush}$	β_1(Broadforb)+β_2(Rabbitbrush)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + % canopy cover[a]
20	$S_{Totgrass+Rabbitbrush+Shrubhgt}$	β_1(Totgrass)+β_2(Rabbitbrush)+β_3(Shrubhgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	% canopy cover[a] + % canopy cover[a] + cm[b]
21	$S_{Shrubhgt}$	β_1(Shrubhgt)	$\beta_1>0$	cm[b]

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[a] Summarized from 84 measurements of 0.1-m2 quadrats from 3 30-m radius sites

[b] Summarized from 84 measurements from 3 30-m radius sites

[c] Summarized from 36 measurements from 3 30-m radius sites

[d] Number of cm > 50% visually obstructed among 4 22.9-cm tall sections on a Robel pole; summarized from 48 measurements at 3 30-m radius sites

CHAPTER 2 - BROOD-REARING SITE SELECTION BY GREATER SAGE-GROUSE IN WYOMING

ABSTRACT

Habitat quality of sagebrush (*Artemisia* spp.) communities used by Greater sage-grouse (*Centrocercus urophasianus*; hereafter: sage-grouse) broods may affect chick survival, which is an important determinant of sage-grouse abundance. We monitored radio-equipped female sage-grouse (*n* = 44 in 2011; 52 in 2012; 46 in 2013) in south-central Wyoming to assess brood-rearing resource selection prior to construction of a wind energy facility. We fit discrete choice models within an information theoretic framework to identify selection of structural, vegetation, and arthropod microhabitat components by female sage-grouse rearing broods. Sage-grouse selected brood-rearing sites (*n* = 105) with greater lateral visual obstruction close to the ground, more sagebrush canopy cover, and greater relative abundance of arthropods compared to available sites. Our study is the first to report sage-grouse broods' selection of areas with greater relative arthropod abundance, but not necessarily greater forb cover. We noted that females with broods avoided areas with greater biomass of Coleoptera (beetles), probably due to habitat segregation by beetle body size. Management practices aimed at conserving vegetation that provides concealing cover, such as the sagebrush/bunchgrass plant community, intermixed with vegetation that supports arthropods, such as numerous, small patches of wet meadows with tall grass, might help improve sage-grouse chick survival on our study area.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations throughout North America were recently listed as “warranted but precluded” under the Endangered Species Act, because sage-grouse populations are declining as a result of loss and degradation of obligatory sagebrush (*Artemisia* spp.) habitat (Connelly and Braun 1997, United States Fish and Wildlife Service 2010). Habitat used by female sage-grouse rearing broods may affect the survival of sage-grouse chicks through a variety of extrinsic factors, including cover and food availability (Gregg 2006, Thompson et al. 2006, Dahlgren 2009). The quality of brood-rearing habitat varies temporally and spatially due to biotic and abiotic factors (Aldridge and Boyce 2007, Aldridge et al. 2008, Dahlgren et al. 2010). The survival of sage-grouse chicks in this area is low (Chapter 3), so it is important to study resource selection to understand how chicks are using their environment.

Animals try to balance the tradeoff between nutrient/energy intake (i.e., foraging) and predation risk (Lima 1998). Maternal female sage-grouse must balance cover and food requirements for their chicks with the relative risk of predation. Thus, protective cover is needed during the brood-rearing stage (Schroeder et al. 1999), along with specific food resources (i.e., forbs and arthropods) for growth and development of chicks (Johnson and Boyce 1990, Drut et al. 1994). Previous research has identified high-protein arthropods as a critical food source for precocial tetraonid chicks for several weeks post-hatch (Hill 1985, Johnson and Boyce 1990, Jamison et al. 2002, Hannon and Martin 2006). After this critical early brood-rearing period, their diet gradually transitions to mostly forbs (Klebenow 1969). In addition, forbs may attract arthropods (Blenden et al. 1986, Hull et al. 1996, Jamison et al. 2002) and provide a diverse plant community which may support higher abundances of arthropods (Wenninger and Inouye 2008). Previous sage-grouse studies examining the relative importance of cover versus food during brood-rearing have yielded inconsistent results. Some studies found broods selected areas with increasing food resources consisting of forbs and arthropods (Drut et al. 1994, Sveum et al. 1998, Holloran 1999, Gregg 2006, Rebholz 2007), but others found broods selected areas with increasing protective cover provided by sagebrush and grass (Aldridge and Brigham 2002, Thompson et al. 2006, Kaczor et al. 2011, Kirol et al. 2012). Our objective was to evaluate resource selection patterns by female sage-grouse with broods.

STUDY AREA

Our study area is located in south-central Wyoming, USA and encompasses the approximately 1,295 km^2 Overland Trail Ranch (hereafter, the ranch) and surrounding areas (Figure 4). The area is 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. The ranch is managed as an open range yearling cattle operation and the Power Company of Wyoming, LLC has proposed to build a wind energy facility on the ranch consisting of ~1,000 turbines capable of generating 2,000–3,000 megawatts (see Bureau of Land Management 2012).

Annual precipitation over the past 60 years averaged 22.8 cm in Rawlins, WY which is 6 km from the northern boundary of the study area and 24.6 cm in Saratoga, WY which is 14 km from the eastern edge of the study area (Western Regional Climate Center 2013). Higher elevation areas up to 2,590 m near the Continental Divide in the southwestern portion of the study area receive more precipitation than lower elevation areas (i.e., 1,890 m) near the North Platte River (Google Earth, Google, Inc., Mountain View, CA). Sources of water on the ranch include livestock impoundments, natural springs, ephemeral drainages, the North Platte River, and Sage Creek. The study area is characterized topographically by a central basin that transitions 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 range is 0.7–12.7 C between November and April and 15.3–28.5 C between May and October (Western Regional Climate Center 2013).

Vegetation cover on the ranch is categorized into 3 ecoregions: rolling sagebrush steppe, salt desert shrub basins, and foothill shrublands (Chapman et al. 2004). The dominant ecoregion is rolling sagebrush steppe which is characterized by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations, mountain big sagebrush (*A. t. vaseyana*) at higher elevations, silver sagebrush (*A. cana*) in areas where the water table is ≤ 1 m of the soil surface (Thatcher 2006), and black sagebrush (*A. nova*) in exposed, rocky soils (Chapman et al. 2004). Other shrubs include various species of rabbitbrush (*Chrysothamnus* spp. and *Ericameria nauseosa*); common forbs include cushion-like phlox (*Phlox* spp.), goldenweed (*Stenotus acaulis*), clover (*Trifolium* spp.), madwort (*Alyssum* spp.), and vetch (*Astragalus* spp.); common grasses include western wheatgrass (*Elymus smithii*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), Sandberg bluegrass (*Poa secunda*), and prairie junegrass (*Koeleria macrantha*; Bureau of Land Management 2012).

The low elevation center of the ranch is characterized by a salt desert shrub basin which comprises approximately 19% of the study area and is characterized by sparse vegetation cover of Gardner's saltbush (*Atriplex gardneri*), shadscale (*Atriplex confertifolia*), and black greasewood (*Sarcobatus vermiculatus*; Chapman et al. 2004). Forbs are scarce and are usually comprised of cushion-like phlox. Grass species include alkali cordgrass (*Spartina gracilis*), Indian ricegrass (*Oryzopsis hymenoides*), blowout grass (*Redfieldia flexuosa*), alkali wildrye (*Leymus simplex*), and needle-and-thread (Bureau of Land Management 2012).

The higher-elevation portion of the study area consists of montane deciduous shrublands comprising approximately 15% of the study area with 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*; Chapman et al. 2004). A variety of broadleaf forbs are abundant including vetch, clover, and lupine (*Lupinus spp.*). Common grasses are blue grama, prairie junegrass, and western wheatgrass (Bureau of Land Management 2012). Vegetation communities found in moist areas are dissimilar to the surrounding ecoregion. Generally, moist areas are dominated by grasses, forbs, wetland sedges (*Carex* spp.), and rushes (*Juncus* spp.) creating green, open patches within a mosaic of sagebrush (Chapman et al. 2004).

METHODS

Field Methods

We assessed brood-rearing site selection by monitoring radio-equipped female sage-grouse with broods. During March and April of 2010–2013, we captured female sage-grouse near leks equally distributed among anticipated wind energy development regions and regions without anticipated wind energy development. After capturing female sage-grouse using spotlighting techniques (Giesen et al. 1982), we attached 30-g rump-mounted (Rappole and Tipton 1991) Global Positioning System Platform Transmitter Terminals (GPS PTTs; Microwave Telemetry, Inc., Columbia, MD). Capture and handling was conducted under protocols approved by the University of Missouri Animal Care and Use Committee permit number 6750.

Each GPS PTT collected 8 locations/day during the summer while females were rearing broods and was equipped with an Ultra High Frequency (UHF) transmitter operational for approximately 8 hrs/day to facilitate ground-tracking. We downloaded GPS PTT location data from Argos satellites every 3−5 days. After a nest successfully hatched (see Chapter 1), we initiated our efforts to conduct field measurements to assess brood-rearing site selection by characterizing the vegetation and arthropod community at locations used by a female with chicks. We verified the female had chicks by spotlighting (see Chapter 3) the brood within the 4 days prior to measuring resources at the site. To select a location where resources would be measured, we randomly selected, without replacement, 1 GPS PTT location that the female used within the past 4 days during daylight hours. For each brooding female, we selected and measured resources at a minimum of 1 location during the first 7 days-post-hatch, 1 location during 8−14 days-post- hatch, and 1 location approximately every 14 days until the chicks were absent or reached 70 days of age. We measured the vegetation characteristics along 4 20-m transects centered on the used location radiating in the cardinal directions and recorded data in Allegro CX and MX data loggers (Juniper Systems, Logan, UT).

Along each transect we measured lateral visual obstruction using a modified Robel pole (Robel et al. 1970, Benkobi et al. 2000) as a coverboard in which we partitioned the Robel pole into 4 vertical sections, each with 18 1.27-cm segments. We tallied the number of segments having >50% obstruction in each segment from a distance of 4 m and a height of 1 m while facing the used location. We recorded these visual obstruction measurements at the used location in each cardinal direction and at 5-m increments out to 20 m along each transect.

We estimated canopy cover using a 0.1 m^2 quadrat (Daubenmire 1959) for which we estimated the cover class of each of the following categories: big sagebrush, black sagebrush, silver sagebrush, total sagebrush, greasewood, rabbitbrush, saltbush, other non-sagebrush shrubs, total non-sagebrush shrubs, cushion-like phlox, goldenweed , vetch, clover, madwort, unknown forb, total broadleaf forb, total cushion forb, total forb, bunchgrass, rhizomatous grass, sedges, cheatgrass (*Bromus tectorum*), and total grass. We measured the height of the plant closest to the corner of the quadrat nearest the transect increment for sagebrush, non-sagebrush shrub, forb, and grass. We measured canopy cover and height at the used location in each cardinal direction and at 2.5-m increments out to 20 m along each transect.

We estimated sagebrush density using the point-centered-quarter method (Cottam and Curtis 1956) at the used location and at 10-m increments out to 20 m along each transect. At each increment along the transect, we measured the distance to the nearest sagebrush plant and the nearest sagebrush plant >20 cm tall in each quarter of a variable radius circular plot. All measurements were truncated at 5 m radius.

To estimate relative abundance of arthropods at the used site, we collected arthropods along 4 20-m transects centered on the used location radiating in the intercardinal directions (i.e., NE, SE, SW, and NW) with a gasoline-powered backpack aspirator with a collection bag (model 1612; John W. Hock Company, Gainesville, FL). We collected arthropods from 1-m^2 quadrats located 10 m and 20 m along the NE transect, 20 m along the SE transect, 10 m and 20 m along the SW transect, and 20 m along the NW transect ($n = 6$). Each 1-m^2 quadrat was covered with netting (0.0635 cm diameter opening) to keep arthropods from escaping. We dropped the netting over the ground and vegetation in a manner so as not to disturb the vegetation and arthropods prematurely. We vacuumed soil and vegetation surfaces within the net for 2 minutes, putting equal effort into collecting ground-dwelling, vegetation-dwelling, and flying arthropods. We transferred the collected material to a labeled, re-sealable bag and placed in a freezer at the end of the day.

To quantify available brood-rearing habitat, we measured vegetation and collected arthropods using the techniques described above at 3 available sites 50 m, 250 m, and 500 m away from the used location. We used a table of random numbers to select the azimuth (0º−360º) to each available site. We completed our field measurements at the available sites within 2 days of measuring the used site to ensure conditions were comparable between the used and available sites.

We investigated whether arthropod activity varied throughout the day (e.g., Lewis and Taylor 1965, Saunders et al. 2002) and biased our estimates if not collected at the same time of day that the female and brood were present. We identified 6 sites used by female sage-grouse with broods and collected arthropods 4 times a day [morning (07:00−09:00), noon (11:00−13:00), afternoon (14:00−17:00), and evening (18:00−20:00)] at each location using the methods described above during July and August 2012. We collected arthropods at a site used by a sage-grouse brood and a site representing an available site 100 m away from the used site. In the morning, we collected arthropods along the *intercardinal* direction using the protocols described above at the used and available site. At noon, we collected arthropods along the *cardinal* directions at the same used and available sites. To avoid collecting arthropods at a site disturbed earlier in the day, we collected arthropods in the afternoon at a site directly adjacent (i.e., 40 m center to center) to the used and available site along the intercardinal transects. In the evening, we collected arthropods at the adjacent sites along the cardinal transects.

***A priori* Model Development**

We developed a set of *a priori* hypotheses to evaluate the relationship between sage-grouse brood-rearing site selection and vegetation and arthropod habitat components. We developed 17 candidate models (Appendix C) divided into 2 broad sections testing hypotheses related to the relative importance of cover (Models 2−7, Appendix C) vs. food (Models 8−17, Appendix C). Specifically, previous research found that selection of brood-rearing sites increases with increasing cover provided by sagebrush and native bunchgrasses, but decreases with forbs, cheatgrass (*Bromus tectorum*), and rabbitbrush (Aldridge and Brigham 2002, Kirol et al. 2012). Therefore, we created Models 2−4 (Appendix C) incorporating these variables. Thompson et al. (2006) found that brooding sage-grouse in Wyoming selected sites with more cover of sagebrush and bunchgrass, fewer arthropods, and forbs were inconsequential to selection. Thus, Models 5−7 (Appendix C) incorporate varying combinations of sagebrush, grass, forb, and arthropod variables. In addition to canopy cover, vegetation provides lateral visual obstruction which may be positively correlated with brood-rearing site selection; therefore, we included this variable in Models 3, 5, and 6 (Appendix C).

Alternatively, female sage-grouse with broods may select areas with more food resources for chicks. Models 8−11 (Appendix C) test whether selection increases with increasing herbaceous vegetation and decreasing sagebrush cover (Klebenow 1969, Klott and Lindzey 1990, Sveum et al. 1998, Holloran 1999, Lyon 2000). Bringing arthropods into the equation, Models 12−15 (Appendix C) incorporate herbaceous covariates and different arthropod Orders, given that previous research suggests that selection increases with increasing herbaceous vegetation and relative arthropod abundance, but decreasing sagebrush cover (Fischer et al. 1996, Rebholz 2007, Gregg and Crawford 2009). We included visual obstruction in Models 10 and 12 (Appendix C), because herbaceous vegetation can also provide lateral visual obstruction. Models 16−17 (Appendix C) assess the relationship between brood-rearing sites and grass height, annual forb cover, and rabbitbrush cover which were all previously found to be positively correlated Lepidopteron caterpillars and adults (Ersch 2009). While Lepidopteron caterpillars represent a high-protein food source, they also have natural defense mechanisms including stinging hairs, glands that emit repellant chemicals, and storage of allelochemicals. Consequently, palatability of caterpillars may affect chicks' selection patterns (Ersch 2009).

Analytical Methods

Canopy cover categories were recoded to the mid-points of the range for each quadrat. We summarized the vegetation covariates by calculating the mean value for each used and available site. Frozen intact arthropods and identifiable pieces were sorted to Order, oven-dried at 55 C for 24 hrs, and weighed to 0.001 g. The author trained technicians sorting arthropods and conducted random quality control checks. Technicians used a dissecting microscope, key (Triplehorn and Johnson 2004), and color field guide (Eaton and Kaufman 2007) to sort arthropods. Intact arthropods were counted. Unidentifiable arthropods and pieces were placed in an “unknown” category and weighed but not counted. We maintained count and biomass by Order for each used and available site in addition to summarizing total count and biomass per site. After the 2012 field season, we dropped arthropods from our sampling protocol due to the expense to collect and sort these data. To test whether there were differences in arthropod availability during different times of the day, we conducted a single-factor ANOVA on total arthropod biomass at used and representative available sites.

We pooled 2011 and 2012 data which allowed us to analyze models incorporating vegetation and arthropod covariates (Appendix C). We analyzed vegetation models from all 3 years (Appendix D) in a separate analysis. We fit brood-rearing site selection models in 2 stages. The first stage consisted of a screening process during which we analyzed individual vegetation and arthropod covariates and compared models containing different structural forms (i.e., linear, pseudothreshold, quadratic). We compared and ranked models using Akaike’s Information Criterion for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002). For the vegetation covariates, we selected nonlinear forms if the nonlinear form was > 2 ΔAIC_c above the linear form and an intuitive biological interpretation existed. During the screening process, we also compared models containing different measures of sagebrush density, sagebrush canopy cover, and lateral visual obstruction. For the arthropod covariates, we identified the most supported structural form and either biomass or count as the most supported metric for the summed data and by Order. For the arthropod covariates, we considered all covariates ≤ 4 ΔAIC_c of the top covariate for each category, because we did not want to be too stringent during the screening process. After the most supported structural form of each covariate had been identified, we calculated a correlation matrix for those variables and selected the most biological reasonable variable for each pair if Pearson's $r > |0.5|$.

During the second stage, we fit discrete choice models related to our hypotheses about cover and food (Appendix C, Appendix D) using the covariates identified by the screening process (Cooper and Millspaugh 1999, Cooper and Millspaugh 2001). Our discrete choice models contained a random error term to account for the variability in multiple observations of the same female, within years and across years. After fitting our *a priori* models (Appendix C, Appendix D) using the Multinomial Discrete Choice procedure in SAS 9.3 (SAS Institute, Inc., Cary, NC), we searched for appropriate models during *post-hoc* analyses. We addressed model selection uncertainty by calculating model-averaged parameter estimates and unconditional standard errors from the 90% Akaike weight confidence set (Burnham and Anderson 2002). We estimated relative selection probabilities by varying explanatory variables of interest while holding other variables in the models at their mean values.

To assess which parameters in the 90% Akaike weight confidence set had a stronger relationship with brood-rearing site selection, we calculated odds ratios and 95% confidence intervals for parameter estimates. We determined goodness-of-fit of our models by calculating the likelihood ratio index (ρ) for each model using:

$$\rho = 1 - \frac{LL(\hat{\beta})}{LL(\emptyset)}$$

where $LL(\hat{\beta})$ is the log-likelihood of the parameterized model and $LL(\emptyset)$ is the log-likelihood of the null model (Train 2003). The likelihood ratio index ranges from 0 to 1, with higher values closer to 1 signifying a better performing model compared to the null model (Train 2003).

We evaluated the predictive ability of our top models by using a modified k-fold cross-validation design (Boyce et al. 2002). The probability of a brood-rearing site's selection is conditional on the available choice set; therefore, we randomly divided the data into 5 random subsets, each containing 20% of the choice sets. We successively removed 1 subset (testing data) and refit the model-averaged model using the remaining 80% (training data) which results in the calculation of new parameter coefficients each time. Validation was based on the testing data, where we fit selection probabilities to each option in every unique choice set and ranked them based on relative probability of use. We assessed model performance by examining the percentage of brood-rearing sites correctly predicted by the model. Given that the choice set consisted of 4 options, we would expect predictive success of 25% due to random chance alone. We expect a good predictive model to demonstrate a large proportion of brood-rearing sites to be ranked as number 1.

RESULTS

We captured, radio-marked, and monitored 44 female sage-grouse (*n* = 12 yearlings, *n* = 32 adults) in 2011, 52 females (*n* = 2 yearlings, *n* = 50 adults) in 2012, and 46 female sage-grouse (*n* = 1 yearlings, *n* = 45 adults) in 2013. Twenty nests were successful in 2011, 16 in 2012, and 12 in 2013. Across all used and available sites, we collected 14 orders of arthropods weighing 24.5 g consisting of 9,117 intact arthropods plus pieces. The 3 most common orders by weight were Coleoptera (8.462 g; beetles), Hymenoptera (6.257 g; ants, bees, and wasps), and Orthoptera (2.092 g; grasshoppers and crickets). Arthropod biomass in the unknown category was 14% of total biomass. Total arthropod biomass did not differ throughout the day at representative used sites ($p = 0.541$; $df = 3$; $F = 0.739$) or available sites ($p = 0.599$; $df = 3$; $F = 0.638$). The screening process for the 2011−2012 analysis found that the most supported sagebrush covariates (Table 5) were density of sagebrush plants ≥ 20 cm tall and canopy cover of total sagebrush. All vegetation covariates had a linear relationship with the response variable except for a pseudothreshold form of lateral visual obstruction 0−22.9 cm in height. For arthropods, the most supported structural form for all covariates was linear except for the pseudothreshold forms of Coleoptera biomass and total number of arthropods. For the summarized arthropod data, total number was more supported than total biomass.

We measured 105 brood-rearing sites ($n = 42$ in 2011, $n = 31$ in 2012, $n = 32$ in 2013) to assess brood-rearing-site selection models. The 2011−2012 *post-hoc* analysis found that female sage-grouse with broods selected areas providing both cover and food resources (Table 6), consisting of a combination of covariates from multiple *a priori* hypotheses (Appendix C). Specifically, broods selected areas with sagebrush cover in addition to lateral visual obstruction close to the ground (Figure 5). Increasing sagebrush canopy cover from 15% to 33% or doubling the number of cm visually obstructed close to the ground doubled the relative probability of selection by female sage-grouse with broods (Figure 5). In regard to food resources, broods selected areas with more arthropods, but surprisingly forbs were inconsequential to selection (Table 6, Figure 6). Contrary to our predictions, broods avoided areas with greater biomass of Coleoptera (beetles; Figure 6). The 2011−2012 top model had a relatively low likelihood ratio value of 0.195 (Table 6), but *k*-fold cross validation procedures correctly classified the actual brood-rearing sites in the test data ranked first 43% of the time, with 36% ranked as the second-most probable, 16% third, and 5% fourth. For the 2011−2013 vegetation analysis, model selection uncertainty existed with model-averaged estimates and odds ratios indicating the only significant covariate was lateral visual obstruction 0−22.9 cm in height. The 3 year dataset provides support for the shorter 2 year dataset regarding the importance of lateral visual obstruction to brood-rearing site selection.

DISCUSSION

Our study is the first to report sage-grouse broods selecting for greater relative arthropod abundance, but not necessarily more forbs. Forbs and grasses are positively correlated with arthropod abundance (Hull et al. 1996, Jamison et al. 2002), and several studies have documented sage-grouse broods selecting areas with increased forbs (Klebenow and Gray 1968, Drut et al. 1994, Sveum et al. 1998, Holloran 1999, Gregg 2006). However, whether broods were selecting these areas for the forbs or the arthropods found on the forbs was unclear. Separating the influence of forbs and arthropods on brood-rearing site selection is difficult. On the Overland Trail Ranch, sage-grouse broods selected for arthropods regardless of their proximity to forbs. Thompson et al. (2006) reported that sage-grouse broods in Wyoming avoided areas with higher relative abundance of arthropods, but Thompson et al. (2006) used pitfall traps for collecting arthropods. Pitfall traps primarily collect ground-dwelling arthropods including Coleoptera and Hymenoptera, specifically ants (Formicidae; Thompson et al. 2006). Our results indicate that ants were unimportant to selection while Coleoptera biomass was negatively related with selection. Pitfall traps may limit the user from adequately describing the arthropod community available to sage-grouse chicks. Other research suggesting that brooding sage-grouse select for cover almost exclusively (e.g., Aldridge and Brigham 2002, Kaczor et al. 2011, Kirol et al. 2012) did not quantify arthropods.

Our result of sage-grouse broods avoiding areas with greater biomass of beetles may be an artifact of habitat segregation by beetle body size. Vegetation heterogeneity has a strong bottom-up influence on the small-scale distribution of ground-dwelling beetles (Noemí Mazía et al. 2006), because they are attracted to shrubs for food, shade, and protection from predators (Whicker and Tracy 1987, Parmenter et al. 1989, Stapp 1997, Groner and Ayal 2001). Previous research suggests that larger-bodied beetles were restricted to shrub habitats providing predator protection and avoided open habitats, while smaller-bodied beetles were equally distributed among shrub-covered and open habitats (Groner and Ayal 2001). During our study, we observed a wide range of body sizes ranging from large scarabs (Scarabaeidae) and darkling beetles (Tenebrionidae) to intermediate ground beetles (Carabidae) to tiny leaf beetles (Chrysomelidae) and weevils (Curculionidae). We found that beetle biomass was correlated with sagebrush canopy cover ($r = 0.32$), height ($r = 0.25$) and density ($r = 0.38$). During years with average precipitation on our study area (2011, 2013), a healthy herbaceous understory supporting large quantities of arthropods can experience widespread growth beneath the shrub overstory. However, during droughts (2012) arthropod production may be limited to open habitats such as wet meadows, swales, springs, ditches, and reservoirs (Wenninger and Inouye 2008). The pattern of broods avoiding beetles was strongest in 2012 during which time we would expect broods to stay near open wet meadows, the areas that large-bodied beetles likely avoided (e.g., Groner and Ayal 2001).

In addition to arthropod food resources, sage-grouse broods on our study area selected areas with concealing cover, specifically lateral visual obstruction and sagebrush canopy cover. Broods may be balancing the risk of predation with the reward of food (e.g., Holbrook and Schmitt 1988, Lima 1998). Predator avoidance has been suggested to constrain selection of foraging habitats for Merriam's turkey (*Meleagris gallopavo merriam*; Rumble and Anderson 1996), white-throated sparrows (*Zonotrichia albicollis*; Schneider 1984), and sharp-tailed grouse (*Tympanuchus phasianellus*; Kobridger 1965). Our findings lend support to previous sage-grouse researchers who suggested that high quality brood-rearing habitat consists of areas with abundant food resources in close proximity to protective sagebrush cover (Klebenow 1969, Klott and Lindzey 1990, Sveum et al. 1998).

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Table 5. Description for covariates used in models related to brood-rearing site selection by Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Type	**Covariate**	**Description**
Canopy Cover	Bunchgrass	Bunchgrass canopy cover (%)[a]
	Rhizograss	Rhizomatous grass canopy cover (%)[a]
	Totgrass	Total grass canopy cover (%)[a]
	Bigsage	Big sagebrush (*Artemisia tridentata*) canopy cover (%)[a]
	Totsage	Total sagebrush (*Artemisia* spp.) canopy cover (%)[a]
	Cheatgrass	Cheatgrass (*Bromus tectorum*) canopy cover (%)[a]
	Broadforb	Broadleaf forb canopy cover (%)[a]
	Rabbitbrush	Rabbitbrush (*Chrysothamnus* spp. and *Ericameria nauseosa*) canopy cover (%)[a]
	Totshrub	Total shrub (non-sagebrush) canopy cover (%)[a]
	Totforb	Total forb canopy cover (%)[a]
	Annualforb	Annual forb canopy cover (%)[a]
Sagebrush Density	Totdensity	Density of sagebrush (plants/m^2)[b]
	Density20	Density of sagebrush $\geq$ 20 cm tall (plants/m^2)[b]
Height	Grasshgt	Average grass height (cm)[c]
	Sagehgt	Average sagebrush (*Artemisia* spp.) height (cm)[c]
Visual Obstruction	SectA	Number of cm > 50% visually obstructed from 0 cm to 22.9 cm in height[d]
	SectB	Number of cm > 50% visually obstructed from 22.9 cm to 45.7 cm in height[d]

	SectC	Number of cm > 50% visually obstructed from 45.7 cm to 68.6 cm in height[d]
	SectD	Number of cm > 50% visually obstructed from 68.6 cm to 91.5 cm in height[d]
	SectAB	Number of cm > 50% visually obstructed from 0 cm to 45.7 cm in height[d]
Arthropods	BmColeoptera	Biomass of Coleoptera (g)[e]
	NoColeoptera	Number of Coleoptera [e]
	BmHymenoptera	Biomass of Hymenoptera (g) [e]
	NoHymenoptera	Number of Hymenoptera [e]
	BmLepidoptera	Biomass of Lepidoptera adults (g) [e]
	NoLepidoptera	Number of Lepidoptera adults [e]
	BmSoftbodylarva	Biomass of soft body larva including caterpillars (g) [e]
	NoSoftbodylarva	Number of soft body larva including caterpillars [e]
	BmOrthoptera	Biomass of Orthoptera (g) [e]
	NoOrthoptera	Number of Orthoptera [e]
	BmTotal	Total arthropod biomass (g) [e]
	NoTotal	Total number of arthropods [e]

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[a] Summarized from 144 measurements of 0.1-m^2 quadrats from 4 20-m radius sites

[b] Summarized from 144 measurements from 4 20-m radius sites

[c] Summarized from 144 measurements from 4 20-m radius sites

[d] Summarized from 80 measurements from 4 20-m radius sites

[e] Summarized from arthropods collected from 24 1-m^2 quadrats from 4 20-m radius sites

Table 6. Support for post-hoc models in 90% confidence set (based on Akaike weights) explaining Greater sage-grouse brood-rearing site selection in 2011–2012 (n = 73) on the Overland Trail Ranch, Wyoming, USA.

Model	**LL**[a]	**K**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	w_i[e]	ρ[f]
LSectA[g], LBmColeoptera, LNoTotal, Totsage	-81.471	5	173.837	0.000	0.986	0.195

[a] LL: log likelihood

[b] K: no. of parameters in each model

[c] AIC$_c$: Akaike's information criterion for small sample sizes

[d] ΔAIC$_c$: difference in AIC*c* between the model and the best performing model

[e] w_i: Akaike weights

[f] ρ: likelihood ratio index value

[g] L: pseudothreshold form (e.g., Franklin et al. 2000)

Table 7. Parameter estimates, standard errors (SE), odds ratios, and 95% odds ratio confidence intervals for the models in the 90% confidence set (based on Akaike weights) explaining brood-rearing site selection by female Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA.

Parameter	**Estimate**	**SE**	**Odds Ratio**	**Lower 90% CI**	**Upper 90% CI**
LSectA[a]	1.322	0.549	3.750	1.516	9.274
LColeoptera biomass	-1.951	0.722	0.142	0.043	0.468
LTotal no. of arthropods	0.395	0.195	1.485	1.076	2.048
Sagebrush canopy cover	0.039	0.023	1.039	1.001	1.079

[a] L: pseudothreshold form (e.g., Franklin et al. 2000)

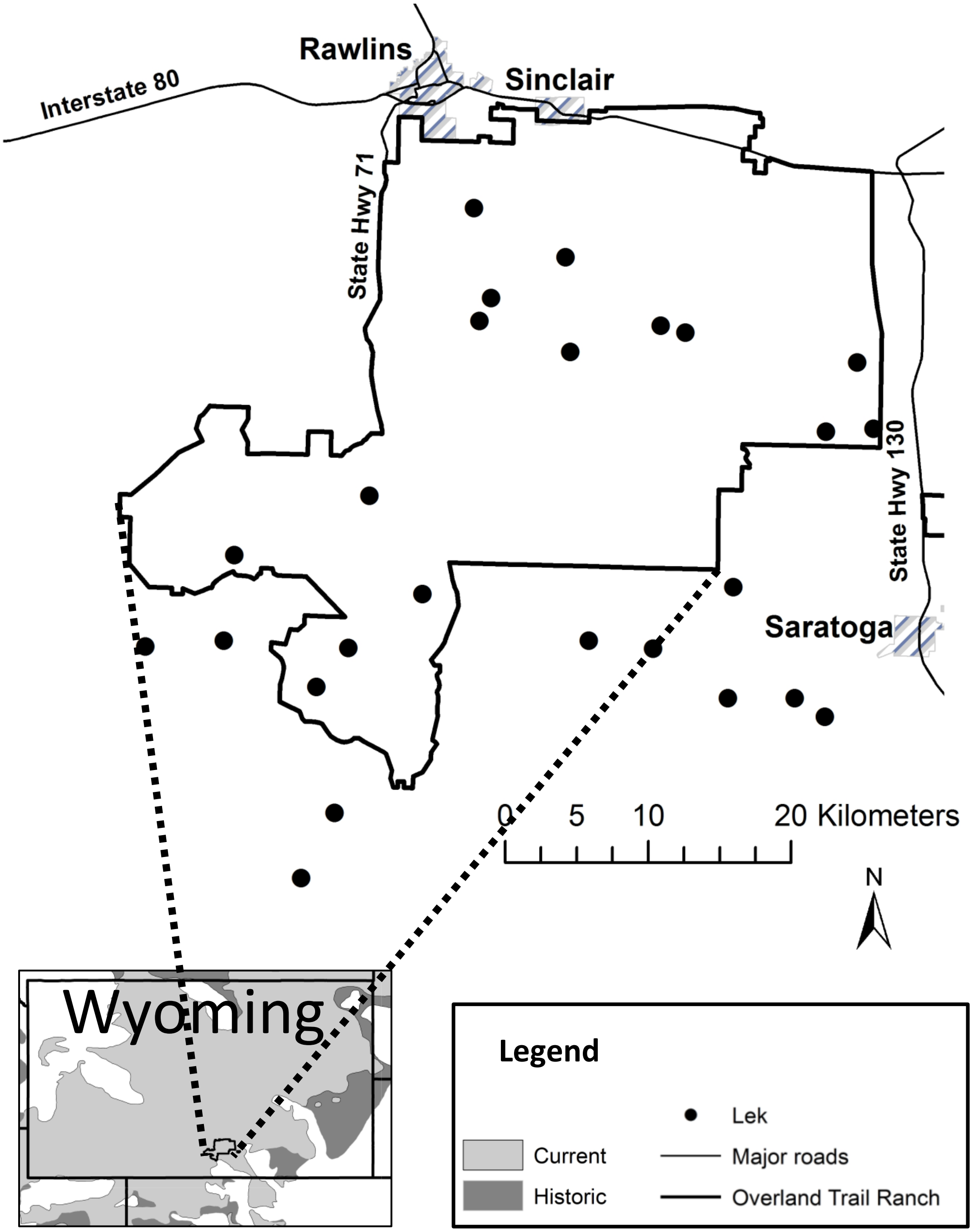
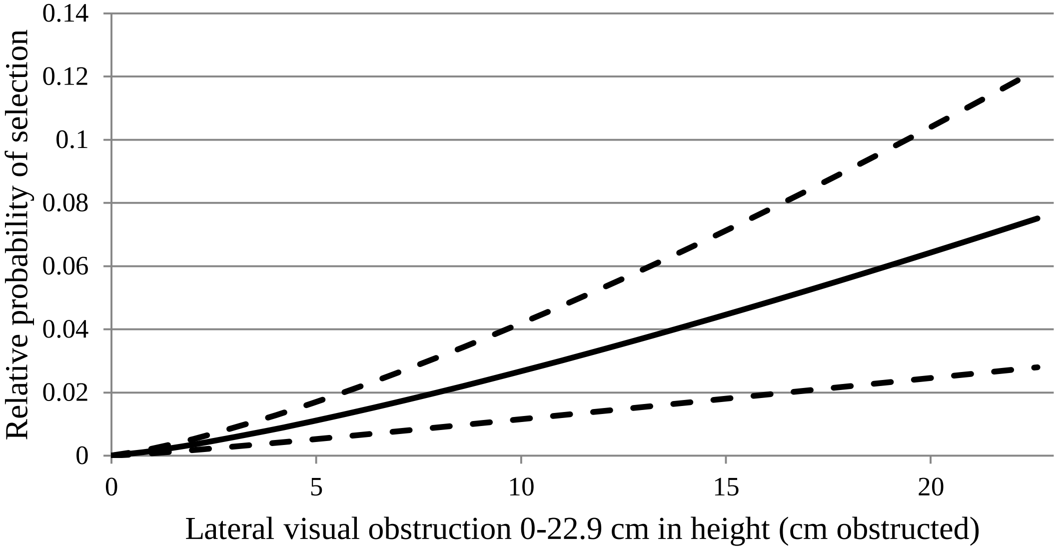


Figure 4. Map of study area showing the current and historic range of Greater sage-grouse (inset; Schroeder 2002), the Overland Trail Ranch, and locations of leks females were captured at during March and April 2010−2013 in Carbon County, Wyoming, USA.



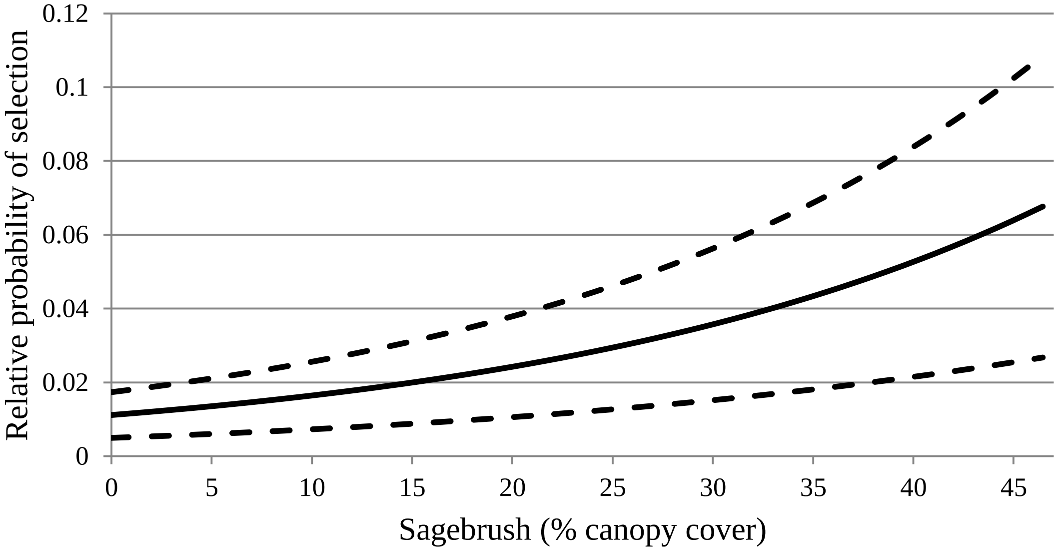
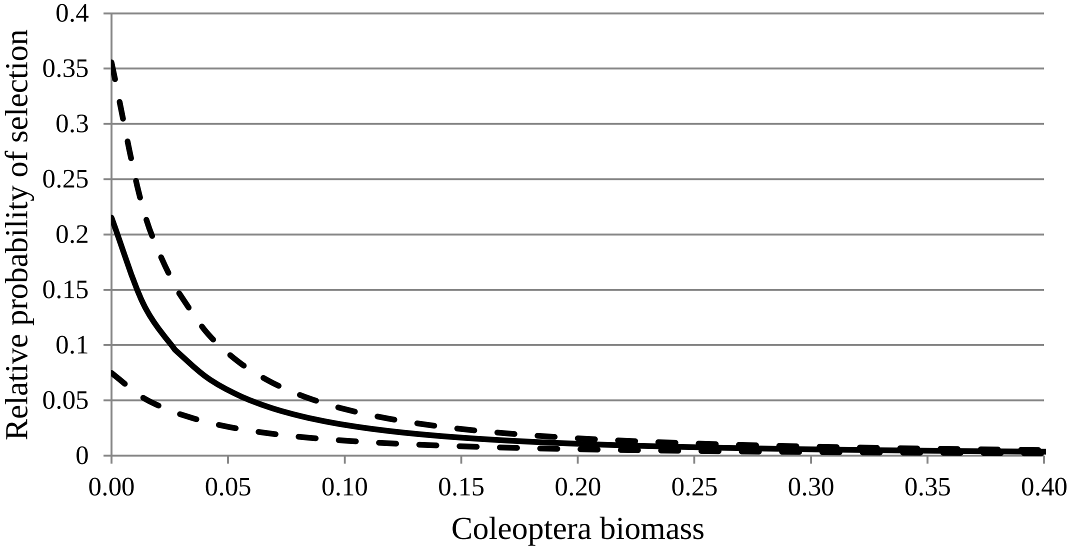


Figure 5. Influence of lateral visual obstruction up to 22.9 cm in height and sagebrush canopy cover on the relative probability of brood-rearing site selection for 73 brood-rearing sites on the Overland Trail Ranch, Wyoming, USA, 2011−2012. Dashed lines represent bootstrapped 95% confidence intervals.



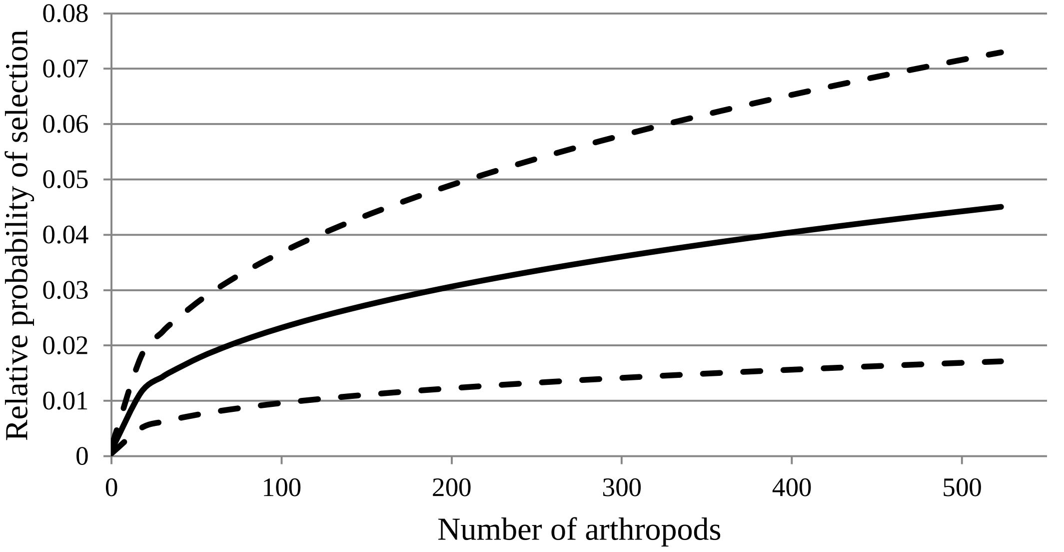


Figure 6. Influence of Coleoptera biomass and total number of arthropods on the relative probability of brood-rearing site selection for 73 brood-rearing sites on the Overland Trail Ranch, Wyoming, USA, 2011−2012. Dashed lines represent bootstrapped 95% confidence intervals.

Appendix C. Models representing specific hypotheses about the influence of vegetation and arthropods within 20 m on brood-rearing site selection by female Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2012.

Model No.	Model Structure	Predicted Result(s)	Units of Measurement
1	Null	Random Selection	
2	β_1(Totsage)+β_2(Grasshgt)+β_3(Bunchgrass)+β_4(Broadforb)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$	% canopy cover^a + cm^b + % canopy cover^a + % canopy cover^a
3	β_1(Density)+β_2(Bunchgrass)+β_3(VOR)+β_4(Sagehgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	No. plants/sq. m^c + % canopy cover^a + cm^d + cm^b
4	β_1(Density)+β_2(Cheatgrass)+β_3(Rabbitbrush)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$	No. plants/sq. m^c + % canopy cover^a + % canopy cover^a
5	β_1(VOR)+β_2(Totsage)+β_3(Bunchgrass)+β_4(Broadforb)+ β_5(Coleoptera)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$, $\beta_5<0$	cm^d + % canopy cover^a + % canopy cover^a + % canopy cover^a + g or No.^{e}
6	β_1(VOR)+β_2(Density)+β_3(Broadforb)+β_4(Hymenoptera)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$, $\beta_4<0$	cm^d + No. plants/sq. m^c + % canopy cover^b + g or No.^{e}
7	β_1(Totsage)+β_2(Density)+β_3(Totgrass)+β_4(Grasshgt)+ β_5(TotalArthropod)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$, $\beta_5<0$	% canopy cover^a + No. plants/sq. m^c + % canopy cover^a + cm^b + g or No.^{e}
8	β_1(Broadforb)+β_2(Totgrass)+β_3(Totsage)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$	% canopy cover^a + % canopy cover^a + % canopy cover^a
9	β_1(Sagehgt)+β_2(Grasshgt)+β_3(Totgrass)+β_4(Totforb)	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	cm^b + cm^b + % canopy cover^a + % canopy cover^a

10	β_1(Density)+β_2(Totgrass)+β_3(VOR)+β_4(Broadforb)	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	No. plants/sq. m[c] + % canopy cover[a] + cm[d] + % canopy cover[a]
11	β_1(Totsage)+β_2(Totshrub)+β_3(Broadforb)	$\beta_1<0$, $\beta_2<0$, $\beta_3>0$	% canopy cover[a] + % canopy cover[a] + % canopy cover[a]
12	β_1(Broadforb)+β_2(Rhizograss)+β_3(VOR)+ β_4(TotalArthropod)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	% canopy cover[a] + % canopy cover[a] + cm[d] + g or No.[e]
13	β_1(Rhizograss)+β_2(Bunchgrass)+β_3(Coleoptera)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	% canopy cover[a] + % canopy cover[a] + g or No.[e]
14	β_1(Rhizograss)+β_2(Bunchgrass)+β_3(Hymenoptera)+ β_4(Density)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$	% canopy cover[a] + % canopy cover[a] + g or No.[e] + No. plants/sq. m[c]
15	β_1(Totgrass)+β_2(Grasshgt)+β_3(Totforb)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	% canopy cover[a] + cm[b] + % canopy cover[a]
16	β_1(Lepidoptera)+β_2(Softbodylarva)+β_3(Rabbitbrush)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	g or No.[e] + g or No.[e] + % canopy cover[a]
17	β_1(Lepidoptera)+β_2(Softbodylarva)+β_3(Annualforb)+ β_4(Grasshgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$	g or No.[e] + g or No.[e] + % canopy cover[a] + cm[b]

[a] Summarized from 144 measurements of 0.1-m^2 quadrats from 4 20-m radius sites

[b] Summarized from 144 measurements from 4 20-m radius sites

[c] Summarized from 144 measurements from 4 20-m radius sites

[d] Number of cm > 50% visually obstructed on 4 22.9-cm tall sections of a Robel pole; Summarized from 80 measurements from 4 20-m radius sites

[e] Either biomass or count of collected arthropods; Summarized from 24 1-m^2 quadrats from 4 20-m radius sites

Appendix D. Models representing specific hypotheses about the influence of vegetation within 20 m on brood-rearing site selection by female Greater sage-grouse on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Model No.	Model Structure	Predicted Result(s)	Units of Measurement
1	Null	Random Selection	
2	β_1(Totsage)+β_2(Grasshgt)+β_3(Bunchgrass)+β_4(Broadforb)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$	% canopy cover^{a} + cm^{b} + % canopy cover^{a} + % canopy cover^{a}
3	β_1(Density)+β_2(Bunchgrass)+β_3(VOR)+β_4(Sagehgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	No. plants/sq. m^{c} + % canopy cover^{a} + cm^{d} + cm^{b}
4	β_1(Density)+β_2(Cheatgrass)+β_3(Rabbitbrush)	$\beta_1>0$, $\beta_2<0$, $\beta_3<0$	No. plants/sq. m^{c} + % canopy cover^{a} + % canopy cover^{a}
5	β_1(VOR)+β_2(Totsage)+β_3(Bunchgrass)+β_4(Broadforb)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4<0$	cm^{d} + % canopy cover^{a} + % canopy cover^{a} + % canopy cover^{a}
6	β_1(Totsage)+β_2(Density)+β_3(Totgrass)+β_4(Grasshgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$, $\beta_4>0$	% canopy cover^{a} + No. plants/sq. m^{c} + % canopy cover^{a} + cm^{b}
7	β_1(Broadforb)+β_2(Totgrass)+β_3(Totsage)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$	% canopy cover^{a} + % canopy cover^{a} + % canopy cover^{a}
8	β_1(Sagehgt)+β_2(Grasshgt)+β_3(Totforb)	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$	cm^{b} + cm^{b} + % canopy cover^{a}

9	β_1(Density)+β_2(Totgrass)+β_3(VOR)	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$	No. plants/sq. m[c] + % canopy cover[a] + cm[d]
10	β_1(Totsage)+β_2(Totshrub)+β_3(Broadforb)	$\beta_1<0$, $\beta_2<0$, $\beta_3>0$	% canopy cover[a] + % canopy cover[a] + % canopy cover[a]
11	β_1(Broadforb)+β_2(VOR)	$\beta_1>0$, $\beta_2>0$	% canopy cover[a] + cm[d]
12	β_1(Rhizograss)+β_2(Bunchgrass)+β_3(Density)	$\beta_1>0$, $\beta_2>0$, $\beta_3<0$	% canopy cover[a] + % canopy cover[a] + No. plants/sq. m[c]
13	β_1(Grasshgt)+β_2(Totforb)	$\beta_1>0$, $\beta_2>0$	cm[b] + % canopy cover[a]
14	β_1(Rabbitbrush)+β_2(Annualforb)+β_3(Grasshgt)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$	% canopy cover[a] + % canopy cover[a] + cm[b]

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[a] Summarized from 144 measurements of 0.1-m^2 quadrats from 4 20-m radius sites

[b] Summarized from 144 measurements from 4 20-m radius sites

[c] Summarized from 144 measurements from 4 20-m radius sites

[d] Number of cm > 50% visually obstructed on 4 22.9-cm tall sections of a Robel pole; Summarized from 80 measurements from 4 20-m radius sites

CHAPTER 3 - GREATER SAGE-GROUSE CHICK SURVIVAL AND NEST PRODUCTIVITY PRIOR TO WIND ENERGY DEVELOPMENT IN WYOMING

ABSTRACT

Small changes in nest productivity and chick survival in Greater sage-grouse (*Centrocercus urophasianus*) populations can have large effects on the population growth rate and abundance. Knowledge of sage-grouse population demographic rates is necessary because the species is considered “warranted but precluded” under the Endangered Species Act (1973). As part of a study quantifying sage-grouse demographics prior to construction of a wind energy facility, we estimated net nest productivity of radio-equipped female sage-grouse (*n* = 44 in 2011; 52 in 2012; 46 in 2013) and estimated the survival rate of chicks associated with each radio-equipped female on the Overland Trail Ranch in south-central Wyoming, USA. Our post-hatch estimates of nest productivity [2.79 ± 0.68 (SE) chicks/female in 2011; 2.00 ± 2.87 (SE) chicks/female in 2012; and 1.54 ± 0.47 (SE) chicks/female in 2013] were low when compared to estimates from other studies. We estimated chick survival by conducting repeated nocturnal spotlight surveys in which we counted the chicks associated with each radio-equipped female (*n* = 14 in 2011; 14 in 2012; 9 in 2013). We used a modified logistic-exposure method to estimate daily chick survival rates and survival over a 70-day time period while examining relationships between chick survival and weather and temporal variables. Chick survival rates to 70 days-post-hatch [2011: 0.120 ± 0.082 (SE), 2012: 0.031 ± 0.034 (SE), 2013: 0.157 ± 0.049 (SE)] were very low. However, these rates should be placed in the broader context of sage-grouse chick survival which exhibits high annual variation due to a variety of extrinsic factors. The low rates of nest

productivity and chick survival suggest that this area may be of marginal quality for sage-grouse. Research is needed to elucidate the mechanisms behind the persistence of birds on the area and the low demographic rates we observed.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) depend on sagebrush (*Artemisia* spp.) communities for food and shelter year-round (Patterson 1952, Connelly et al. 2011). Sage-grouse populations across North America have declined at an average rate of 2% per year since 1965 (Connelly et al. 2004) and these population declines have been attributed to loss and degradation of sagebrush (*Artemisia* spp.) habitat. Sage-grouse were recently listed as “warranted but precluded” for protection under the Endangered Species Act (United States Fish and Wildlife Service 2010).

Declining tetraonid populations may be the result of reduced nest productivity and chick survival (Blank et al. 1967, Bergerud 1988). Sage-grouse population growth rates are sensitive to small changes in chick survival (Taylor et al. 2012). Sage-grouse nest productivity and chick survival rates are often mediated by sagebrush habitat associated with these life stages (Connelly et al. 2000). Sagebrush habitat quality varies across the species’ range due to environmental gradients which influence nest productivity and chick survival rates (Connelly et al. 2004). Consequently, it is necessary to have estimates of nest productivity and chick survival rates applicable at a local scale when evaluating demographics of sage-grouse populations that are of concern.

Previous research has shown that tetraonid chick survival is affected by weather and age-related factors which are site-specific (Bergerud 1988). Weather may directly influence chick survival through exposure (Huwer et al. 2008), or indirectly by winter and spring precipitation that affects grass and forb growth in the summer (Skinner et al. 2002). Tetraonid chick survival is generally low during the first 2-3 weeks of age with survival increasing as chicks age (Bergerud 1988). Furthermore, adult sage-grouse may be more successful at rearing chicks than yearling sage-grouse (Curio 1983, Aldridge and Brigham 2001), because older females are more experienced (Wiebe and Martin 1998) or have better nutrition stores (Gregg 2006). Lastly, sage-grouse initiate nests throughout the spring and early summer under fluctuating environmental conditions resulting in different hatch dates and subsequently different chick survival rates (Thompson 2012).

Sage-grouse demographics can be influenced by human alterations to the environment such as energy development (Holloran 2005, Walker et al. 2007, Naugle et al. 2011). The United States' demand for renewable energy has prompted a nationwide increase in wind energy development (Deparment of Energy 2008). Long-term studies directly investigating potential effects of large-scale wind energy development on sage-grouse demographics are nonexistent (Stewart et al. 2007). The Power Company of Wyoming, LLC proposes to construct North America's largest wind energy facility consisting of ~1,000 turbines in an area occupied by sage-grouse. Our objectives were to 1) estimate sage-grouse nest productivity; 2) estimate sage-grouse chick survival rates; and 3) evaluate hypotheses related to the influence of weather and temporal variables on sage-grouse chick survival. This study was part of a Before-After-Control-Impact project collecting baseline sage-grouse demographics prior to construction of the wind energy facility.

STUDY AREA

Our study area encompassed 1,295 km^2 in south-central Wyoming, south of Rawlins and east of Saratoga (Figure 7). The study area is managed as an open range yearling cattle operation and land ownership pattern of the study area resembles a checkerboard with approximately half of the land under private ownership by the Overland Trail Cattle Company, half administered by the Bureau of Land Management, and a small portion owned by the State of Wyoming (collectively hereafter, the ranch). Elevations range from about 1,890 m at the North Platte River to about 2,590 m near the Continental Divide in the southwestern portion of the study area (Google Earth, Google, Inc., Mountain View, CA). Over the past 60 years, annual precipitation averaged 22.8 cm in Rawlins, WY which is 6 km from the northern boundary of the study area and 24.6 cm in Saratoga, WY which is 14 km from the eastern edge of the study area (Western Regional Climate Center 2013). The average monthly temperature range is 0.7–12.7 C between November and April and 15.3–28.5 C between May and October (Western Regional Climate Center 2013). The dominant ecoregion in the study area is rolling sagebrush steppe characterized by vegetation cover of big sagebrush (*Artemisia tridentata*), silver sagebrush (*A. cana*), and black sagebrush (*A. nova*; Chapman et al. 2004).

METHODS

Field Methods

We captured female sage-grouse near leks equally distributed among regions slated for wind turbine placement and regions without anticipated wind turbines. During March and April 2010–2013, we captured female sage-grouse using spotlighting techniques (Giesen et al. 1982) and fit them with 30-g rump-mounted (Rappole and

Tipton 1991) Global Positioning System Platform Transmitter Terminals (GPS PTTs; Microwave Telemetry, Inc., Columbia, MD). Age of female sage-grouse was determined from characteristics of primary feathers on wings (Eng 1955). Capture and handling was conducted under protocols approved by the University of Missouri Animal Care and Use Committee permit number 6750.

Nest Productivity – During spring and summer, GPS PTTs collected 8 locations/day which were downloaded from Argos satellites every 3−5 days. Field personnel investigated multiple (>3) GPS locations occurring within a 50 m radius over 48 hrs to confirm a female was nesting. In addition, each GPS PTT was equipped with an Ultra High Frequency (UHF) transmitter that was operational approximately 8 hrs/day to facilitate ground-tracking. Using UHF telemetry to locate the nesting female, we visually observed the bird using binoculars >10 m from the nest to avoid disturbing the female. We estimated an approximate hatch date using an incubation period of 27 days (Schroeder 1997). Starting the day before the approximate hatch date, we began daily visual observations of the nesting female until incubation ceased. If we were unable to perform field observations due to logistics, we used GPS PTT data to inform us of the exact hatch date, evidenced by >3 GPS locations >50 m from the nest. After the female left the nest, we inspected the nest to estimate the number of successfully hatched chicks by counting eggshells with detached membranes (Girard 1939).

Chick Survival – We conducted repeated nocturnal spotlight surveys from May to September 2011–2013 to count the chicks associated with each radio-equipped female with a successful nest. We located maternal females at night using GPS locations and a hand-held UHF telemetry antenna. When the female was located, we carefully approached her on foot and counted the chicks using a handheld spotlight (e.g., Dahlgren et al. 2010b). When chicks were < 42 days of age, it was often necessary to flush the maternal female to count the chicks roosting underneath her (D.K. Dahlgren, Kansas Dept. of Wildlife and Parks, personal communication). After counting the chicks, we immediately left the site to minimize disturbance. We did not spotlight chicks if it was raining or had just rained to lessen the risk of exposure related mortality. We initiated spotlight surveys as early as the night after hatching and repeated the survey at 1–2 week intervals until all chicks were absent (assumed dead) or the brood had reached 70 days of age at which time it was difficult to differentiate chicks from adults based on size. We assumed perfect detection based on our field observations which is a reasonable assumption (Dahlgren et al. 2010b). Nonetheless, we could not assess the possibility of chick adoption by females (e.g., Dahlgen et al. 2010a) because chicks were not marked.

Analytical Methods

Nest Productivity – We estimated average brood sizes for initial nests and renests. We assumed that all eggs in the nest were fertilized. We estimated net nest productivity using a weighted mean of the average brood size which is the product of the average brood size and the rate of nest success for initial nests and renests (Skalski et al. 2005: 100).

Chick Survival – We modified the logistic-exposure method typically used for modeling nest survival (Shaffer 2004, Shaffer and Thompson 2007) to analyze chick survival. The logistic exposure method estimates survival as an exponential function of the number of days in the interval between observations; for nest survival each observation interval is a single binary trial with a survival event indicating the nest survived the interval. We similarly applied the method to brood observations only each brood observation consisted of multiple binary trials representing the number of chicks alive at the start of the interval and survival events were the number of chicks alive at the end of the interval. Due to the lack of independence among chicks within the same brood, we fit repeated measures models using generalized estimating equations in PROC GENMOD (SAS 9.3, SAS Institute, Inc., Cary, NC) with the individual female as the repeated effect. Mixed models require identification of the appropriate covariance structure of the data to obtain unbiased parameter estimates (Littell et al. 2006). Consequently, we evaluated exchangeable, independent, and unstructured covariance structures using the Quasilikelihood under the Independence model Criterion (QIC) statistic (Pan 2001). The most supported correlation structure was used in all subsequent models.

We evaluated the relative support among models representing different hypotheses about chick survival (Appendix E). We hypothesized chick survival would vary by year (Bergerud 1988); increase with maternal female age (Curio 1983); decrease with advancing hatch date (Thompson 2012); increase with chick age (Bergerud 1988); increase with mean temperature over the interval between observations (Thompson et al. 2006); and decrease with the sum of precipitation over the interval between observations due to exposure (Bergerud 1988), or alternatively increase with the sum of precipitation over the interval between observations due to subsequent increases in food and cover resources (Gregg and Crawford 2009). Daily measurements of temperature and precipitation were obtained from a weather station in Rawlins, WY (National Oceanic and Atmospheric Administration 2013). The greatest distance from the weather station in

Rawlins to a nest in our study was 58 km. We checked for multicollinearity between covariates using tolerance values from PROC REG in SAS 9.3, and if multicollinearity was present (tolerance <0.4; Allison 2012), we selected the most biological meaningful covariate. We used Akaike's Information Criterion for small sample sizes (AIC$_c$) to select the most supported structural form (i.e., linear, pseudothreshold, or quadratic) for each covariate and evaluate the relative support among models (Appendix E). We ranked all models based on AIC$_c$ and used the top model or models with parameters adjusted by generalized estimating equations for repeated measures for inference and to generate predictions. We estimated survival rates by varying explanatory variables of interest while holding other variables in the models at their mean values.

RESULTS

We captured, radio-marked, and monitored 44 female sage-grouse (n = 12 yearlings, n = 32 adults) in 2011, 52 female sage-grouse (n = 2 yearlings, n = 50 adults) in 2012, and 46 female sage-grouse (n = 1 yearlings, n = 45 adults) in 2013. In 2011, we verified 38 initial nests (n = 16 successful) and 10 renests (n = 4 successful); 37 initial nests (n = 14 successful) and 4 renests (n = 2 successful) in 2012; and 37 initial nests (n = 11 successful) and 8 renests (n = 1 successful) in 2013. Average hatch date was approximately 3 weeks earlier in 2012 [22 May ± 8.6 days (SE)] than in 2011 [13 June ± 12.2 days (SE)] and 2013 [10 June ± 13.0 days (SE)].

Nest Productivity – Females that died during their first nesting attempt (n = 3 in 2011; n = 5 in 2012; n = 1 in 2013) were censored from renesting productivity calculations. Clutch size for successful nests averaged 6.05 ± 1.32 (SE) eggs/nest in 2011, 6.43 ± 1.09 (SE) eggs/nest in 2012, and 5.89 ± 1.17 (SE) eggs/nest in 2013. Net nest productivity in 2013 [1.54 ± 0.47 (SE) chicks/female] was only 55% of nest productivity in 2011 [2.79 ± 0.68 (SE) chicks/female] and 77% of nest productivity in 2012 [2.00 ± 0.51 (SE) chicks/female].

Chick Survival – We monitored chicks from 14 broods in 2011, 14 broods in 2012, and 9 broods in 2013 (*n* = 2 yearling maternal females, and *n* = 35 adult maternal females). Average number of days between consecutive spotlight observations was 8.0 ± 3.9 (SE) days. In 2011, we were unable to monitor chicks from all the successful nests, because 1 brood was on private land that we could not access, and 5 broods were associated with females with transmitters whose UHF transmitters did not turn on until after our monitoring period ended. Of those UHF transmitters that were on during our monitoring period, 4 turned off prematurely on 31 July preventing us from monitoring those broods to 70 days. Data from these broods were truncated to the time available and included in the survival analysis. In 2012, we were unable to obtain access to private land for 1 brood. Another brood in 2012 was apparently predated before the first spotlight survey, but for which the presence of eggshell membranes suggested this nest hatched, but we were unable to accurately count the eggshells, because the eggs were crushed. In 2013, we were unable to obtain access to private land for 1 nest that successfully hatched. We censored observations when obvious chick adoption (e.g., Dahlgren et al. 2010a) occurred (2011: *n* = 3, 2012: *n* = 1, 2013: *n* = 0).

The daily survival rate (DSR) was lowest in 2012 [0.952 ± 0.014 (SE)] compared to 2011 [0.970 ± 0.011 (SE)] and 2013 [0.974 ± 0.004 (SE)]. The exchangeable correlation structure was most supported indicating that the life-fates of chicks within a brood were not independent. Due to the small number of radio-marked yearling maternal females (*n* = 2), we did not evaluate candidate models that included female age as a covariate (Models 8 and 5; Appendix E). Of the 9 models we evaluated, Akaike weights indicated only 1 model was supported (w_i = 0.987; Table **8**). The covariates in the top model included chick age, year, and hatch date for which we calculated parameter estimates and standard errors (Table 9). As hatch date advanced from mid-May to early-July, the DSR increased linearly and was lower in 2012 compared to 2011 and 2013 (Figure 8). The DSR was lowest during the first few weeks post-hatch, but increased to its maximum as the chicks approached 70 days with lower survival in 2012 compared to 2011 and 2013 (Figure 8).

DISCUSSION

Tetraonid chick survival rates exhibit high annual variation due to a variety of extrinsic factors including weather, food availability, and predator abundance (Blank et al. 1967, Bergerud 1988, Riley et al. 1998, Goddard and Dawson 2009, Taylor et al. 2012). Our estimates of chick survival varied by a factor of 4 over 3 years. However, our highest estimate is still low when compared to other published survival rates (Table 10), but similar to chick survival estimates from the highly altered environments in the Great Basin (Gregg and Crawford 2009) and Alberta, Canada (Table 10; Aldridge and Brigham 2001, Aldridge and Boyce 2007). Our study area consisted of relatively unaltered sagebrush habitat, but our survival estimates were approximately half the survival rates recorded from other intact sagebrush habitat (Table 10; Dahlgren et al. 2010a, Thompson 2012). Even though we have examined survival rates over a broad array of conditions occurring over 3 years, we have not accounted for factors varying over decades, such as predator populations. As such, our low chick survival rates may not represent the long-term average for this population.

Our chick survival estimate in 2012 was 3% to 70 days-post-hatch. The hot, dry conditions associated with the drought in 2012 were a prevailing and obvious condition that could be tied to the abnormally low survival rate. Droughts have previously been shown to negatively affect chick survival (June 1963, Aldridge 2005). Average temperature during April and May was 10.6 C and precipitation from April to August was only 44% of the long-term average (National Oceanic and Atmospheric Administration 2013). Conversely, the weather in 2011 and 2013 was average: the average temperature during April and May was 4.4 C in 2011 and 6.3 C in 2013 with approximately 110% of the long-term average precipitation from April to August in both years (National Oceanic and Atmospheric Administration 2013). During 2011 and 2013, the cooler and wetter weather would have resulted in herbaceous production well into May; however, if April is hot and dry (2012), subsequent precipitation will have limited effect on annual herbaceous production (Cagney et al. 2010). Annual herbaceous production affects food and cover resources available to sage-grouse chicks (Connelly et al. 2000). While our models did not support temperature and precipitation affecting chick survival, they only considered weather conditions over the interval between brood observations, and not weather conditions prior to hatching occurring in April. The only variable other than chick age correlated with survival was hatch date where we observed increased survival as hatch date advanced. Overall, the chick to female ratios we observed of 1.5-2.8 chicks/female in early spring were similar to those observed elsewhere in the fall (Connelly and Braun 1997, Holloran 2005), suggesting that this population of sage-grouse exhibited low recruitment that began with nesting.

The low estimates of chick survival suggest this area may be of marginal quality for sage-grouse. Low habitat quality could be due to inherent low capacity possibly caused by relatively arid site conditions (Whitford et al. 1995) or poor or degraded soils (Knight 1996). Because our estimates of nest productivity and chick survival are low compared to the literature, our research highlights the importance of collecting baseline, preconstruction data when evaluating effects of wind energy development on sage-grouse. If improving sage-grouse populations is a priority, managers should consider practices aimed at enhancing nesting and brood-rearing resources (Chapter 1, 2).

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Table 8. Support for models explaining Greater sage-grouse chick survival for 37 broods on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Model	**LL**[a]	**K**[b]	**AIC$_c$**[c]	**ΔAIC$_c$**[d]	***w_i***[e]
Chick age, Hatch date, Year	-245.351	5	502.637	0.000	0.987
Chick age, Temp, Precip	-251.369	4	511.987	9.350	0.009
Chick age, Temp*Precip, Temp, Precip	-251.265	5	514.466	11.829	0.003
Temp, Precip	-255.418	3	517.564	14.927	0.001
Temp*Precip, Temp, Precip	-255.185	4	519.621	16.984	0.000
Chick age	-258.426	2	521.205	18.568	0.000
Year	-267.409	3	541.546	38.909	0.000
Year, Hatch date	-266.789	4	542.828	40.191	0.000
Null	-285.822	1	573.758	71.121	0.000

[a] LL: log likelihood
[b] K: no. of parameters in each model
[c] AIC$_c$: Akaike's information criterion for small sample sizes
[d] ΔAIC$_c$: difference in AIC*c* between the model and the best performing model
[e] w_i: Akaike weights

Table 9. Parameter estimates and standard errors explaining Greater sage-grouse chick survival for 37 broods on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Parameter	**Level**	**Estimate**	**SE**
Chick age		0.0338	0.0110
Intercept		0.5741	2.0448
Year	2011	-0.1398	0.3284
Year	2012	-0.6415	0.2717
Year	2013	0.0000	0.0000
Hatch date		0.0133	0.0128

Table 10. Comparison of Greater sage-grouse chick survival rates from previously published estimates and from 37 broods on the Overland Trail Ranch, Wyoming, USA, 2011–2013. Daily survival rates from previously published studies were converted to 70-day period survival to allow direct comparison.

Reference	**Location**	**Daily Survival Rate**	**Survival to 70 days**	**Sagebrush Habitat**
This study	WY	0.970, 0.952, 0.974[a]	12%, 3%, 16%[a]	Relatively intact
Aldridge and Brigham 2001, Aldridge and Boyce 2007	Alberta	0.963	7%	Highly altered by oil/gas & agriculture
Gregg and Crawford 2009	Great Basin/ NV & OR	0.967	10%	Relatively intact
Dahlgren et al. 2010	UT	0.984	32%	Relatively intact
Thompson 2012	CO	0.984–0.993[b]	32%–61%[b]	Relatively intact

[a] 2011, 2012, 2013, respectively

[b] range over 4 consecutive years

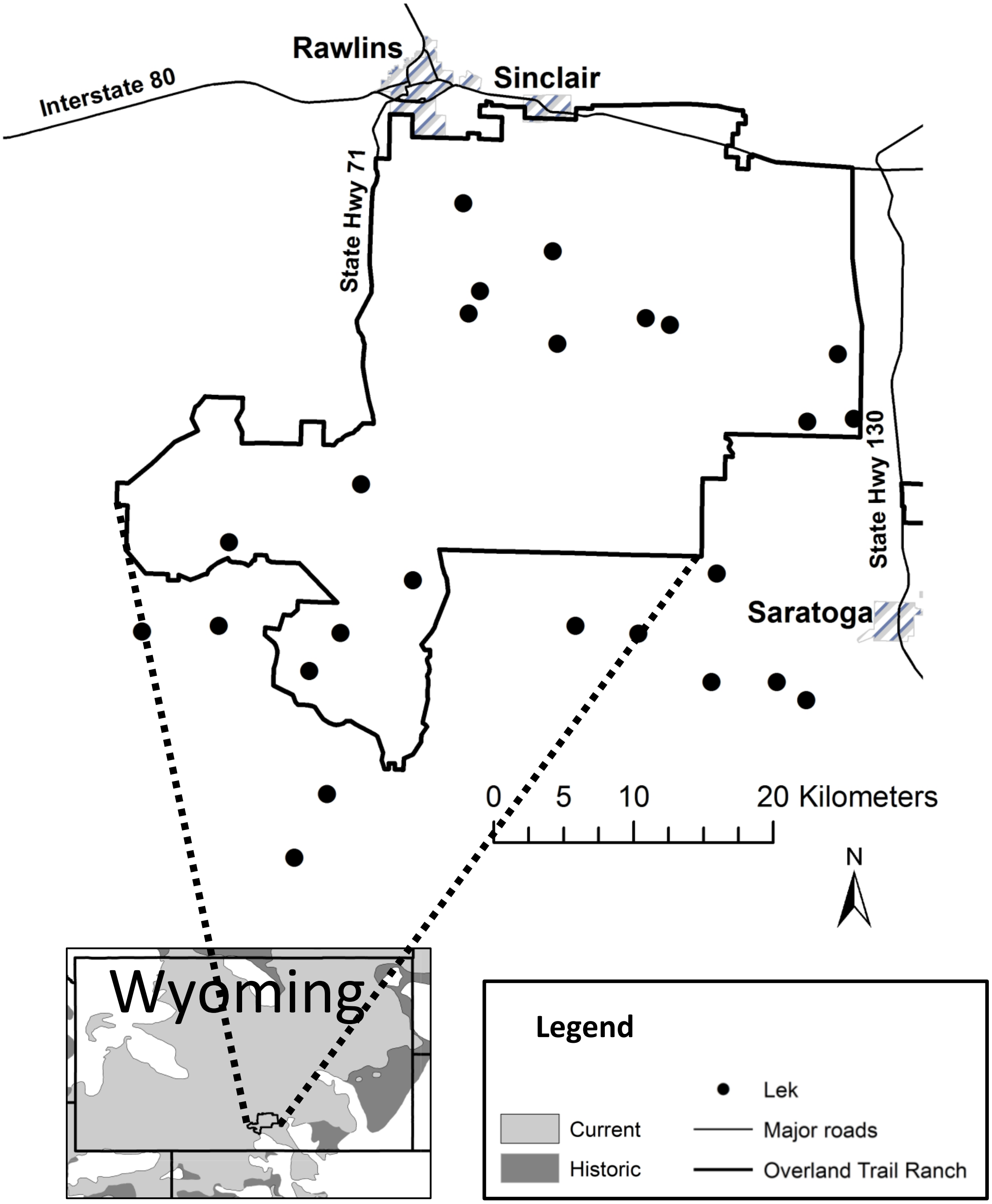

Figure 7. Map of study area showing the current and historic range of Greater sage-grouse (inset; Schroeder 2002), the Overland Trail Ranch, and locations of leks females were captured at during March and April 2010−2013 in Carbon County, Wyoming, USA.

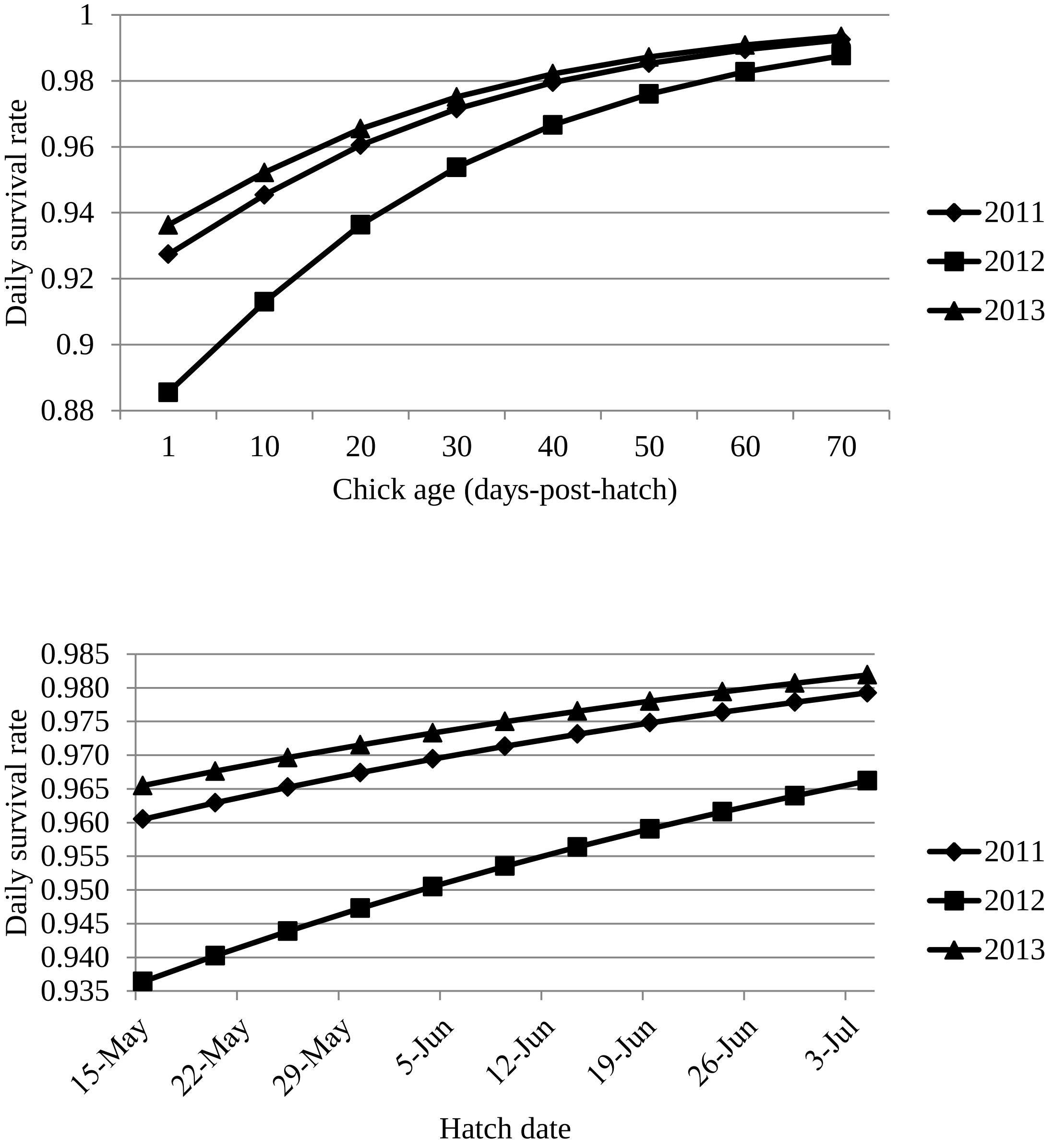

Figure 8. Daily survival rate by year of Greater sage-grouse chicks from 37 broods as a function of chick age and hatch date on the Overland Trail Ranch, Wyoming, USA, 2011–2013. Lines representing 95% confidence intervals were omitted for clarity.

Appendix E. Models representing specific hypotheses about the influence of weather and temporal factors on Greater sage-grouse chick survival on the Overland Trail Ranch, Wyoming, USA, 2011–2013.

Model No.	Model Structure	Predicted Result(s)	Units of Measurement
1	Null	Random Selection	
2	β_1(Temp)+β_2(Precip)	$\beta_1>0$, $\beta_2>0$ or $\beta_2<0$	C^{a} + cm^{b}
3	β_1(Temp*Precip)+β_2(Temp)+β_3(Precip)	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$ or $\beta_3<0$	$C*cm^{ab}$ + C^{a} + cm^{b}
4	β_1(Year)	β_1(2011>0, 2012<0, 2013>0)	year
5	β_1(Year)+β_2(Maternal female age)	β_1(2011>0, 2012<0, 2013>0), β_2(Adult>0, Yearling<0)	year + adult/yearling^{c}
6	β_1(Year)+β_2(Hatch date)	β_1(2011>0, 2012<0, 2013>0), $\beta_2<0$	year + ordinal date
7	β_1(Chick age)	$\beta_1>0$	days-post-hatch
8	β_1(Chick age)+β_2(Maternal female age)	$\beta_1>0$, β_2(Adult>0, Yearling<0)	days-post-hatch + adult/yearling^{c}
9	β_1(Chick age)+β_2(Hatch date)+β_3(Year)	$\beta_1>0$, $\beta_2<0$, β_3(2011>0, 2012<0, 2013>0)	days-post-hatch + ordinal date + year
10	β_1(Chick age)+β_2(Temp)+β_3(Precip)	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$ or $\beta_3<0$	days-post-hatch + C^{a} + cm^{b}
11	β_1(Chick age)+β_2(Temp*Precip)+ β_3(Temp)+β_4(Precip)	$\beta_1>0$, $\beta_2<0$, $\beta_3>0$, $\beta_4>0$ or $\beta_4<0$	days-post-hatch + $C*cm^{ab}$ + C^{a} + cm^{b}

[a] mean temperature (C) that occurred during the interval between observations measured at the Rawlins Airport, Wyoming
[b] sum precipitation (cm) that occurred during the interval between observations measured at the Rawlins Airport, Wyoming
[c] maternal female is either a yearling (born the previous year) or adult (>1 year old)