THE CONDOR
Ornithological Applications
www.cooper.org

Volume 116, 2014, pp. 629–642
DOI: 10.1650/CONDOR-13-163.1

RESEARCH ARTICLE

Greater Sage-Grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features

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Submitted December 20, 2013; Accepted September 5, 2014; Published November 5, 2014

ABSTRACT

Prey species minimize the risk of predation directly by avoiding predators and indirectly by avoiding risky habitat. Habitat loss and fragmentation have been prevalent in Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") habitat, which has necessitated a better understanding of mechanisms driving habitat use. Using multinomial logistic regression, we compared landscape attributes and anthropogenic features (indirect mechanisms) and densities of avian predators (direct mechanisms) among 792 sage-grouse locations (340 nests, 331 early brood, and 121 late brood) and 660 random locations in Wyoming, USA, in 2008–2011. Anthropogenic features included oil and gas structures, communication towers, power lines, roads, and rural houses; and landscape attributes included a normalized difference vegetation index (NDVI), topographic ruggedness, the proportion of big sagebrush (*Artemisia* spp.), and proximity and proportion variables for forested and riparian habitats. Sage-grouse locations were best described with models that included multiple habitat variables and densities of small, medium, and large avian predators. Thus, both indirect and direct mechanisms of predator avoidance were employed by sage-grouse to select habitat and presumably lower their exposure to predation and nest predation. At all reproductive stages, sage-grouse selected flatter locations with a greater proportion of big sagebrush, a higher NDVI, and lower densities of oil and gas structures. Nest locations had a lower density of major roads and were farther away from riparian habitat; early-brood locations had a lower density of power lines and were closer to rural houses; and late-brood locations were closer to riparian habitat. The magnitudes of direct and indirect avoidance by sage-grouse hens were dependent on a sage-grouse's reproductive stage. Differential habitat use of female sage-grouse relative to predation risk and food availability was a means for sage-grouse hens to lower their risk of predation and nest predation, while using habitat to meet their energetic requirements and those of their chicks.

Keywords: brood-site selection, corvid, habitat use, Greater Sage-Grouse, nest-site selection, predator avoidance, predation risk, raptor

Centrocercus urophasianus selecciona el hábitat basado en las aves depredadoras, la composición del paisaje y las características antropogénicas

RESUMEN

Las especies de presa minimizan el riesgo de depredación evitando directamente a los depredadores e indirectamente evitado los hábitats riesgosos. La pérdida de hábitat y la fragmentación han sido determinantes en el hábitat de *Centrocercus urophasianus*, lo que ha hecho necesaria una mejor comprensión de los mecanismos que determinan el uso del hábitat. Usando regresión logística multinomial, comparamos los atributos del paisaje y las características antropogénicas (mecanismos indirectos) y la densidad de aves depredadoras (mecanismos directos) entre 792 localizaciones de *C. urophasianus* (340 nidos, 331 crías recientes y 121 crías tardías) y 660 localizaciones al azar en Wyoming, entre 2008 y 2011. Las características antropogénicas incluyeron estructuras de petróleo y gas, torres de comunicación, tendidos eléctricos, caminos y casas rurales; y los atributos del paisaje incluyeron el índice normalizado de diferencia de vegetación (NDVI), rugosidad topográfica, proporción de especies de *Artemisia* y proximidad y proporción de hábitats boscosos y ribereños. Las localizaciones de *C. urophasianus* fueron mejor descritas con modelos que incluyeron múltiples variables de hábitat y densidad de aves predadoras pequeñas, medianas y grandes. Así, *C. urophasianus* usó mecanismos indirectos y directos de evasión de los depredadores para seleccionar los hábitats y bajar presumiblemente su exposición a la depredación y a la depredación de los nidos. En todos los estadios reproductivos, *C. urophasianus* seleccionó localizaciones más planas con una mayor proporción de especies de *Artemisia*, NDVI más elevado y densidades más bajas de estructuras de petróleo y gas. Las localizaciones de los nidos tuvieron menor densidad de caminos principales y estuvieron más alejadas de los hábitats ribereños; las localizaciones

de las nidadas tuvieron menor densidad de tendidos eléctricos y estuvieron más cercanas a casa rurales; y las localizaciones de las nidadas tardías estuvieron más cerca a los hábitats ribereños. Las magnitudes de la evasión directa e indirecta por parte de los individuos de *C. urophasianus* dependieron del estadio reproductivo de *C. urophasianus*. Los diferentes usos de hábitat de las hembras de *C. urophasianus* con relación al riesgo de depredación y a la disponibilidad de alimentos fue aprovechada por los individuos de *C. urophasianus* para bajar su riesgo de depredación y la depredación de los nidos, durante el uso del hábitat para alcanzar los requerimientos energéticos de los adultos y los pichones.

Palabras clave: aves depredadores, *Centrocercus urophasianus*, córvido, evasión del depredador, rapaz, riesgo de depredación, selección de sitio de la nidada, selección de sitio del nido, uso de hábitat

INTRODUCTION

Predator avoidance behaviors influence habitat selection indirectly by reducing the use of risky habitats (habitats correlated with higher risk of predation) or directly by avoiding predators once they are seen (Lima 1998, Verdolin 2006, Cresswell 2008, Dinkins et al. 2012). Both indirect and direct mechanisms of predator avoidance are connected with an animal's perceived risk of predation (Cresswell 2008, Martin and Briskie 2009). For example, the risk of predation taken by male Red-breasted Nuthatches (*Sitta canadensis*) and White-breasted Nuthatches (*S. carolinensis*) to feed females on nests was lower in the presence of House Wrens (*Troglodytes aedon*) and Sharp-shinned Hawks (*Accipiter striatus*), which indicates direct avoidance of predators (Ghalambor and Martin 2000). Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") use habitat with lower densities of avian predators (Dinkins et al. 2012). Dinkins et al. (2012) suggested that the potential mechanism for this pattern was direct predator avoidance, but the pattern could also be explained in part as avoidance of habitat correlated with higher avian predator densities (e.g., oil and gas structures, power lines, forested habitat, etc.).

Anthropogenic features can be used as perches or nest structures by avian predators or can be associated with food subsides. American Kestrels (*Falco sparverius*; hereafter "kestrel"), Common Ravens (*Corvus corax*; hereafter "raven"), Golden Eagles (*Aquila chrysaetos*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*Buteo jamaicensis*), and Swainson's Hawks (*Buteo swainsoni*) use power lines for perching or nesting and areas around power lines for foraging (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010, Coates et al. 2014, Howe et al. 2014). Road-killed animals also attract mammalian and avian predators (Bradley and Fagre 1988, Boarman 1993, Boarman et al. 1995, Frey and Conover 2006). Several studies have demonstrated that sagebrush-obligate birds, including Brewer's Sparrows (*Spizella breweri*), Sagebrush Sparrows (*Artemisiospiza nevadensis*), Vesper Sparrows (*Pooecetes gramineus*), and sage-grouse are negatively associated with oil and gas infrastructure (Aldridge 2005, Walker et al. 2007, Doherty 2008, Carpenter et al. 2010, Holloran et al. 2010, Gilbert and Chalfoun 2011). In addition, sage-grouse avoid power lines (Hanser et al. 2011) and roads (Holloran 2005, Aldridge and Boyce 2007). Thus, sagebrush birds, including sage-grouse, may avoid man-made features to indirectly reduce predation risk.

In addition to avoiding tall man-made structures (structures >2 m tall) and roads, prey species including sage-grouse may indirectly avoid avian predators by avoiding other landscape attributes that represent riskier habitat, such as riparian areas, coniferous forests, and rough terrain. In northeastern Wyoming, USA, Doherty et al. (2010) found that sage-grouse selected nesting habitat with lower terrain roughness and percent cover of conifer, grassland, and riparian habitat; they also found that sage-grouse selected areas with a greater density of sagebrush (*Artemisia* spp.) at the scale of 100 to 350 m compared with random locations within sagebrush. Greater density of sagebrush at relatively large spatial extents may reduce the foraging efficiency of visual predators. Reduced predation has the potential to increase not just sage-grouse adult survival but also nest success. For example, Brewer's Sparrows nesting in areas with greater shrub cover and a greater density of vacant potential nest sites had better nest success (Chalfoun and Martin 2009).

A better understanding of habitat quality and mechanisms driving habitat use is a key component of conservation of sage-grouse, a species of conservation concern (Braun 1998, Schroeder et al. 2004, Connelly et al. 2011). Little research has explicitly compared the relative importance of indirect vs. direct predator avoidance mechanisms in relation to the use of habitat by prey species, which could have implications for management recommendations. Sage-grouse may avoid avian predators indirectly by avoiding landscape attributes or anthropogenic features that might attract avian predators or directly by observing them; however, it is more likely that sage-grouse use both indirect and direct means of avoiding predators. We used sage-grouse as a model prey species to test the importance of both indirect and direct predator avoidance. From 2008 to 2011, we recorded avian predator densities and calculated distances from landscape attributes and anthropogenic features to radio-tagged sage-grouse hens to determine the importance of direct and indirect predator avoidance by sage-grouse hens. For

precocial species such as sage-grouse, predator avoidance may differ among reproductive stages (Ghalambor and Martin 2000). Thus, we also evaluated habitat use of sage-grouse females during two reproductive stages, nesting and brood-rearing. We hypothesized that sage-grouse primarily would avoid nesting and raising their chicks in areas with high densities of avian predators and secondarily would avoid landscape attributes and anthropogenic features that posed a greater risk of predation. We also hypothesized that sage-grouse hens would respond to multiple predator species by always avoiding avian predators, which are a threat to adult hen survival during all reproductive stages, but by avoiding predators that are threats to just nests and chicks only during those reproductive stages. Finally, we predicted that hens would use more productive, but riskier, riparian habitat only when chicks were less vulnerable to predation.

METHODS

Study Area

Our study was conducted at 12 sites in southwestern and south-central Wyoming, USA. Holloran and Anderson (2005) found that 93% of 415 observed nests were within 8.5 km of leks at which females were captured in central and southwestern Wyoming. Thus, our eight sites in southwestern Wyoming (Lincoln, Sweetwater, and Uinta counties) were 16 km in diameter, approximately centered around leks where hens were captured. The four sites in south-central Wyoming (Carbon and Sweetwater counties) were 24 km in diameter, because sage-grouse were captured at several nearby leks over a larger area. Sites were chosen to provide a representation of overall sage-grouse nesting habitat in southern Wyoming, with a variety of land uses and topographic features. Elevation ranged from 1,950 m to 2,600 m. Most of the area within our sites was federally owned and administered by the Bureau of Land Management, with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in our sites. All sites had anthropogenic development, which consisted mostly of unimproved four-wheel drive roads. Conventional natural gas, coalbed methane natural gas, and/or conventional oil extraction activities were present in six (50%) of our sites; mean well density among all sites was 0.12 ± 0.22 SD wells km^{-2} (minimum–maximum = 0.00–0.64 wells km^{-2}).

The landscape at all sites was dominated by sagebrush; Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and little sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species included alderleaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), chokecherry (*Prunus virginiana*), common snowberry (*Symphoricarpos albus*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), and spiny hopsage (*Grayia spinosa*). Isolated stands of juniper (*Juniperus* spp.) and quaking aspen (*Populus tremuloides*) were found at the higher elevations on north-facing hillsides.

Sage-grouse Capture and Monitoring

We monitored sage-grouse hens during nesting and brood-rearing from 2008 to 2011. Hens were captured, radio-tagged, and released in April of each year. We captured hens at night using all-terrain vehicles (ATVs), spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Sage-grouse hens were fitted with 17.5-g or 22-g ($<$1.5% body mass) necklace radio-collars (RI-2D, Holohil Systems, Carp, Ontario, Canada; or A4060, Advanced Telemetry Systems, Isanti, Minnesota, USA).

We located hens weekly with Communications Specialists receivers (R-1000, Communications Specialists, Orange, California, USA) and three-way Yagi antennas. Potential nests were identified with binoculars from $\sim$15 m away by visually locating a radio-tagged hen under a shrub. Nests were verified by triangulating the hen under the same shrub from $>$50 m away or thoroughly searching the area of the potential nest when the hen was absent. We continued monitoring nests weekly until the nest hatched or failed.

We located the broods of radio-tagged hens weekly with binoculars from $\sim$15 m distance. Brood hens were identified either by visually detecting chicks or by observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, clucking). If there was evidence of at least one chick with a sage-grouse hen, we classified the hen as early brood (chicks $<$4 weeks of age) or late brood (chicks 4–8 weeks of age). Monitoring of broods continued for as long as possible, which was usually until the chicks were 3–8 weeks posthatch, the hen lost her brood, the hen died, or the hen could no longer be located.

Avian Predator Monitoring

To quantify avian predators, we used standard distance sampling techniques (Ralph et al. 1995, Buckland et al. 2001, Thomas et al. 2010), which entailed counting all avian predators observed during point counts and recording their distance from the observer. Point counts were conducted at random and sage-grouse (nest, early brood, and late brood) locations. Random locations were selected from habitat dominated by sagebrush within 8 km of the leks where sage-grouse were captured. This was intended to quantify avian predator density in habitat available for use by sage-grouse (Dinkins et al. 2012). Within each year, random locations were $>$2,000 m apart.

Point counts at sage-grouse nests were established when hens had begun incubating; thus, we assumed that we detected raptors and corvids that were present when nests were initiated. For a detailed description of point count methods see Dinkins et al. (2012) and Dinkins (2013). All avian predator variables were calculated from the raw count data within effective detection radii (EDR) estimated with DISTANCE version 6.0 release 2 (Thomas et al. 2010), as specified in Dinkins et al. (2012). Thus, *Buteo* spp. hawk, Golden Eagle, Northern Harrier (*Circus cyaneus*; hereafter "harrier"), kestrel, Black-billed Magpie (*Pica hudsonia*; hereafter "magpie"), and raven densities were individually calculated within 450 m, 1,000 m, 350 m, 400 m, 300 m, and 600 m, respectively, of each point count location (see Dinkins et al. 2012 for further details). We did not include other falcons or owls because they were rarely detected during point counts. Raw densities were standardized by the number of visits to each point count location and were log-transformed.

Anthropogenic and Landscape Feature Variables

We used ArcMap 10.0 (Esri, Redlands, California, USA) to calculate point count proximity (Euclidean distance) to anthropogenic features that could be used as perch or nest sites by avian predators or could provide food subsidies. We quantified the distance from each point count location to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy-extraction-related building), major road, any road type, communication tower, house, or power line. Densities of anthropogenic structures were calculated at four spatial extents (0.27-km, 0.54-km, 1.00-km, and 3.00-km radii) for oil and gas structures (number km^{-2}), major roads (km km^{-2}), all road types (km km^{-2}), houses (number km^{-2}), and power lines (km km^{-2}). The four spatial extents were derived from previous research on sage-grouse (Holloran and Anderson 2005, Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2010, Aldridge et al. 2011, Hanser et al. 2011). Ongoing energy development was occurring in half of our sites, which required us to assess the dates that energy-related structures and roads were added or removed from the landscape.

In distance calculations, we included only oil and gas structures and roads that existed when each point count was conducted. We obtained information on oil and gas structures, including the date that construction started on the structure and the date when wells were plugged and abandoned (the date that the structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC; http://wogcc.state.wy.us). We verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture 2010). Aerial imagery from NAIP is produced by the U.S. Department of Agriculture (USDA) on a 3-yr rotation; thus, we used WOGCC data and on-the-ground GPS units to map energy development that occurred after August 2009.

We used 2009 NAIP imagery to digitize the location of major roads, all roads, communication towers, and houses within a 5-km buffer around sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. Major roads included paved roads, improved gravel roads, and railroads; all roads included major roads and all unimproved four-wheel drive roads. All transmission and distribution power lines within a 5-km buffer around sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in power-line mapping.

Sage-grouse were likely to respond to many different types of anthropogenic structure in a similar manner (e.g., select locations farther away from all tall structures). Thus, we created two anthropogenic structure variables that represented the nearest: (1) distance to an oil and gas structure, communication tower, or house (WCH); and (2) distance to an oil and gas structure, communication tower, house, or power line (ANTH). This was in addition to distances from point count locations to individual types of anthropogenic structures.

Similarly to anthropogenic feature calculations, we used ArcMap 10.0 to calculate the distance from every point count location to landscape attributes including forested (deciduous or coniferous stands) and riparian habitats. Tree stands and riparian habitat were identified with Northwest ReGAP landcover data (http://gap.uidaho.edu/index.php/nw-gap/land-cover) from 2011, and verified with NAIP imagery from 2009. At our sites, riparian habitat from ReGAP consisted of mesic areas with patchy shrubs. In addition to distance variables, we calculated a normalized difference vegetation index (NDVI) and the proportion of forested, riparian, and big sagebrush habitats around all point count locations. We extracted NDVI values that were generated by Aldridge et al. (2011) and Hanser et al. (2011) for the Wyoming Basins Ecoregion, which were created from 250 m MODIS (Moderate Resolution Imaging Spectroradiometer) satellite imagery (http://modis.gsfc.nasa.gov/) between May and August of 2004. These NDVI values represent relative NDVI among point count locations during the sage-grouse nesting and brood-rearing season. Topography with greater surface roughness had the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that could provide vantage points for avian predators. Riley et al. (1999) created a topographic ruggedness index (TRI) to describe the roughness of landscapes, quantified as the difference in elevation among adjacent pixels of a digital

elevation map averaged over a user-defined area. For every point count location, we used ArcMap 10.0 to extract TRI values generated by Aldridge et al. (2011) and Hanser et al. (2011). Proportion of habitat (big sagebrush, forested, and riparian), NDVI, and TRI variables were constructed at four spatial extents (0.23-km^2, 0.92-km^2, 3.14-km^2, and 28.26-km^2) by using a moving window analysis within 0.27-km, 0.54-km, 1.00-km, and 3.00-km radii, respectively (Aldridge et al. 2011, Hanser et al. 2011).

Euclidean distance is not a good measure of habitat selection by wildlife, because the response of a species to landscape attributes or anthropogenic features often declines as distance increases (Carpenter et al. 2010, Aldridge et al. 2011, Fedy and Martin 2011, Hanser et al. 2011). Thus, we calculated distance decay functions to allow for nonlinear avoidance of landscape attributes or anthropogenic features, expressed as:

$$\text{Decay function} = \exp^{(\text{Euclidean distance to feature(km)}/-\text{decay distance})}.$$

We calculated all decay functions with three decay distances (0.25 km, 0.50 km, and 1.00 km). The value of the 0.25-, 0.50-, and 1.00-km decay functions approached 0 at ~1.2, ~2.4, and ~4.5 km, respectively. The distance at which decay function values approached 0 approximated the home range size of Golden Eagles and ravens (Boarman and Heinrich 1999, DeLong 2004). Decay functions scaled distance variables between 0 and 1, with greater values corresponding to point count locations closer to landscape attributes or anthropogenic features.

Data Analyses

We fit multinomial logistic regression models with maximum likelihood using function multinom in package nnet version 7.3–4 in R (R 2.14.2; R Development Core Team 2012) to evaluate habitat selection of nesting and brood-rearing sage-grouse hens. In addition to our full analysis, we conducted the same analysis with the exclusion of anthropogenic features on a subset of random and sage-grouse locations that were at least 3 km away from oil and gas structures, communication towers, power lines, rural houses, and major roads. This analysis was intended to verify whether sage-grouse response to avian predators was consistent regardless of influences from anthropogenic structures. Multinomial logistic regression models have been used to model habitat selection of wildlife species with >2 response categories (McCracken et al. 1998, McDonald et al. 2006, Bañuelos et al. 2008). We categorized point count locations into four response categories: (1) random, (2) sage-grouse nest, (3) early brood, and (4) late brood. Random point counts were kept in a single category across the summer, because we did not detect differences in avian densities between the first and second half of summer (Dinkins 2013); thus, modeling with multinomial logistic regression was more efficient as we could compare all response categories simultaneously rather than having to conduct a series of binomial regressions. Multinomial logistic regression uses one category as the reference for comparisons with all other categories; thus, each analysis can directly compare all categories among themselves by iteratively changing the reference category in the same model. To compare sage-grouse habitat selection with available sagebrush habitat (random locations), we made comparisons of sage-grouse locations with random locations by coding random locations as the reference category. We then alternated nest and early-brood location as the reference category to directly compare among sage-grouse locations.

Modeling of sage-grouse habitat selection was conducted using an information-theoretic approach (Anderson 2008). We compared models with Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002) using function aictab in package AICcmodavg version 1.25 in R (Mazerolle 2012). We employed sequential AIC_c modeling of covariate sets (anthropogenic, landscape, and avian predator), which Arnold (2010) suggested as an appropriate approach for identifying and ranking the most parsimonious models. Noninformative covariates (85% confidence intervals [CIs] of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC_c-selected models among covariate sets (Arnold 2010). We classified models within 2 AIC_c of the null model as being noncompetitive (Burnham and Anderson 2002); thus, any model within 2 AIC_c of the null was omitted from further analyses.

The best spatial extent and functional form of variables describing the effects of landscape attributes and anthropogenic features on habitat selection by sage-grouse were determined through AIC_c prior to sequential modeling of covariate sets (Step 1). We did not include WCH or ANTH with any anthropogenic structure variable that was used to create WCH or ANTH. For all distance decay functions, we chose the best decay distance (0.25 km, 0.50 km, and 1.00 km) for each distance variable by comparing AIC_c values. We compared models with individual density, proportion, and TRI variables measured at 0.27-km, 0.54-km, 1.00-km, and 3.00-km radii using AIC_c to choose the best spatial extent for each of those variable groups to be used in the anthropogenic and landscape covariate sets. Density and proportion variables were compared to the analogous proximity variables with AIC_c, and the best functional form of each variable was used in all further modeling (Table 1).

In Step 2, anthropogenic and landscape covariate sets were evaluated sequentially to identify the variables to be included in the best models for each of those covariate sets

TABLE 1. Variables selected in Step 1 of our modeling process and used in analysis of habitat selection by sage-grouse hens at nest ($n = 340$), early-brood ($n = 331$), and late-brood ($n = 121$) locations at 12 sites in southern Wyoming, USA, 2008–2011. Subscripts indicate best spatial extent or distance decay (km), and descriptions indicate best functional form (see Results).

Covariate set and variable name	Variable description
Anthropogenic	
$OGSden_{3.0}$	Density of oil and gas structures (energy wells, compressor stations, transfer stations, refineries, and other energy extraction related buildings; no. km^{-2})
$POWden_{3.0}$	Density of power lines (km km^{-2})
$MRDden_{3.0}$	Density of major roads (km km^{-2})
$HOM_{1.0}$	Distance decay function to nearest rural house
$WCHden_{1.0}$	Density of oil and gas structures, communication towers, and houses (no. km^{-2})
$ANTH_{0.25}$	Distance decay function to nearest oil and gas structure, communication tower, house, or power line
Landscape	
$SAGEpro_{1.0}$	Proportion of big sagebrush (*Artemisia* spp.) landcover
$TREE_{0.25}$	Distance decay function to nearest forested habitat including deciduous and coniferous stands
$RIP_{1.0}$	Distance decay function to nearest riparian habitat
$TRI_{0.54}$	Topographic ruggedness index
$NDVI_{0.27}$	Normalized difference vegetation index
Avian predator	
Small avian predators	Aggregated density of Black-billed Magpies and American Kestrels calculated from raw point counts within species-specific effective detection radii (300 m and 400 m, respectively)
Medium avian predators	Aggregated density of Common Ravens, *Buteo* hawks, and Northern Harriers calculated from raw point counts within species-specific effective detection radii (600 m, 450 m, and 350 m, respectively)
Large avian predators	Density of Golden Eagles calculated from raw point counts within the species-specific effective detection radius of 1,000 m

(i.e. models within 2 AIC_c of the top model within each covariate set). As the final modeling step (Step 3), we compared all top AIC_c-selected models from anthropogenic and landscape covariate sets and the best avian predator model from Dinkins et al. (2012) among each other and as additive models. The avian predator model included three avian predator variables (small, medium, and large avian predators), and three of the four years of data were from Dinkins et al. (2012). The three avian predator variables were constructed by aggregating raw avian predator densities calculated within species-specific EDRs based on the size of the avian predator, which resulted in small (magpie and kestrel), medium (*Buteo* hawk, harrier, and raven), and large (Golden Eagle) avian predator variables. This avian predator model was shown by Dinkins et al. (2012) to describe potential sage-grouse avoidance of avian predators better than models based on: individual species; distinguishing among different avian predator foraging styles; or avian predator threat to sage-grouse hens, nests, or broods. We based our inference on models within 2 AIC_c of the top selected model (Burnham and Anderson 2002). We prevented multicollinearity by not including in any model any two variables that covaried ($r > 0.65$) as determined with a Pearson's correlation matrix; thus, we eliminated one covarying variable from further analysis by retaining the variable that made the most biological sense.

Although we could not test for spatial autocorrelation in multinomial logistic regressions, avian predator densities derived from distance-sampling techniques were robust to lack of independence of observation locations because distance sampling was set up to be a snapshot in time (Thomas et al. 2010). Our avian predator sampling was designed to count the greatest proportion of the actual number of avian predators within a site each week while not counting the same avian predator more than once per week, as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a site in one day reduced the possibility of double-counting individual avian predators during that week's visit. Counting the same individual avian predator during different weeks, regardless of the particular point count location, was properly scaled by accounting for survey effort. We replicated point counts in multiple weeks to increase detection of avian predators (Thomas et al. 2010). When evaluating avian predator densities between sage-grouse and random locations, Dinkins et al. (2012) accounted for spatial autocorrelation in generalized linear mixed models; however, accounting for spatial autocorrelation did not significantly change the coefficient values of their avian predator models. Furthermore, multinomial logistic regression only requires that successive habitat selection choices be independent (Agresti 2007).

TABLE 2. Multinomial logistic regression models comparing landscape-attribute and anthropogenic-feature variables as covariate sets among locations used by sage-grouse (nest: $n = 340$, early-brood: $n = 331$, and late-brood: $n = 121$ locations) and random locations ($n = 660$) at 12 sites in southern Wyoming, USA, 2008–2011. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight. See Table 1 for variable descriptions.

Model	K	ΔAIC_c	w_i	Deviance
Anthropogenic covariate set				
$OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$ [a]	15	0.00	0.98	3522.16
$OGSden_{3.0}$, $POWden_{3.0}$, $HOM_{1.0}$	12	8.02	0.02	3536.30
$OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$	12	17.17	0.00	3545.44
$OGSden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$	12	19.84	0.00	3548.12
$OGSden_{3.0}$, $POWden_{3.0}$	9	20.62	0.00	3555.00
$POWden_{3.0}$, $MRDden_{3.0}$, $HOM_{1.0}$	12	22.22	0.00	3550.50
$POWden_{3.0}$, $HOM_{1.0}$	9	27.69	0.00	3562.06
$OGSden_{3.0}$, $MRDden_{3.0}$	9	34.02	0.00	3568.38
$POWden_{3.0}$, $MRDden_{3.0}$	9	40.72	0.00	3575.08
$POWden_{3.0}$	6	42.27	0.00	3582.70
Landscape covariate set				
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$ [b]	15	0.00	0.80	3432.84
$SAGEpro_{1.0}$, $TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	18	2.80	0.20	3429.50
$SAGEpro_{1.0}$, $TREE_{0.25}$, $RIP_{1.0}$, $NDVI_{0.27}$	15	16.19	0.00	3449.02
$SAGEpro_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	19.05	0.00	3458.00
$SAGEpro_{1.0}$, $TREE_{0.25}$, $TRI_{0.54}$, $NDVI_{0.27}$	15	23.25	0.00	3456.10
$SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$	12	27.12	0.00	3466.08
$SAGEpro_{1.0}$, $TREE_{0.25}$, $NDVI_{0.27}$	12	37.21	0.00	3476.16
$TREE_{0.25}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	15	38.59	0.00	3471.42
$RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	39.71	0.00	3478.66
$SAGEpro_{1.0}$, $NDVI_{0.27}$	9	44.24	0.00	3489.30

[a] $AIC_c = 3552.49$.
[b] $AIC_c = 3463.17$.

RESULTS

Avian Predators, Landscape Attributes, and Anthropogenic Features Analysis

We conducted 4,441 point count surveys at 1,452 locations during 2008–2011, including 340 sage-grouse nest, 331 sage-grouse early-brood, 121 sage-grouse late-brood, and 660 random locations. These locations were compiled from 289 hens with a mean of 1.2 nests per hen, 2.9 early-brood locations per hen, and 3.0 late-brood locations per hen. Brood locations were compiled from 124 separate sage-grouse broods from 114 sage-grouse hens. We counted 196 *Buteo* hawks, 295 Golden Eagles, 77 harriers, 105 kestrels, 143 magpies, and 688 ravens within species-specific EDRs (Dinkins et al. 2012), which equated to 248 small, 961 medium, and 295 large avian predators. These counts do not necessarily indicate unique individuals, but rather detections used to quantify density around localized areas. Brood, nest, and random locations aggregated across all years were on average 598.0 m (38.8 m SE), 908.6 m (9.6 m SE), and 1,189 m (25.5 m SE) apart, respectively. Avian predator variables did not covary with any other variables ($r^2 < 0.02$, variance inflation factor [VIF] ≤ 2.2), indicating no multicollinearity between avian predator variables and anthropogenic or landscape feature variables.

During Step 1, our modeling generally suggested that anthropogenic features were influencing sage-grouse habitat selection at a larger spatial extent (3-km radius) than were landscape attributes (<1-km radius; Table 1). The best spatial extent for density variables was within 3 km of a point count location. Densities of oil and gas structures ($OGSden_{3.0}$), power lines ($POWden_{3.0}$), and major roads ($MRDden_{3.0}$) fit the data better than raw distance or distance decay functions. The best spatial extents for the proportion of big sagebrush ($SAGEpro_{1.0}$), TRI ($TRI_{0.54}$), and NDVI ($NDVI_{0.27}$) were within 1.00 km, 0.54 km, and 0.27 km, respectively. Distance to rural houses ($HOM_{1.0}$) and riparian habitat ($RIP_{1.0}$) as 1-km distance decay functions fit the data better than Euclidean distance or densities. The effects of $HOM_{1.0}$ and $RIP_{1.0}$ on sage-grouse selection of nesting and brood locations became negligible beyond approximately 4 km (i.e. 1 km distance decay approaches zero at approximately 4 km away from an object of interest).

During Step 2 of sequential modeling, we found that sage-grouse selection of nest and brood locations was partially based on landscape attributes and anthropogenic features (Table 2). The top AIC_c-selected anthropogenic feature model ($w_i = 0.98$) included $OGSden_{3.0}$, $POWden_{3.0}$, $MRDden_{3.0}$, and $HOM_{1.0}$ (Table 2). The top AIC_c-selected

TABLE 3. Multinomial logistic regression models comparing anthropogenic and landscape covariate sets (top models from Table 2) and the avian predator model (including small, medium, and large avian predator densities) among locations used by sage-grouse (nest, early-brood, and late-brood locations) and random locations at 12 sites in southern Wyoming, USA, 2008–2011. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight.

Model	K	ΔAIC_c	w_i	Deviance
Avian, anthropogenic, landscape [a]	36	0.00	1.00	3042.14
Avian, landscape	24	38.24	0.00	3105.42
Avian, anthropogenic	24	141.46	0.00	3208.62
Avian	12	203.45	0.00	3295.24
Anthropogenic, landscape	27	295.98	0.00	3356.92
Landscape	15	347.16	0.00	3432.84
Anthropogenic	15	436.48	0.00	3522.16
Intercept only	3	509.13	0.00	3619.12

[a] $AIC_c = 3116.01$.

landscape feature model ($w_i = 0.80$) included $SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$, and $TRI_{0.54}$ (Table 2). During Step 3 of sequential modeling, our analyses indicated that sage-grouse hen selection of nest and brood locations was best described by small, medium, and large avian predator densities (avian predator model) in conjunction with many landscape attributes and anthropogenic features ($w_i = 1.00$; Table 3). This indicates that sage-grouse respond to multiple factors related to habitat quality, including factors related to perceived predation risk (landscape attributes and anthropogenic features) and direct predation risk (avian predator densities).

Greater densities of small, medium, and large avian predators were negatively correlated with sage-grouse nest, early-brood, and late-brood locations compared with random locations (Table 4). Early-brood and late-brood sage-grouse locations had lower avian predator densities than nesting sage-grouse locations (Table 5). Within each reproductive stage, sage-grouse locations had similar negative coefficient values for small and medium avian predators, but exhibited greater negative coefficient values for large avian predators (Golden Eagles) compared with small and medium avian predators (Tables 4 and 5).

In general, sage-grouse responded to most anthropogenic features by avoiding them, regardless of the sage-grouse's reproductive stage; however, many of these effects had parameter estimates with 95% CI that overlapped zero for all reproductive stages (Tables 4 and 5). In contrast to the avoidance of other anthropogenic structures, our analyses indicated that early-brood and late-brood sage-grouse were closer to rural houses ($HOM_{1.0}$ parameter estimate was positive) compared with random locations and nest locations (Tables 4 and 5). We found that nesting, early-brood, and late-brood sage-grouse were in areas with lower $OGSden_{3.0}$ compared with random locations (Table 4). However, the effect of $OGSden_{3.0}$ on sage-grouse habitat use during nesting had a parameter estimate with 95% CI that overlapped zero (Table 4). Sage-grouse use of habitat was negatively associated with $MRDden_{3.0}$ during all reproductive stages, with 95% CI of parameter estimates overlapping zero for brood locations (Table 4). Early-brood and late-brood sage-grouse locations had lower $POWden_{3.0}$ compared with random locations (Table 4).

For landscape attribute variables, we found that sage-grouse differed in their response to proximity to riparian habitat ($RIP_{1.0}$) depending on their reproductive stage. Compared with random locations, sage-grouse selected nest locations farther away from riparian habitat ($RIP_{1.0}$ parameter estimate was negative), but early-brood sage-grouse neither selected nor avoided habitat based on

TABLE 4. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 2 and 3). This analysis compares either nest, early-brood, or late-brood locations used by sage-grouse with random (reference category) locations at 12 sites in southern Wyoming, USA, 2008–2011. See Table 1 for variable descriptions.

	Nest vs. random			Early-brood vs. random			Late-brood vs. random		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−7.83 (0.91)	−9.61	−6.05*	−17.57 (1.51)	−20.54	−14.60*	−18.25 (1.98)	−22.14	−14.35*
Small avian predator	−0.09 (0.03)	−0.15	−0.02*	−0.34 (0.06)	−0.47	−0.21*	−0.33 (0.09)	−0.52	−0.16*
Medium avian predator	−0.08 (0.02)	−0.12	−0.04*	−0.28 (0.03)	−0.34	−0.21*	−0.28 (0.05)	−0.38	−0.19*
Large avian predator	−0.14 (0.05)	−0.23	−0.05*	−0.59 (0.12)	−0.82	−0.36*	−0.45 (0.14)	−0.73	−0.19*
$OGSden_{3.0}$	−0.37 (0.20)	−0.75	0.02	−0.56 (0.24)	−1.03	−0.09*	−3.18 (1.01)	−5.16	−1.20*
$POWden_{3.0}$	0.44 (0.67)	−0.88	1.76	−2.52 (0.97)	−4.44	−0.61*	−5.28 (1.71)	−8.64	−1.92*
$HOM_{1.0}$	0.12 (0.84)	−1.53	1.76	2.16 (0.79)	0.59	3.73*	2.56 (0.99)	0.62	4.50*
$MRDden_{3.0}$	−2.99 (1.31)	−5.58	−0.41*	−1.52 (1.48)	−4.44	1.40	−2.00 (2.54)	−7.01	3.02
$SAGEpro_{1.0}$	3.42 (0.58)	2.28	4.55*	2.17 (0.59)	1.02	3.33*	1.21 (0.78)	−0.32	2.75
$RIP_{1.0}$	−0.86 (0.28)	−1.42	−0.31*	−0.26 (0.29)	−0.83	0.31	0.85 (0.40)	0.05	1.64*
$TRI_{0.54}$	−0.04 (0.01)	−0.05	−0.02*	−0.02 (0.01)	−0.03	−0.01*	0.02 (0.01)	−0.04	<0.00*
$NDVI_{0.27}$	6.72 (1.06)	4.62	8.81*	5.97 (1.11)	3.78	8.16*	9.00 (1.36)	6.32	11.68*

* Denotes a 95% confidence interval that does not include zero.

TABLE 5. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 2 and 3). The reference category was alternated from random to nest or early-brood location to facilitate direct comparison of locations used by sage-grouse at 12 sites in southern Wyoming, USA, 2008–2011. See Table 1 for variable descriptions.

	Early-brood vs. nest [a]			Late-brood vs. nest [a]			Late-brood vs. early-brood [b]		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−9.74 (1.56)	−12.82	−6.66*	−10.42 (2.01)	−14.38	−6.45*	−0.68 (2.27)	−5.15	3.79*
Small avian predator	−0.26 (0.07)	−0.39	−0.13*	−0.25 (0.09)	−0.42	−0.07*	0.01 (0.10)	−0.20	0.21
Medium avian predator	−0.20 (0.03)	−0.27	−0.13*	−0.21 (0.05)	−0.30	−0.11*	0.00 (0.05)	−0.11	0.10
Large avian predator	−0.45 (0.12)	−0.69	−0.22*	−0.32 (0.14)	−0.60	−0.04*	0.14 (0.18)	−0.21	0.49
$OGSden_{3.0}$	−0.19 (0.27)	−0.72	0.33	−2.82 (1.01)	−4.81	−0.82*	−2.62 (1.01)	−4.61	−0.63*
$POWden_{3.0}$	−2.97 (1.01)	−4.94	−0.98*	−5.73 (1.72)	−9.11	−2.34*	−2.76 (1.76)	−6.22	0.70
$HOM_{1.0}$	2.04 (0.88)	0.32	3.78*	2.44 (1.05)	0.37	4.52*	0.40 (0.88)	−1.34	2.14
$MRDden_{3.0}$	1.47 (1.71)	−1.89	4.83	0.99 (2.68)	−4.28	6.27	−0.48 (2.62)	−5.64	4.68
$SAGEpro_{1.0}$	−1.24 (0.66)	−2.54	0.05	−2.20 (0.83)	−3.85	−0.56*	−0.96 (0.80)	−2.54	0.62
$RIP_{1.0}$	0.60 (0.32)	0.03	1.23	1.71 (0.43)	0.87	2.54*	1.11 (0.41)	0.30	1.91*
$TRI_{0.54}$	0.02 (0.01)	0.00	0.04*	0.02 (0.01)	0.00	0.04*	0.00 (0.01)	−0.02	0.02
$NDVI_{0.27}$	−0.75 (1.12)	−2.97	1.47	2.28 (1.36)	−0.41	4.97	3.03 (1.29)	0.48	5.58*

* Denotes a 95% confidence interval that does not include zero.
[a] Nest as reference category. This analysis also included random locations; however, those results are in Table 4.
[b] Early-brood as reference category. This analysis also included random and nest locations; however, those results are in the early-brood vs. nest and late-brood vs. nest columns and Table 4.

proximity to riparian habitat, and late-brood sage-grouse selected locations closer to riparian habitat ($RIP_{1.0}$ parameter estimate was positive; Table 4). However, both early-brood and late-brood locations were closer to riparian habitat compared with nest locations ($RIP_{1.0}$ parameter estimate was positive), and late-brood locations were closer to riparian habitat than early-brood locations ($RIP_{1.0}$ parameter estimate was positive; Table 5). $SAGEpro_{1.0}$ was positively associated with sage-grouse locations during nesting and early brood rearing (Table 4). $NDVI_{0.27}$ was positively associated with sage-grouse locations at all reproductive stages (Table 4). Sage-grouse during all reproductive stages were located in areas with flatter topography ($TRI_{0.54}$ parameter estimates were negative) compared with random locations (Table 4).

Avian Predators and Landscape Attributes Analysis

Our analysis that excluded locations within 3 km of anthropogenic structures comprised 2,406 point count surveys at 803 locations during 2008–2011. This equated to 153 sage-grouse nest locations (45% of total nest data), 207 sage-grouse early-brood locations (63% of total early-brood data), 93 sage-grouse late-brood locations (77% of total late-brood data), and 350 random locations (53% of total random data). Similar to the full analysis, avian predator variables did not covary with any other variable ($r^2 < 0.05$, VIF ≤ 2.3), indicating no multicollinearity between avian predator variables and anthropogenic or landscape feature variables. The subset analysis illustrated that the pattern of habitat use by sage-grouse was nearly the same as that in our full analysis in relation to avian predator densities and sage-grouse response to landscape attributes (Tables 6 and 7). Unlike in the full dataset, late-brood sage-grouse did not select for $SAGEpro_{1.0}$ or $RIP_{1.0}$; even so, the coefficients had the same positive values as in the full analysis (Table 7).

DISCUSSION

Sage-grouse hens used both indirect and direct mechanisms of predator avoidance to select habitat, which may have partially lowered their exposure to predation and nest predation. We did not quantify the effects of olfactory (mammalian) predators on sage-grouse selection of habitat. However, sage-grouse have not been found to hide their nests from olfactory predators at a microhabitat scale (Conover et al. 2010). In general, sage-grouse were located in less risky habitat that was farther away from potential perches and had lower densities of small, medium, and large avian predators. This result is largely concordant with the finding of Dinkins et al. (2012), who included some of the same bird location data but did not include landscape attribute or anthropogenic feature variables. The pattern of lower avian predator densities at sage-grouse locations was consistent between our full analysis and our analysis of locations >3 km away from anthropogenic structures (Tables 3 and 4 compared with Tables 6 and 7), which provided additional evidence that sage-grouse used direct predator avoidance. We found that sage-grouse locations were best described with models that included multiple habitat variables and avian predator densities. This implies that information on avian predator

TABLE 6. Multinomial logistic regression models comparing landscape-attribute variables and then comparing the top model from the landscape covariate set with the avian predator model (small, medium, and large avian predator densities) among locations used by sage-grouse (nest: $n = 153$, early-brood: $n = 207$, and late-brood: $n = 93$ locations) and random locations ($n = 350$) at 12 sites in southern Wyoming, USA, 2008–2011. Sage-grouse and random locations were greater than 3 km from anthropogenic features. K is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, and w_i is the model weight. See Table 1 for variable descriptions.

Model	K	ΔAIC_c	w_i	Deviance
Landscape covariate set				
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$ [a]	15	0.00	0.75	1930.96
$SAGEpro_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	2.78	0.19	1939.96
$SAGEpro_{1.0}$, $RIP_{1.0}$, $NDVI_{0.27}$	12	5.29	0.05	1942.46
$SAGEpro_{1.0}$, $NDVI_{0.27}$	9	8.50	0.01	1951.84
$RIP_{1.0}$, $TRI_{0.54}$, $NDVI_{0.27}$	12	26.35	0.00	1963.52
$RIP_{1.0}$, $NDVI_{0.27}$	9	34.32	0.00	1977.66
$TRI_{0.54}$, $NDVI_{0.27}$	9	40.04	0.00	1983.38
$SAGEpro_{1.0}$, $RIP_{1.0}$	9	40.40	0.00	1983.74
$SAGEpro_{1.0}$, $RIP_{1.0}$, $TRI_{0.54}$	12	44.26	0.00	1984.44
$NDVI_{0.27}$	6	48.83	0.00	1998.30
Avian and landscape comparison				
Avian, landscape [b]	24	0.00	1.00	1715.40
Avian	12	109.55	0.00	1850.08
Landscape	15	196.64	0.00	1930.96
Intercept only	3	291.92	0.00	2050.82

[a] $AIC_c = 1961.57$.
[b] $AIC_c = 1764.93$.

use of sagebrush habitat, even sagebrush habitat little influenced by anthropogenic structures, could improve understanding of how sage-grouse are distributed in sagebrush habitat.

Sage-grouse exhibit high individual (among seasons) and generational site fidelity (Fisher et al. 1993, Holloran and Anderson 2005, Thompson 2012), which likely limits their ability to move in response to changing distributions of avian predators. Site fidelity has been suggested to delay nonuse patterns of sage-grouse in response to developing oil and gas fields, with older birds displaying strong fidelity despite low productivity and yearling birds (first nesting season) avoiding new anthropogenic structures (Holloran et al. 2010, Naugle et al. 2011). Older sage-grouse hens with failed nests in a previous nesting season had lower nest site fidelity compared with hens with successful nests (i.e. eggs hatched), but the average distances between their sequential nests were 512 m and 283 m, respectively, hardly landscape-level movements (Holloran and Anderson 2005). Distances between sequential nests from our study also indicated lower nest-site fidelity for hens with previously failed nests compared with hens with successful nests, especially when stratified by sites with low vs. high raven density (average distance to previously failed nests: 0.66 km [0.26 km SE] and 1.16 km [0.20 km SE], respectively; average distance to previously hatched nests: 0.53 km [0.20 km SE] and 0.36 km [0.08 km SE], respectively; Dinkins 2013). The greatest average distance between subsequent nests was for birds with previously failed nests in areas with comparatively higher raven density. Yearling birds seem to adjust spatial location at relatively large spatial extents, whereas older birds changed spatial location at smaller scales.

Rather than indirect and direct predator avoidance explaining our results, sage-grouse habitat use patterns could also be explained by areas of relatively greater predation over time leading to low sage-grouse productivity (i.e. sage-grouse disappear from a localized area, resembling nonuse by sage-grouse). It is plausible that our random locations were areas with greater avian predator densities associated with historically lower productivity for sage-grouse. Temporal stability in location of nesting structures for avian predators in sagebrush habitat could generate areas with greater predation risk for sage-grouse. However, stability also correlates with relatively constant spatial habitat use by avian predators, which might allow

TABLE 7. Parameter estimates with 95% confidence intervals (LCL and UCL) from top AIC_c-selected multinomial logistic regression models (Tables 6). This analysis compares either nest, early-brood, or late-brood locations used by sage-grouse at 12 sites in southern Wyoming, USA, 2008–2011, with random (reference category) locations. See Table 1 for variable descriptions.

	Nest vs. random			Early-brood vs. random			Late-brood vs. random		
Variable	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL	Estimate (SE)	LCL	UCL
Intercept	−7.83 (1.25)	−10.60	−5.69*	−20.30 (2.30)	−24.83	−15.77*	−19.98 (2.46)	−24.82	−15.13*
Small avian predator	−0.09 (0.05)	−0.18	<0.00*	−0.43 (0.10)	−0.62	−0.23*	−0.45 (0.12)	−0.69	−0.21*
Medium avian predator	−0.06 (0.03)	−0.11	<0.00*	−0.30 (0.05)	−0.39	−0.21*	−0.29 (0.06)	−0.40	−0.18*
Large avian predator	−0.13 (0.07)	−0.26	0.01	−0.73 (0.20)	−1.13	−0.34*	−0.40 (0.14)	−0.69	−0.12*
$SAGEpro_{1.0}$	3.65 (0.80)	2.07	5.23*	2.22 (0.74)	0.76	3.68*	0.29 (0.91)	−1.50	2.07
$RIP_{1.0}$	−0.85 (0.42)	−1.67	−0.03*	−0.06 (0.38)	−0.81	0.68	0.59 (0.49)	−0.38	1.56
$TRI_{0.54}$	−0.03 (0.01)	−0.04	−0.01*	−0.02 (0.01)	−0.03	<0.00*	−0.03 (0.01)	−0.05	−0.01*
$NDVI_{0.27}$	6.53 (1.50)	3.57	9.50*	6.01 (1.52)	3.02	8.99*	12.94 (1.72)	9.56	16.32*

* Denotes a 95% confidence interval that does not include zero.

sage-grouse to directly avoid them. Even small distance adjustments in sequential nest locations have the potential to move a sage-grouse outside of a corvid's or a raptor's home range or use hotspots. Lower nest-site fidelity of sage-grouse illustrates the capacity of sage-grouse to at least partially adjust their use of habitat by moving away from threats after nest failure. Our results indicate that sage-grouse habitat use patterns were likely a remnant of multiple factors. Predator avoidance (indirect and direct mechanisms) and localized disappearance of sage-grouse were unlikely to be mutually exclusive processes shaping habitat use patterns of sage-grouse.

Avian predators including *Buteo* hawks (MacLaren et al. 1988, Schroeder et al. 1999, Schroeder and Baydack 2001), Golden Eagles (MacLaren et al. 1988, Danvir 2002), harriers (Schroeder et al. 1999, Thirgood et al. 2000, Fletcher et al. 2003), kestrels (Schroeder et al. 1999), magpies (Holloran and Anderson 2003, Vander Haegen et al. 2002), and ravens (Manzer and Hannon 2005, Bui et al. 2010, Coates and Delehanty 2010) negatively affect nest success or potentially prey on sage-grouse adults and chicks. One of the responses of prey species to the presence of these predators is direct avoidance (Lima 1998, Evans 2004, Cresswell 2008, Dinkins et al. 2012). Similarly to the results of Dinkins et al. (2012), our analyses indicated that sage-grouse avoided avian predators during all reproductive stages—nesting, early brood, and late brood—but at different magnitudes. Our results also suggest that sage-grouse hens have the ability to distinguish among threats to their own survival, their nests, and their offspring.

Sage-grouse are a relatively long-lived bird (Connelly et al. 2011). Johnson and Braun (1999) and Taylor et al. (2012) found that adult survival was the most influential demographic parameter on sage-grouse population growth, followed by chick survival and then nest success. Golden Eagles have been identified as the primary predator of adult sage-grouse (Schroeder et al. 1999, Schroeder and Baydack 2001, Mezquida et al. 2006). Sage-grouse hens avoided Golden Eagles (large avian predators) at greater magnitudes than smaller avian predators within each reproductive stage (i.e. more strongly negative parameter estimates for large avian predators than for small and medium avian predators when comparing sage-grouse locations to random locations; Table 4), suggesting that sage-grouse hens were predominantly concerned with their own survival. Our results also indicated that the magnitudes of avian predator avoidance for predators of all sizes were greater at early-brood and late-brood locations than at nest locations, suggesting that broods moved in a way that reduced predation risk to both adults and chicks.

In addition to direct avoidance of avian predators, sage-grouse selected habitat in response to landscape attributes and anthropogenic features. Direct and indirect avoidance of avian predators were not necessarily linked (correlated) from the perspective of a sage-grouse, because indirect cues (perches and areas with food subsidies for predators) were not correlated with the density of any avian predator species ($r^2 < 0.02$). Similarly to previous research, our analyses confirmed that sage-grouse select locations farther away from landscape attributes that could be used as perches or provide subsidized food resources for predators, including oil and gas structures (Aldridge 2005, Holloran 2005, Walker et al. 2007, Doherty 2008, Holloran et al. 2010, Kirol 2012) at all reproductive stages, power lines at brood locations, and major roads (Holloran 2005, Aldridge and Boyce 2007) and riparian habitat (Doherty et al. 2010, Dzialak et al. 2011) at nest locations. Sage-grouse also chose flatter locations, similarly to findings by Doherty et al. (2010), Dzialak et al. (2011), and Kirol (2012). A greater proportion of big sagebrush and higher NDVI values were positively associated with sage-grouse locations. Greater proportion of sagebrush habitat has been positively correlated with abundance of sagebrush-obligate and associated birds including Brewer's Sparrows, Green-tailed Towhees (*Pipilo chlorurus*), sage-grouse, Sagebrush Sparrows, and Sage Thrashers (*Oreoscoptes montanus*; Knick et al. 2005, Noson et al. 2006, Aldridge et al. 2011). Sage-grouse population growth and recruitment have also been associated with a greater NDVI (Blomberg et al. 2012); however, Guttery et al. (2013) did not find a connection between NDVI values and sage-grouse chick survival.

Habitat use involves tradeoffs among risks of weather exposure and predation and benefits of food acquisition (Verdolin 2006). Similarly to the findings of Dzialak et al. (2011), our results confirmed that sage-grouse have opposing associations with riparian habitat depending on reproductive stage. Sage-grouse were farther away from riparian habitat compared with random locations while nesting, but were closer to it compared with random locations during late brood rearing. Nesting may have occurred away from riparian areas because concealment cover and lower predator abundance was more important than food availability for nesting sage-grouse hens. However, chicks have increasing energetic needs as they grow, and sage-grouse hens typically move broods to riparian areas after early brood rearing (Crawford et al. 2004, Gregg and Crawford 2009). Sage-grouse hens also move broods to align with changes in food availability as the breeding season progresses. Riparian habitats provide forbs and invertebrates that meet the energetic demands of growing sage-grouse chicks (Connelly et al. 2004, Aldridge and Boyce 2007, Dzialak et al. 2011), but riparian habitats have a higher risk of brood failure (Aldridge and Boyce 2007). Sage-grouse appear to minimize the negative effects of increased predation risk associated with riparian areas directly by avoiding avian predators and indirectly by

avoiding riparian habitat during relatively more vulnerable reproductive stages (nest and early brood). Sage-grouse early-brood and late-brood locations were closer to rural houses than random and nest locations, which may be explained by the distribution of rural houses in more productive sagebrush habitat. This is speculative and deserves more research. If rural houses are in better habitat for brood foraging, sage-grouse movements to these areas may show similar patterns as movements to riparian habitat.

A prey species' ability to predict and avoid risky habitat increases survival and reproductive success, but the ability to directly avoid predators is more beneficial than avoiding indirect cues of predation risk (Thomson et al. 2006). Both mechanisms presumably achieve reduced predation rates; however, there may be other population-limiting effects as a result of indirect and direct predator avoidance, such as reduced foraging ability of prey species in areas of lower habitat quality (Lima 1998, Evans 2004, Cresswell 2008). High densities of avian predators and close proximity to landscape attributes and anthropogenic features—specifically riparian habitat, rugged topography, oil and gas infrastructure, power lines, and major roads—are likely to result in reduced adult survival and higher predation of sage-grouse eggs and chicks. Sage-grouse use of habitat was negatively associated with avian predator densities, with quality sage-grouse habitat presumably having lower densities of small, medium, and large avian predators. Increased avian predator abundance may induce changes in sage-grouse behavior associated with habitat usage. Thus, human manipulation of habitat that promotes increased densities of avian predators may limit sage-grouse populations, because even habitat that has high-quality cover and forage may become functionally unavailable to sage-grouse as avian predator densities increase.

ACKNOWLEDGMENTS

Research funding was provided by the Anadarko Petroleum Corporation, Jack H. Berryman Institute, Lincoln County Predator Management Board, Predatory Animal District of Sweetwater County, School of Energy Resources at the University of Wyoming, South Central and Southwest Wyoming Sage-grouse Local Working Groups, Utah Agricultural Experiment Station (Utah State University, publication number 8718), Uinta County Predator Management Board, Wyoming Animal Damage Management Board, and Wyoming Game and Fish Department. We greatly appreciate the logistical support provided by N. Tratnik, T. Christiansen, M. Zornes, N. Hymas, T. Clayson, M. Holloran, D. Oles, L. Oles, F. Blomquist, C. Morton, L. McCarthy, C. Powell, R. Etzelmiller, M. Murry, and many others. We thank our many field technicians, who are too numerous to name. We would also like to give a special thanks to the cooperation of the many landowners throughout southwestern and south-central Wyoming for allowing access to private lands.

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