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Microhabitat Selection by Greater Sage-Grouse Hens in Southern Wyoming

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MICROHABITAT SELECTION BY GREATER SAGE-GROUSE

HENS IN SOUTHERN WYOMING

by

Scott T. Mabray

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ABSTRACT

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Utah State University, 2015

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Greater sage-grouse (*Centrocercus urophasianus*) populations have declined throughout the western United States over the past 3 decades. Habitat loss within the sagebrush steppe ecosystem is a major factor leading to sage-grouse population decline. Hen sage-grouse were captured, marked, and tracked during the summer of 2012 in southwestern and south-central Wyoming. I performed vegetation surveys, and avian point counts were performed at 1 early-season brood location, 1 late-season brood location, and an accompanying random location for each marked hen regardless of reproductive status. Multinomial models were run to determine what habitat variables were most informative in predicting site selection by hen sage-grouse. During early-brood season, hen sage-grouse with chicks selected sites that had high total shrub cover density; these areas also exhibited high densities of American kestrels (*Falco sparverius*). They did not avoid areas with common ravens (*Corvus corax*). Hen sage-grouse not accompanied by a brood selected sites with high total shrub cover and low densities of common ravens and American kestrels. During late-brood season, hen sage-grouse that were accompanied by a brood selected sites with high shrub cover and low densities of small avian predators, such as black-billed magpies (*Pica hudsonia*) and American kestrels as well as medium-sized predators, such as common ravens, buteo hawks (*Buteo* spp.), and northern harriers (*Circus cyaneus*). Hens that were not accompanied by broods were more often found in sites with high total shrub cover and low densities of small avian predators, but selected sites with higher densities of medium-sized predators. Hen sage-grouse select areas with high total shrub cover during early and late-brood season regardless of their reproductive status. By avoiding predators and selecting areas with cover, hens with broods can reduce the risk of their chicks being depredated.

(53 pages)

PUBLIC ABSTRACT

Microhabitat Selection by Greater Sage-Grouse

Hens in Southern Wyoming

Scott Thomas Mabray

Greater sage-grouse (*Centrocercus urophasianus*) populations have been declining throughout the western United States over the past 3 decades. Habitat loss within the range sagebrush steppe ecosystem is a major factor leading to sage-grouse population decline. Understanding the use of microhabitats by hen sage-grouse may provide data that will allow managers to reduce the decline in the sage-grouse population.

My objective was to determine the factors lead to site selection by hen sage-grouse hens. This was accomplished by addressing several questions regarding the interactions of habitat selection and predator avoidance among sage-grouse hens. I examined if (1) sites occupied by sage-grouse hens with broods differ from random sites, (2) sites occupied by sage-grouse hens with broods differ from sites occupied by sage-grouse hens without broods, (3) sites occupied by sage-grouse hens with young broods differ from sites occupied by sage-grouse hens with old broods, and (4) sites where hen sage-grouse were killed differ from sites occupied by live sage-grouse hens or random sites.

Previous studies have looked at microhabitat selection by hen sage-grouse with active broods. To my knowledge, there have been no studies that have determined if hen sage-grouse will select the same habitat if they are not accompanied by a brood.

I determined that hen sage-grouse select area with high total shrub cover throughout the summer regardless of their reproductive status. By avoiding predators and selecting areas with high shrub cover, hens with broods can reduce the risk of their chicks being depredated.

Hen sage-grouse may avoid otherwise suitable habitat based on perceived risk due to higher densities of avian predators. I recommend that managers should focus efforts on maintaining and increasing shrub cover in sage-grouse habitat and refrain from practices that lead to reduce shrub cover within sage-grouse habitat.

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INTRODUCTION

The sage-grouse (*Centrocercus urophasianus*), is a long-lived species with high annual survival and low reproductive rates (Connelly et al. 2000). Over the past few decades, greater sage-grouse populations have declined throughout the western United States (Patterson 1952, Connelly and Braun 1997, Connelly et al. 2004, Connelly et al. 2011). Sage-grouse use sagebrush (*Artemisia* spp.*)* throughout the year for food, shelter, and nest cover (Patterson 1952, Bent 1963, Connelly et al. 2011). Loss of sagebrush-dominated habitat is a major factor in the decline in sage-grouse populations throughout the western United States (Schroeder et al. 2004, Connelly et al. 2011, Kirol 2012).

Sage-grouse are a polygamous species that breed on leks or strutting grounds. Like most polygamous birds, sage-grouse males provide neither parental care nor resources (Schroeder et al. 1999, Kirol 2012). In Wyoming, female sage-grouse generally breed in late March and April, depending on annual weather conditions (Schroeder et al. 1999). Females start building their nest within a few days of breeding and remain close to the nest bowl until laying is complete (Patterson 1952). Female sage-grouse show high fidelity to nesting areas and often nest close to the previous year's nest (Patterson 1952, Schroeder et al. 1999, Holloran and Anderson 2005, Dinkins 2013). After an incubation period of 25-29 days, sage-grouse eggs hatch in late May and early June (Schroeder et al. 1999). Clutch size, on average, is 7 eggs with a range of 6 to 9 (Patterson 1952, Schroeder et al. 1999, Connelly et al. 2011, Kirol 2012). After hatching, hen sage-grouse move their chicks to habitat more suitable for brood rearing.

Previous research has improved our understanding of the microhabitat characteristics of early- and late-brooding sites of adult hen sage-grouse with broods

(Holloran and Anderson 2005, Dinkins et al. 2012, Kirol 2012). Sage-grouse brood hens selected locations with higher densities of sagebrush and grass cover compared to available sage-grouse habitat (Aldridge and Brigham 2002, Kirol et al. 2012).

Early-brood and nesting habitats have similar characteristics (Holloran and Anderson 2005, Connelly 2011, Kirol 2012). Sage-grouse hens keep their newly-hatched broods in sagebrush highlands for 2-3 weeks, until the chicks have the ability to fly and are more mobile. 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). The height of chick mortality occurs during early-brood rearing (up to 3 weeks after hatching); (Patterson 1952). In the Atlantic Rim area of south-central Wyoming, early-brood locations were 1.6 to 3.2 km from nest sites (Holloran and Anderson 2005). Slater (2003) found that 80% of early-brood locations were found within 1.5 km of nests in the Kemmerer, Wyoming area. Crawford et al. (1992) concluded that a key factor that determines sage-grouse productivity is the availability of brood habitat. Early-brood habitat is characterized by thick sagebrush canopy cover and an understory rich in nutrients (Connelly et al. 2000, Aldridge and Brigham 2002, Kirol 2012). Thompson et al. (2006) concluded that early-brood sites were characterized by high density sagebrush cover, grass cover, and abundance of insects. Guttery (2011) found that early-brood habitat is characterized by high density of black sagebrush (*Artemisia nova*).

Late-brooding sites are characterized by mesic sites containing increased numbers of forbs and insects compared to early-brood sites; forbs and insects are important food sources for both the chicks and hens (Holloran 1999, Connelly et al. 2000). If suitable microhabitat conditions are available, hen sage-grouse will keep their broods in upland habitat similar to early-brood sites (Wallestad 1971). Hens with late-broods selected for habitat with increased visual obstruction in the Farson, Wyoming area, and increased total shrub cover in the Pinedale, Wyoming area when compared to available sage-grouse habitat (Holloran and Anderson 2005).

As the summer progresses, forb abundance declines in the upland habitats that are used during early-brood rearing. When this occurs, hens move their broods to more nutrient-rich riparian zones (Dinkins 2013). Sometimes, hen sage-grouse with broods remained in sagebrush-dominated habitat throughout the summer and only move to riparian zones after forbs dried up and died. This happened in the Casper, Wyoming area during the summer of 1998, as well as in the Pindale, Wyoming area during the summer of 2004. In areas where there is little or no difference in sage-grouse selection of habitat between early- and late-brood seasons, this is most likely due to the fact that there is no difference in availability of forbs in the area (Aldridge and Brigham 2002). Late-brood sites characteristics can change from year to year based on the availability of food supply in the sagebrush-dominated upland habitat preferred for nesting and early-brood rearing.

Most habitat selection studies performed during the summer months have focused on hen sage-grouse that have broods. Summer habitat selected by hens with broods contains high densities of nutrient-rich forbs and insects (Connelly et al. 1997, Connelly et al. 2011). Few studies have looked at site selection by non-brooding sage-grouse hens. Dinkins (2013) and Kirol (2012) compared brood hens to non-brood hens but did not look at what factors influence a non-brood hen to select a given site.

Predator avoidance can have dramatic effects on the selection of habitat by birds and other terrestrial animals. Predator avoidance may occur indirectly, through reduced use of habitats correlated with higher risk of predation, or directly through avoidance of predators that are seen or heard (Lima 1998, Verdolin 2006, Cresswell 2008, Dinkins et al. 2012, Dinkins 2013). Avoiding predators has played a vital role on shaping all aspects of the life history of ground-nesting birds (Holloran and Anderson 2005). Both indirect and direct mechanisms of predator avoidance are connected to an animal's perceived risk of predation (Cresswell 2008, Martin and Briskie 2009). Greater sage-grouse select habitat with lower densities of avian predators (Dinkins et al. 2012), especially during nesting and brood rearing. More than 95% of failed sage-grouse nests were due to predation (Holloran and Anderson 2005). Other studies have shown that mortality on sage-grouse is highest during early-brood rearing. Willis et al. (1993) documented high rates of depredation on chicks in Oregon during the first few weeks of brood rearing, Cote and Sutherland (1997) concluded that high mortality rates early in life were due to depredation. Dinkins et al. (2012) found that sage-grouse avoided avian predators at nest and brood locations based on the size of avian predator rather than identity of individual species. During brood rearing, ravens and various hawk species are the main predators of sage-grouse (Girard 1937, Patterson 1952). Summer survival of sage-grouse is lowest in areas with high densities of risky habitat (natural and man-made roosts and rugged habitats) as well as higher densities of raptors, most notably golden eagles (*Aquila chrysaetos*) (Dinkins 2013). Along with golden eagles, Buteo hawks (*Buteo* spp.), and northern harriers (*Circus cyaneus*) pose a significant threat to the survival of sage-grouse (Schroeder et al. 1999). Sage-grouse that select habitat that minimize predation risk have a higher survival rate than those that choose riskier habitat.

Effects of nest depredation on productivity of sage-grouse have been well documented; in fact, most sage-grouse nests are lost to depredation (Gregg et al 1994, Connelly et al. 2004, Coates et al. 2008, Dinkins 2013). Coates et al. (2008) documented sage-grouse nest depredation by common ravens on camera traps in Nevada. High depredation rates of sage-grouse chicks have also been documented throughout the West during early-brood season (Aldridge 2005, Gregg and Crawford 2009, Guttery 2011).

As a result of the predation risk, hen sage-grouse and other ground-nesting birds place their nests in areas with the greatest concealment (Connelly et al. 1994, Connelly et al. 2004, Conover et al. 2010, Kirol 2012, Dinkins et al. 2012). Hen sage-grouse select nest sites based on a variety of concealment characteristics, including: sagebrush density (Connelly et al. 2003), sagebrush cover (Doherty et al. 2010, Kirol 2012), shrub height (Gregg et al. 1994), grass height (Holloran 2005), and grass cover (Kirol 2012). Conover et al. (2010) reported that sage-grouse hens select nest sites that provide concealment from visual (avian) predators but not olfactory (mammalian) predators.

The purpose of this study was to determine what factors lead to site selection by hen sage-grouse hens. This was accomplished by addressing several questions regarding the interactions of habitat selection and predator avoidance among sage-grouse hens. I examined if (1) sites occupied by sage-grouse hens with broods differ from random sites, (2) sites occupied by sage-grouse hens with broods differ from sites occupied by sage-grouse hens without broods, (3) sites occupied by sage-grouse hens with young broods differ from sites occupied by sage-grouse hens with old broods, and (4) sites where hen sage-grouse were killed differ from sites occupied by live sage-grouse hens or random sites.

STUDY AREA

My 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; Fig. 1). Five study sites were located in Lincoln County (16-km diameter each), two in Sweetwater County (one 16-km diameter and one 24-km diameter), two in Uinta County (both 16-km diameter), and three in Carbon County (24-km diameter each). The study sites in southwest Wyoming were all 16-km in diameter and centered around leks where hens had been captured. Study sites in south-central Wyoming were all 24-km because sage-grouse were captured at several nearby leks over a larger area. 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 2012). Elevation ranged from 1,950 m to 2,530 m at all study sites. Land at most of my study sites was federally owned and administered by the United States Bureau of Land Management; a small percentage of sites were on private lands. 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, coal-bed methane natural gas, and/or conventional oil extraction activities were present in 50% of my 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 (Dinkins et al. 2012).

The landscape at all study sites was dominated by sagebrush (*Artemisia* spp.); Wyoming big sagebrush (*A. tridentata wyomingensis*) and mountain big sagebrush (*A. t. vaseyana*) were the most common. Black sagebrush (*A. nova*) and dwarf sagebrush (*A. arbuscula*) were found on exposed ridges. Other common shrub species in my 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 aspen (*Populus tremuloides*) were found at the higher elevations on north-facing slopes.

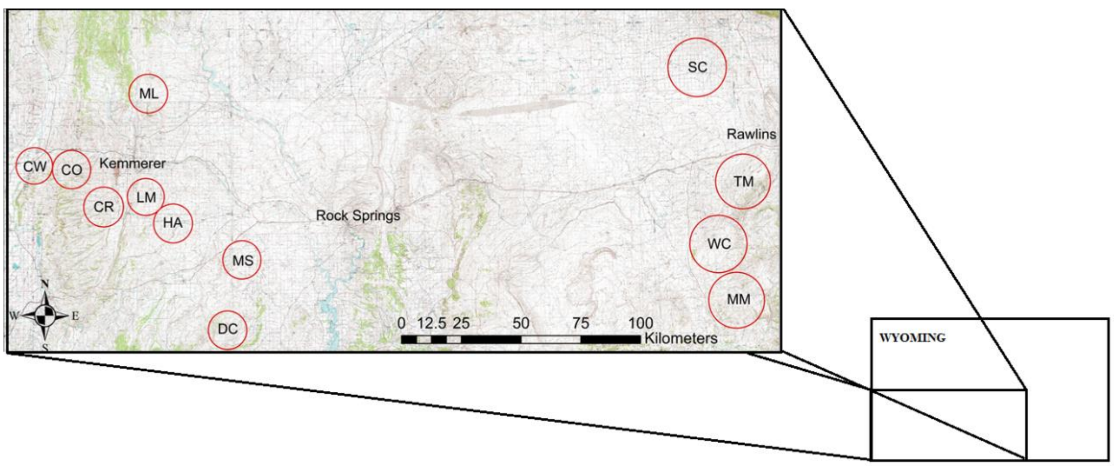

Figure 1 Sage-grouse study site in southwestern and south central Wyoming. Western sites are 16-km in diameter; eastern sites are 24-km in diameter.

METHODS

Sage-Grouse Capture and Monitoring

In April 2008-2011, hens were captured, radio-collared, and released. Hens were captured at night using 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 (Holohil Systems Ltd, RI-2D, Carp, Ontario, Canada or Advanced Telemetry Systems Inc, A4060, Isanti, Minnesota).

I monitored sage-grouse hens during nesting and early-brood-rearing from late March to mid-July 2012. I located radio-tagged hens weekly with Communications Specialists receivers and 3-way Yagi antennas (Communications Specialists, Orange, California). Collared hens were identified with binoculars while I was approximately 25-m away by circling the hen until it was visually located. I monitored hens for survival and brood presence throughout brood rearing. I determined the fate of nests after incubating hens had left and classified it as either successful or unsuccessful. A nest was considered successful if there was evidence that ≥1egg from the clutch has hatched based on membrane condition (Dinkins et al. 2012). I considered a nest to be unsuccessful if it was abandoned by the hen or if any one egg in a given clutch showed signs of a depredation and no eggs in the clutch had hatched (Dinkins et al. 2012).

All radio-collared hens were located on a weekly basis throughout brooding season. Successful hens were located using radio telemetry and then by circling the hen's location in attempt to visualize the hen and brood without flushing her from her brood. Locations within 20 days after hatching were considered early-brood locations (Thompson et al. 2006). Late-brood locations were defined as those locations in which the brood hen was visualized ≥21 days post-hatch. (Early and late brood dates were calculated based on the average hatch date of monitored nests). Hens unaccompanied by broods, as determined by diligent searching for chicks and by hen behavior, were located over the same time as hens with broods. I used the average of the hatching days of all successful nests as the starting point to label unaccompanied hens as early- or late-brood.

Vegetation Surveys

To determine micro-habitat characteristics, I conducted vegetation surveys at locations where radio-collared hens were located during early- and late-brood seasons. 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, I used ArcMap 10.1 (ESRI Inc., Redlands, California) 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. Random selection averaged >2000 m from their nearest neighbor (Dinkins et al. 2012, Dinkins 2013). I 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 non-brood hens. Brood hens were identified as such if I located a chick with that hen. Non-brooding hens were identified as such if I was unable to locate a chick. An early brood hen that was not found with chicks in the late brood season was considered to be a non-brood hen during that survey period. 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 observed bird location 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 (2011), and Kirol (2012). I measured the highest point (cm) of all shrub species encountered on the transect and averaged their heights per location (hereafter called total shrub height). I 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, Dinkins 2013, and Kirol 2012) 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 (Figure 2).

The lowest observable point on the Robel pole not obscured by vegetation from each distance was recorded. Canopy or ground cover was 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 (Fig. 2).

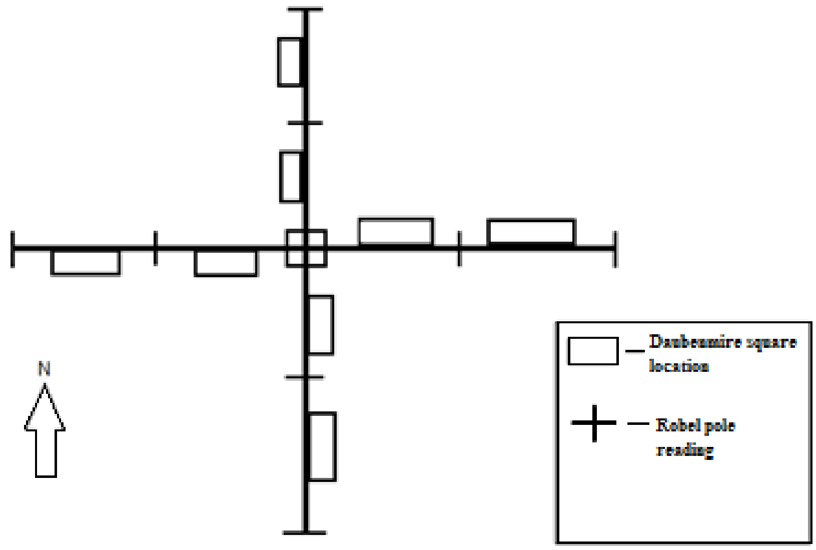

Figure 2 Schematic of Robel pole and Daubenmire square placement along transect lines at all vegetation survey locations.

Canopy and ground cover classes were categorized from 1 to 6 based on the percent of ground covered by vegetation with: 1 = 0–1% coverage, 2 = 1.1–5% coverage, 3 = 5.1–25% coverage, 4 = 25.1–50% coverage, 5 = 50.1–75% coverage, and 6 = 75.1–100% coverage. Canopy or ground cover categories were: annual grasses (i.e. grass species that complete their life cycle in one year), perennial grasses (i.e. grass species that complete their life cycle over multiple years), residual perennial grasses (i.e. dead sections of grass still standing from previous years of a perennial grass species growth), food forb (forbs that are known to be eaten by sage-grouse [Patterson 1952, Peterson 1970, Kirol 2012], Appendix 1), non-food forb (species sage-grouse are not known to eat, Appendix 1), 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, I 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 2013). Avian-predator point counts consisted of 10-minute observation periods during which I recorded all avian-predators including: common raven (*Covus corax*), black-billed magpie (*Pica hudsonia*), golden eagle, Buteo hawks, northern harrier, and American kestrel (*Falco sparverius*). I 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 course of the summer.

Data Analysis

I 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 I tested included all vegetation covariates including shrub cover, ground cover, and visual-obscurity. The objective of my analysis was to determine the variables that hen sage-grouse selected for during early- and late-brood rearing season regardless of their reproductive status. Therefore, I compared site selection by all hens compared to available habitat. All hen-location combinations (early-season non-brood hens, early-season brood hens, late-season non-brood hens, 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 me to determine what environmental factors hen sage-grouse select for during early- and late-brooding seasons. I 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

I grouped avian predators by body size (Dinkins et al. 2012). 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). I considered golden eagles (GOEA) (mean mass = 4500 g) to be the only large avian predator (LARGE) on the landscape. Average body mass was obtained from Sibley (2003).

I 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 perennial 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 was converted to a single value per plot (SHRUB).

Model Construction and Selection

I 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). I kept all variables that performed better than the null and whose 85% confidence intervals did not overlap zero, and I 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 (Tables 2 and 3). All models that ranked within 4 AICc of the top model were kept for further analysis.

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, non-brood 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 Avian			
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 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

Table 2. 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, non-brood 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
Late Avian			
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
Late Vegetation			
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

RESULTS

Vegetation sampling and avian-predator point counts were each performed at 173 sage-grouse and random-point locations throughout the summer of 2012. Samples included 40 early-season bird locations, 35 late-season locations, 92 random-points and 7 locations where I located a dead sage-grouse hen. The 40 early-season locations included locations for 8 brood hens and 32 non-brood hens. Late-season locations contained 7 brood hens and 33 non-brood hens.

Early Season

Habitat used by hen sage-grouse during early-brood season differed from available sage-grouse habitat in having more total shrub cover, more visual obscurity, and lower densities of common ravens and American kestrels (Table 3). Two models 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).

Table 3. Top models for early- and late-brood seasons based on their AICc scores. Top models compared locations of sage-grouse brood hens, non-brood 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

Parameters used to derive inference are found in Table 4. Lower density of common ravens and American kestrels, as well as the higher percent total shrub cover, were significant predictors of a site being occupied by a hen sage-grouse versus a random location in available sage-grouse habitat. Bare ground and visual obscurity were in the top models, but they were not significant predictors of site selection.

Table 4. 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, non-brood hens, and random points. Early-season locations included locations for 8 brood hens, 32 non-brood 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
Non-Brood			
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.**			

As the density of common ravens increased, the probability of a hen sage-grouse, regardless of her reproductive status, selecting a given site decreased significantly. Non-brood hens avoided areas where densities of American kestrels were high; brood hens, however, did not avoid sites with higher densities of American kestrels. The probability of a hen with a brood selecting a site increased as the density of American kestrels increased. Shrub cover was a significant predictor of site selection by all hen sage-grouse.

When compared to random available habitat, hen sage-grouse selected sites with higher percentage of shrub cover. As the shrub cover increased, so did the probability of selection by all hen sage-grouse during the early-brood season regardless of reproductive status.

Late Season

My best-fit models for describing variation in site selection by hen sage-grouse during late-brood season contained shrub cover and densities of small and medium-sized avian predators (Table 5). 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). Parameters used to derive inference are found in Table 5.

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, non-brood hens, and random points. Late-season locations included 7 brood hens, 33 non-brood hens, and 92 random locations.

Variable	**Estimate**	**SE**	**95 % CI Lower**	**Upper**
Brood				
Intercept	*- 1.17*	1.80	-4.70	2.36
Small	- 18.89	4.67E -8	-18.90	- 18.90*
Medium	- 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
Non-Brood				
Intercept	*- 1.17*	0.88	-1.90	2.36
Small	- 2.24	6.37E -6	-25.42	-25.42*
Medium	- 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.

The presence of small and medium-sized predators were significant predictors of whether a hen sage-grouse would select a given site when compared to a random location in suitable sage-grouse habitat. Hen sage-grouse were much less likely to select a site with high densities of small predators (black-billed magpies and American kestrels) regardless of their reproductive status. I found that sage-grouse hens that had an active brood during late-season selected against sites where medium-sized predators (common ravens, Buteo hawks, and northern harriers) were present. As the density of medium-sized predators per square km increased, the probability of a hen sage-grouse with a brood selecting a given site decreased dramatically. Non-brood hens during late-brood season were found at a similar rate at sites where medium-sized predators were present when compared to random locations. Hens, both with and without broods, selected sites that had a higher shrub cover than random sites in available sage-grouse habitat. As the shrub cover increased the probability of use by all hen sage-grouse increased significantly.

Mortality Sites

Vegetation surveys and avian point counts were performed at sites where a hen sage-grouse was found depredated. During 2012, 5 collared hens were found depredated by mammalian or avian predators. When models were run when comparing mortality sites to random sites, no variables were found to be significant.

DISCUSSION

Do sites occupied by sage-grouse hens differ from random sites?

I found that sites occupied by hen sage-grouse, regardless of whether they were accompanied by a brood, differ from random sites based on multiple variables. Hen sage-grouse select sites based on shrub cover and the densities of small and medium-sized avian predators. Occupied sites had a high percentage of overall shrub cover and lower densities of small and medium-sized avian predators when compared to random locations in available sage-grouse habitat. My findings are consistent with other sage-grouse studies. Dinkins et al. (2102) concluded that hens with broods select sites with lower densities of avian predators. They did not, however, determine if there is a variation in site selection based on early and late-season brood-sites. Conover et al. (2010) concluded that sage-grouse selected nest sites to avoid visual (avian) predators but did not select nest sites to avoid olfactory (mammalian) predators. They did not, however, look at the avoidance of olfactory predatory at brood rearing sites. I did not look at olfactory predators directly; no mammalian predators were directly surveyed for or used in data analysis. My data does suggest that there may be some avoidance of mammalian predator based on selection for sites with greater visual obscurity.

Do sites occupied by brood hens differ from those occupied by non-brood hens?

I found that brood hens were more likely than non-brood hens to select sites with high total shrub cover and low densities of small- and medium-sized predators. Aldridge and Brigham (2002) concluded that hen sage-grouse selected for brood sites with high sagebrush cover. They were unable to find a significant difference between early and late-brood sites so they grouped those together for analysis. My data are consistent with theirs— hen sage-grouse with an active brood during late-brood season select for sites that have high total shrub cover (percent of a site that was covered by a shrub of any species). My findings are not specific to sagebrush cover; however, total shrub cover included sagebrush of all species and all of my study sites were composed of sagebrush-dominated vegetation. Therefore, the most common shrub species found in my study site was sagebrush. I used total-shrub cover in analysis instead of sagebrush cover only. Total shrub cover and sagebrush cover were found to be collinear. I used total shrub cover in my analysis because I felt that it provided a more complete representation of the habitat that was surveyed. Antelope bitter brush, rabbit brush and other woody shrubs can be used as cover by both sage-grouse adults and chicks. The selection for higher total shrub cover by both reproductively active and inactive hens allowed for concealment from avian predators.

What factors do hens select for in early season?

During early summer, when sage-grouse broods are young, brood hens not only select sites that differ from random locations but also differ from sites non-brood hens select. Holloran and Anderson (2005), Connelly et al. (2011), and Kirol (2012) report that early-brood habitat is similar to nesting habitat. Hens with broods during early-season selected sites with higher densities of American kestrels when compared to available sage-grouse habitat. 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 allows for chick concealment without visual obstruction (Guttery 2011). The structure of black sagebrush is such that total-shrub cover can be high but visual obstruction can be low, a more fitting shrub composition for American kestrel hunting strategy (Hoffman 1985).

Hens that are not accompanied by a brood during the same time period show a slightly different response to avian predator densities. Hens without a brood select sites with high total shrub cover, similar to those hens with a brood. They also select sites with low densities of common ravens and American kestrels.While brood hens select areas with high densities of American kestrels, hens without a brood avoid areas with high densities of American kestrels. I hypothesize that reproductively inactive sage-grouse hens are avoiding small avian predators inadvertently. By selecting sites with greater shrub cover, the hen is also selecting cover types in which black-billed magpies and American kestrels do not hunt. Hoffmann (1985) concluded that shrub cover was negatively correlated with amount of time spent foraging by American kestrels in the White Mountains of California. The most important variable for site selection is not the avoidance of small predators but the presence of high percentage of total shrub cover. Thus, hen sage-grouse use different microhabitats during early-brood season depending on their reproductive status.

What factors do hens select for in late season?

My data indicate that hen sage-grouse without broods avoid small-sized predators during late-brood season. Medium-sized avian predators pose a threat to both adult and chick sage-grouse; small avian predators pose a threat only to chick sage-grouse. Even though medium-sized predators, buteo hawks in particular, threaten adult sage-grouse, reproductively inactive hens did not select sites during late summer with lower densities of medium-sized predators. Connelly et al. (2000) report 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 whereas medium predators (common ravens, buteo hawks, and northern harriers) were avoided only by those hens that had an active brood during the late-season.

MANAGEMENT IMPLICATIONS

Expanding development of anthropogenic resources across their range has limited the amount of suitable habitat that sage-grouse can occupy. Previously widespread loss of sagebrush habitat have resulted in the range of the sage grouse to reduce by almost 50% (Schroeder et al. 2004). Healthy sagebrush shrub lands support the highest densities of sage-grouse and other sagebrush obligate species (Connelly et al. 2004). This same area is also within the area of the greatest expansion of energy development throughout the western United States.

Anthropogenic development not only leads to the loss and fragmentation of suitable sagebrush habitat but also leads to an increase in predator densities (Dinkins et al. 2014). 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 leads to an increase in predator densities and hunting success in avian predators (Dinkins et al. 2014).

The direct loss of habitat by development and fragmentation of sagebrush habitat as well as the increase in predator densities associated with human development has led to a decrease in suitable sage-grouse habitat. Sage-grouse can minimize the threat of predation by directly and indirectly avoiding predators. Sage-grouse avoid areas in which they directly observe predators as well as avoid habitats in which they perceive as "riskier". Sage-grouse may avoid otherwise suitable habitat based on the proximity to tall structures, other anthropogenic resources. Avoidance of avian predators and anthropogenic features allows hen sage-grouse to lower their risk of predation while using habitat to meet energetic requirements of hens and chicks.

My results indicated that hen sage-grouse select sites based on shrub cover and predator avoidance regardless of whether they are accompanied by a brood. These results correspond with Kirol (2012). My results also show that hen sage-grouse avoid avian predators. Coates (2007), Bui et al. (2010), and Hagen (2011) suggested that predator removal may provide a short-term release in predation rates within fragmented habitats. However, Hagen (2011) indicated that predator removal will prevent sage-grouse population declines throughout the range of sage-grouse. My results indicate that sage-grouse hens may avoid otherwise stable habitat due to predators. This avoidance suggests that predator abundance may result in even less suitable habitat for sage-grouse throughout their range.

I recommend that managers should focus efforts on maintaining and increasing shrub cover in sage-grouse habitat. As found in Kirol (2012), my data suggests managers should refrain from practices that reduce shrub cover in sage-grouse habitat.

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APPENDIXES

Appendix 1. List of grouse food and non-food forbs (Patterson 1952, Peterson 1970, and Kirol 2012)

Scientific name	**Common name**	**Code**
Food forbs		
Achillea millefolium	Yarrow	ACME
Agoseris spp.	Agoseris or mountain dandelion	AGOSERIS
Allium spp.	Wild onion	ALLIUM
Antennaria spp.	Pussytoes or everlasting	ANTENNARIA
Artemisia frigida	Fringed sagewort	ARFR
Aster spp.	Aster	ASTER
Astragalus spp.	Milkvetch	ASTRAGALUS
Balsamorhiza sagittata	Arrowleaf and other balsamroots	BASA
Bassia scoparia	Burningbush (an annual)	BASC
Calochortus nuttallii	Sego lily	CANU
Castilleja spp.	Indian paintbrush	CASTILLEJA
Crepis spp.	Hawksbeard	CREPIS
Dalea spp.	Prairie clover	DALEA
Erigeron spp.	Fleabane	ERIGERON
Eriogonum spp.	Buckwheat	ERIOGONUM
Gilia spp	Shooting stars	GILIA
Grindelia squarrosa	Curlycup gumweed	GRSQ
Hedysarum boreale	Northern sweetvetch	HEBO
Krascheninnikovia lanata	Winterfat	KRLA
Lactuca serriola	Prickly lettuce	LASE
Lepidium densiflorum	Common pepperweed	LEDE
Linum spp.	Flax	LINUM

Lomatium spp.	Desert parsley/biscuitroot	LOMATIUM
Lupinus spp.	Lupine	LUPINE
Medicago sativa	Alfalfa	MESA
Melilotus officinalis	Sweetclover	MEOF
Mertensia spp.	Bluebells	MERTENSIA
Microsteris gracilis	Slender phlox	MIGR
Nothocalais troximoides	Sagebrush false dandelion	NOTR
Penstemon spp.	Penstemon	PENSTEMON
Onobrychis vicifolia	Sainfoin	ONVI
Orobanche spp.	Broomrape	OROBANCHE
Phlox longifolia	Longleaf phlox	PHLO
Sanguisorba minor	Small burnet	SAMI
Sphaeralcea spp.	Globemallow	SPHAERALCEA
Taraxacum officinale	Common dandelion	TAOF
Tragopogon spp.	Goatsbeard of salisfy	TRAOPOGON
Trifolium spp.	Clover	TRIFOLIUM
Vicia spp.	Vetch	VICIA
Zigadenus spp.	Deathcamas	ZIGADENUS
Non-food forbs		
Atriplex gardneri	Gardner’s saltbush	ATGA
Phlox hoodii	Spiny phlox	PHHO
Delphinium occidentale	Western larkspur	DEOC

Appendix 2. Covariate statistics. Minimum, maximum, mean and standard deviation for all covariates in early and late season.

EARLY				
Variable	Min	Max	Mean	SD
Common Raven Denstiy	0.00	2.61	0.14	0.36
Black-Billed Magpie Density	0.00	3.69	0.15	0.68
Golden Eagle Density	0.00	0.63	0.06	0.13
Northen Harrier Density	0.00	3.14	0.04	0.31
Buteo Hawk Density	0.00	4.96	0.12	0.52
American Kestrel Density	0.00	2.99	0.11	0.43
Average Robel	0.00	61.25	14.23	14.53
Total Shrub	0.30	79.65	26.45	15.63
Total Sage-brush	0.00	56.03	21.29	12.47
Percent Annual Grass	0.00	0.08	0.00	0.01
Percent Perenial Grass	0.00	38.42	2.90	4.38
Percent Reisdual Annual Grass	0.00	39.96	8.52	6.19
Percent Food Forb	0.00	20.85	1.97	3.71
Percent Non-Food Forb	0.00	12.88	2.52	3.04
Percent Bare Ground	0.00	55.35	21.38	14.40
Percent Cactus	0.00	4.85	0.17	0.64
Percent Cryptobiotic Crust	0.00	10.00	1.32	2.12
Percent Gravel	0.00	59.00	9.84	13.54
Percent Litter	0.35	55.35	21.37	13.33
Inside Grass Height (cm)	0.00	48.00	10.37	6.71
Outside Grass Height (cm)	0.00	65.67	17.44	8.48
Outside Residual Grass Height (cm)	3.85	85.55	23.11	8.77
LATE				
Variable	Min	Max	Mean	SD
Common Raven Denstiy	0.00	3.48	0.21	0.54
Black-Billed Magpie Density	0.00	3.69	0.10	0.52
Golden Eagle Density	0.00	0.63	0.07	0.14
Northen Harrier Density	0.00	3.14	0.04	0.31
Buteo Hawk Density	0.00	4.96	0.17	0.59
American Kestrel Density	0.00	2.99	0.08	0.37
Average Robel	0.00	61.88	13.62	14.53
Total Shrub	0.00	79.35	24.70	14.89
Total Sage-brush	0.00	50.23	19.99	12.04
Percent Annual Grass	0.00	0.08	0.00	0.01
Percent Perenial Grass	0.00	38.42	2.91	4.48
Percent Reisdual Annual Grass	0.00	39.23	8.56	5.84
Percent Food Forb	0.00	16.46	2.00	3.25
Percent Non-Food Forb	0.00	12.35	2.44	2.83
Percent Bare Ground	0.00	55.35	22.28	14.43
Percent Cactus	0.00	4.85	0.18	0.69
Percent Cryptobiotic Crust	0.00	10.00	1.27	2.13
Percent Gravel	0.00	59.00	10.06	13.52
Percent Litter	0.35	47.65	20.55	12.54
Inside Grass Height (cm)	0.00	48.00	10.18	6.61
Outside Grass Height (cm)	0.00	65.67	17.16	8.36
Outside Residual Grass Height (cm)	3.85	85.55	22.61	8.30