Habitat Selection by Two K-Selected Species: An
Application to Bison and Sage-Grouse in Utah

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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Masters of Science

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December 2013

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ABSTRACT

Habitat Selection by Two K-Selected Species: An Application to Bison and Sage-Grouse in Utah

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Population growth for species with long lifespans and low reproductive rates (i.e., K-selected species) is influenced primarily by both survival of adult females and survival of young. Because survival of adults and young is influenced by habitat quality and resource availability, it is important for managers to understand factors that influence habitat selection during the period of reproduction. My thesis contains two chapters addressing this issue for K-selected species in Utah. Chapter one evaluates habitat selection of greater sage-grouse (Centrocercus urophasianus) on Diamond Mountain during the critical nesting and brood-rearing period. Chapter two address selection of birth sites by bison (Bison bison) on Antelope Island, Utah.

We collected micro-habitat data for 88 nests and 138 brood locations of greater sage-grouse from 2010-2012 to determine habitat preferences of nesting and brooding sage-grouse. Using random forests modeling techniques, we found that percent sagebrush, percent canopy cover, percent total shrubs, and percent obscurity (Robel pole) best differentiated nest locations from random locations with selection of higher values in each case. We used a 26-day nesting period to determine an average nest survival rate of 0.35 (95% CI = 0.23 – 0.47) for adults and 0.31 (95% CI = 0.14 – 0.50) for juvenile grouse. Brood sites were closer to habitat edges, contained more forbs and less rock than random locations. Average annual adult female survival across the two-year study period was 0.52 (95% CI= 0.38 – 0.65) compared to 0.43 (95% CI= 0.28 – 0.59) for yearlings. Brooding and nesting habitat at use locations on Diamond Mountain met or exceeded published guidelines for everything but forb cover at nest sites. Adult and juvenile survival rates were in line with average values from around the range whereas nest success was on the low end of reported values.

For bison, we quantified variables surrounding 35 birth sites and 100 random sites during 2010 and 2011 on Antelope Island State Park. We found females selected birth sites based on landscape attributes such as curvature and elevation, but also distance to anthropogenic features (i.e., human structures such as roads or trails). Models with variables quantifying the surrounding vegetation received no support. Coefficients associated with top models indicated that areas near anthropogenic features had a lower probability of selection as birth sites. Our model predicted 91% of observed birth sites in medium-high or high probability categories. This model of birthing habitat, in cooperation with data of birth timing, provides biologists with a map of high-probability birthing areas and a time of year in which human access to trails or roads could be minimized to reduce conflict between recreation and female bison.

Keywords: Antelope Island State Park, Diamond Mountain, human disturbance, nest survival, random forests, reproductive habitat, sagebrush, sage-grouse, sage-grouse management guidelines
ACKNOWLEDGEMENTS

I would first like to thank my family, particularly my wife, Hayley. She was supportive and understanding as I spent many months in the field collecting data. I would also like to personally thank my Dad, Taft. My father is responsible for whatever work ethic and personal integrity I possess.

I would also like to thank Brigham Young University, especially the Plant and Wildlife Science Department for creating a learning environment where I was able to be instructed, challenged, and edified. I am most grateful for my graduate advisor, Dr. Randy Larsen. Dr. Larsen is a great mentor scholastically, but he also has become a personal role model and I consider him a friend. I would also like to thank those who served on my graduate committee (Dr. Steve Petersen and Dr. Rick Baxter) and Jericho Whiting for his invaluable help with all my research, particularly the bison chapter. I had many undergraduate technicians that worked tirelessly and I will always appreciate their diligence and honesty.

I would also like to thank the Utah Division of Wildlife Resources for their support, financially and otherwise.
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CHAPTER 1

Abstract

Human activities can affect habitat selection by a wide diversity of ungulate species, particularly during parturition (birthing period). Minimizing human-wildlife conflicts during parturition can be critical in areas like national and state parks that have high rates of human visitation. We investigated birth-site selection by bison (Bison bison) on Antelope Island State Park (AISP), Utah at multiple spatial scales to determine the relative influence of vegetation, topography, and distance to anthropogenic features (i.e., buildings, trails, or roads) on selection of birthing habitat. We used vaginal implant transmitters (VITs) to identify bison birth sites, and the timing of births. We used logistic regression within a model-selection framework to differentiate between birth sites and random locations based on a suite of potential explanatory variables. We quantified variables surrounding 35 birth sites and 100 random sites during birthing in 2010 and 2011. Our best model of birth-site selection for bison included the landscape features curvature (averaged at a 500-m radius around site), elevation (averaged at a 500-m radius around site), and distance to nearest anthropogenic feature. Coefficients associated with top models indicated areas near anthropogenic features had a lower probability of selection. Our model predicted 91% of observed birth sites in medium-high or high probability categories. We also estimated birthdates from 41 expelled VITs, and 81% of births occurred in April (range = March 22 to May 20). Our model of birthing habitat and data concerning timing of birth provides biologists with a map of high-probability birthing areas and a time of year in which human access to trails or roads could be minimized to reduce conflict between recreation and female bison on AISP.

Key words: Antelope Island State Park, birth synchrony, Bison bison, human disturbance, parturition, predators, ungulate
Introduction

Female ungulates select parturition sites that maximize fitness for themselves and their offspring. A tradeoff usually occurs between adequate opportunities for the mother to fulfill nutritional requirements during late gestation and early lactation and habitat that offers favorable micro-climates and/or protection from predators (Festa-Bianchet 1988, Rachlow and Bowyer 1998, Ciuti et al. 2006, Barbknecht et al. 2011, Rearden et al. 2011). Strategies to minimize predation risk during parturition include the following: use of habitat that offers concealment from predators (Ciuti et al. 2006, Barbknecht et al. 2011), selection of habitat with fewer predators—often due to difficulty in predators accessing the area (Festa-Bianchet 1988, Eastland et al. 1989, Rachlow and Bowyer 1998), or use of topography that offers unobstructed views of approaching predators (Bowyer et al. 1999). Often, females from different populations or even within the same population will demonstrate different strategies for selecting birthing locations. For example, some female bison (Bison bison) in one population isolated themselves prior to parturition and selected habitat that provided vegetative cover (Lott and Galland 1985). Conversely, in the same population other females selected open grasslands with limited visual obscurity where they gave birth in groups (Lott and Galland 1985). Finally, in another population bison selected parturition sites in open grasslands, and those areas consisted of rolling hills that were bisected by ravines, but were still almost 250% more flat and open than topography selected by non-pregnant females (Berger and Cunningham 1994).

Birth-site selection in ungulates can be further influenced by human disturbance. Animals can perceive humans as predators, which can elicit alarm responses from the observing animal (Fairbanks and Tullous 2002, Frid and Dill 2002, Taylor and Knight 2003). Saiga antelope (Saiga tatarica), for example, avoided human-use areas while selecting birthing sites (Singh et al. 2010). Similarly, female elk (Cervus elaphus) adjusted their spatio-temporal
movements to avoid human disturbance during calving (Dzialak et al. 2011). Elk avoided high-
human use areas during the day by selecting cover that offered concealment, but continued to 
utilize areas of high human use at night (Dzialak et al. 2011). Moreover, human disturbance may 
negatively influence population growth in ungulates. For example, in an area that was 
intentionally disturbed by humans during calving, counts of calves/female elk were 22.5% lower 
than undisturbed herds (Philips and Alldredge 2000). After termination of human disturbance, 
elk reproductive rates increased to pre-disturbance levels (Phillips and Alldredge 2000, Shively 
et al. 2005). Previous studies have documented that human disturbance can also influence bison 
by increasing the daily use radius of these ungulates (Fortin and Andruskiw 2003); however, 
little is known regarding how human disturbance may influence selection of birth sites by this 
species.

Human-wildlife interactions can be critical in areas like national and state parks due to 
high rates of human visitation and goals that include both conservation of natural resources and 
facilitation of recreation. Antelope Island State Park (AISP) is located in northern Utah, USA. 
Almost 300,000 people visit AISP each year with the majority of those recreationists visiting to 
view wildlife (UDSPR 2009). Visitor access on the island is limited to a small network of 
designated roads and trails. Because human-wildlife interactions are mostly limited to existing 
roads and trails, animals on AISP have access to areas with limited human disturbance: therefore, 
AISP offers an opportunity to study effects of human influences on wildlife. Recently, plans 
have been initiated to allow access to more of the island for recreation (hiking, biking, camping, 
etc.). Although previous research has indicated that human recreation may negatively influence 
ungulates on AISP (Fairbanks and Tullous 2002, Taylor and Knight 2003), no studies have been 
conducted regarding the potential for humans to disturb bison during calving. Such information
is important for the conservation and management of this species and its habitat on Antelope Island State Park.

We investigated birth-site selection by bison on Antelope Island using vaginal implant transmitters (VITs) to identify bison birth sites, as well as to determine the timing of births for those ungulates. We analyzed birth sites at multiple spatial scales and measured the influence of vegetative, topographical, and anthropogenic features on bison birth-site selection. We predicted that bison would select open areas with relatively high visibility for parturition. We also predicted that bison would avoid anthropogenic features when selecting birth sites. Our model of birthing habitat, and data concerning timing of births, will provide biologists with areas and a time of year in which human access to trails and roads can be minimized in order to reduce conflict between recreation and bison on Antelope Island State Park.

Study Area

Antelope Island State Park is located in the southeast corner of the Great Salt Lake in northern Utah, USA, and depending on lake levels, the park could be an island or a peninsula connected to the main land by marsh and mud flats (Fig. 1). The distinguishing feature of the island is the north to south mountain range that extends much of the length of the island. This mountain range consists of steep hills that descend gradually into flat areas that eventually meet the water. Major vegetation in this area during our study years was mixed grasslands with communities of sagebrush (Artemisia spp.) and rabbitbrush (Chrysothamnus spp.). Few, scattered junipers (Juniperus spp.) also occurred on the island, and bigtooth maple (Acer grandidentatum) were located around fresh water springs. Russian olive (Elaeagnus angustifolia) was abundantly located on the east side of the island at the lower elevation and in
wetland areas. The highest peak is 2,011 m, and the lake shore, while fluctuating, was near 1280 m during our study years.

Animals inhabiting the island included bighorn sheep (*Ovis canadensis*), bison, black-tailed jackrabbits (*Lepus californicus*), bobcats (*Felis rufus*), coyotes (*Canis latrans*), pronghorn (*Antilocapra americana*), porcupines (*Erethizon dorsatum*), and mule deer (*Odocoileus hemionus*) (Whiting et al. 2009 and 2010). Average monthly temperatures over 29 years (1971 – 2000) ranged from 33.3 °C in July, to -8.3 °C during January and average annual precipitation was 45.6 cm (www.noaa.gov). Access to AISP was obtained via an 11.3 km causeway connecting the island to Davis County at the north end of the island (Fig. 1). Off-road and off-trail access to the island was restricted during our study years to protect the island’s natural resources. One paved road extended across one half of the length of the eastern side of the island, and hiking was allowed on an established trail system consisting of four primary routes (Fig. 1). Also, service roads crossed the island and had limited vehicle use by park personnel and wildlife researchers (Fig. 1). Of the approximate 300,000 annual visitors, roughly 86,000 (~30 %) visit AISP in March, April, and May (UDSPR 2009) during the birthing season for bison.

Methods

*Data Collection*

In November 2009 and 2010, Antelope Island State Park employees and volunteers herded all bison (except mature bulls) into holding pens on the north end of the island. While in holding pens, AISP employees and volunteers identified (using ear tags or RFID tags) and weighed each bison while also testing females for pregnancy. Using a previously compiled database of all individuals on the island, we randomly selected mature (≥ 2 years old) females in 2009 and 2010 (mean age = 8 years old, SD = 3.6, range = 2 to 15 years old). A certified
veterinarian implanted a vaginal implant transmitter (VIT; Advanced Telemetry Systems, Isanti Michigan) into the birth canal of each randomly selected female that was confirmed to be pregnant. After VITs were inserted, the selected females were immediately released back into the herd remaining on the island. Each VIT weighed 45 g, and was equipped with a temperature-sensitive switch that increased the pulse rate from 40 to 80 pulses per minute once the temperature of the transmitter dropped below 32° C. We deployed 50 VITs each year in 2009 and 2010. Treatment of handled bison and practices of veterinarians and AISP officials were consistent with animal care and use standards (Wolfe et al. 1999, Sikes and Gannon 2011).

Following release of female bison from the holding pen to the island, we monitored VIT signals using radio telemetry equipment (Communications Specialists, R1000). Due to the low probability of calving, VIT signals were monitored only one time per month during December and January. Beginning in February, we monitored VIT signals once a week through mid-March to determine a general location or pattern of movement for each female. After March 15 of each year, we monitored each VIT signal 2-3 times weekly to determine birth sites and estimate timing of births. We maintained this monitoring schedule until all VITs were expelled or signals were lost due to battery failure. During those surveys, we exercised care not to disturb females with young (Rachlow and Bowyer 1991, Gannon and Sikes 2007).

When we located an expelled VIT, we determined if the location was a birth site or if the transmitter was expelled early. We classified locations where VITs were expelled as birth sites when we observed evidence of disturbed soil with bison tracks generally in a circle pattern, and afterbirth or grass matted down from consumption and licking of the afterbirth was observed coupled with at least one of the following: a) presence of bison teeth marks in the transmitter, b) absence of predator teeth marks in the transmitter, c) tracks from bison calf attempting first steps,
or d) visual observation of the birth with transmitter found at site. Some of these classifications have been used in other studies to determine birth sites for bison and other ungulates (Lott and Galland 1985, Barbknecht et al. 2009, Bishop et al. 2011).

In each year, we also selected 50 random locations (100 total) using ArcGIS 10.0 (ESRI, Redlands California) for comparison of the surrounding vegetation between birth and random locations. At each birth and random location, we established four, 50-m transects in each cardinal direction centered at the birth or random point. We used the line intercept method to obtain canopy cover estimates by measuring all trees and shrubs (≥ 10 cm in height) that intersected transects (Canfield 1941). Along those transects, we also determined density by counting all rooted trees and shrubs (≥ 10 cm in height) within 0.5 m of each side of all four line transects. We used a Robel pole to measure visual obscurity at the birth site by determining the amount of pole that was obscured at 5, 10, and 25 m along each transect associated with birth or random locations (Robel et al. 1970). The obscurity of the pole was assessed at a height of 0.5 m above ground level, to simulate an approaching predator. We collected vegetative characteristics from both birth and random sites during the same time each year (March 25 to June 1) to ensure consistent phenology of vegetation.

In addition to measuring the surrounding vegetation at each site, we calculated landscape metrics across multiple spatial scales by creating buffers of 0, 50, and 500-m radius for each birth site and random location using ArcGIS 10.0. We used these three scales at which to consider potential habitat characteristics selected by parturient bison based on the following reasons: First, we wanted to quantify topographic characteristics at the birth site or random location (0 m). Second, we expanded our analysis to include characteristics that bison might select at 50 m (vegetation, concealment, topography, etc.). Lastly, we arbitrarily selected 500 m
after considering that bison can see stationary objects, like a horse and a rider, at 1000 m and moving objects as far as 2000 m (McHugh 1958). We used a 2-m digital elevation model (DEM, Utah GIS portal) to quantify elevation (m), slope, aspect, and curvature for each birth and random site. We then averaged the raster values calculated for both a 50 and 500-m radius around each site using zonal statistics and used these average values for analyses. Additionally, we determined the percentage of the area within a 50 and 500-m radius of each site that was visible from the birth or random site using the viewshed spatial analyst tool in ArcGIS 10.0.

Because we were also interested in any influence from anthropogenic features on birth-site selection, we determined the distance (near tool in ArcGIS) from each birth site to anthropogenic features. We recorded the distance in meters from each site to structures, trails, public roads, service roads, all roads (not distinguishing between service or public roads), and any anthropogenic development (a measurement from each site to the nearest feature regardless of whether it was a structure, road, or trail).

Statistical Analyses

To understand the relationship between bison birth sites and potential explanatory variables (site vegetation, topographic, and anthropogenic structures), we used logistic regression models where the response variable was birth (1) or random (0) site. We created candidate models representing our predictions about birth-site selection as a function of surrounding vegetation, topographic, and anthropogenic features (Table 1). After evaluating explanatory variables for multi-collinearity, we used a multi-step process to identify variables that influenced bison birth-site selection. First, we used Akaike’s information criterion adjusted for small sample sizes (AICc) to rank models (Akaike 1973, Burnham and Anderson 2002) within each variable type (e.g., surrounding vegetation, topographic, and anthropogenic features). For topographical
variables, we analyzed each variable at the birth site and random site, as well as at 50 and 500 m. Next, we then used the top and competing models (ΔAICc< 2.0) within each variable type (Doherty et al. 2008). In this second stage, we combined variables (moved up from the first step) and then ranked models based on AICc values to identify a best approximating model and any competing models (Burnham and Anderson 2002). Following completion of this step, we evaluated supported models (AICc weight > 5%) and looked at AICc and log-likelihood values to identify and remove any uninformative parameters (Arnold 2010).

In the case of model-selection uncertainty, we obtained model-averaged parameter estimates to determine the direction and strength of correlations between the response and explanatory variables. We then used those model-averaged coefficients and the raster calculator in ArcGIS 10.0 to project our model onto Antelope Island State Park. The output of this function produced a raster file that assigned each cell (1x1m) a numerical value associated with the resource selection function. We then partitioned AISP into low, medium low, medium, medium high, and high probability of birthing habitat based on quantiles (Sawyer et al. 2006). We then estimated the accuracy of our model by determining what percentage of birth sites (both those from VITs used to build the model and 5 opportunistically observed births not used in analyses) were located in each quantile.

We used the date on which we first heard a distress signal from an expelled VIT as an estimated birthdate of young. We then pooled those dates into sampling intervals and calculated a corrected mean (timing of births) and SD (synchrony of births) (Johnson et al. 2004, Whiting et al. 2010, Whiting et al. 2011). This calculation was a robust technique that allowed comparison of unequal sampling intervals (bin sizes) in determining timing and synchrony of births (Johnson et al., 2004). We could only calculate those measures partially in 2011, because the nine
remaining transmitters failed after April 30 before they were expelled by females. Using data from 2010, however, 84% of births occurred before April 30; therefore, although transmitters failed during the latter part of the birthing season in 2011, we likely estimated most birthdates of young in that year.

Results

No VITs (n = 46) collected before March 1 of either year were at locations that contained any evidence of parturition. In spring 2010, one VIT battery failed, 25 were expelled prematurely (before March 1), and five did not exhibit enough evidence for us to classify the location as a birth site. In 2011, one transmitter broke while being inserted, 9 batteries failed, 21 were expelled early (before March 1), and three were expelled during the birthing period but did not exhibit sufficient evidence to be classified as a birth site. Thus, of the 100 VIT transmitters we implanted in female bison, only 35 (35%) transmitters were expelled between March 23 and May 28 at sites that contained evidence of recent parturition (Fig. 2). Our earliest birth site was recorded on March 23, 2010 and our latest birth site was recorded on May 28, 2010.

Our top two models accounted for 93% of AICc weight. No other model received > 5% AICc weight. Our most supported (AICc weight = 53.9%) model of bison birth-site selection relative to vegetative, topographic, and anthropogenic features included curvature (averaged at a 500-m radius around birth site) and elevation (averaged at a 500-m radius around birth site). An additional competing model (AICc weight = 39.1%) included those two variables and the distance to all combined anthropogenic features (i.e., minimum distance to any trial, road, or structure) (Table 2). Evaluation of the log-likelihood value associated with our second model showed modest improvement in fit from the top model, but not enough to overcome the penalty associated with the additional parameter (Table 2). We found little support for any other models.
The coefficient for curvature was negative (Table 3), indicating that bison selected areas of concave topography at the 500-m scale; therefore, a one unit change in curvature (more convex) was associated with a very slight decrease in odds of birthing habitat (change < 0.01). For elevation, a one meter increase in this variable increased likelihood of birthing habitat by a factor of 1.01. Similarly, converting the anthropogenic coefficient to an odds ratio suggested that each 10-meter increase in distance from anthropogenic features was associated with a 1.1% increase in likelihood of birthing habitat.

Using model-averaged coefficients from the top two supported models, we determined that 26 of 35 (74%) birth sites occurred in the category designated as high, 6 of 35 (17%) were located in the category designated as medium high, and 3 of 35 (9%) occurred in the category designated as medium (Fig. 2). Conversely, of our 100 random locations 24 were located in low, 9 were located in medium low, 24 were located in medium, 29 were located in medium high, and 15 were located in high. In addition, 4 of 5 (80%) opportunistically observed birth sites occurred in the category designated as high and 1 was located in the category designated as medium high.

In 2010, we estimated birthdates for 25 young. Mean (± SD) birthdate for bison on Antelope Island during that year was April 14 (± 18 days, range = March 22 to May 20). In 2011, we estimated birthdates for 16 young, and mean (± SD) birthdate for bison on the island during that year was April 20 (± 8 days, range = April 5 to April 30).

Discussion

Our data indicated that parturient bison selected topographic variables and avoided anthropogenic features during calving. Other ungulates have similarly shown selection for landscape characteristics while choosing birthing habitat (Alldredge et al. 1991, Singh et al. 2010, Barbknecht et al. 2011, Rearden et al. 2011). Large-scale curvature at the 500-m scale was
the most predictive variable for birth sites of bison on Antelope Island State Park. The coefficient for large-scale curvature was negative, indicating that bison selected areas of concave topography at the 500-m scale. Because we only considered selection at three scales (point, 50-m, and 500-m), we recognize that bison could have selected for topographic features at a different scale. Our results are only relative to each other; meaning a 500-m scale better represented bison birth-sites than a 50-m scale. Other studies described bison selecting the tops of rolling hills bisected with ravines for parturition (Berger and Cunningham 1994). Although we found selection for birth sites in concave areas at a 500-m scale, we did note that many birth sites were located on the tops of small ridges within large concave valleys similar to areas described by Berger and Cunningham (1994). We hypothesize that these small rolling hills and ridges within a large concave valley, where many births occurred, provided increased visibility for female bison on AISP. Future work can test this hypothesis in other areas.

Other ungulates use areas of high visibility for detecting predators while selecting birth sites (Bowyer et al. 1999, Rearden et al. 2011). In the last 10,000 years, bison have faced predation from mountain lions (Puma concolor) and grizzly bears (Ursus arctos), but most predation was caused by wolves (Canis lupis) (Lott 1991). Coyotes are also a potential predator of bison. Gese (1999) observed bison acting aggressively to coyotes, indicating that coyotes were viewed as a threat. Sheldon, Reed et al. (2009) observed a male coyote killing a bison calf, although the calf had become isolated from the herd after failing to ford a river. Indeed, these canids are the most prominent, potential predator of bison on Antelope Island State Park. Biologists on Antelope Island have observed coyotes harassing a parturient bison that had not yet given birth but had either the chorioallantionic sac or the emniotic sac protruding. On AISP, we hypothesize that bison select birth sites with increased visibility due to the presence of coyotes, or that this
behavior is a life-history strategy that bison have continued to use even though they likely do not experience excessive predation.

Elevation at 500 m was our second most predictive variable (Table 3). Bison on AISP selected birth sites at higher elevation than random locations. Elevation has been identified as an influential variable in other studies documenting birth-site selection in ungulates (Bergerud and Page 1987, Festa-Bianchet 1988, Wilton and Garner 1991, Barten et al. 2001, Gustine et al. 2006, Poole et al. 2007, Barnowe-Meyer et al. 2010). Several of those studies indicated that females used birth sites at higher elevation to potentially avoid predators (Festa-Bianchet 1988, Barten et al. 2001, Poole et al. 2007). With no information on the spatial use of predators on AISP, however, it would be difficult to determine if higher elevations offered protection for parturient bison from predators. Moreover, selection for higher elevation could also be related to forage condition (Hebblewhite et al. 2008, Plumb et al. 2009), favorable micro-climates (Barbknecht et al. 2011), or avoidance of insects (Mooring et al. 2003), and increased distance from anthropogenic structures which also influenced selection of habitat.

Distance from the birth site to all combined anthropogenic features was the final predictive variable supported in our analyses (Tables 2 and 3). This variable is a combination of the distance from a birth site to trails, roads, and structures. We recognize that some of these individual variables may influence birth-site selection in bison more than others; however, our results indicated that all anthropogenic features combined predicted birth-site selection for bison on Antelope Island better than any individual factor. Our findings are similar to those in other studies of ungulates, which show that anthropogenic influences can affect birth-site selection (Shively et al. 2005, Brook 2010, Singh et al. 2010, Dzialak et al. 2011). For example, parturient elk in Colorado avoided roads, selected areas with higher elevation and more security cover
during the day, and used lower elevations regardless of human infrastructures at night (Dzialak et al. 2011). In Kazakhstan, saiga antelope avoided anthropogenic features for calving sites (Singh et al. 2010). In Prince Albert National Park, female bison increased their average daily radius of movement by 27-30% due to human disturbance (Fortin and Andruskiw 2003). Very little information exists, however, regarding anthropogenic influences on birth-site selection of bison. Our study provides important, basic insight regarding variables that influence birth-site selection by these ungulates.

We documented 81% of birthdates of bison occurring in April with birthdates ranging from March 22 to May 20. Data collected at AISP between 1985 and 1989 reported bison births occurring between March and October with 40% of births occurring between August and October (Wolfe and Kimball 1989). Additionally, from 1987 to 1997, Wolfe et al. (1999) reported a protracted birthing period of > 60 to 90 days (first birth to 80% of births) with calves reported in every month of the year. Our data indicated that bison birthing on Antelope Island has become much more synchronous in the last 20 years, and that most of this synchronization has occurred since 1998. Berger (1992) suggested an inverse relationship between food quality and length of parturition period. Similarly, Wolfe et al. (1999) suggested nutritional deficiencies as a possible explanation for the protracted birthing period for bison on Antelope Island. Since 1987, wildlife managers have taken multiple steps to improve habitat on the island, including the termination of the grazing of approximately 1,500 domestic cattle and multiple habitat reclamation projects like noxious weed control and seeding projects. Also, since 2005, non-pregnant bison are routinely culled from the herd during the annual round-up. These management decisions, coupled with improving habitat conditions, potentially have led to a more synchronous birthing period.
Previous to European-American settlement, bison numbered in the tens of millions and occupied areas from New York to California and from Alaska to Mexico (Hornaday 1927, Hall 1959, Shaw 1995, Isenberg 2000). Due to overhunting and other factors, the number of bison decreased to only a few hundred animals by the late 1800s (Hornaday 1927, Isenberg 2000). Currently, bison inhabit less than one percent of their historic range, which has resulted in the ecological extinction of this species (Boyd 2003, Freese et al. 2007, Sanderson et al. 2008). With only 4% of the entire bison population managed for conservation, and most of those areas in National Parks with high-human visitation, it is imperative to delineate the habitat used by bison and then to avoid potential negative impacts of anthropogenic influences on bison, especially parturient females. We modeled birth-site habitat and determined the timing of births for bison on Antelope Island. Our model of birthing habitat, and data concerning timing of births, will provide biologists with a map of high-probability birthing areas and a time of year in which human access to trails and roads can be minimized in order to reduce conflict between recreation and bison on AISP.

Acknowledgements

We thank the Utah State Parks especially Antelope Island State Park. We thank Jolene Rose-Greer and Nate Duncan for their help collecting field data. We also thank Brigham Young University.
Literature Cited


Chapter 1 Tables

Table 1. Vegetation attributes and GIS-generated variables, as well as variable descriptions for potential factors influencing birth-site selection of bison on Antelope Island State Park in Utah, USA, from 2009 to 2011.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vegetation</strong></td>
<td></td>
</tr>
<tr>
<td>Robel</td>
<td>Amount of pole obscured at 5, 10, and 15 meters</td>
</tr>
<tr>
<td>Rooting Density</td>
<td>Number of trees and shrubs rooted in a 1-m area along 50m transect</td>
</tr>
<tr>
<td>CanopyCover</td>
<td>Total amount of tree and shrub cover along 50m transect</td>
</tr>
<tr>
<td><strong>Topographic</strong></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>Elevation (at point and an average at 50 and 500 m)</td>
</tr>
<tr>
<td>Aspect</td>
<td>Aspect (at point and an average at 50 and 500 m)</td>
</tr>
<tr>
<td>Slope</td>
<td>Slope (at point and an average at 50 and 500 m)</td>
</tr>
<tr>
<td>Curvature</td>
<td>Curvature (at point and an average at 50 and 500 m)</td>
</tr>
<tr>
<td>Visibility</td>
<td>Area visible (at point and an average at 50 and 500 m)</td>
</tr>
<tr>
<td><strong>Water</strong></td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>Distance (m) to nearest water</td>
</tr>
<tr>
<td><strong>Anthropogenic</strong></td>
<td></td>
</tr>
<tr>
<td>Trials</td>
<td>Distance (m) to nearest trail</td>
</tr>
<tr>
<td>Service Roads</td>
<td>Distance (m) to nearest service road</td>
</tr>
<tr>
<td>Public Roads</td>
<td>Distance (m) to nearest public road</td>
</tr>
<tr>
<td>All Roads</td>
<td>Distance (m) to nearest road of any kind</td>
</tr>
<tr>
<td>Structures</td>
<td>Distance (m) to nearest structure</td>
</tr>
<tr>
<td>DistHuman</td>
<td>Distance (m) to all combined anthropogenic features</td>
</tr>
</tbody>
</table>
Table 2. Model information associated with supported (AICc weight > 5%) models of bison birth-site selection on Antelope Island State Park in Utah, USA, from 2009 to 2011.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K^a$</th>
<th>$\text{AICc}^b$</th>
<th>$\Delta \text{AICc}^c$</th>
<th>$W_i^d$</th>
<th>Log likelihood$^e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curv(500 m) + Elev(500 m)</td>
<td>3</td>
<td>110.96</td>
<td>0.00</td>
<td>0.539</td>
<td>-52.01</td>
</tr>
<tr>
<td>Curv(500 m + Elev(500 m) + DistHuman</td>
<td>4</td>
<td>111.60</td>
<td>0.64</td>
<td>0.391</td>
<td>-51.13</td>
</tr>
</tbody>
</table>

$^a$Number of parameters

$^b$Akaike’s information criterion adjusted for small sample sizes

$^c$Difference in AICc value compared to top model

$^d$AICc model weight

$^e$Log likelihood
Table 3. Parameter estimates for the model that best accounted for bison birth site selection at Antelope Island State Park 2010 and 2011.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Z Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.162</td>
<td>4.313</td>
<td>-3.77</td>
</tr>
<tr>
<td>Curv (500 m)</td>
<td>-0.3856</td>
<td>8.979</td>
<td>-4.23</td>
</tr>
<tr>
<td>DistHuman</td>
<td>0.0009124</td>
<td>0.0006650</td>
<td>1.37</td>
</tr>
<tr>
<td>Elev (500 m)</td>
<td>0.009881</td>
<td>0.003056</td>
<td>3.23</td>
</tr>
</tbody>
</table>
Figure 1. Roads, trails, and other structures on Antelope Island State Park in the Great Salt Lake in Utah, USA.
Figure 2. Probability map indicating likely bison birthing habitat on Antelope Island State Park, Utah, USA, during 2010 and 2011. Seventy-four percent (n = 26) of birth sites occurred in high likelihood areas, 17% (n = 6) in the high-medium areas, 9% (n = 3) in medium areas, and none in the low or medium low areas.
CHAPTER 2

Abstract

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage grouse or grouse) declines have been well documented and principally linked to the loss of sagebrush (*Artemisia spp.*) habitat. Published guidelines provide a benchmark for managers to determine health of habitat where sage-grouse occur. The Diamond Mountain plateau provides habitat for one of the four largest populations of sage-grouse in Utah. Nonetheless, little information is available about nesting and brood-rearing habitat on Diamond Mountain. We monitored female sage-grouse from April 1 through the failure or success of individual nests and for ~50 days post hatch for brooding females. We collected micro-habitat data for 88 nests and 138 brood locations from 2010-2012 to determine habitat preferences of nesting and brooding sage-grouse. Using random forests, we found that percent sagebrush, percent canopy cover, percent total shrubs, and percent obscurity (Robel pole) best differentiated nest from random locations. We were unable to identify any micro-scale habitat variables that predicted nest success. Nests were located in habitat that met guidelines for sagebrush canopy cover, sagebrush height, grass height, grass canopy cover, but not forb cover. We used a 26-day nesting period to determine an average nest survival rate of 0.35 (95% CI = 0.23 – 0.47) for adults and 0.31 (95% CI = 0.14 – 0.50) for juvenile grouse. Brood sites were closer to habitat edges, contained more forbs and less rock than random locations. Grass height and sagebrush canopy cover also received support as important elements selected by grouse with brood sites consisting of higher grass heights and greater sagebrush canopy cover compared to random sites. Brood habitat at use locations on Diamond Mountain met or exceeded published guidelines. We found no significant habitat differences between early (hatch - 30 days) and late (30 – 50 days) brooding habitat. Annual
survival of female sage grouse was 0.50 (95% CI = 0.37 – 0.63) during the first year (April 1, 2010 – March 31, 2011) and 0.45 (95% CI = 0.28 – 0.63) in the second year of this study (April 1, 2011 – March 31, 2012). Average annual adult female survival across the two-year study period was 0.52 (95% CI= 0.38 – 0.65) compared to 0.43 (95% CI= 0.28 – 0.59) for yearlings. Adult survival of female sage-grouse was relatively high, but nest success was rather low.

Introduction

Declines of greater sage-grouse (Centrocercus urophasianus; hereafter sage-grouse) have been well documented and principally linked to the loss of sagebrush (Artemisia spp.) habitat which has occurred since European-American settlement (Connelly et al. 2004, Schroeder et al. 2004). Currently, sage-grouse only occupy about 56 percent of their historic sagebrush habitat (Schroeder et al. 2004). Sagebrush habitat has declined due to many factors including habitat conversion for agriculture, habitat loss due to invasive weeds, altered fire regimes, pinyon/juniper invasion, and fragmentation from anthropogenic influences such as energy extraction (Connelly et al. 2004). The decline in sagebrush has impacted a wide variety of sagebrush obligate or facultative species that rely on sagebrush for food and concealment from predators throughout their life cycle (Connelly and Braun 1997, Connelly et al. 2000).

Although sagebrush is important throughout their life cycle, sage-grouse select different habitat features depending on time of year, sex, and reproductive status (Connelly et al. 2011a, Fedy et al. 2012). During winter, for example, sage-grouse select tall stands of sagebrush that offer forage and concealment when snow is deep (Patterson 1952, Remington and Braun 1985). Conversely, during the spring breeding season, males select lek locations that occur in open areas with reduced vegetation that are adjacent to nesting habitat (Wiley 1973, Wakkinen et al. 1992a). Sage-grouse also preferentially select specific habitat characteristics for nesting and brooding
locations (Klebenow 1969, Aldridge and Brigham 2002, Connelly et al. 2004, Crawford et al. 2004). Sage-grouse nest on the ground, under shrubs, and rely on their cryptic camouflage and vegetation obscurity to protect against predators (Patterson 1952, Wallestad and Pyrah 1974). Nests are generally placed in areas with taller shrubs, more canopy cover, and more understory obstruction than what is available (Braun et al. 1977, Aldridge and Brigham 2002, Crawford et al. 2004, Holloran et al. 2005). Once females hatch chicks, however, they select areas with less sagebrush cover, taller grass, greater forb abundance, and greater grass cover (Hagen et al. 2007, Connelly et al. 2011a). These different requirements complicate management and create a need for a mosaic of habitat types. Although a mosaic of habitats are needed, research suggests that reproductive success is critical to maintain current sage-grouse population levels (Taylor et al. 2012), especially in human modified landscapes (Dzialak et al. 2011). Therefore, features associated with nesting and brood-rearing habitat must be present to ensure sage-grouse persistence (Connelly et al. 2011a).

Connelly et al. (2000) published guidelines to manage sage-grouse that included habitat requirements for nesting and brooding sage-grouse. In 2007 Hagen et al. (2007), furthering Schultz (2004), published a meta-analysis of studies that quantified vegetative characteristics at nesting and brooding locations. This meta-analysis supported published guidelines for the management of sage-grouse habitat during the reproductive phase of their life cycle. Ideal nesting habitat was described as sites with percent shrub canopy cover ranging from 15% – 25%, sagebrush heights from 40-80 cm, grass heights ≥18 cm, percent grass canopy cover ≥ 15%, and percent forb canopy cover ≥ 10%. Similarly, guidelines for brooding habitat included percent forb/grass canopy cover > 15%, percent sagebrush canopy cover ranging from 10% – 25%, and sagebrush height from 40 – 80 cm. These guidelines provide a benchmark for managers to
determine the quality of habitat for sage-grouse during the reproductive phase of their life cycle which contributes most to population growth. Assessment of habitat quality via published guidelines provides an important piece of information for managers attempting to prioritize conservation efforts for greater sage-grouse.

Diamond Mountain, in northeastern Utah, provides habitat for one of the four largest populations of sage-grouse in Utah (UDWR 2009). The Utah Division of Wildlife Resources has created a Comprehensive Wildlife Action Strategies plan that classifies the Diamond Mountain sage-grouse population as one of the core breeding populations that must be maintained if sage-grouse are to persist in Utah (UDWR 2009). Despite this designation, however, little information is available about the basic reproductive ecology of sage-grouse on Diamond Mountain. To address this lack of information, we radio-marked and monitored female sage-grouse and collected information on habitat composition at nest, brood-rearing, and random locations. Our objectives were to: (1) identify habitat preferences of nesting and brooding sage-grouse, (2) determine any habitat differences between successful and unsuccessful nests or early versus late brooding locations, and (3) compare nesting and brooding habitat on Diamond Mountain to published guidelines. In addition, we used data from radio-marked grouse to document survival and reproductive output of female sage-grouse on Diamond Mountain. We predicted that sage-grouse nest locations would occur in areas of greater shrub cover and greater grass heights (Hagen et al. 2007). We also predicted that successful nests would occur in areas with increased grass height compared to unsuccessful nests (Kaczor 2008). We further predicted that sage-grouse would select brooding areas with less percent sagebrush cover and greater percent forb and grass cover (Connelly et al. 2000, Hagen et al. 2007). Because of the stable nature of this relatively large population over the past several decades, we anticipated habitat
composition would meet published guidelines and that observed survival, nest initiation, nest success, and brood survival rates would be on the high end of those observed for greater sage-grouse throughout their range.

Methods

Study Area

Our study area was located 25-km northeast of Vernal, Utah (Figure 1) and consisted of a mountain plateau bordered to the south and west by sharp canyons that fall into the Vernal valley and to the north and east by the Diamond Mountains that extend north and south. The plateau was dominated by mountain big sagebrush (*Artemisia tridentata ssp. vaseyana*). Other shrubs in the area included bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos oreophilus*), and mountain mahogany (*Cercocarpus montanus*). A mix of grasses and forbs occurred in the understory. Dominant species included Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), crested wheatgrass (*Agropyron cristatum*), needle-and-thread grass (*Stipa comata*), and downy brome (*Bromus tectorum*). The plateau was comprised largely of private property and most parcels were used for summer grazing of cattle and some sheep.

Data Collection

We captured female sage-grouse on and around known leks during the spring of 2010-2012. We used spotlights and nets to trap sage-grouse from ATV's or on foot (Giesen et al. 1982, Wakkinen et al. 1992b). Following capture, we aged (Crunden 1963), weighed, and recorded a capture location using a Global Positioning System (GPS) for each individual. We then fitted females with a 22-gram, necklace-style telemetry unit (Advanced Telemetry
Radio transmitters emitted 45 pulses per minute and had a 19-hour duty cycle with a mortality signal after 8 hours of inactivity. Maximum battery life of radio transmitters was estimated at 30 months.

Once marked, we located sage-grouse once or twice a week beginning in April until the middle of August using VHF radio telemetry equipment (Communications Specialists Incorporated, Orange, CA). We approached potentially nesting females with caution and attempted to locate nests from a distance to reduce disturbance. If females were located under shrubs and did not flush from close distances, we assumed nesting. We confirmed this assumption by returning to the location within a few days. We monitored nests once a week until the nesting attempt was successful, terminated by a predator, or the female abandoned unhatched eggs. We considered nests successful if at least one egg showed evidence of a detached membrane (Klebenow 1969, Wallestad and Pyrah 1974). When nests failed, we attempted to identify predators (i.e.; tracks, feathers, marks in egg shell remains, etc.) and recorded number of destroyed eggs by counting crowns and bases of remaining eggshells. Following successful hatching, we located brooding females at least once a week for 50 days.

**Micro-site vegetation data**

To define an area within which to sample habitat at random locations, we used the SWReGAP landcover analysis (USGS 2005) to identify sagebrush on the Diamond Mountain plateau. We then buffered known leks using ArcGIS, v. 10.0 (ESRI, Redlands California, USA) with a 5-km radius circle. We chose this distance because it was within the middle of reported values for distances to leks for nesting and on the lower end of published distances to leks for brooding sage-grouse (Wallestad 1971, Wakkinen et al. 1992a, Schroeder et al. 1999, Peck et al. 2012). Following creation of buffers, we dissolved the boundaries to create a single layer and
used the extract by mask tool to remove any area within buffers that was not designated as sagebrush habitat by the SWReGAP. The resulting sampling area encompassed all but one of our nesting and brood-rearing locations during three years. Finally, we used ArcGIS, v.10.0 (ESRI, Redlands California) to generate random locations within this area.

In each year, we began collecting data from nest and random sites after the first nest was successful (egg hatch) or failed (egg predation or nest abandonment). We finished collecting data at locations within one week after the fate of the last nest was determined (Hausleitner et al. 2005). We matched the timing of data collection at random sites to that of data collection at nest sites to ensure consistent phenology of vegetation. Similarly, for broods we collected habitat data during the first week that a brood was located in a given year and we measured habitat at random locations within the window associated with brood rearing. We considered early brood rearing the period from 0-21 days post hatch and late brood rearing as 22 - 50 days post hatch (Connelly et al. 2000). We completed measurement of habitat at brooding and random locations by August 10th of each year.

To measure habitat composition at nesting, brooding, and random locations, we centered two 50-m line transects at the nest, brood, or random location. We then used the line intercept method to obtain estimates of percent cover for sagebrush, other shrubs, and combined shrubs (Table 1) (Canfield 1941). For understory composition, we used 0.5 m² quadrats placed every 2.5 m (n=41 per site) (Daubenmire 1959). Within each quadrat, we made an ocular estimate of percent bare-ground, rock, litter, perennial grass, annual grass, forbs, sagebrush, and other shrubs. We estimated cover as one of 11 classes 0-10 (0=5%, 1=15%, 2=25%, 3=35%, 4=45%, 5=55%, 6=65%, 7=75%, 8=85%, 9=95%, 10=100%). For shrubs rooted within quadrats, we recorded shrub height to generate an average height for shrubs at each site. We measured shrub
obscurity cover using a 135 cm Robel pole placed at 2.5, 5, and 10 m along each transect (Table 1) (Robel et al. 1970). We read Robel poles from a height of 30 cm, to simulate visual obscurity of an approaching predator. We obtained grass height measurements by measuring the height (cm) of the grass nearest the nest, brood, or random location. Additionally, we measured distance to nearest habitat edge with a laser range finder. We considered edge habitat as any shift in dominant vegetation type.

**Statistical analysis**

We used random forests in program R (R Development Core Team 2011) to differentiate between nest and random locations, successful and unsuccessful nests, brooding and random locations, and early and late brood-rearing locations (Cutler et al. 2007). Random forests is a non-parametric classifier that determines predictive ability for each variable by building classification trees then iteratively scrambling data associated with explanatory variables to determine change in associated predictive ability for each variable. Random forests produces a mean decrease in accuracy (MDA) for each explanatory variable that helps quantify variable importance. Variables can then be ranked in predictive ability according to MDA scores. One advantage of using random forests is its ability to model complex interactions without potential complications associated with multi-collinearity. Moreover, compared to other classifiers (e.g. logistic regression or discriminate function analysis) random forests has high accuracy (Cutler et al. 2007).

To provide estimates of survival for radio-marked females and their nests, we used Program MARK 6.1 (White and Burnham 1999). We used the nest survival model to estimate daily nest survival rates and grouped the nest data by years with an individual covariate for grouse age (juvenile or adult). Grouping data by years allowed us to graduate sage-grouse from
juvenile to adult in our analysis if as juveniles they survived the year. We specified a list of a priori models and used Akaike's Information Criterion adjusted for small sample sizes (AICc) and AICc weights to evaluate relative support for candidate models (Burnham and Anderson 2002). We used a 26-day nesting period to determine nest success rates (Connelly et al. 2004). We also used Program MARK to estimate annual survival for birds using known fate models (White and Burnham 1999) and followed similar protocol as above for specification and ranking of models. For this analysis, we specified year as a group variable and included individual covariates of age (yearling or adult), initiation of nest, and whether or not the bird had a brood during a given year.

Results

Nesting

We trapped 30 female sage grouse in 2010, 42 in 2011, and 15 in 2012 (total of 87). From these sage grouse, we located 21 nests from 30 birds (0.70 apparent nest initiation) in 2010, 47 nests from 56 birds in 2011 (0.84 apparent nest initiation), and 20 nests from 35 birds in 2012 (0.57 apparent nest initiation). We considered 45/88 nests to be successful, 11 of 21 in 2010, 20 of 47 in 2011, and 14 of 20 in 2012. Average daily nest survival from Program MARK was 0.96. We used a 26-day nesting period to determine an average nest survival rate of 0.35 (CI = 0.23 – 0.47) for adults and 0.31 (CI = 0.14 – 0.50) for juvenile grouse.

Percent sagebrush, percent canopy cover, percent total shrubs, and percent obscurity (Robel pole) were the highest ranked (MDA > 1.0) variables best able to differentiate between nest and random locations (Figures 2 and 3). Percent sagebrush was ranked highest with sage-grouse selecting nesting sites with an average of 10% more sagebrush than random locations (Figure 3). Similarly, sage-grouse selected nesting sites with more canopy cover, total shrubs,
and greater obscurity compared to random locations (Figure 3). For our comparison of habitat at successful versus unsuccessful nests, random forests did not identify any explanatory variables with an MDA above 1.0. Moreover, for the highest ranked variables in this analysis (percent sagebrush MDA = 0.58; percent rock MDA = 0.43) significant overlap in confidence intervals between mean values at successful versus unsuccessful nests was present.

**Brooding**

We had 11 birds hatch at least one egg in 2010 and 20 in 2011 for a total of 31 birds with broods. We obtained 138 (mean = 4.45; range 1-7 locations per brood) brooding locations from these birds and measured vegetation data at 146 random locations. Early brood-rearing sites made up 64 of these sites and 74 were late brood-rearing sites. Similar to successful and unsuccessful nests, however, we did not identify any variables with an MDA > 1.0 when comparing early to late brooding habitat. Moreover, the two highest ranked variables (grass height MDA = 0.52 and percent litter MDA = 0.47) demonstrated significant overlap in confidence intervals around mean values. Consequently, we combined early and late brooding locations prior to comparison with random locations. Distance to edge habitat, percent forbs, and percent rock were the highest ranked explanatory variables differentiating brooding and random locations (Figure 4 and 5). These variables were followed by grass height and percent canopy cover of sagebrush (Figure 4). Sage-grouse with broods selected areas closer to edges with more forbs and less rock than random locations (Figure 5).

**Survival**

Our best model of annual survival (null model) carried 0.28 percent AICc weight (Table 3). The next closest model contained nest initiation and held 0.17 percent AICc weight. Models containing covariates of age, brood, and our grouping year variable were next and received some
support (Table 3). In each of these cases, the β value associated with individual covariates (e.g., age, nest initiation, etc.) was positive, but in every case, the confidence interval around these estimates overlapped zero (nest initiation $β = 0.51$, 95% CI = -0.47 – 1.48; age $β = 0.20$, 95% CI = -0.50 – 1.23; brood $β = 0.31$, 95% CI = -0.55 – 1.18). Annual survival of female grouse was 0.50 (95% CI = 0.37 – 0.63) in the first year (April 1, 2010 – March 31, 2011) and 0.45 (95% CI = 0.28 – 0.63) in the second year (April 1, 2011 – March 31, 2012). Average annual adult female survival across years was 0.52 (95% CI = 0.38 – 0.65) and annual yearling survival averaged across years was 0.43 (95% CI = 0.28 – 0.59).

Discussion

The variables that best differentiated nest locations from random locations (percent sagebrush, percent sagebrush canopy cover, percent total shrubs, and obscurity) (Figures 2 and 3) have been identified in other areas as important for sage-grouse (Connelly et al. 2000, Hagen et al. 2007). For nests, 3 of the top 4 explanatory variables (percent sagebrush, sagebrush canopy cover, and percent total shrubs) are related to sagebrush and all showed positive selection (i.e., preference for increased percentages). This finding reaffirms the importance of sagebrush for sage-grouse and highlights the need to identify and maintain quality nesting habitat for sage-grouse in sagebrush systems.

We suspected that grass height would be taller at nest sites than at random sites, but grass height ranked 19th out of 22 variables with an MDA of 0.51. Moreover, mean grass height at nest (30.96 cm) and random (29.17 cm) locations was similar. Guidelines to manage grouse report sufficient grass height for nesting grouse above 18 cm (Connelly et al. 2000), Hagen et al. (2007) reported average grass height at nests from 27 other studies at approximately 19cm.
Thus, grass heights on Diamond Mountain are likely adequate for nesting sage grouse and do not play a large role in habitat selection in this area.

We found no evidence for a difference in habitat at successful versus unsuccessful nests. We suspected that grass heights would be taller at successful nests because it was important in South Dakota (Kaczor 2008). Nonetheless, grass height ranked 15th out of 22 variables with an MDA of only 0.09. Moreover, the variable with the highest MDA (0.70 for percent sage) for comparison of successful versus unsuccessful nests showed significant overlap in confidence intervals around mean values. Therefore, the factors we measured were not associated with success or failure of nests. It could be that nest failure was more influenced by scenting conditions (i.e., position on the landscape to prevailing wind (Conover 2007)), landscape scale influences, topographic features, or other unknown environmental variables we didn't measure.

Connelly et al. (2000) suggested that habitat should be managed to offer 0.15-0.25 sagebrush canopy cover, sagebrush heights of 40-80 cm, grass heights of >18 cm, grass canopy cover of ≥ 0.15, and ≥0.10 forbs (Table 2) for nesting sage grouse. Nest sites at Diamond Mountain met all of these guidelines with the exception of forb cover (Table 2). Percent forbs at random locations (0.09, 95% CI = 0.07–0.11) was close to the guidance of ≥ 0.10, but not at nest sites (0.06, 95% CI= 0.05 – 0.07) suggesting grouse made tradeoffs of cover over forbs, which could imply a shortage of forbs within sufficient cover, or that nesting sage-grouse on Diamond Mountain did not select for forbs while selecting nesting locations.

Averaged over the three years of our study, apparent nest initiation rates were 0.73. This average, however, includes 2012 (apparent nest initiation of 0.57) when failing collars made it difficult to track birds. Excluding 2012’s apparent nest initiation rate, average apparent nest initiation was 0.79. Nesting initiation rates in the literature range from 1.0 (Aldridge and
Brigham 2001) to 0.67 (Jensen 2006, Connelly et al. 2011b). The overall apparent nest initiation rate from Diamond Mountain is similar to most other studies where the mean has been reported as 0.82 (SD of 10.2) (Wallestad and Pyrah 1974, Holloran 1999, Holloran et al. 2005, Connelly et al. 2011a, Connelly et al. 2011b). Taylor et al. (2012) offered the most comprehensive collection of nest initiation rates from multiple studies, and after correcting for rates that were reported as apparent initiation, reported an average initiation rate of 0.96 (CI: 0.94 – 0.97) for adults and 0.89 (CI: 0.87 – 0.91) for yearlings. We report herein, apparent nest initiation, so our nest initiation rates are likely biased low.

The nest survival rate at Diamond Mountain calculated from Program MARK was 0.35 (95% CI = 0.23 – 0.47) for adults and 0.31 (95% CI = 0.14 – 0.50) for juvenile grouse which was lower than many other studies. Connelly et al. (2011b) combined data from 16 different studies of nest survival from Alberta, Colorado, Montana, North Dakota, South Dakota, and Wyoming and reported an average nest survival rate of 0.48 (SD 0.13). Taylor et al. (2012) used nest survival data from 50 studies, and after accounting for results reported as apparent nest survival, reported an average nest survival rate of 0.44 (CI: 0.41 – 0.48) for adults and 0.38 (CI: 0.34 – 0.42) for juveniles. Despite nesting habitat meeting most of the published guidelines for nesting sage-grouse, nest success on Diamond Mountain over the three years of our study was relatively low. Inherent to any radio-telemetry studies of nesting sage-grouse, is the possibility that researches approaching the nest location could result in greater potential for nest mortality. We attempted to avoid this by scanning for potential predators before approaching the nests, minimizing time spent at the nests, and not leaving any identifying markers at nest locations. Even with efforts to minimize the potential effects of the researchers, there is a chance that reported nest success could have been influenced by the presence of researchers.
Because we detected no difference between early and late brooding locations, we combined early and late brood locations together to compare with random locations. No difference in early and late brooding locations could have been influenced by an uncommonly wet spring and summer in 2011, or the fact that the Diamond Mountain plateau is a high elevation area that does not experience as much of a climatic shift between spring and summertime periods as other areas throughout the range of sage-grouse. Previous research has shown that if no difference between early and late brooding habitat exists, it may be due to prolonged availability of forbs in late periods (Aldridge and Brigham 2002, Connelly et al. 2011a). In support of this idea, we found no difference in forb abundance between early and late brooding locations or early or late random locations.

Once combined, we found evidence that brooding sage grouse selected locations that were closer to habitat edges, contained greater amounts of forbs, and reduced presence of rock (Figure 4). Similarly, Klott and Lindzey (1990) reported sage-grouse using the edges of sagebrush and grass areas in Wyoming. In northwest Colorado, sage-grouse selected brooding areas that were closer to changes in dominant vegetation types, or edge, than random locations (Dunn and Braun 1986). The most common edge habitat on Diamond Mountain was transition from sagebrush dominated habitats to grassy meadows, or mesic areas associated with wetland meadows. We hypothesize that these edge areas were preferred by sage-grouse with broods on Diamond Mountain because they contained greater access to forbs while still providing sagebrush cover for concealment and protection from predators. Average forb cover at brooding locations was 0.11 (95% CI = 0.10 – 0.13) compared to 0.08 (95% CI = 0.07 – 0.09) at random locations. Guidelines to manage sage-grouse habitat include forb and grass cover together and suggest that this category be >0.15 of the composition at brooding locations (Connelly et al.
When combined, grasses and forbs at brooding locations on Diamond Mountain averaged 0.31—well above suggested guidelines. Furthermore, in a meta-analysis of brooding studies that considered early and late brood-rearing sites together, values for forb canopy cover ranged from 0.05 – 0.16 and averaged 0.09 (95% CI= 0.03 – 0.14). These values differ from Aldridge and Brigham (2002) who suggested a minimum of 12-14 percent forb cover was needed for brooding sage-grouse. Other research has shown sage-grouse using brooding locations in the state of Washington with between 0.19 and 0.27 canopy cover of forbs for late brooding (Sveum et al. 1998). Furthermore, in Montana, sage-grouse selected late brooding areas with canopy cover of 0.33 forbs (Peterson 1970). Although forb abundance on Diamond Mountain met guidelines for brooding sage-grouse, observed values were on the low end and efforts to increase forb diversity while maintaining sagebrush cover could benefit this population.

Sage-grouse on Diamond Mountain selected brooding areas that on average contained less rock than random locations (Figure 5). We were not able to find any other examples in the literature where composition of rock differentiated brood and random locations. Bare ground, however, has previously been described as meaningful when characterizing brooding locations. Hausleitner (2003) and Lyon (2000) reported that brooding sage-grouse selected areas with less bare ground than random locations. Although, it is important to note that our analysis did contain a bare ground measure, others did not and may have lumped these two categories together. Another potential explanation could be that occurrence of rock was associated with less vegetative cover that would offer concealment or foraging opportunity for female sage-grouse.
In the guidelines to manage sage-grouse, sagebrush canopy cover is suggested to be between 0.10 and 0.25. We suspected that brood sites would contain less overall shrubs than random sites, but we found no evidence to support this idea as sagebrush canopy cover averaged 0.21 (95% CI = 0.19 – 0.23) at brood sites and 0.18 (95% CI = 0.16 – 0.20) at random locations. The guidelines also suggest a sagebrush height of 40-80 cm. Average sagebrush height at brooding locations on Diamond Mountain was within these guidelines at 55 cm (95% CI = 52 – 58 cm). Brooding locations at Diamond Mountain met all the vegetation related habitat variables in published guidelines (Connelly et al. 2000) suggesting managers should work to conserve and maintain existing habitats.

Average annual survival of female sage-grouse on Diamond Mountain between 2010 - 2012 was 0.48 (95% CI = 0.38 – 0.59). Between years, survival ranged from 0.50 (95% CI = 0.37 – 0.62) in the first year to 0.45 (95% CI = 0.28 – 0.62) during the second. Average annual survival of adults was 0.52 (95% CI = 0.38 – 0.65) compared to 0.43 (95% CI = 0.28 – 0.59) for yearlings. Mean survival from a large meta-analysis was 0.58 (CI: 0.54 – 0.61) for adults and 0.65 (CI: 0.61 – 0.69) for juveniles (Taylor et al. 2012). Rates for sage grouse on Diamond Mountain were on the low end of these reported values. We suggest continued monitoring of survival for this population because annual survival of females has recently been indicated as having the most impact on λ (Taylor et al. 2012).

Management Implications

According to lek counts, the Diamond Mountain sage-grouse population is currently stable (≥10 years), to growing (≥3 years) (Personal communication with Sensitive Species Biologist Brian Maxfield, Utah Division of Wildlife Resources). Our analysis found vegetation related habitat variables to be well within the guidelines for sage-grouse management furthering
this assessment. Nonetheless, the lower than average annual female survival is of some concern and should be monitored. We recommend managers continue to monitor annual survival of adult and yearling females in this population. If annual survival continues to be low, further management action could be recommended.

Acknowledgements

We would like to thank the Bureau of Land Management (BLM) Utah Division of Wildlife Resources (UDWR) for the funding and support of this project. We would especially like to thank Brian Maxfield and Jason Robinson as well as the Uinta Basin Adaptive Resource Management (UBARM) local working group for their contributions to the project. We would like to acknowledge and thank the Diamond Mountain Grazers association and the other private landowners on Diamond Mountain that allowed us access to their property. We thank Brad Horrocks, Josh Horrocks, and Mitch Hacking for allowing us to lodge at their cabin during the field data collection portion of this project. We also thank Austin Brewer, Austin Wooley, Cooper McCourtney, Eric Freeman, Greg Bush, Jared Oyster, and Jay Olsen for their help capturing grouse and collecting data.
Literature Cited


USGS. 2005. National Gap Analysis Program, Southwest Regional GAP Analysis Project—Land Cover Descriptions. RS/GIS Laboratory, College of Natural Resources. College of Natural Resources, Utah State University.


Table 1. Habitat variables measured at greater sage-grouse nest, brooding, and random locations on Diamond Mountain, Utah, 2010-2012.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge</td>
<td>EDGE</td>
<td>Distance from site to nearest change in habitat type</td>
</tr>
<tr>
<td>Grass height</td>
<td>GRASSHEIGHT</td>
<td>Grass height at nest bowl or random site</td>
</tr>
<tr>
<td>Robel 1</td>
<td>ROBL</td>
<td>Average Robel pole obscurity at 2.5 meters</td>
</tr>
<tr>
<td>Robel 2</td>
<td>ROBM</td>
<td>Average Robel pole obscurity at 5 meters</td>
</tr>
<tr>
<td>Robel 3</td>
<td>ROBH</td>
<td>Average Robel pole obscurity at 10 meters</td>
</tr>
<tr>
<td>Robel total</td>
<td>ROBELT</td>
<td>Average Robel pole at 2.5, 5, 10 meters</td>
</tr>
<tr>
<td>Sage canopy cover(a)</td>
<td>CCS</td>
<td>Average percent sagebrush canopy cover</td>
</tr>
<tr>
<td>Other shrubs(a)</td>
<td>CCO</td>
<td>Average percent canopy cover other shrubs</td>
</tr>
<tr>
<td>Total canopy cover(a)</td>
<td>CCT</td>
<td>Average percent canopy cover of all shrubs</td>
</tr>
<tr>
<td>Bare ground(b)</td>
<td>BG</td>
<td>Average percent bare ground</td>
</tr>
<tr>
<td>Rock(b)</td>
<td>ROCK</td>
<td>Average percent rock</td>
</tr>
<tr>
<td>Litter(b)</td>
<td>LITTER</td>
<td>Average percent litter</td>
</tr>
<tr>
<td>Perennial grass(b)</td>
<td>PERGRASS</td>
<td>Average percent perennial grasses</td>
</tr>
<tr>
<td>Annual grass(b)</td>
<td>ANNGRASS</td>
<td>Average percent annual grasses</td>
</tr>
<tr>
<td>Forbs(b)</td>
<td>FORB</td>
<td>Average percent forbs</td>
</tr>
<tr>
<td>Sagebrush(b)</td>
<td>SB</td>
<td>Average percent sagebrush</td>
</tr>
<tr>
<td>Other shrubs(b)</td>
<td>OTHER</td>
<td>Average percent other shrubs</td>
</tr>
<tr>
<td>Total shrubs(b)</td>
<td>TOTSHRUBS</td>
<td>Average percent all shrubs</td>
</tr>
</tbody>
</table>

\(a\) Measured using the line-intercept along 50-m transects centered at use or random location.

\(b\) Measured within 0.5 m quadrats (n=41) along transects.
Table 2. Comparison of habitat characteristics at nesting and brooding locations for greater sage-grouse at Diamond Mountain, Utah (2010-2012) to Connelly et al.’s (2000) guidelines.

<table>
<thead>
<tr>
<th></th>
<th>Guidelines</th>
<th>Diamond Mountain ($\bar{x}$ and 95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nesting</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy cover</td>
<td>15-25%</td>
<td>31.63% (CI = 29.16 – 34.09)</td>
</tr>
<tr>
<td>Sagebrush height</td>
<td>40-80 cm</td>
<td>59.29 cm (CI = 56.21 – 62.37)</td>
</tr>
<tr>
<td>Grass height</td>
<td>$\geq$ 18 cm</td>
<td>30.97 cm (CI = 28.02 – 33.91)</td>
</tr>
<tr>
<td>Grass canopy cover</td>
<td>$\geq$ 15%</td>
<td>16.18% (CI = 14.58 – 17.79)</td>
</tr>
<tr>
<td>Forb canopy cover</td>
<td>$\geq$ 10%</td>
<td>5.92% (CI = 5.22 – 6.63)</td>
</tr>
<tr>
<td><strong>Brooding</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forb/grass canopy cover</td>
<td>$&gt; 15%$</td>
<td>30.68%</td>
</tr>
<tr>
<td>Sagebrush canopy cover</td>
<td>10-25%</td>
<td>21.35 (95% CI= 19.4 – 23.31)</td>
</tr>
<tr>
<td>Sagebrush height</td>
<td>40-80 cm</td>
<td>55.13 (95% CI= 52.16 – 58.1)</td>
</tr>
</tbody>
</table>
Table 3. Supported models of annual survival of female sage-grouse on Diamond Mountain, Utah from 2010-2012.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>AICcWeights</th>
<th>Likelihood</th>
<th>K</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(.)</td>
<td>119.78</td>
<td>0.00</td>
<td>0.28</td>
<td>1.00</td>
<td>1</td>
<td>117.73</td>
</tr>
<tr>
<td>S(nest)</td>
<td>120.82</td>
<td>1.04</td>
<td>0.17</td>
<td>0.59</td>
<td>2</td>
<td>116.67</td>
</tr>
<tr>
<td>S(age)</td>
<td>121.18</td>
<td>1.41</td>
<td>0.14</td>
<td>0.49</td>
<td>2</td>
<td>117.04</td>
</tr>
<tr>
<td>S(brood)</td>
<td>121.37</td>
<td>1.60</td>
<td>0.13</td>
<td>0.45</td>
<td>2</td>
<td>117.23</td>
</tr>
<tr>
<td>S(year)</td>
<td>121.67</td>
<td>1.89</td>
<td>0.11</td>
<td>0.39</td>
<td>2</td>
<td>117.52</td>
</tr>
<tr>
<td>S(year*nest)</td>
<td>122.89</td>
<td>3.12</td>
<td>0.06</td>
<td>0.21</td>
<td>3</td>
<td>116.60</td>
</tr>
<tr>
<td>S(year*age)</td>
<td>123.27</td>
<td>3.49</td>
<td>0.05</td>
<td>0.17</td>
<td>3</td>
<td>116.98</td>
</tr>
<tr>
<td>S(year*brood)</td>
<td>123.34</td>
<td>3.56</td>
<td>0.05</td>
<td>0.17</td>
<td>3</td>
<td>117.04</td>
</tr>
<tr>
<td>S(year+age+brood+nest)</td>
<td>126.69</td>
<td>6.91</td>
<td>0.01</td>
<td>0.03</td>
<td>5</td>
<td>115.93</td>
</tr>
</tbody>
</table>

aThe components of the models are defined as follows: S(.) = constant survival across years; (S(nest) = nest initiation; S(age) = age of grouse (yearling/adult); S(brood) = occurrence of a brood; S(year) = survival by year; S(year*nest) = survival by year and nest initiation; S(year*age) = survival by year and age; S(year*brood) = survival by year and occurrence of brood; S(year+age+brood+nest) = survival by year, age, occurrence of a brood, and nest initiation

bAICc = Akaike's Information Criterion adjusted for small sample sizes; Δ AICc = AIC relative to the most parsimonious model; AICc Weights = Akaike weights; Likelihood = model likelihood; K = number of parameters
Figure 1. Map of western United States showing location of Diamond Mountain, Utah where we evaluated reproductive ecology of greater sage-grouse, 2010-2012.
Figure 2. Ranking of variable importance (MDA) from random forests comparison of habitat features at nest and random locations on Diamond Mountain, Utah, USA, 2010-2012. Variable names on y-axis follow those from Table 1.
Figure 3. Comparison of habitat features at nests and random locations for variables identified as most influential in a random forests analysis for greater sage-grouse on Diamond Mountain, Utah, USA, 2010-2012. Error bars represent 95 percent confidence intervals.
Figure 4. Mean decrease in accuracy (MDA) from random forests analysis comparing habitat variables at brooding and random locations for sage grouse on Diamond Mountain, Utah USA during 2010 and 2011. Variables names match those in Table 1.
Figure 5. Comparison of habitat features at brood and random locations for variables identified as most able to discriminate between brood locations and random locations in a random forests analysis for greater sage-grouse on Diamond Mountain, Utah, USA, 2010-2012.