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Microhabitat selection by greater sage-grouse hens during brood rearing

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Abstract: Greater sage-grouse (*Centrocercus urophasianus*) populations have declined throughout the western United States over the past century. Loss of large stands of sagebrush is a major factor leading to the decline of sage-grouse populations. We captured, marked, and tracked hen sage-grouse in Wyoming during the summer of 2012 to study where sage-grouse hens keep their chicks given the dual needs to provide them with food and to keep them safe from avian predators. Vegetation surveys and avian point counts were performed at early-season brood locations, late-season brood locations, and random locations. We conducted multinomial models to determine which habitat variables were most informative in predicting site selection by hen sage-grouse. Hens with and without broods selected sites that had more shrub cover during the early-brood season but not during the late-brood season. During the early-brood season, hens without broods avoided sites where there were American kestrels (*Falco sparverius*) and common ravens (*Corvus corax*), but brood hens did not avoid these sites. During late-brood season, brood hens chose sites with fewer small-avian predators (e.g., black-billed magpies [*Pica hudsonia*] and American kestrels), as well as medium-sized avian predators, such as common ravens, Buteo hawks (*Buteo* spp.), and northern harriers (*Circus cyaneus*). Our results suggest that habitat selection by sage-grouse hens is focused more on avoiding predators than on finding food.

Key words: brood site selection, *Centrocercus urophasianus*, habitat selection, microhabitat, predator avoidance, predator–prey interactions, sage-grouse

Over the past century, greater sage-grouse (*Centrocercus urophasianus*; Figure 1) populations have declined throughout the western United States (Patterson 1952, Connelly and Braun 1997, Connelly et al. 2004, Connelly et al. 2011). Greater sage-grouse (hereafter, referred to as sage-grouse, hens, broods, or chicks) use sagebrush (*Artemisia* spp.) throughout the year for food, shelter, and cover (Bent 1963, Connelly et al. 2011). Loss of sagebrush-dominated habitat has played a major role in the decline in sage-grouse populations throughout the West (Schroeder et al. 2004, Connelly et al. 2011, Kirol et al. 2012).

One way to stabilize sage-grouse populations is to increase the production of juvenile sage-grouse, but this requires suitable brood habitat (Crawford et al. 1992). Most chick mortality occurs when chicks are <3 weeks old (Patterson 1952). Sage-grouse hens keep their newly-hatched broods in sagebrush highlands for 2 to 3 weeks, until the chicks develop the ability to fly. The amount of time that hens keep their broods close to nesting habitat varies each year based on weather and food availability (Holloran and Anderson 2005). In Wyoming, most young broods were located within 3 km of their nest sites (Slater 2003, Holloran and Anderson 2005).

Forbs and insects are important foods for sage-grouse chicks. Therefore, it is not surprising that early-brood habitat is characterized by thick stands of sagebrush with a forb and grass understory containing an abundance of insects (Connelly et al. 2000, Aldridge and Brigham 2002, Kirol 2012). Late-brooding sites often are mesic sites that contain forbs and insects (Holloran 1999, Connelly et al. 2000, Holloran and Anderson 2005, Connelly 2011, Kirol 2012). Hens with late-broods also select for habitat with increased visual obstruction where chicks can hide from predators (Holloran and Anderson 2005).

Predators, including common ravens (*Corvus corax*) and hawks, are a common source of mortality of young sage-grouse (Girard 1937, Patterson 1952, Willis et al. 1993, Cote and Sutherland 1997, Guttery 2011). Survival of sage-grouse during the summer is lowest in: (1) risky habitat where there are perches that hawks can use for hunting; and (2) areas frequented by Buteo hawks (*Buteo* spp.),

Figure 1. Greater sage-grouse. (*Photo by D. Menke, courtesy U.S. Fish and Wildlife Service*)

northern harriers (*Circus cyaneus*) and golden eagles (*Aquila chrysaetos*; Schroeder et al. 1999, Dinkins et al. 2014*b*). Sage-grouse hens can protect their broods from predators by moving them to areas where there are fewer avian predators (Dinkins et al. 2012, 2014*a*, *b*).

The purpose of this study was to examine how habitat selection by sage-grouse hens with broods is impacted by the dual needs to provide food for their chicks and to keep them safe from avian predators. We examined if sage-grouse hens with and without broods differed in their habitat selection and predator avoidance during the early- and the late-brood seasons. We also compared sites occupied by sage-grouse hens to sites where sage-grouse were killed by predators to determine if some habitats were more risky than others.

Study area

Our study area included 11 circular sites in southwest and south-central Wyoming, each 16 or 24 km in diameter (7 study sites of 16-km diameter and 4 study sites of 24-km diameter). Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Each study site in southwest Wyoming was 16-km in diameter and centered on the specific lek where hens had been captured. Study sites in south-central Wyoming all were 24-km in diameter, because sage-grouse were captured at several adjacent leks. Study site diameters were based on Holloran and Anderson (2005); they found that 93% of observed nests were <8.5 km from leks where they bred. Study sites were chosen to provide a representation of overall sage-grouse brood-rearing habitat in southern Wyoming with a variety of land uses and topographic features (Holloran 2005, Dinkins et al. 2012, Kirol et al. 2012). Elevation ranged from 1,950 m to 2,530 m at all study sites. Land at most of our study sites was federally owned, and administered by the U.S. Bureau of Land Management; a small percentage of sites were on private land. Domestic sheep (*Ovis aries*) and cattle (*Bos taurus*) grazing were the dominant land uses. All study sites had anthropogenic development, which consisted mostly of unimproved 4-wheel drive roads. Conventional natural gas, conventional oil, and coal-bed methane natural gas extraction activities were present in 50% of our study sites. Removal of common ravens for the benefit of the local livestock producers was conducted by USDA Wildlife Services in 50% of the study sites. The vegetation at all study sites was dominated most commonly by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), black sagebrush (*A. nova*), or dwarf sagebrush (*A. arbuscula*). Other common shrub species in our study sites included antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), alderleaf mountain mahogany (*Cercocarpus montanus*), rabbitbrush (*Chrysothamnus* spp.), greasewood (*Sarcobatus vermiculatus*), 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 slopes.

Methods

Sage-grouse capture and monitoring

Each April from 2008 to 2011, we captured sage-grouse hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982, Wakkinen et al. 1992). Hens were released at capture sites after we fitted them with 17.5-g or 22-g (<1.5% body mass) necklace radio collars made by Holohil Systems Ltd. (Carp, Ontario, Canada or Advanced Telemetry Systems Inc, Isanti, Minn.).

We monitored sage-grouse hens during nesting and brood rearing from late March

through July 2012. We located radio-tagged hens weekly with Communications Specialists receivers and 3-element Yagi antennas (Communications Specialists, Orange, Calif.). Collared hens were identified with binoculars while we were approximately 25 m away by circling each hen until it was visually located. We monitored hens weekly for survival and brood presence throughout the brood-rearing season. Locations within 20 days after hatching were considered early-brood locations (Thompson et al. 2006). We identified hens unaccompanied by broods after we repeatedly failed to observe any brooding behavior by the hen or chicks. Hens without broods were located at the same time as hens with broods. We used the average of the hatching days of all successful nests as the starting point to label unaccompanied hens as early- or late-brood.

Table 1. Top avian and vegetation models from all possible combinations of informative variables for the early-brood season. Top models were used to compare locations of sage-grouse brood hens, nonbrood hens, and random points. (LARGE = golden eagle density; MED = common raven, Buteo hawk, and northern harrier density; BUTEO = Buteo hawk density; CORA = common raven density; AMKE = American kestrel density; SHRUB = percent shrub cover; BARE = percent bare ground, INGRASS = height of tallest grass in plot; OUTGRASS = height of tallest grass within 1 m outside plot; ROBEL = average Robel pole reading; RESGR = height of residual perennial grass).

Model	K	ΔAIC_c	w_i
Early-brood season — Avian predators			
LARGE + CORA + AMKE	8	0.00	0.20
MED + MAKE	6	0.35	0.17
CORA + MAKE	6	0.39	0.17
CORA + BUTEO + MAKE	8	0.58	0.15
LARGE + AMKE	6	3.05	0.04
LARGE + MED	6	3.26	0.04
LARGE + AMKE + BUTEO	8	3.30	0.04
LARGE + CORA	6	3.61	0.03
AMKE + BUTEO	6	3.79	0.03
MED	4	3.82	0.03
NULL (INTERCEPT ONLY)	2	8.32	0.00
Early-brood season—Vegetation			
SHRUB	6	0.00	0.27
SHRUB + BARE + INGRASS	8	2.12	0.09
SHRUB + BARE + ROBEL	8	2.23	0.09
SHRUB + ROBEL	6	2.65	0.07
SHRUB + BARE + OUTGRASS	8	3.40	0.05
SHRUB + BARE + INGRASS + RESGRASS	10	3.91	0.04
SHRUB + BARE + GRAVEL	8	4.18	0.03
SHRUB + RESGRASS	8	4.32	0.03
SHRUB + BARE + GRAVEL + INGRASS	10	4.73	0.03
SHRUB + INGRASS + RESGRASS	8	4.83	0.02
NULL (INTERCEPT ONLY)	2	25.0	0

Vegetation surveys

We conducted vegetation surveys at sites where radio-collared hens were located during early- and late-brood seasons to determine micro-habitat characteristics. Surveys were also conducted at an equal number of randomly generated points within each study site. To restrict random locations to habitat considered available to sage-grouse for brood-rearing, we used ArcMap 10.1 (ESRI Inc., Redlands, Calif.) to generate random locations only in sagebrush-dominated habitat as classified by the Northwest ReGAP land cover data during 2008 (Lennartz 2007). Random locations were selected to be >1000 m apart from each other. We generated 12 random locations in each 16-km diameter study site and 20 random locations in each 24-km diameter study site.

Hereafter, hens with broods will be referred to as brood hens, and hens without broods will be referred to as nonbrood hens. Each early- and late-brood location was paired with a random-point location and surveyed for shrub height, shrub density, ground cover, and visual obscurity.

At each location, shrub height and density were determined along 20-m transects in the

north-south and east-west directions centered on the location of observed hen or random point. Height, size and species of shrub (i.e. woody vegetation) were documented on the same transects using techniques previously reported by Gregg et al. (1994), Thompson et al. (2006), Connelly et al. (2011), and Kirol et al. (2012). We measured the highest point (cm) of all shrub species encountered on the transect and averaged their heights per location (hereafter, called shrub height). We calculated shrub density by counting the number of live shrubs within 1 m of each transect line. Visual obscurity was determined by using a 1-m Robel pole (Robel et al. 1970) placed at each hen's location and random point. Visual obscurity was measured at 5-m increments from each cardinal direction by looking back at the Robel pole at a height of 1-m. We recorded the lowest observable point on the Robel pole that was not obscured by vegetation from each distance. Canopy and ground cover were determined visually within 6 cover classes in 20 × 50-cm quadrants (Daubenmire 1959). Quadrants were placed along each transect along the north-south and east-west transects at distances of 0, 4, 6, 8, 10, 12, and 14 m radiating from the center point.

Canopy and ground cover were grouped into 6 categories based on the percent of ground covered by vegetation with: 1 = 0 to 1% coverage; 2 = 1.1 to 5% coverage; 3 = 5.1 to 25% coverage; 4 = 25.1 to 50% coverage; 5 = 50.1 to 75% coverage; and 6 = 75.1 to 100% coverage. Ground-cover categories were: annual grass, perennial grass, residual grass (i.e., dead sections of grass still standing from the previous year); food forb (forbs that are known to be eaten by sage-grouse (Mabray 2015); nonfood forb (species sage-grouse are not known to eat); gravel and rock (crushed stone of any size); bare soil (soil not covered by any other material); cryptobiotic crust (cyanobacteria, lichens, moss, green algae, microfungi and bacteria); cacti (*Opuntia* spp., *Pediocactus* spp.); and litter (dead vegetative matter, or scat). In addition, we measured the tallest portion of annual, perennial, and residual perennial grass (cm) blades within 1 m of the leading outer edge of each Daubenmire quadrant.

Avian-predator point counts

Avian predator point counts were performed at each sage-grouse location and weekly at an equal number of randomly generated locations (Dinkins et al. 2012, Dinkins et al. 2014*a*). Avian-predator point counts consisted of 10-minute observation periods during which we recorded all avian predators including, common raven, black-billed magpie (*Pica hudsonia*), golden eagle, Buteo hawks, northern harrier, and American kestrel (*Falco sparverius*). We determined a weighted average for avian-predator densities to eliminate differences in number of visits that each random point and sage-grouse location received over the summer.

Data analysis

We compared multinomial models using Akaike's information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i; Burnham and Anderson 2002) with function aictab in package AICCMODAVG R. Multinomial models were used because of the multiple plot type variables (early-brood, early-hen, late-brood, late-hen, mortality, and random). The following multinomial equation was used:

$$(x_1 + x_2 + \cdots + x_k)^n = \sum_{n_1,n_2,\ldots,n_1 \geq 0} \frac{n!}{n_1!\, n_2! \ldots n_k!} x_1^{n_1} x_2^{n_2} \ldots x_k^{n_1}$$

AICc was used to determine the model that best described the variation in the data collected. Variables that we tested included all vegetation covariates, including shrub cover, ground cover, and visual-obscurity. The objective of our analysis was to determine the variables that hen sage-grouse selected during early- and late-brood rearing season regardless of their reproductive status. Therefore, we compared site selection by all hens compared to available habitat. All combinations of season and hens (early-season nonbrood hens, early-season brood hens, late-season nonbrood hens, and late-season brood hens) were compared to random-site locations. Bird locations were analyzed based on the temporal group (early-season or late-season) in which they were observed, regardless of reproductive status. This allowed us to determine what

Table 2. Top models for both early- and late-brood seasons based on their AICc scores. Top models compared locations of sage-grouse brood hens, nonbrood hens, and random points. (LARGE = golden eagle density, MED = common raven, buteo hawk, and northern harrier density, SMALL = black-billed magpie and American kestrel density, CORA = common raven density, AMKE = American kestrel density, SHRUB = percent shrub cover, BARE = percent bare ground, INGRASS = height of tallest grass in plot, OUTGRASS = height of tallest grass within 1 m outside plot, ROBEL = average robel pole reading, RESGRASS = height of residual perennial grass in plot, GRAVEL = percentage of gravel cover).

Model	K	ΔAIC_c	w_i
SHRUB + CORA + AMKE	8	0.00	0.20
SHRUB + BARE + ROBEL + CORA + AMKE	12	0.01	0.19
SHRUB + BARE + ROBEL + LARGE + CORA + AMKE	14	2.69	0.05
SHRUB + BARE + OUTGRASS + CORA + AMKE	12	2.75	0.05
SHRUB + BARE + INGRASS + CORA + AMKE	12	2.82	0.05
SHRUB + ROBEL + CORA + MAKE	10	3.05	0.04
SHRUB + LARGE + CORA + MAKE	10	3.07	0.04
SHRUB + CORA + BUTEO + AMKE	10	3.13	0.04
SHRUB + BARE + ROBEL + CORA + BUTEO + AMKE	14	3.35	0.04
SHRUB + MED + MAKE	8	3.94	0.03
NULL (intercept only)	2	28.65	0.00
SMALL + MED + SHRUB + BARE + GRAVEL + ROBEL	10	0.00	0.37
SMALL + MED + SHRUB	12	1.61	0.16
SMALL + MED + LARGE + SHRUB + BARE + GRAVEL + ROBEL	12	2.95	0.08
SMALL + MED + LARGE	8	3.21	0.07
SMALL + MED + LARGE + SHRUB + OUTGRASS + ROBEL	10	4.80	0.03
SMALL + MED + SHRUB + OUTGRASS + ROBEL	10	4.80	0.03
SMALL + MED + SHRUB + ROBEL	12	4.96	0.03
SMALL + MED + LARGE + SHRUB	14	5.26	0.03
SMALL + CORA + SHRUB	12	5.32	0.03
SMALL + MED + SHRUB + BARE + OUTGRASS	14	5.83	0.02
SMALL + MED + BARE + GRAVEL	12	5.84	0.02
NULL (intercept only)	2	18.64	0.00

environmental factors hen sage-grouse selected during early- and late-brooding seasons. We based inference on multinomial models within 4 AIC_c of the top-selected model and conducted model averaging of parameter estimates from models within 4 AIC_c of the top-selected model (Burnham and Anderson 2002). Variable importance was calculated for each parameter estimate that was model averaged by summing the w_i across all models with that variable (Arnold 2010).

Covariates

We grouped avian predators by body size (Dinkins et al. 2012, 2014*b*). Small predators (SMALL) included black-billed magpies (BBMA; mean mass = 178 g) and American kestrels (AMKE; mean mass = 117 g). Medium predators (MED) included: common ravens (CORA; mean mass = 1150 g); buteo hawks (BUTEO; mean mass = 1000 g); and northern harriers (NOHA; mean mass = 890 g). We considered golden eagles (GOEA; mean mass = 4500 g) to be the only large avian predator (LARGE) on the landscape. Average body mass

Table. 3. Parameter estimates for the early-brood season with 95% confidence intervals (CI) for top AICc selected multinomial regressions. The top model compared avian-predator densities (CORA = Common raven; AMKE = American kestrel) and vegetation data (Shrub cover = percent shrub cover) at locations of sage-grouse brood hens, nonbrood hens, and random points. Early-season locations included locations for 8 brood hens, 32 nonbrood hens, and 92 random locations.

Variable	Estimate	SE	95 % CI	
			Lower	Upper
Brood intercept	*- 12.72*	38.94	-89.05	63.61
Shrub cover	0.10	0.03	0.04	0.11*
CORA density	- 1.35	5.64	-12.40	9.69
AMKE Density	0.28	0.15	-0.02	0.58
Nonbrood intercept	-15.26	0.02	-15.03	-15.21*
Shrub cover	0.08	0.02	0.04	0.15*
CORA density	- 0.32	0.13	-0.57	-0.07*
AMKE Density	- 1.47	0.16	-1.77	-1.15*

* Denotes 95% CI that does not include zero.

was obtained from Sibley (2003).

We considered 3 main sub-groups of vegetation covariates: shrub cover, ground cover, and visual obscurity. Shrub cover included all data collected during transect surveys; these covariates include: live-shrub cover (LIVESHR); live-shrub height (LIVESHR_HT); dead-shrub cover (DEADSHR); dead-shrub height (DEADSHR_HT); live-sagebrush cover (LIVEART); live-sagebrush height (LIVEART_HT); dead-sagebrush cover (DEADART); dead-sagebrush height (DEADART_HT); total-sagebrush cover (TOTALART); and total-sagebrush height (TOTALART_HT). Ground cover covariates included: annual grass cover (AGRASS); annual grass height (AGRASS_HT), perennial grass cover (PGRASS); perennial grass height (PGRASS_HT); residual grass cover (RESGR); bare dirt cover (BARE); litter cover (LITTER); cryptobiotic crust cover (CRYPTO); and gravel cover (GRAVEL). Visual obscurity was composed of a single covariate per site, the average measurements from all Robel pole readings at all vegetation plot locations (ROBEL). All shrub cover data were converted to a single value per plot (SHRUB).

Model construction and selection

We ran multinomial models containing all variables independently to determine informative variables from the overall set of collected data for early- and late-brood seasons for sage-grouse hens with and without broods. All models with a ΔAICc below that of the null model (the null model functions as a statistical null hypothesis for detecting pattern) were removed from all further analysis (Gotelli 2006, Arnold 2010). We kept all variables that performed better than the null and had an 85% confidence intervals did not overlap zero. We ran them in all possible combinations to determine the most informative avian and vegetation models for both early- and late-brood seasons to be used in final analysis. All models that ranked within 4 AICc of the top model were kept for further analysis. An individual variable was considered statistically significant if the 95% confidence interval of its regression did not overlap zero.

Results

Vegetation sampling and avian-predator point counts were each performed at 173 sage-grouse and random-point locations. Samples included 40 early-season bird locations, 35 late-season locations, 92 random-points and 7 locations where we located a dead sage-grouse hen that had been depredated. The 40 early-season locations included locations for 8 brood hens and 32 nonbrood hens. Late-season locations contained 7 brood hens and 33 nonbrood hens.

Habitat used by hen sage-grouse during early-brood season differed from available sage-grouse habitat (i.e., random points) in having more shrub cover, more visual obscurity, and lower densities of common ravens and American kestrels (Tables 1 and 2). Two models

Table. 4. Top avian and vegetation models using all possible combinations of variables for the late-brood season. Top models were used to compare locations of sage-grouse brood hens, nonbrood hens, and random points. (LARGE = golden eagle density; MED = common raven, Buteo hawk, and northern harrier density; SMALL = black-billed magpie and American kestrel density; NOHA = northern harrier density; CORA = common raven density; AMKE = American kestrel density; SHRUB = percent shrub cover; BARE = percent bare ground; INGRASS = height of tallest grass in plot; OUTGRASS = height of tallest grass within 1 m outside plot; ROBEL = average Robel pole reading; RESGRASS = height of residual perennial grass in plot; GRAVEL = percentage of gravel cover).

Model	K	ΔAIC_c	w_i
Avian models			
SMALL + MED	6	0.00	0.42
SMALL + MED + LARGE	8	2.18	0.14
SMALL + CORA	6	3.38	0.08
MED + MAKE	6	4.49	0.04
SMALL	4	4.92	0.04
SMALL + CORA + NOHA	8	4.97	0.04
SMALL + LARGE + CORA	8	5.90	0.02
SMALL + CORA + BUTEO	8	6.08	0.02
MED	4	6.34	0.02
MED + LARGE + MAKE	8	6.55	0.02
NULL (intercept only)	3	215.63	0.00
Vegetation models			
SHRUB + ROBEL	6	0.00	0.17
BARE + GRAVEL	6	1.11	0.10
SHRUB + BARE + ROBEL	6	2.04	0.06
SHRUB	8	2.26	0.06
SHRUB + INGRASS + RESGRASS	8	2.39	0.05
BARE + GRAVEL + RESGRASS	8	2.67	0.05
SHRUB + BARE + OUTGRASS	8	2.86	0.04
SHRUB + GRAVEL + ROBEL	8	2.95	0.04
SHRUB + INGRASS + ROBEL	8	3.22	0.03
SHRUB + BARE + GRAVEL + ROBEL	10	3.93	0.02
NULL (intercept only)	3	214.91	0.00

scored within 2 AICc; they were (SHRUB) + (CORA + AMKE) (AICc = 176.69 with a log likelihood of -79.76) and (SHRUB + BARE + ROBEL) + (CORA + AMKE) (AICc=176.70 and a log likelihood of -75.03). During the early-brood season, hens with and without broods preferred areas with more shrubs (Table 3). Nonbrood hens avoided sites where there were common ravens or American kestrels, but nonbrood hens did not.

Our best-fit models for describing site selection by hen sage-grouse during late-brood season contained shrub cover and densities of small and medium-sized avian predators (Table 4). The top 2 models, within 2 AICc, were (SMALL+ MED) + (SHRUB + BARE + GRAVEL + ROBEL) (AIC = 163.06 and a log likelihood of -70.57), and (SMALL + MED) + SHRUB (AIC = 164.67 and a log likelihood of -68.96). During the late season, sage-grouse hens, both with and without broods, selected sites that had more shrub cover than random sites (Table 5). Hens with broods avoided sites with either small avian predators (black-billed magpies

Table. 5. Parameter estimates for the late-brood season with 95% confidence intervals (CI) for top AICc selected multinomial regressions. The top model compared avian-predator densities (Small = American kestrel and black-billed magpies, Medium = buteo hawks, common ravens and northern harriers) and vegetation data (Shrub cover = percent shrub cover) at locations of sage-grouse brood hens, nonbrood hens, and random points. Late-season locations included 7 brood hens, 33 nonbrood hens, and 92 random locations.

Variable	Estimate	SE	95 % CI	
			Lower	Upper
	Brood			
Intercept	- 1.17	1.80	-4.70	2.36
Small predators	- 18.89	4.67E -8	-18.90	-18.90*
Medium predators	- 24.96	6.05E -5	-24.96	-24.96*
Shrub cover	0.05	0.05	-0.03	0.14
Bare ground	- 0.07	0.05	-0.17	0.01
Gravel	- 0.11	0.11	-0.27	0.17
Robel pole	- 0.04	0.04	-0.12	0.03
	Nonbrood			
Intercept	- 1.17	0.88	-1.90	2.36
Small predators	- 2.24	6.37E -6	-25.42	-25.42*
Medium predators	- 0.29	2.31E -1	-0.07	0.83
Shrub cover	0.08	0.02	-0.01	0.07
Bare ground	0.01	0.02	-0.11	0.01
Gravel	0.03	0.02	-0.08	0.01
Robel pole	- 0.07	0.04	-0.07	0.01

* Denotes 95% CI that does not include zero.

and American kestrels) or medium-sized avian predators (common raven, Buteo hawk, and northern harrier).

Vegetation surveys and avian point counts were performed at sites where 5 hen sage-grouse had been killed by either avian or mammalian predators. When models were run comparing mortality sites to random sites, no variables were significant.

Discussion

We found that sites occupied by hen sage-grouse, regardless of whether they were accompanied by a brood, differed from random sites based on multiple variables. During the early-brood season, hens select sites that contained more shrub cover. Guttery (2011) found during early-brood season that hen sage-grouse select sites with high density of black sagebrush. Black sagebrush is shorter and denser than big sagebrush (Wyoming big sagebrush and mountain big sagebrush) and provides concealment for chicks without the brush obscuring the vision of hens.

We found that sage-grouse hens, both with and without broods, avoided sites where there were higher densities of small and medium-sized avian predators when compared to random locations although the results for brood hens were not statistically significant during the early season. Dinkins et al. (2012, 2014*a*) also reported that hens with broods select sites with lower densities of avian predators. Small and medium-sized avian predators kill sage-grouse chicks, and medium-sized predators, Buteo hawks in particular, can kill adult sage-grouse. Connelly et al. (2000) reported that predation is not a limiting factor on sage-grouse populations. However, sage-grouse will avoid the predators that pose a threat to their survival. Small predators, such as black-billed magpies and American kestrels, were avoided by all hen sage-grouse during both the early and late seasons, whereas medium-sized predators were avoided only by those hens that had an active brood during the late-season. Other than this one variable, habitat selection was similar between the early-brood season and late-brood season. Our results indicate that sage-grouse hens select sites based more on avoiding predators than on the sites vegetation.

Management implications

Anthropogenic development of sagebrush stands not only leads to the loss of suitable habitat for sage-grouse but also leads to an increase in predator densities (Dinkins et al. 2014*b*). Tall structures, including rural homes, communication towers, oil and gas structures, and power poles provide nesting and perching opportunities for raptor species. Increase in

nesting and perching opportunities across the landscape has caused an increase in predator densities (Dinkins et al. 2014*b*).

Sage-grouse minimize the threat of predation by avoiding areas where they observe predators (Conover et al. 2010). The results of this study and Dinkins et al. (2014*a*) demonstated that sage-grouse also avoiding habitat that the birds perceive as riskier, such as areas near tall structures and other anthropogenic features. Avoidance of avian predators and anthropogenic features allows hen sage-grouse to lower their risk of predation, but also has the unfortunate effect of concentrating sage-grouse into smaller areas.

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