2014

Determining Impacts of Mountain Lions on Bighorn Sheep and Other Prey Sources in the Black Hills

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Recommended Citation

Smith, Joshua B., "Determining Impacts of Mountain Lions on Bighorn Sheep and Other Prey Sources in the Black Hills" (2014). *Electronic Theses and Dissertations*. 649.
https://openprairie.sdstate.edu/etd/649

DETERMINING IMPACTS OF MOUNTAIN LIONS ON BIGHORN SHEEP AND OTHER PREY SOURCES IN THE BLACK HILLS

BY

JOSHUA B. SMITH

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Major in Wildlife and Fisheries Sciences

South Dakota State University

2014

DETERMINING IMPACTS OF MOUNTAIN LIONS ON BIGHORN SHEEP AND OTHER PREY SOURCES IN THE BLACK HILLS

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy in Wildlife and Fisheries Science degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidates are necessarily the conclusions of the major department.

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ACKNOWLEDGEMENTS

I would like to offer a sincere appreciation to my advisor Dr. Jon Jenks for allowing me to take the reins on a project of this scope and magnitude. I have grown both personally and professionally under your mentorship and look forward to future collaborations. Thank you to my graduate committee, Dr. Scott Pederson, Dr. Troy Grovenburg, Dr. Dan Thompson, and Dr. Allan Jones for challenging me throughout this process and for providing helpful feedback. Troy, I have appreciated the many conversations we have shared, however, I feel I may have completed this weeks earlier had I cut back on a few of them. I would also like to thank Dr. Robert Klaver for his insightful comments and statistical prowess as well.

Intense field projects such as this require the efforts of numerous people in order to succeed, and I would like to thank all the folks at South Dakota Department of Game, Fish, and Parks for providing assistance with the many aspects of this study. A special thanks to Jack Alexander and all the hounds for their assistance with captures and helping a southern boy learn the ways of the cougar. Steve Griffin was also an essential cog in too many aspects of this study to enumerate, and I will always be appreciative of your assistance. John Broecher’s assistance with field work, database management and willingness to come and pull me out of numerous messes was also crucial, and for this I will always be indebted. Hope you are enjoying San Diego now! I would also like to thank John Kanta, Luke Meduna, Brandon Tycz, Lauren Wiechman, Tom Berdan, Andy Lindbloom, Kevin Roebling, Kris Cudmore, and Ted Benzon specifically for their assistance as well. Thanks also to Greg Shroeder, Duane Weber, and Dan Roddy at Wind Cave National Park for field assistance as well.

I thank all the SDSU graduate students for their assistance with data analysis, review of manuscripts, political talks, broomball, and overall helping me keep my sanity while finishing this dissertation. A special thanks to a few: my office mates Ben Simpson, David Wilckens, Datta Shubham, Kristin Sternhagen, Carri-Ann Hayer and Brandi Crider for listening to my daily rants and offering assistance when I needed just a little jolt to get me over a hump. Thanks to Matt Wagner for assistance with making graphs and figures for publications. Adam Janke also provided invaluable help with numerous statistical problems that I came across, and I have enjoyed our many political and philosophical conversations over the years. Thanks also to Terri, Di, and Dawn for all you have done for me and the department. I am also appreciative of all the help provided by the South Dakota Civil Air patrol, especially Leo Becht and Gerald Kirk, your both great pilots.

I have to give a special thanks to Beckie Juarez, not only for her assistance in the field, but also for listening to me ramble on repeatedly about data analysis and my complaining when things weren’t going as planned. Your cool southern California vibe always kept me grounded. Last, but not least, I need to thank Darwin for all his help in the field; nothing is as effective at helping find dead deer as a corgi’s nose!

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ABSTRACT

DETERMINING IMPACTS OF MOUNTAIN LIONS ON BIGHORN SHEEP AND OTHER PREY SOURCES IN THE BLACK HILLS

JOSHUA SMITH

2014

From 2009 to 2013, we assessed cougar (*Puma concolor*) feeding habits and bighorn sheep (*Ovis canadensis*) population dynamics in the Black Hills, South Dakota. We used Global Positioning System (GPS) telemetry to locate 1,506 cougar feeding events and found deer (*Odocoileus spp*.; 83%), primarily white-tailed deer (*O. virginianus*), dominated cougar diets. Overall ungulate kill rate averaged 0.79 ungulates/week (range = 0.13–1.75 ungulates/week), and was significantly higher ($P < 0.001$) in summer ($\bar{x} = 0.92$; SE = 0.06) than in winter ($\bar{x} = 0.62$; SE = 0.06). In contrast, biomass consumed was significantly higher ($P = 0.033$) in winter ($\bar{x} = 8.23$ kg/day; SE = 0.96) than in summer ($\bar{x} = 5.45$ kg/day; SE = 0.43), primarily as a result of increased scavenging (winter = 0.21 events/week; summer = 0.08 events/week), which represents the highest documented rate for cougar populations studied. We also documented a relatively high rate of chronic wasting disease- (CWD) infected elk in 2 cougar (1 male; 1 female) diets (64%; 95% CI = 50.3–78.3%) and speculate that CWD infection likely increased elk predation risk. Annual lamb survival was 0.02 (SE = 0.01) with pneumonia (36%) and predation (30%) the leading causes of mortality. We found pneumonia and predation were temporally heterogeneous with lambs most susceptible to predation during the first 2–3 weeks of life, while the greatest risk from pneumonia occurred from weeks 4–8. Annual ewe survival was 0.81 (SE = 0.04) with pneumonia (19%) and predation (19%) the leading causes of documented mortality; 48% were unknown. Additionally, we used vaginal implant transmitters (VITs) to assess capture efficiency and document parturition and neonate lamb bed site selection for bighorn sheep. We found successful VITs increased capture efficiency (95%) over unsuccessfully-vitted ewes (81%) and ewes not equipped with VITs (70%). Bighorn ewes selected for rugged terrain at both macro- and microhabitat scales, while at the macrohabitat scale ewes selected for areas that were close to perennial streams on south and west facing slopes and against anthropogenic disturbance. At the microhabitat scale, neonate lambs tended to select for greater cover and against north facing slopes.

CHAPTER 1: COUGAR FEEDING HABITS IN THE BLACK HILLS: NATURAL OR ANTHROPOGENICALLY IMPACTED

This chapter is being prepared for submission in the Journal of Mammalogy and was coauthored by David T. Wilckens, John W. Broecher, and Jonathan A. Jenks.

ABSTRACT

The recolonization of cougars (*Puma concolor*) to the upper Midwest provides a unique opportunity to assess the role of this apex predator on prey population dynamics and ecosystem processes in areas where anthropogenic influences may be significantly higher than in other regions. From 2009–2012, we captured 41 cougars (29 females; 12 males) and used Global Positioning System (GPS) telemetry to locate 1,506 feeding events in the Black Hills, South Dakota and Wyoming, USA. Deer (*Odocoileus spp*.) comprised the majority of cougar diets (83%), and in cases where we could identify species, white-tailed deer (*Odocoileus virginianus*) dominated (63%). We used a subset of 25 GPS-collared cougars monitored for 6,358 days to estimate feeding rates and biomass consumed across seasons and demographic classes. We visited 93% of GPS cluster sites: logistic regression was used to predict consumption and biomass for 7% of potential feeding sites. Overall ungulate kill rate averaged 0.79 ungulates/week, but was highly variable (range = 0.13–1.75 ungulates/week) among individuals. We found kill rates were significantly higher ($P < 0.001$) in summer ($\bar{x} = 0.92$; 95% CI = 0.81–1.03) than in winter ($\bar{x} = 0.62$; 95% CI = 0.51–0.74); however, we found no differences by demographic status (e.g., sex, age, or presence of cubs) within the same season (summer: $P = 0.581$; winter: $P = 0.607$). In contrast, biomass consumed was significantly higher ($P = 0.033$) in winter ($\bar{x} = 8.23$ kg/day; 95% CI = 6.35 – 10.12) than in summer ($\bar{x} = 5.45$ kg/day; 95% CI = 4.63 – 6.27), primarily as a result of increased scavenging. Scavenging accounted for 17.3% ($n = 260$) of all prey items found in terms of relative frequency with higher rates observed in winter ($\bar{x} = 0.21$ events/week) than in summer ($\bar{x} = 0.08$ events/week). The high rate of scavenging indicated that anthropogenic activities influenced feeding activity of cougars within the Black Hills ecosystem. Our results highlight how adaptable and opportunistic cougars are at foraging for prey in an area of heavy human use interspersed with suitable cougar habitat.

Key words: biomass, Black Hills, consumption rates, cougar, global positioning system (GPS collars) collars, kill rates, predator-prey dynamics, *Puma concolor*, scavenge, South Dakota.

INTRODUCTION

Following historic declines of large carnivore populations in the 19th and 20th centuries (Pyare et al. 2004), recent reintroductions (e.g., wolves [*Canis lupus*] in Yellowstone National Park [YNP]) and range expansions (e.g., cougars [*Puma concolor*] into the Dakotas and Nebraska) are restoring these species to areas where they have been extirpated for up to 100 years (Wilson et al. 2010). While there is considerable ecological research supporting the thesis that carnivores can affect ecosystem functions and community structure (Ripple and Beschta 2004), less is known about the conditions in which predators do exert major influences (Holling 1973). Understanding when and/or the degree to which predators regulate the structure and function of prey populations hinges on deciphering the underlying mechanisms that drive predation, such as kill rate and prey composition.

In North America, cougar-prey relationships have been the focus of extensive research over the past 60 years (e.g., Connely 1949, Hornocker 1970, Knopff et al. 2010b), shedding light on important ecological questions. However, even fundamental questions such as the number of ungulates killed per week (i.e., kill rate) have varied significantly based on methodology and/or study area (see Knopff et al. 2010b Table 1).

Reasons for these discrepancies have received substantial attention in recent years (e.g., Knopff et al. 2010b, Ruth et al. 2010). Prior to Global Positioning System (GPS) technology, methods for estimating kill rate relied on snow tracking (Connely 1949, Hornocker 1970), energetic models (Ackerman et al. 1986, Laundre 2005), or intensely monitoring radiocollared individuals (Beier et al. 1995). These techniques are labor intensive, dependent upon season, or snow, and thus, tend to produce short monitoring intervals that require extrapolation to the remainder of the year, or to monitoring periods where kill rates may differ substantially (Vucetich et al. 2012). Following Anderson and Lindzey's (2003) initial study of cougar kill rates, predation studies based on GPS data have allowed monitoring of a greater number of individuals for longer continuous periods across seasons, resulting in increased precision and decreased bias (Knopff et al. 2010b, Ruth et al. 2010). Despite the increased efficiency and accuracy of these new techniques, applying kill rates across geographic areas can be problematic. For instance, cougar kill rates may differ by prey species composition, prey migratory behavior (Elbroch et al. 2013), or through interference competition with bears (*Ursus sps*.; Murphy et al. 1998) or wolves (Bartnick et al. 2013).

In addition to regional variation, ecological factors also have been shown to influence variability in kill rates within a population. Significant differences in kill rates of cougars by season have been noted from several regions (Murphy 1998, Nowak 1999, Knopff et al. 2010b), although others have found no effect (Cruickshank 2004, Cooley et al. 2008). Furthermore, demographic structure has been implicated in influencing cougar kill rates (Anderson and Lindzey 2003, Knopff et al. 2010b), which can be important for hunted populations (Robinson et al. 2008). Finally, while most studies of cougar predation habits have estimated (e.g., Knopff et al. 2009) or assumed (Anderson and Lindzey 2003) scavenging is rare, recent studies have found that scavenging can account for a significant portion of biomass consumed, especially in winter months (Knopff et al. 2010a). However, most studies of cougar predation habits have been conducted in remote settings where human population densities are relatively low; consequently, sources of scavenging from anthropogenic sources may be limited. Thus, even the most thorough assessments of cougar kill rates may not be applicable to other populations.

Recolonization of cougars of former ranges within the upper Midwest (Thompson and Jenks 2005, North Dakota Game and Fish Department 2006, Wilson et al. 2010, Thompson et al. 2014) through dispersal (Thompson and Jenks 2010) provides a unique opportunity to assess the role of this apex predator on prey population dynamics and ecosystem processes in the absence of other large carnivores, and in areas where anthropogenic influences may differ (e.g., higher road densities, higher human populations) from previous studies. Our objectives were to: 1) determine prey composition of cougar diets, 2) quantify ungulate kill rates, 3) assess the influence of season and demographic status on predation rates, and 4) determine the influence of scavenging on overall cougar consumption rates in the Black Hills of South Dakota and Wyoming.

MATERIALS AND METHODS

Study Area.—We studied cougar predation in and around the approximately 8,400 km^2 (Fecske et al. 2004) Black Hills of southwestern South Dakota and eastern Wyoming, USA, from 2009–2012 (Figure 1). Topography of the area varied from steep ridges, rock outcrops, canyonlands, and gulches to upland prairie, rolling hills, and tablelands. Elevations ranged from 973 to 2,202 m above mean sea level (msl; Froiland 1990). Average annual precipitation was 53 cm and mean temperatures ranged from a maximum of 28° C in July to a minimum of −10° C in January. Climate values were based on data collected at the Hill City, South Dakota, USA, weather station from 1981–2010 (National Oceanic and Atmospheric Administration [NOAA] 2013). The Black Hills ecosystem is comprised of 4 distinct vegetation complexes: 1) Rocky Mountain coniferous forest, 2) Northern coniferous forest, 3) Grassland complex, and 4) Deciduous complex (Froiland 1990). Ponderosa pine (*Pinus ponderosa*) was the most abundant tree species comprising 84% of the forested landscape (Rumble and Anderson 1996). Other important tree species included quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), giving way to burr oak (*Quercus macrocarpa*) in the eastern and northern foothills (Larson and Johnson 1999). Ungulates in the study area included bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), mountain goats (*Oreamnos americanus*), pronghorn (*Antilocapra americana*), and elk (*Cervus elaphus*); bison (*Bison bison*) occur in portions of Custer State Park and Wind Cave National Park in the southeastern Black Hills. Other potential prey items of cougars included turkey (*Meleagris gallapavo*), porcupine (*Erethizon dorsatum*), and marmot (*Marmota flaviventris*), along with an assortment of other small mammals and domestic/livestock species. In addition to cougars, other predators included coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

Capture and monitoring. — From 2009–2012 we captured cougars primarily with the aid of hounds, as well as opportunistic use of walk-in live traps, foot-hold snares (Logan et al. 1999), and foot-hold traps. We immobilized cougars with a mixture of telazol (5.0 mg/kg) and xylazine (1.0 mg/kg; Kreeger and Arnemo 2007) based on estimated live animal body weight via dart rifle (Dan-Inject, Børkop, Denmark, EU). We weighed, measured, sexed, and estimated age of cougars by tooth wear and pelage characteristics (Anderson and Lindzey 2000). We classified cougars as cubs (dependent on mother), subadults (dispersal until 2.5–3.0 yrs), or adults (>3 yrs) and fitted independent cougars (i.e., not dependent on adult female) with one of 2 brands of GPS radiocollars (Northstar D-cell, King George, Virginia, USA; Advanced Telemetry Systems [ATS] G2110E, Isanti, Minnesota, USA). Upon completion of handling, we administered 0.125 mg/kg yohimbine to reverse xylazine, released cougars on site, and monitored them from a distance to ensure safe recovery. All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

We programmed GPS collars with one of 2 location schedules: 1) 4 locations/day – 0000, 0400, 1200, and 1900 hrs or 2) 8 locations/day – 0000, 0300, 0600, 0900, 1200, 1500, 1800, and 2100 hrs. We downloaded data weekly and used a Python script (Python software Foundation, Hampton, New Hampshire, USA) developed by Knopff et al. (2009) to identify potential kill sites. We considered a cluster (i.e., a potential kill site) as sites with ≥2 GPS locations within a 200 m radius over a 6-day period (Knopff et al. 2009). We visited clusters of GPS locations as soon as possible thereafter to determine possible predation events by programming geometric centers and all GPS locations associated with clusters into handheld GPS units (Garmin International, Olathe, KS, USA). We conducted a systematic search at each cluster by walking 5−10 m wide (depending on visibility) zig-zag patterns at each location and the cluster centroid out to 30 m. Prior to October 2011, we attempted to visit all identified clusters. After 1 October 2011, we had equipped all cougars with ATS collars set to take locations at 3 hr intervals. We experienced fix success >80% and found a near-zero probability of 2 location clusters containing kills (1 probable kill out of 237 clusters investigated; 0.5%) outside of the fawning season (May–August). Therefore, after 1 October 2011 we visited clusters with ≥3 locations outside of the fawning season and all clusters with ≥2 locations during the fawning season.

Prey composition. — We categorized prey remains found at cluster locations as either predation or scavenge events provided there was evidence the cougar had killed or fed on the carcass. Our default category was to classify prey remains as a probable cougar kill provided the age of prey remains closely matched the dates over which the cluster was created and there was no evidence to contradict cougar predation (e.g., antlers sawed off, hunter license attached). We assigned scavenging in cases where it was clear the animal had been killed by something other than the cougar assigned to that cluster (e.g., 2 cougars on same kill, road-kill) or if the carcass age greatly preceded the dates the cougar spent at the cluster (Knopff et al. 2010b).

We identified prey species and sex by anatomical characteristics (e.g., tail, metatarsal glands, horns, and antlers; Demarais and Krausman 2000), and determined age from tooth eruption and wear (Severinghaus and Cheatum 1956). In cases where we could not determine species, sex, or age we assigned “unknown”. We assigned each predation event to either summer (15 May–15 November) or winter (16 November–14 May) based on time of first GPS location at cluster site. Seasonal cutoffs were selected to ensure we encapsulated the neonatal birth pulse within one season (Knopff et al. 2010b).

We calculated species composition by percent frequency seasonally for 3 cougar demographic classes; adult female, adult male, and subadults. We collapsed prey into 3 categories: small ungulates (bighorn sheep, deer, and pronghorn), large ungulates (elk, bison), and nonungulate, and used chi-square tests to compare prey among cougar classes, prey categories, and between seasons within demographic classes. We performed these analyses using SYSTAT 11.0 (Systat Software Inc., Chicago, Illinois, USA).

To estimate biomass (kg) consumed, we assigned approximate live weights to adult prey based on values from the literature. For, elk and deer (white-tailed and mule deer combined) we assigned weights to adults based on average values from Jensen (2002). For bighorn sheep, we assigned values based on known weights from the Black Hills, South Dakota (J. Smith, South Dakota State University, unpublished data). To estimate yearling and young of the year ungulate biomass, we used a von Bertalanffy growth equation (Ricker 1979) modified from Knopff et al. (2010a). For example, we used an inflection point (I) of 140 days (Knopff et al. 2010a) and adjusted the growth rate (K) until birth weights approximated known ungulate birth weights for the region (e.g., Smith et al. 2014). We then assigned median weights for each of 4 age classes (0–3 months, 3–6 months, 6–12 months, and 12–24 months; Table 1). In cases where we could not determine age class, we assigned yearling weight to the kill (Knopff et al. 2010b). When we could determine that the prey was an adult but were unable to determine sex, we assigned the average adult weight (i.e., [ad M + ad F]/2). For nonungulate prey we did not differentiate between sex or age classes; instead, we assigned mean weights given by Higgins et al. (2002) for mammals and Dunn and Alderfer (2006) for birds. As it was often difficult to ascertain the amount of biomass consumed at scavenge sites, we used predictions from a large- vs small-prey model developed to assign scavenge events to one of the 2 categories. We then applied the average biomass from all known small-prey kills or large-prey kills to each scavenged item within the same respective category.

Model development.—We attempted to census cougar predation of ungulates throughout the monitoring period for each marked cougar by visiting all generated GPS clusters. However, not all sites could be investigated (e.g., private property, cougars dispersing); therefore, we used a multivariate logistic regression model (Hosmer and Lemeshow 2000) to predict predation events at non-investigated clusters. First, we developed a model to predict presence or absence of prey items ≥4kg using data from investigated clusters. We only included data from cougars fitted with ATS GPS collars scheduled to take 8 fixes/day in our model development. We removed clusters associated with initial collarings, collar removals, and den sites prior to modeling our data. We used season (summer and winter) and 8 variables generated from the Python script and for model development: 1) number of GPS locations in cluster, 2) fidelity (number of GPS locations in the cluster minus number of locations away from cluster during cluster duration), 3) hours (number of hours between the first and last locations in the cluster), 4) days (number of 24-hour periods in which at least one location was collected within the cluster), 5) night points (total number of locations within cluster that were obtained between 1800-0600 hrs), 6) night proportion (number of night locations in cluster divided by total number of locations in cluster, 7) average distance (average distance that each location was from cluster centroid, and 8) cluster radius (difference between cluster centroid and the farthest cluster location)

After testing for correlation between variables (r ≥0.7) in SYSTAT, we developed a priori models using various combinations of uncorrelated variables, and fit them to our investigated GPS clusters. We assessed model fit using Akaike's Information Criteria (AIC; Burnham and Anderson 2002). We applied coefficients from our top regression model to our investigated cluster data to calculate a prediction value for each cluster. We then used a receiver operating characteristic (ROC) curve generated in package *ROCR* (Sing et al. 2005) in Program *R* to determine an optimal cutoff value for our model predictions to classify a cluster as containing a prey item or not (Boyce et al. 2002, Knopff et al, 2009, Miller et al. 2013). Proper selection of cutoff values is imperative for optimal prediction performance of the model (Knopff et al 2009, Merrill et al. 2010, Miller et al. 2013, Webb et al. 2008). Selecting a cutoff that maximizes the true positive rate, or sensitivity, may lead to the overestimation of kill rate due to the increased number of false positives generated by the model. However, maximizing the true negative rate, or specificity, may lead to the underestimation of kill rate by misclassifying many sites as not having a ≥4kg prey carcass present. We chose our cutoff values by maximizing the overall model accuracy, defined as the sum of the true positive predictions and true negative predictions, divided by the sum of actual positives and actual negatives (Sing et al. 2005).

We developed a second logistic model using this same methodology to further predict clusters containing large (≥32kg) or small (<32kg) prey items. We used 32kg as a cut point to allow deer fawns ≥6 mo to be incorporated as large prey items. We applied our top regression models to non-investigated GPS clusters allowing us to categorize them as no-prey, large prey, or small prey. We assigned a consumption category (ungulate kill, nonungulate kill, scavenge) to non-investigated clusters based upon percentage of each category found at investigated clusters within the same prey-size class and season (e.g., large prey, winter) as the predicted cluster. We estimated a predicted biomass value for each non-investigated cluster based upon the average biomass from investigated clusters within the same prey-size class and season. We used the *lme4* package (Bates et al. 2014) in Program *R* for model development.

Feeding rates.— For cougars fitted with GPS collars that had ≥45% fix success and were monitored for ≥28 days within a given season and demographic class (Knopff et al. 2010b), we calculated 3 feeding rates: 1) ungulate kill rate, using feeding events where we determined the ungulate prey was killed by the cougar that generated the cluster, 2) ungulate consumption rate, using both cougar-killed ungulates and scavenged ungulates, and 3) biomass consumed, included ungulate and nonungulate prey items consumed. We used a ratio estimator to calculate feeding rates using total number of weeks (or days for biomass) monitored as the denominator, and total number (actual + predicted) of ungulate kills, ungulate consumptions, or biomass as the numerator (Knopff et al. 2010b).

We used all 3 rates to estimate annual feeding rates by using individuals as the unit of analysis and pooling data across season and demographic classes. We also calculated seasonal feeding rates for 6 demographic classes: subadult female (SF), subadult male (SM), adult male (AM), adult female (AF), adult female with young >6 months (FG > 6 months), and adult female with young <6 months (FG < 6 months;

Knopff et al. 2010b). We calculated feeding rates more than once for individual cougars if they transitioned between age or reproductive class during our study. We obtained initial cub counts and estimated cub age by visiting dens sites or when they were encountered while collaring adult females. We assessed cub retention by following tracks in the snow or mud and by placing infrared cameras at feeding sites. When we were unable to assess the exact dispersal date, we reclassified females as solitary when cubs reached 15 months of age, the average age of dispersal for cougars in the Black Hills (Jansen and Jenks 2012). We assessed the effects of demographic class on feeding rates using a single-factor analysis of variance for each season. Demographic and season-specific feeding rates were the unit of analysis. To quantify these effects, we used cougars that maintained the same demographic class across seasons to compare kill rate and consumption rates by season.

We calculated the number of days between ungulate kills and consumptions for each month by summing the number of days cougars were on air and dividing by the number of ungulate kills or consumptions in the respective month. To avoid problems with calculating rates over short monitoring periods (e.g., collar failures or initial collaring), we only used cougars that were on air for ≥7 days per month. If no ungulate kills or consumptions were made in a given month, we used the number of days the cougar was on air as the estimate. For example, if a cougar was on air for 28 days within a month and failed to make an ungulate kill, we assigned a value of 28 days between kills for that cougar. To determine the impact of the ungulate birth pulse on cougar kill rates, we evaluated the relationship between the percentage of juvenile ungulates in cougar diets by month in relation to the average number of days between kills using a Pearson's correlation.

RESULTS

From October 2009 to September 2012, we captured 41 cougars; 16 adult females, 13 subadult females, 10 adult males, and 2 subadult males. Of these, 6 subadult females transitioned to adults while radiocollared. We visited >5,500 cluster locations and documented 1,506 feeding events (kills = 1,246; scavenge = 260). We were able to identify species (with white-tailed deer and mule deer combined) at 1,487 feeding events, age at 1,135 feeding events, and sex at 1,015 feeding events.

We documented 26 unique species of prey at cougar feeding sites. Wild ungulates (white-tailed deer, mule deer, elk, bighorn sheep, and pronghorn*)* comprised the majority of identified prey items found in terms of relative frequency (89.4%) with deer (*Odocoileus spp*.) being most common prey item consumed (83.0%), and in cases where we could identify species (*n* = 947) white-tailed deer dominated (62.9%). Elk (5.5%), mule deer (3.7%), bighorn sheep (0.6%), and pronghorn (0.2%) occurred at much lower frequencies. Ungulates dominated prey composition across all months (Table 2). However, during April and May, when ungulate densities should be at their lowest (i.e., just before the birth pulse in June), we observed considerably more nonungulate prey in cougar diets (20%; range = 20–21%) versus the remainder of the year (8%; range = 3–13%; Figure 2). Other important prey items included turkey (3.1*%),* coyote (1.1%), and domestic cattle (1.0%) with the remainder of species occurring at <1% each. Scavenged prey accounted for 17.3% (*n* = 260) of diets in terms of relative frequency.

Cougars in the Black Hills did not exhibit significant seasonal shifts in prey composition by season (ad F, $\chi^2_2 = 0.20$, $P = 0.904$; ad M, $\chi^2_2 = 3.13$, $P = 0.210$; subad, $\chi^2_2 = 4.59$, $P = 0.105$; Table 2); however, prey composition did vary significantly ($\chi^2_4 = 27.219$, $P < 0.001$) among cougar age-sex classes. Small ungulates comprised the majority of prey consumed for all categories, but annually were lower for adult males (69.4%) than adult females (87.1%) or subadults (82.9%). Subadults consumed more nonungulate prey (14.9%) than adult males (10.5%) or adult females (9.3%), whereas adult males consumed more large ungulates (20.1%) than either adult females (3.7%) or subadults (2.1%).

Kill rate.—We estimated ungulate kill rates, consumption rates (kills plus scavenges), and biomass consumed using a subset of 25 GPS-collared cougars monitored for 6,358 days ($\bar{x} = 248.3$ days/cougar, SD = 136.5 days), separated between 3,696 days (58%) in summer versus 2,662 days (42%) in winter, from November 2010 to December 2012. Our sample of collared cougars included 14 adult females (4 of which were collared as subadults but transitioned to adults during the study), 8 subadult females, 5 adult males, and 2 subadult males. On average, we investigated 92.9% (range = 100–13.8%) of all clusters generated/cougar. Both subadult males and 2 subadult females dispersed outside of the Black Hills for part of the monitoring period; excluding these 4 cougars, we investigated 97.6% (range = 100–85.7%) of all clusters generated per cougar. We visited cluster sites an average of 13.4 days (SD = 11.7 days) after the first cougar location was identified. We did not calculate rates for cougars wearing Northstar GPS collars because fix success averaged <30%. We calculated 63 season- and demographic-specific rates during which monitoring averaged 101 days (SD = 51.5). We excluded rates for 11 monitoring periods because duration was <28 days.

Our top model for differentiating cougar feeding sites from non-feeding sites included hours at the site, average distance between GPS locations, night locations, proportion of nighttime locations, and fidelity to the site (Table 3). Feeding sites were more likely to be present when hours, night locations, proportion of nighttime locations, and fidelity increased, and when the average distance between locations decreased (Table 4). We considered this as our best approximating model as it contained 67% of model weight, which was 2.0 times greater than all other models combined. While one additional model was within 1.4 ΔAIC units from this model, the maximized log likelihood from our top model (–1402.295) was essentially unchanged with the addition of season (–1401.999); thus, we considered season to be an uninformative variable and precluded this model from consideration (Burnham and Anderson 2002, Arnold 2010). Our top model fit the data well with a ROC area under the curve of 0.91 (Hosmer and Lemeshow 2000). The maximized probability cutoff for which we considered a cluster a feeding event was 0.29, which corresponded to a classification success rate of 88%.

For discriminating between large and small prey items consumed, our best predictive model included; days at cluster, season, and fidelity. Prey were more likely to be large as days and fidelity increased during the winter (Table 5). We considered this as our best predictive model for the following reasons: 1) this model contained 66% of model weight, which was 2.0 times greater than all other models combined, 2) the second ranked model was >2 ΔAIC units from our top model, and 3) our second ranked model exhibited a higher maximized log likelihood (–449.091) than our top model (–447.189) despite containing an additional 3 parameters. Our top model for distinguishing large- from small-bodied feeding events fit the data well with an ROC area under the curve of 0.84. The maximized probability cutoff for which we considered a predicted kill a large-bodied prey item was 0.45, which corresponded to a classification success rate of 77%.

Cougar kill rate (not accounting for seasonal or demographic effects) averaged 0.79 ungulates/week (95% CI = 0.70–0.88), but was highly variable among individuals (range = 0.13 – 1.75 ungulates/week) and varied significantly ($F_{1,61} = 14.574$, $P < 0.001$) from summer ($\bar{x} = 0.92$; 95% CI = 0.81–1.03) to winter ($\bar{x} = 0.62$; 95% CI = 0.51–0.74). When accounting for scavenged ungulates, cougar consumption rate increased to 0.94 ungulates/week (95% CI = 0.86–1.0) and was primarily driven by significant seasonal variation in scavenging ($F_{1,61} = 21.185$, $P < 0.001$) with higher rates observed in winter ($\bar{x} = 0.23$ events/week; 95% CI = 0.17–0.28) than in summer ($\bar{x} = 0.08$ events/week; 95% CI = 0.06–0.11). Additionally, while we observed no statistical difference in consumption (summer: $F_{5,29} = 0.833$, $P = 0.537$; winter: $F_{5,22} = 0.916$, $P = 0.489$) or kill rates (summer: $F_{5,29} = 0.767$, $P = 0.581$; winter: $F_{5,22} = 1.170$, $P = 0.607$) across demographic classes within the same season, we did see considerable variation (Figure 3). Annually, the average number of ungulates killed was 52 for females with cubs >6 months, 42 for females with cubs <6 months, 39 for adult females, 38 for subadult males, 35 for adult males, and 33 for subadult females. Similar to Knopff et al. (2010a), we found ungulate kill rate increased as reliance upon juvenile prey increased, and that the interval between feeding events varied substantially by month but decreased rapidly during the ungulate birth pulse (Jun) before increasing after a low in July (Figure 4). Days between ungulate kills were strongly and negatively correlated (r^2 = 0.64, P = 0.002) with the proportion of juveniles in cougar diet.

Biomass consumed by cougars averaged 6.61 kg/day (95% CI = 5.64–7.59) across all season and demographic classes. In contrast to our observed kill rate, biomass consumed by cougars was significantly higher ($F_{1,61}$ = 4.774, P = 0.033) in winter ($\bar{x}$ = 8.23 kg/day; 95% CI = 6.35–10.12) than in summer ($\bar{x}$ = 5.45 kg/day; 95% CI = 4.63–6.27; Figure 5). However, when accessing only cougar-killed biomass (i.e., removing scavenged biomass), biomass consumed was not significantly different ($F_{1,61}$ = 0.330, P = 0.568) for summer ($\bar{x}$ = 5.05 kg/day; 95% CI = 4.21–5.88) and winter ($\bar{x}$ = 6.15 kg/day; 95% CI = 4.14–8.16). Similar to our kill rate estimates, we observed no difference in biomass consumed across seasons within demographic classes (summer: $F_{5,29}$ = 1.398, P = 0.254; winter: $F_{5,22}$ = 1.072, P = 0.402). Overall, scavenging averaged 1.11 kg/day (95% CI = 0.80–1.41), but was significantly higher ($F_{1,61}$ = 37.68, P < 0.001) in winter ($\bar{x}$ = 2.08 kg/day; 95% CI = 1.58–2.58) than in summer ($\bar{x}$ = 0.40 kg/day; 95% CI = 0.20–0.62; Figure 5). Annually, live-weight biomass consumed by cougars averaged 3,336 kg for females with cubs >6 months, 2,383 kg for females with cubs <6 months, 2,101 kg for adult females, 2,162 kg for subadult males, 3,483 kg for adult males, and 1,882 kg for subadult females.

Using paired data from 17 individual cougars that maintained demographic status across seasons, we estimated that on average cougars killed 1.30 times as many ungulates in summer ($\bar{x}$ = 0.749 ungulates/week; 95% CI = 0.645–0.853) as in winter ($\bar{x}$ = 0.576 ungulates/week; 95% CI = 0.450–0.703). In contrast, scavenging increased consumption rates 1.30 times in winter ($\bar{x}$ = 0.800 ungulates/week; 95% CI = 0.694–0.904

ungulates/week) versus 1.13 times in summer ($\bar{x}$ = 0.901 ungulates/week; 95% CI = 0.799–1.00 ungulates/week) above the respective kill rate. Total biomass consumed averaged 1.32 times higher in winter ($\bar{x}$ = 7.37 kg/day; 95% CI = 6.42–8.31) than in summer ($\bar{x}$ = 5.56 kg/day; 95% CI = 4.52–6.61), while scavenged biomass averaged 5.10 times higher in winter ($\bar{x}$ = 2.13 kg/day; 95% CI = 1.56–2.71) than summer ($\bar{x}$ = 0.42 kg/day; 95% CI = 0.28–0.55).

DISCUSSION

To our knowledge, the amount of scavenging we observed in the Black Hills represents the highest documented rate for cougar populations studied. Earlier studies relying on VHF-collared animals tended to report relatively infrequent events. Murphy (1998) reported a single instance of scavenging during a 9-yr study, and Ross and Jalkotzy (1996) reported 4 instances over a 13-yr period. However, Nowak et al. (2000) documented a cougar scavenging from 4 different sources over a 22-day period in Oregon. Others have attempted to quantify the frequency of scavenging by either observing ungulates that died of nonpredation causes (Logan and Sweanor 2001) or by placing carcasses as bait and documenting the number visited by cougars (Bauer et al. 2005). Visitation rates to these sites ranged from 9% in New Mexico (Logan and Sweanor 2001) to 44% in southern California (Bauer et al. 2005). These estimates illustrate that scavenging does occur in other systems, although they should not be misconstrued as a scavenging rate as they do not represent a true proportion of scavenge events in cougar diets.

The use of GPS telemetry has recently allowed researchers to investigate cougar feeding habits that incorporate a larger number of individuals while decreasing the amount of time between feeding events and field visitation. Recent application of these techniques in areas of low anthropogenic influence, such as Yellowstone National Park (3.5%; Ruth et al. 2010) and Patagonia (1%; Elbrock and Wittmer 2013), indicated that scavenging is a relatively small proportion of cougar diets. In contrast, Knopff et al. (2010b) documented higher scavenging rates in Alberta where anthropogenic influences were considerably higher (e.g., trapping, hunting), and noted an increase in scavenging from summer (0.04 events/week) to winter (0.12 events/week). The fact that we observed essentially twice the scavenging rate reported by Knopff et al. (2010b) is likely due to higher anthropogenic influences in the Black Hills. For instance, the Black Hills contains the highest road density of any western national forest (3.5 km/km^2; USDA Forest Service 1997); thus, contributing to road-killed animals and allowing greater access for dumping carcasses. Additionally, the Black Hills also contains numerous private inholdings and several domestic livestock farms. At one farm, a male cougar visited a landowner’s cattle dumpsite (an area where dead cattle were discarded) on 7 occasions over a roughly 5 month period.

While we attempted to continuously census cougar predation events across all monitoring periods, several factors led to our inability to do so. First, the Black Hills represent a matrix of public and private lands, and while numerous private landowners were amicable to allowing us access to investigate cougar clusters, there were times when access was denied or where landowners could not be contacted. Second, we had 4 subadult cougars (2 males, 2 females) that dispersed outside the Black Hills for various periods of time that made cluster investigation logistically unfeasible. This lack of continuous monitoring was especially important for subadult males as we were only able to investigate 41% (range = 81–14%) of clusters generated. Thus, as others have noted a tendency of models to overestimate subadult kill rates (Anderson and Lindzey 2003, Knopff et al. 2010b), we also believe our estimates (e.g., kills, biomass) for subadult males likely represents an overestimation. In contrast, we investigated 94% (range = 100–75%) of subadult female clusters; consequently, we believe our assessment of feeding habits for this and other demographic classes is a close approximation to true values.

Demographic effects.—Overall, females with cubs, especially older cubs, averaged more ungulate kills than other classes, and subadults and adult males tended to kill less frequently than adult females. The pattern of ungulate kill rates across demographic classes we observed was similar to previous studies using GPS telemetry (e.g., Anderson and Lindzey 2003, Ruth et al. 2010), although the magnitude of this effect was less pronounced than that found in Alberta (Knopff et al. 2010b). The fact that demographic effects were less variable in the Black Hills was likely the result of 2 main factors. First, differences in prey composition of cougar diets across study sites could influence ungulate kill rates. For instance, while deer were the predominant prey item found in both regions, we found deer occurred nearly 20% (83% vs 64%) more in cougar diets in the Black Hills than in Alberta (Knopff et al. 2010b). Additionally, nonungulate species were consumed in higher proportions across all categories in Alberta, but were consumed considerably more by subadults (34.4%) in Alberta than by subadults in the Black Hills (15.0%). In systems where subadults tend to rely more on nonungulate prey we would expect lower ungulate kill rates for this group; thus, increasing variability across demographic classes.

Second, scavenging also could contribute to reduced variability across demographic classes. We observed slightly lower kill rate estimates for females with cubs, especially females with cubs >6 months in age, in comparison to Knopff et al. (2010a). The lower kill rates we observed for females with cubs >6 months in summer was largely influenced by one female that scavenged frequently. This female subsisted primarily by scavenging from several dumpsites where multiple carcasses were present, and had the lowest kill rate of any female in this demographic class (0.23 ungulate kills/week). Excluding this female, our estimate for females with cubs >6 months increased substantially (1.37 ungulate kills/week), and was within range of kill rates observed in Alberta (1.5 ungulate kills/week; Knopff et al. 2010b). It is possible that our reliance on modeling of some non-investigated clusters could have contributed to our lower estimate of kill rate for females with cubs >6mo. If handling time (time spent consuming prey) of prey was significantly lower for this demographic class our model potentially underestimated consumption events. However, as we investigated 98% of all clusters for adult-aged cougars, we believe this was not likely a significant source of variation. Rather, our inability to detect significant differences across demographic classes was a reflection of the slightly higher ungulate kill rates for subadults and the lower rates we observed for females with older cubs. The overall pattern we documented suggests population structure does influence ungulate kill rates although the magnitude of the effect will likely be a function of the region and prey composition of the system being investigated.

Seasonal effects.—Frequency of ungulate kills increased by a factor of 1.3 during summer when cougars primarily targeted juvenile prey (Figure 3). This pattern of increasing kill rates in tandem with the ungulate birth pulse was similar to that observed for brown bears (*Ursus arctos*) in Sweden (Rauset et al. 2012) and cougars in Alberta (Knopff et al. 2010b). Using criteria from Knopff et al. (2010a) for selection of juvenile ungulates when they comprised >55% of cougar diets by month, we found cougars selected for neonates in June and July when they comprised 75% and 82%, respectively, of cougar diets, and continued to comprise a majority of cougar diets through August (51%). Several mechanisms likely underlie this pattern. First, juvenile ungulates have been found to be highly susceptible to large carnivore predation (Testa et al. 2000, Mech and Peterson 2003, Knopff et al. 2010b, Sand et al. 2012); consequently, they should represent a relatively low-risk prey item relative to adults (Lingle et al. 2008). Second, as cougars prey more frequently on juvenile ungulates they would tend to kill more to obtain the same amount of biomass. Our results support other studies documenting strong seasonal variation in large carnivore predation rates (Sand et al. 2008, Knopff et al. 2010b, Rauset et al. 2012), and highlight the biases that can occur if seasonal effects are ignored.

Scavenging.—When accounting for scavenged ungulates, our consumption rates for cougars were distinctly higher during winter when compared to estimates across most demographic classes for cougars in Alberta (Knopff et al. 2010a). While scavenging was ubiquitous throughout the year, we noticed a marked increase starting in December and lasting through April (Figure 3). This initial increase in scavenging coincided with the end of the Black Hills rifle harvest season for deer, which ends in November, and partially explains the initial increase in scavenging we observed. For example, we documented several instances of scavenged deer that seemed to have been butchered and the carcass subsequently deposited along roads within the Black Hills National Forest, often with multiple carcasses present, and some with kill tags still attached. Additionally, we noted at least 7 instances of animals apparently dying from wounds consumed by cougars; in 6 cases bullet wounds were present and one deer carcass contained an arrow head, all of which were consumed during or shortly after the harvest season had ended. Similar shifts in diet to changing anthropogenic food sources have been documented in other large carnivores (e.g., Yirga et al. 2012).

The fact that scavenging continued to be an important part of cougar diets through April cannot solely be explained by this influx of biomass after the deer harvest season. In addition to hunter-related scavenging events, we documented at least 7 vehicle-killed animals being scavenged, 10 instances of multiple, collared cougars consuming the same carcass, 39 scavenge events where multiple carcasses were present (e.g., boneyards, land-owner cattle graveyards), and 3 observations of non-collared cougars consuming prey remains during times a collared animal also was feeding on the carcass. It is our assumption that many of these areas with multiple carcasses present represent dumpsites where road-killed animals were cast off in the national forest. Many of these "dumpsites" seemed to be fairly well established with carcasses routinely placed at the same spot throughout the year. Additionally, most of the dumpsites we identified where in close proximity to interstate exits and Black Hills National Forest boundaries. These sites were prevalent enough that we identified 2 instances of cougars subsisting for a substantial amount of time simply by scavenging. One older female (estimated age at capture 6–7 years) fed on a wounding loss deer, killed one turkey, and visited 4 dumpsites before being harvested 40 days after capture. A second subadult female, which was apparently injured during capture, subsisted for 138 days off several dumpsites from the time of capture on 13 October 2009 until making her first kill on 28 February 2010.

Our results indicate cougars are facultative scavengers, and when provided the opportunity will take full advantage of readily available low-risk food sources. Scavenging in the Black Hills also bolsters the suspicion of others (Bauer et al. 2005, Knopff et al. 2010a, Ruth et al. 2010) that misclassifying scavenging events as kills can significantly influence kill rate estimates. The fact that we were able to investigate clusters an average of 13 days after they were made likely contributed to our ability to document scavenging events. Although it is possible that investigating clusters shortly after formation could potentially alter feeding habits by prematurely displacing cougars from carcasses, we believe this is not likely a significant source of bias as we routinely observed cougars returning to bait sites from which they were captured.

Application of GPS telemetry has been widely applied in recent years to estimate predation rates and prey requirements for a variety of systems (e.g., Ruth et al. 2010, Rauset et al. 2012, Miller et al. 2013). However, when attempting to quantify the impacts of predation, the influence of prey age composition and the proportion of adults among cougar-killed prey are important, as these can be significant factors in determining the per capita impact of predation (Gervasi et al. 2012). Furthermore, as estimates of variance in kill rate are contingent upon accurate assessments of scavenging rates and prey composition, researchers implementing similar techniques should consider timely investigation of cougar feeding events, especially in highly modified landscapes, as an important step to reduce biases in estimating cougar kill rates.

ACKNOWLEDGMENTS

We thank J. Alexander, S. Griffin, B. Juarez, B. Tycz, L. Wiechman, J. Kanta, A. Lindbloom, T. Berdan, J. Schmit, J. Felio, K. Cudmore, M. Gotlob, and T. Solano for assistance with capture and cluster investigation and T. Grovenburg and A. Janke for help with analysis. Thanks also to the Civil Air Patrol pilots L. Becht and G. Kirk for assistance with flight time. Funding for this study was provided by Federal Aid to Wildlife Restoration administered by South Dakota Department of Game, Fish, and Parks (Study No. 7537).

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Figure 1. Map of Black Hills, South Dakota and Wyoming, USA, where cougars were monitored from 2009–2012.

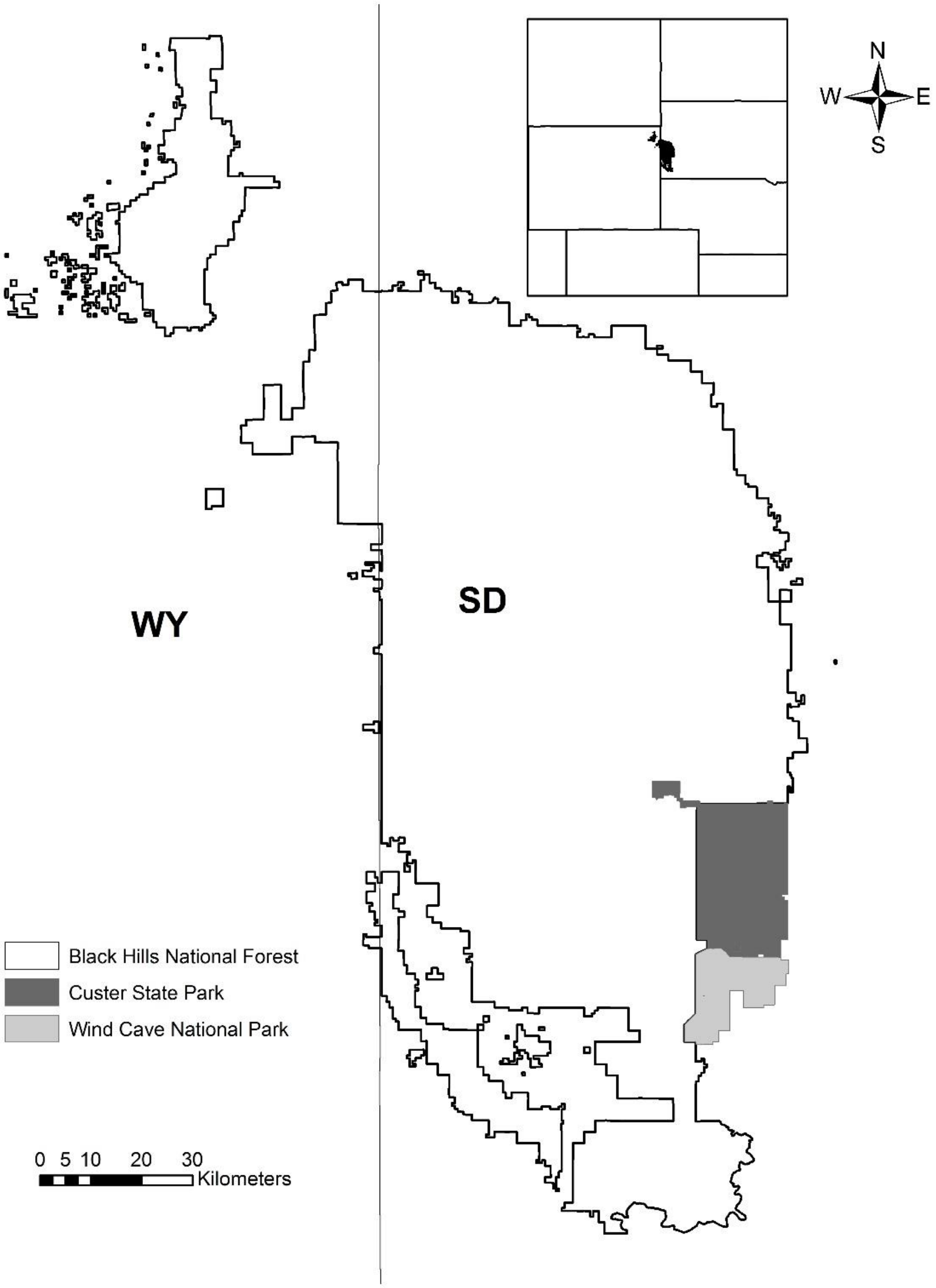


Figure 2. Percentage of ungulate and nonungulate prey items found in cougar (*Puma concolor*) diets in the Black Hills, South Dakota and Wyoming, USA, during 2009–2012.

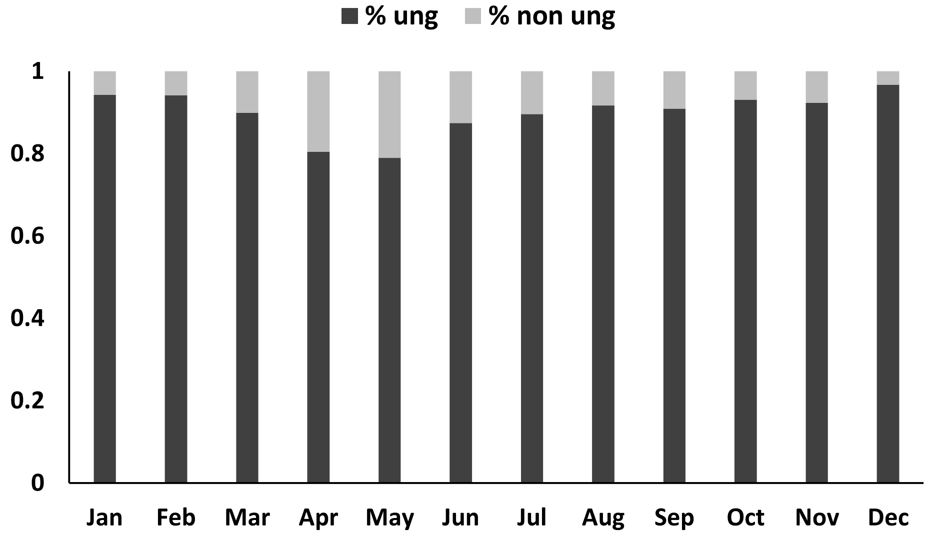


Figure 3. Estimated ungulate kill and consumption (kills + scavenges) rates with associated SEs expressed as a frequency for each demographic class by season (summer = 15 May–15 Nov; winter = 16 Nov–14 May) for 25 cougars (*Puma concolor*) in the Black Hills, South Dakota and Wyoming, USA, from 2010–2012.

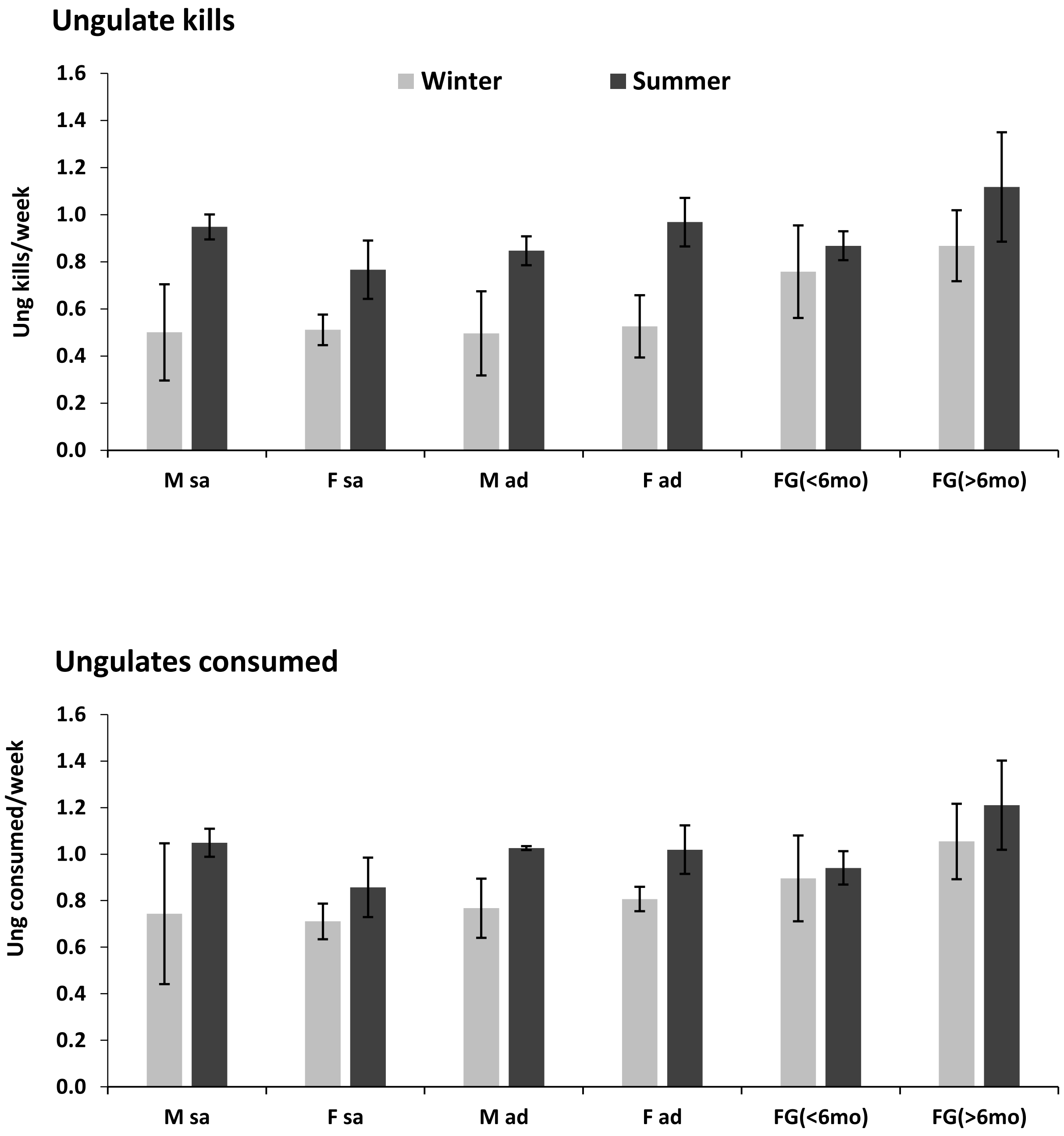


Figure 4. Monthly proportion of juvenile ungulate prey in cougar diets as relative frequency found at cluster sites and average interval in days between ungulate kills (with SEs) and consumptions made each month in the Black Hills, South Dakota and Wyoming, USA, from November 2010 − December 2012. Data pooled from 25 individual cougars (*Puma concolor*) from all sex–age classes.

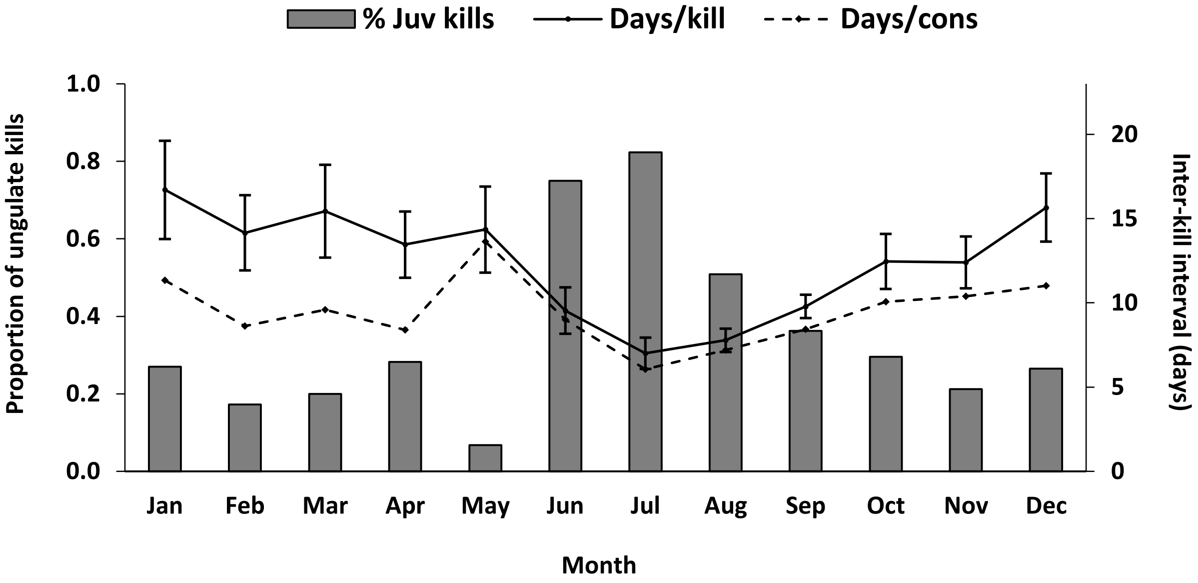
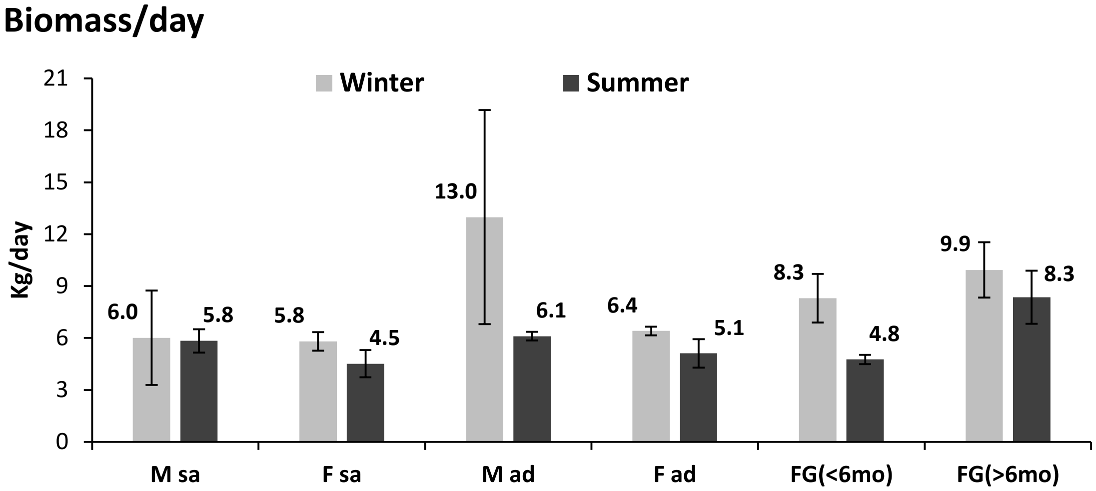
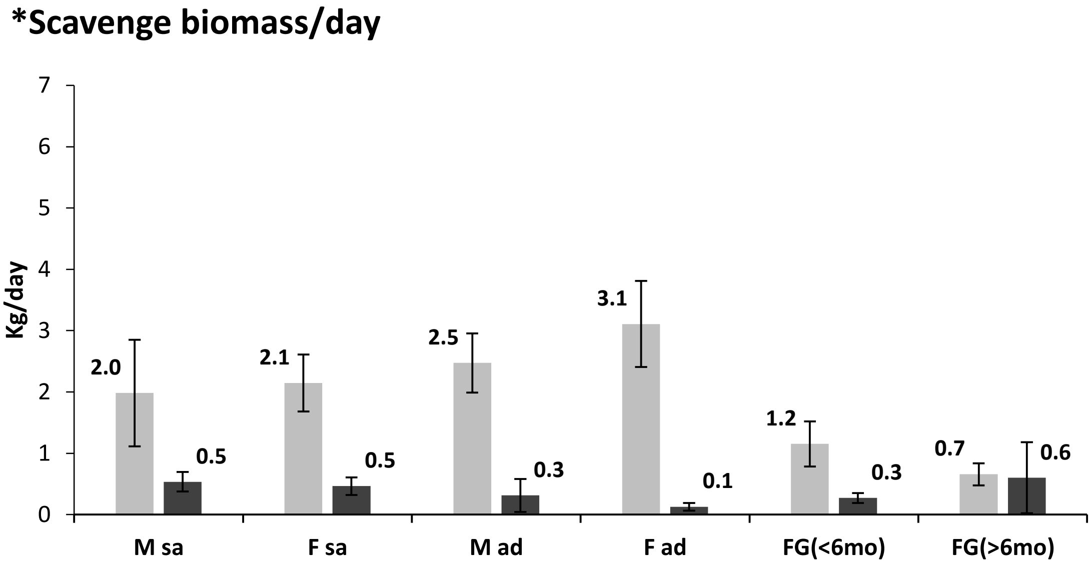


Figure 5. Estimated weekly biomass consumed with associated SEs from all feeding events and from scavenging by demographic class and season (summer = 15 May–15 Nov; winter = 16 Nov–14 May) compiled from 25 cougars (*Puma concolor*) in the Black Hills, South Dakota and Wyoming, USA, from 2010–2012.





*Scale 1/3 of biomass per day.

Table 1. Ungulate weights (kg) used to derive biomass estimates for cougars in the Black Hills, South Dakota and Wyoming, USA, during 2010–2012.

	Species		
Age and sex class	Deer	Elk[a]	Bighorn sheep[b]
Ad M	75[a]	317[a]	104[b]
Ad F weight	61[a]	225[a]	65[b]
Yearling (12–24 months)	50[c]	186[c]	54[c]
YOY[d] (6–12 months)	32[c]	118[c]	34[c]
YOY (3–6 months)	18[c]	65[c]	19[c]
YOY (0–3 months)	8[c]	29[c]	8[c]
Unknown	50[e]	186[e]	54[e]

[a] Weight estimates obtained from Jensen (2000).

[b] Weight estimates obtained from South Dakota State University, unpublished data.

[c] We derived median weight estimates for non-adult age classes using a von Bertalanffy growth equation of the form $M(t) = A[1 - 1/3e^{-K(t-I)}]3$, where $M(t)$ = mass (kg) at age t, A = max. wt. (we used weight of adult female), K = growth rate (we used 0.0042), and I = age at inflection point (we used 140 days).

[d] YOY = young of the year.

[e] For unknowns we used yearling weights.

Table 2. Seasonal comparison by frequency of prey items found for adult female (Ad F), adult male (Ad M), and subadult cougars (*Puma concolor*) in the Black Hills, SD and WY from 2009–2012. Results are presented from 1,506 documented feeding events from 41 cougars.

	Ad F (%)		**Ad M (%)**		**Subadult (%)**	
Prey type	**Summer (n=548)**	**Winter (n=462)**	**Summer (n=101)**	**Winter (n=108)**	**Summer (n=158)**	**Winter (n=129)**
Bighorn sheep	0.18	0.87	0.99	0.93	1.27	0.00
Bison	0.00	0.00	0.99	0.93	0.00	0.00
Coyote	0.55	1.74	0.00	1.85	0.63	2.33
Deer	86.68	85.90	72.28	64.81	77.22	88.37
Domestic	1.10	1.08	1.98	8.33	2.53	0.78
Elk	4.20	3.04	18.81	19.44	1.90	2.33
Lion	0.18	0.00	1.98	0.93	0.00	0.00
Marmot	0.91	0.00	0.00	0.93	2.53	0.00
Misc	0.00	1.08	0.00	0.00	0.00	0.78
Porcupine	0.18	0.22	0.00	0.00	3.80	0.00
Turkey	3.28	2.60	0.00	0.93	6.33	4.65
Unknown	0.73	0.87	2.97	0.00	0.63	0.78
Other	2.01	2.82	0.00	0.93	3.16	0.00
Prey group						
Nonungulate	8.95	9.76	6.93	13.89	19.62	9.30
Small ungulate	86.86	87.42	73.27	65.74	78.48	88.37
Large ungulate	4.20	3.04	19.80	20.37	1.90	2.33
Scavenge	7.30	23.43	18.81	38.89	10.13	27.13

Table 3.—Top 4 multiple logistic regression models for predicting cougar (*Puma concolor*) feeding sites (≥4kg) from non-feeding sites in the Black Hills, South Dakota and Wyoming, USA, 2010–2012.

Model description[a]	n	K^b	AIC^c	ΔAIC^d	w_i^e	Evidence ratio
Hrs + Avgdist + Nightpts + Nightprop + Fidelity	4403	5	2816.590	0.000	0.669	1.000
Hrs + Avgdist + Nightpts + Nightprop + Fidelity + Season	4403	6	2817.998	1.408	0.331	0.495
Hrs[a] + Avgdist + Nightpts + Fidelity	4403	4	2830.789	14.198	0.001	0.001
Days + Avgdist + Nightpts + Nightprop + Fidelity	4403	5	2844.432	27.842	0.000	0.000

[a] Hrs = number of hours between first and last locations in the cluster site, Avgdist = average distance that each location was from cluster centroid, Nightpts = total number of locations within cluster that were obtained between 1800-0600 hrs, Nightprop = number of night locations in cluster divided by total number of locations in cluster, Fidelity = number of locations away from the cluster subtracted from the number of locations over the duration of the cluster, Season = season (summer = 15 May–15 Nov; winter = 16 Nov–14 May) in which cluster was generated, Days = number of 24-hr time periods cougars spent at cluster site.

[b] Number of parameters.

[c] Akaike’s Information Criterion (Burnham and Anderson 2002).

[d] Difference in AIC relative to min AIC.

[e] Akaike wt (Burnham and Anderson 2002).

Table 4.—Beta coefficients from top multiple logistic regression model used to predict cougar (*Puma concolor*) feeding sites from non-feeding sites, and to predict small-prey (<34kg) from large-prey (≥34kg) feeding sites in the Black Hills of South Dakota and Wyoming, USA from 2010–2012.

Pr (kill, no kill)				Pr (large kill, small kill)			
Covariate	Coefficient	SE	*P*-value	Covariate	Coefficient	SE	*P*-value
Constant (β_0)	−3.052	0.142	<0.001	Constant (β_0)	0.705	0.220	0.001
Hours[a]	0.014	0.002	<0.001	Days[f]	0.554	0.062	<0.001
Avg Dist[b]	−0.011	0.002	<0.001	Season[g]	−2.544	0.204	<0.001
Night Points[c]	0.396	0.035	<0.001	Fidelity[e]	0.016	0.006	0.008
Night Proportion[d]	0.795	0.198	<0.001				
Fidelity[e]	0.070	0.009	<0.001				

[a] Hrs = number of hours between first and last locations in the cluster site.
[b] Avgdist = average distance that each location was from cluster centroid.
[c] Nightpts = total number of locations within cluster that were obtained between 1800-0600 hrs.
[d] Nightprop = number of night locations in cluster divided by total number of locations in cluster.
[e] Fidelity = number of locations away from the cluster subtracted from the number of locations over the duration of the cluster.
[f] Days = number of 24-hr time periods cougars spent at cluster site.
[g] Season = season (summer = 15 May–15 Nov; winter = 16 Nov–14 May) in which cluster was generated.

Table 5.—Top 5 multiple logistic regression models for predicting large (≥32kg) from small (<32kg) cougar (*Puma concolor*) feeding sites in the Black Hills, South Dakota and Wyoming, USA, 2010–2012.

Model description[a]	n	K[b]	*AIC*[c]	*ΔAIC*[d]	w_i[e]	Evidence ratio
Days + Season + Fidelity	4403	3	906.183	0.000	0.665	1.000
Days + Radius + Nightpts + Nightprop + Season + Fidelity	4403	6	908.378	2.195	0.222	0.334
Days + Season	4403	2	911.111	4.928	0.057	0.085
Days + Avgdist + Nightpts + Nightprop + Season + Fidelity	4403	6	911.152	4.969	0.055	0.083
Hrs + Avgdist + Nightpts + Nightprop + Season + Fidelity	4403	6	918.171	11.988	0.002	0.002

[a] Days = number of 24-hr time periods cougars spent at cluster site, Season = season (summer = 15 May–15 Nov; winter = 16 Nov–14 May) in which cluster was generated, Fidelity = number of locations away from the cluster subtracted from the number of locations over the duration of the cluster, Radius = difference between cluster centroid and the furthest away location within the cluster. Nightpts = total number of locations within cluster that were obtained between 1800-0600 hrs, Nightprop = number of night locations in cluster divided by total number of locations in cluster, Avgdist = average distance that each location was from cluster centroid, Hrs = number of hours between first and last locations in the cluster site.

[b] Number of parameters.

[c] Akaike's Information Criterion (Burnham and Anderson 2002).

[d] Difference in AIC relative to min AIC.

[e] Akaike wt (Burnham and Anderson 2002).

CHAPTER 2: DO COUGARS SELECT FOR CWD-INFECTED ELK?

This chapter is being prepared for submission in the Journal of Wildlife Diseases and was coauthored by Jonathan A. Jenks, Duane C. Weber, and Steven L. Griffin.

Abstract:

Behavioral modifications from diseases, such as chronic wasting disease (CWD), could increase susceptibility of infected individuals to predation. As part of targeted surveillance to identify CWD-infected elk (*Cervus elaphus*) in Wind Cave National Park (WCNP), we report prevalence of CWD infected elk in the diets of 2 (1 male; 1 female) cougars (*Puma concolor*). From December 2011 to April 2012, we located kill sites using cluster analysis of GPS-locations and collected elk tissue samples from 14 cougar-killed elk (7 male, 7 female) to test for CWD. Of the 14 cougar-killed elk sampled, 7 were taken by both the male and female cougars, respectively. The male cougar accounted for 5 (55.6%) CWD-positive elk kills while the female killed 4 (44.4%) infected elk. Overall proportion of cougar-killed elk that were CWD positive was 64% (95% CI = 50.3–78.3%). The proportion of CWD-positive elk killed by cougars was higher than other regional CWD prevalence estimates (4.9–12.9%; CI = 3.0–19.1%) and higher than adjacent hunting units in the Black Hills (2.8%; 95% CI = 2.0–3.2%). Though speculative, it is possible that CWD infection in elk increased predation risk.

KEY WORDS *Cervus elaphus*, chronic wasting disease, cougar, CWD, elk, predation, *Puma concolor*, vulnerability.

INTRODUCTION

Large terrestrial carnivores often differentially select prey items based on species, size, age or sex, or a character that implies a physically substandard individual. Several hypotheses have been proposed to explain prey selection such as search images (Taylor 1976), energetic benefits and costs (Griffiths 1975, Creel and Creel 1995), or prey vulnerability (Curio 1976, Temple 1987). Yet, despite widespread acceptance that sick or diseased prey should be selected at higher than expected proportions than healthy prey, evidence for this phenomenon has been mixed (Barber-Meyer et al. 2007, Krumm et al. 2009).

In many areas across North America, cervid populations are being affected by chronic wasting disease (CWD), a fatal prion disease of substantial management concern (Williams et al. 2002). Despite widespread application of harvest or selective culling, the disease has continued to spread (Conner et al. 2007). Theoretically, targeted predation of infected cervids by large terrestrial carnivores, such as cougars (*Puma concolor*) or wolves (*Canis lupus*), may be one of the most effective methods of mitigating the effects from, and controlling the spread of, this fatal disease (Wild et al. 2011). Clinical signs of CWD include reduced physical condition, altered behavior, incoordination, and reduced alertness (Williams and Young 1980). Such behavioral modifications would seem to increase susceptibility of infected individuals to predation, and indeed this has been documented for cougars preying on mule deer (*Odocoileus hemionus*; Miller et al. 2008, Krumm et al. 2009) in Colorado. However, disease pathogenesis is different in CWD-infected elk (*Cervus elaphus*) compared with deer (Williams et al. 2002) and elk may not exhibit this same pattern of vulnerability to cougars. As part of a larger study evaluating cougar predation rates in the Black Hills, and as part of targeted surveillance to identify CWD-infected elk in Wind Cave National Park (WCNP; National Park Service 2009), we report prevalence of CWD infected elk in 2 cougar diets.

MATERIALS AND METHODS

Our study encompassed an area of approximately 15,000 ha in the southeastern portion of the Black Hills (South Dakota, USA) and included Wind Cave National Park

(11,450 ha) and a section of the Black Hills National Forest just west of the park. We captured cougars primarily with the aid of hounds and immobilized them with a mixture of telazol (1.0 mg/kg) and xylazine (0.2 mg/kg; Kreeger 2007) via dart rifle (Dan-Inject, Børkop, Denmark, EU). We fitted animals with Global Positioning System (GPS) radiocollars (ATS G2110E, Isanti, MN) programmed to obtain locations at 3-hour intervals. Upon completion of handling, immobilized cougars were administered 0.125 mg/kg yohimbine to reverse xylazine, released on site, and monitored from a distance to ensure safe recovery. All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

To identify possible predation sites, we downloaded GPS locations weekly and used a Python script (Knopff et al. 2009) to classify cluster locations where any combination of ≥ 3 GPS locations occurring within 200 m and 6 days of each other was classified as a cluster (i.e., potential kill site). We visited clusters of GPS locations as soon as possible thereafter to determine possible predation events by programming geometric centers and all GPS locations associated with clusters into handheld GPS units (Garmin International, Olathe, KS, USA). We conducted 30-m grid searches by walking in 5-10 m wide zig-zag patterns (depending on visibility) around all GPS locations as well as the cluster center. We identified prey species by anatomical, skeletal, and pelage characteristics and assigned them as predation or scavenging (i.e., carcass consumed but not killed by cougar) events provided there was evidence the cougar had killed or fed on the carcass. We assigned predation in cases where the carcass age matched the age of the cluster or if there were obvious bite marks or antemortem hemorrhages on the neck or nose of the carcass or if there were signs of a chase sequence (e.g., in the snow) or struggle. If the intact head was available, we collected a sample of brain tissue at the obex for immunohistochemical CWD testing (Spraker et al. 2004); testing was conducted by the Colorado State University Diagnostic Veterinary Laboratory, Ft. Collins, Colorado, USA. We also compared average age of CWD-positive cougar-killed elk to elk where CWD was not detected using an analysis of variance (ANOVA; SYSTAT 11.0, Systat Software Inc., Chicago, Illinois, USA).

RESULTS

Of 41 cougars radiocollared from 2009–2012, 2 adult cougars (1 male; 1 female) used portions of WCNP and thus, were included in our analyses. From December 2011 to June 2012, we found prey remains at 31 cluster sites in WCNP. Prey items consisted of deer (*Odocoileus sp.*), turkey (*Meleagris gallopavo*), coyote (*Canis latrans*), one scavenged bison (*Bison bison*), and 20 elk carcasses. In all, there were 14 cougar-killed elk (7 male, 7 female) with suitable tissue available to test for CWD. Of the remaining 6 elk kills that were not tested for CWD, 2 were elk calves. One radiocollared cow elk was killed 2.7 km west of WCNP; however, because she was known to reside predominately in the park, we included her in our analyses. Average age of cougar-killed elk was 9.8 yrs (SD = 5.6 yrs) and we found no significant difference ($F_{1,12} = 1.229$, $P = 0.289$) between CWD-positive cougar-killed elk (8.6 yrs; SD = 5.9 yrs) and elk where CWD was not detected (12.0 yrs; SD = 4.8 yrs). Of the 14 cougar-killed elk sampled, 7 were taken by both the male and female cougars, respectively. The male cougar accounted for 5 (55.6%) CWD-positive elk kills while the female killed 4 (44.4%) infected elk. Overall proportion of cougar-killed elk that were CWD positive was 64% (95% CI = 50.3–78.3%).

DISCUSSION

The proportion of CWD positive elk killed by cougars in our study area was relatively high given prevalence rates of CWD reported in elk populations in North America. For example, Monello et al. (2013) documented prevalence of 12.9% (95% CI = 8.0–19.1%) for elk in Rocky Mountain National Park using rectal biopsies. In Wyoming, CWD prevalence in elk since 1980 was estimated at 4.9% (95% CI = 3.0-6.8%) overall, but has ranged as high as 10.6% (2009) based on hunter harvest data (H. Edwards, Wyoming Game and Fish Department, Cheyene, Wyoming, personal communication). Additionally, hunter-harvest data (*n* = 517) from 2008–2011 from 3 hunting units adjacent to WCNP in the Black Hills indicated that CWD prevalence rate for elk >1 year of age was 2.8% (95% CI = 2.0–3.2%; South Dakota Department of Game, Fish, and Parks unpublished data), which was similar to elk mortality from CWD in WCNP from 2005–2009 (0.034; SE = 0.012; Sargeant et al. 2011).

Differential selection for injured or substandard prey has been well documented for coursing predators like coyotes (Gese and Grothe 1995), wolves (Mech 1970, Husseman et al. 2003), and African wild dogs (*Lycaon pictus*; Fitzgibbon and Fanshawe 1989, Pole et al. 2004); yet studies examining this phenomenon in cougars has been variable (Ross and Jalkotzy 1996, O’Gara and Harris 1988, Pierce et al. 2000). Recently, Miller et al. (2008) documented that cougars were nearly 4 times as likely to kill CWD-infected mule deer as uninfected deer, though most deer showed no obvious signs of the disease (i.e., were preclinical). Although cougars readily kill healthy deer as illustrated from numerous diet studies (Pierce et al. 2000, Cooley et al. 2009, Knopff et al. 2010), infection from CWD or poor nutritional state could result in a higher predation risk to larger prey such as moose (*Alces americanus*) and elk (Ross and Jalkotzy 1996).

The observed pattern of predation may have resulted from individual cougar specialization as opposed to population-level specialization. Individual cougars in multiprey systems have been shown to specialize on bighorn sheep (*Ovis canadensis*; Ross et al. 1997), feral horse (*Equus caballus*; Knopff and Boyce 2007), moose (Ross and Jalkotzy 1996), mule deer (Robinson et al. 2002), and huemul (*Hippocamelus bisulcus*; Elbroch and Wittmer 2013) and have been implicated in the decline of small and isolated prey populations of bighorn sheep (Rominger et al. 2005) and mountain caribou (*Rangifer tarrandus*; Kinley and Apps 2001). Both radiocollared cougars in our study area were older individuals; the male's estimated age was 10+ years old at time of capture and the female was estimated at 7−8 years old. Thus, they may have had more experience and were more adept at distinguishing CWD-infected elk from healthy individuals. Unfortunately WCNP does not collect standardized data for CWD prevalence, and, though speculative, it is possible that CWD infection in elk increased predation risk.

ACKNOWLEDGEMENTS

This project was funded by Federal Aid to Wildlife Restoration (Study No. 7537) administered through South Dakota Game, Fish and Parks. We thank J. Alexander, J. Broecher, L. Meduna, L. Wiechman, D. Roddy, G Schroeder, and B. Juarez for help with capturing and radio collaring cougars, and for help with data collection activities. K. Schuler and K. Robling provided helpful comments on previous drafts of our manuscript.

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CHAPTER 3: TECHNIQUES FOR CAPTURING BIGHORN SHEEP LAMBS

This chapter is being prepared for submission in the Wildlife Society Bulletin and was coauthored by Daniel P. Walsh, Elise J. Goldstein, Zachary D. Parsons, Rebekah C. Karsch, Julie R. Stiver, James W. Cain, Kenneth J. Raedeke, and Jonathan A. Jenks.

KEY WORDS bighorn sheep, capture, helicopter, lambs, neonates, netgun, *Ovis canadensis*, vaginal implant transmitter.

ABSTRACT Low lamb recruitment is a major challenge facing managers attempting to mitigate the decline of bighorn sheep (*Ovis canadensis*), and investigations into the underlying mechanisms are limited because of the inability to readily capture and monitor bighorn sheep lambs. We evaluated 4 capture techniques for bighorn sheep lambs: 1) hand-capture of lambs from radiocollared females fitted with vaginal implant transmitters (VITs), 2) hand–capture of lambs of intensively monitored radiocollared females, 3) helicopter net-gunning, and 4) hand-capture of lambs from helicopters. During 2010–2012, we successfully captured 90% of lambs from females that retained VITs to ≤1 day of parturition, although we noted differences in capture rates between an area of high road density in the Black Hills (92%–100%) and less accessible areas of New Mexico (71%), USA. Retention of VITs was 78% with pre-partum expulsion the main cause of failure. We were less likely to capture lambs from females that expelled VITs ≥1 day of parturition (range = 80–83%) or females that were collared without VITs (range = 60–78%). We used helicopter net–gunning at several sites in 1999, 2001–2002, and 2011, and it proved a useful technique; however, at one site, attempts to capture lambs led to lamb predation by golden eagles (*Aquila chrysaetos*). We attempted helicopter hand–captures at one site in 1999, and they also were successful in certain circumstances and avoided risk of physical trauma from net-gunning; however, application was limited. In areas of low accessibility or if personnel lack the ability to monitor females and/or VITs for extended periods, helicopter capture may provide a viable option for lamb capture.

INTRODUCTION

During the late 19th and early 20th centuries, bighorn sheep (*Ovis canadensis*) populations declined dramatically. These declines have been attributed to a wide array of factors including diseases, unregulated hunting, loss of habitat, and competition with other ungulate species (Buechner 1960, Capp 1968, Spraker et al. 1984, Beecham et al. 2007, Wehausen et al. 2011). Over the years, trap and transplant efforts were successful in increasing the overall number of bighorn sheep throughout the Western North America, but many of the herds remain small and isolated (Douglas and Leslie 1999, Beecham et al. 2007). Additionally, periodic pneumonia epizootics have occurred in many herds, resulting in significant losses to populations. These die-offs are often followed by years of depressed lamb recruitment, which limits population recovery (Woodard et al. 1974, Spraker et al. 1984, Gross et al. 2000, Monello et al. 2001, Cassirer and Sinclair 2007). Identifying the underlying cause(s) for this poor recruitment is one of the major challenges facing bighorn sheep managers.

One of the difficulties inherent in understanding the causal mechanisms associated with poor recruitment and developing effective mitigating strategies is the inability to readily capture and monitor bighorn sheep lambs. Bighorn lamb capture is problematic due to the rugged and inaccessible terrain typically used for lambing and rearing of young (Shackleton et al. 1999). To date, lambs have been successfully captured in only a few studies. In Alberta, researchers used corral traps baited with salt to attract and capture females and lambs throughout the year (Samson et al. 1987, Festa-Bianchet 1988, Portier et al. 1998), and Scotton and Pletscher (1998) employed helicopter techniques to capture neonatal Dall sheep (*Ovis dalli*). However, most researchers examining lamb survival and juvenile recruitment have relied on intensive monitoring of marked females to determine if lambs were at-heel or lamb:female ratios in the herd (Woodard et al. 1974, Wehausen et al. 1987, Cook et al. 1990, Cassirer and Sinclair 2007, Sirochman et al. 2012). The latter is particularly problematic because it may inaccurately reflect lamb survival resulting from the confounding effects of detection probability, female mortality, changing group associations, and lack of knowledge of female age-structure (Festa-Bianchet 1992, Jorgenson 1992, Bodie et al. 1995, Festa-Bianchet et al. 1996, Shackleton et al. 1999). Reliance on these metrics severely limits the identification of the timing and causes of lamb mortality.

The difficulty in capturing lambs also limits the ability of managers to assess the effectiveness of various efforts, such as the administration of antibiotics or vaccines, aimed at reducing the impacts of periodic pneumonia epizootics and improving lamb survival (Mcadoo et al. 2010, Wolfe et al. 2010, Sirochman et al. 2012). As a consequence, effective methods of capturing bighorn lambs are needed to study and devise improved management strategies for recovering bighorn sheep populations negatively impacted by poor lamb survival.

Here we describe and compare 4 techniques used to capture bighorn sheep lambs that have been employed in several regions across western North America. First, we examined the use of vaginal implant transmitters (VITs) in radiocollared females in combination with intensive monitoring and hand capturing of neonatal lambs. This technique has been successfully used to capture a variety of neonates of other ungulate species because the VIT is designed to remain with the female until parturition, at which time it exits the female and the emits a “deployed” signal (Carstensen et al. 2003, Johnson et al. 2006, Bishop et al. 2007, Bishop et al. 2011). Secondly, we examined the utility of hand-capture of neonatal lambs born to radiocollared females that were intensively monitored. Third, we evaluated a helicopter net-gunning method (Schemnitz 2005) to capture 4–6 week old lambs in several regions. Lastly, we investigated the use of hand-capture of lambs using a helicopter. We detail the strengths and limitations of each of these methods and provide an estimate of associated costs with each technique.

STUDY AREA

Neonatal Capture

New Mexico: Peloncillo Mountains.— This study area for this project was located in the central Peloncillos in the southwestern corner of New Mexico, USA, and contained approximately 8,300 ha of bighorn sheep habitat. Peak elevations ranged from 1,512 to 2,112 m above mean sea level (msl). Sandoval (1982) described 7 land cover types in the Peloncillo Mountains: grass-desert scrub (40%), mixed shrub/grass (27%), desert shrub (12%), grassland (11%), pinyon-juniper (*Pinus edulis and Juniperus* spp.*;* 7%), oak (*Quercus* spp.; 3%), and mountain scrub (<1%). Climate in the Peloncillos was characterized by a monsoon precipitation cycle, with an average precipitation of 5 cm of rain per month during the July to September monsoon season. Average annual precipitation was 28 cm. Temperatures ranged from an average maximum temperature of 35° C in June to an average minimum of -3° C in December. Climate values were based on data collected at the Animas, New Mexico weather station from 1923 to 2012 (Western Regional Climate Center 2013).

South Dakota: East-Central Black Hills.—The Black Hills are located in southwestern South Dakota and eastern Wyoming, USA. The study area for this project was located in the east-central portion of the Black Hills with bighorn sheep habitat encompassing an area of approximately 26,000 ha. Elevations ranged from 973 to 2,202 m above msl. Ponderosa pine (*Pinus ponderosa*) forest comprised 83% of the landscape (USGS Gap Analysis Program 2004). Mixed grass prairie (5%), riparian (4%) , aspen (*Populus tremuloides*)-mixed-conifer forest (3%), and developed open space (2%) were other major land-cover types present in our study area (USGS Gap Analysis Program 2013). Average annual precipitation was 53 cm. Mean temperatures ranged from a maximum of 28° C in July to a minimum of -10° C in January. Climate values were based on data collected at the Hill City, South Dakota weather station from 1981 to 2010 (National Oceanic and Atmospheric Administration [NOAA] 2013).

Helicopter Capture

Colorado: Pikes Peak.—The Pikes Peak study area was located west of Colorado Springs, Colorado, USA, and contains approximately 25,000 ha of bighorn sheep habitat. Elevations range from approximately 2,500 m to 4,300 m above msl. Bear and Jones (1973) provide a detailed description of the range of this herd.

Major land-cover types within this bighorn sheep range were ponderosa pine forest (33%), spruce-fir forest (29%), aspen stands (16%), mixed tundra (15%), and subalpine meadows (4%; USGS Gap Analysis Program 2013). Average annual total precipitation for the region was 60 cm. Average annual temperatures for the region ranged from a maximum of 22˚ C in July to a minimum of −14˚ C in January. Climate values were based on data collected at the Ruxton Park, Colorado weather station from 1959 to 2012 (Western Regional Climate Center 2013).

New Mexico: Fra Cristobal Mountains.—The Fra Cristobal Mountains are located in South-central New Mexico, USA. The range contains approximately 12,000 ha of bighorn sheep habitat, and elevations range from 1,400 to 2,109 m above msl. The study area was dominated by Apacherian-Chihuahuan semi-desert grassland and steppe (84%), the Chihuahuan creosotebush (*Larrea tridentata*), mixed desert and thorn scrub (10%), and Madrean pinyon-juniper woodland (3%) land cover types (USGS Gap Analysis Program 2013). Climate in the Fra Cristobal Mountains is characterized by a monsoon cycle with an average precipitation of 4 cm per month falling in the wettest months of July and August. Average annual precipitation was 24 cm. Mean temperatures ranged from a maximum of 34 º C in July to −2 º C in January. Climate values were based on data collected at Elephant Butte Dam, New Mexico from 1908 to 2012 (Western Regional Climate Center 2013).

South Dakota: Custer State Park.—In Custer State Park, South Dakota, USA, the 2 bighorn sheep sub-herds (East End and West End) resided in the approximately 430-ha French Creek Canyon. The elevation throughout the study area ranges from 1,127 to 1,524 m above msl. Major land cover types of this bighorn sheep range were ponderosa pine forest (80%), deciduous trees (11%) and grasslands (5%; USGS Gap Analysis Program 2013) interspersed with steep cliffs. Average annual precipitation was 50 cm. Average annual temperatures ranged from an average maximum of 27˚ C in July to a minimum of −9.4˚ C in December. Climate values were based on data collected at the Custer, South Dakota weather station from 1981 to 2010 (NOAA 2013).

METHODS

Neonatal Capture

Female capture.–At both sites in New Mexico, adult females were captured via net-gunning during winter months, while in the East-central Black Hills of South Dakota we captured adult females using a drop-net baited with weed-free alfalfa hay or using chemical immobilization (BAM: 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine) via dart rifle (Dan-Inject, Børkop, Denmark, EU).

VIT deployment.–In the Peloncillos and the Black Hills, we used PETTMPF2 or M3930 VITs manufactured by Advanced Telemetry Systems (ATS; Isanti, MN) with a redesigned wing system and antenna length of 6 cm (Bishop et al. 2011). Prior to VIT deployment, pregnancy status of females was checked via ultrasonography at the time of capture. Females that were not pregnant or not checked for pregnancy at the time of capture were not fitted with VITs. Methods of VIT deployment followed Bishop et al. (2011). In addition to receiving VITs, all females were fitted with very high frequency (VHF) collars (ATS) that were uniquely marked to facilitate individual identification.

Lamb capture using females with VITs.– Prior to the lambing season, radiocollared females were monitored 1–3 times/week from the ground using hand-held directional antennas (Telonics, Inc., Mesa, AZ), or from a Cessna 182 (Cessna Aircraft Co., Wichita, KS) airplane. We listened for possible VIT expulsion each time we located females. When we detected an expelled VIT prior to the lambing season, we retrieved it using ground telemetry and ascertained if the female had aborted the fetus on-site, and estimated date of expulsion as the mean date between the first mortality signal and the last active signal received.

During the lambing season in the Peloncillo Mountains of New Mexico, females with VITs were checked each morning and evening to account for daytime temperatures sufficiently warm to affect the temperature sensor in the VIT, and cause its pulse rate to return to an “undeployed mode”. When the expulsion of a VIT was indicated and the precise event transmitter (PET; a component of the PETTMPF2 model VITs that emits a series of single or double beeps that can be used to calculate the amount of time the VIT has been expelled to within 0.5 hours) indicated that a lamb was <3 hours old, we waited until it was >3 hours old to avoid interrupting mother-young bonding, which could result in abandonment (Livezey 1990). When the PET indicated that the lamb was >3 hours old, we immediately attempted to visually locate the associated female through a spotting scope (Nikon Corporation, Tokyo, Japan) from a distance that would minimize disturbance. We observed the female’s behavior and visually searched for a lamb in her vicinity. If a lamb was not seen, we continued to focus our efforts on the location of the female. One person monitored the female (and lamb if detected) through the spotting scope while a 2-person team approached the female and/or lamb. The team used telemetry equipment and guidance from the person with the spotting scope to locate the female and/or lamb.

During the lambing season in the Black Hills of South Dakota, we employed a similar protocol. Females with VITs were checked once daily during the lambing season to determine if the VIT had been expelled. If the radio signal indicated a VIT had been expelled and terrain permitted, personnel would use telemetry to home in on the expelled VIT on foot and retrieve it.

At both study sites if the VIT was located at a birth site and the lamb was present, we attempted to hand-capture it. If the dam had moved away from the VIT or if a lamb was not located in the vicinity of the female, we searched the area surrounding the female's location and the VIT location, and if a lamb was located we attempted capture. In the event the VIT was prematurely expelled based on a lack of evidence of birthing activities at the VIT site and observation of the female without a lamb, we intensively monitored the individual female's behavior. If we subsequently established the female had lambed, we attempted to capture the lamb once it was observed.

Lamb capture using females without VITs.–In the Fra Cristobal Mountains of New Mexico and the Black Hills of South Dakota, we monitored radiocollared females without VITs on a near daily basis for movement patterns indicative of parturition and presence of newborn lambs via radio-telemetry and visual observation from a distance. When we detected a newborn lamb, we assessed its degree of mobility by observations of ambulatory movements. We attempted hand-capture from the ground if the lamb appeared sufficiently immobile and the terrain was accessible. We waited until the animals bedded down before attempting capture. Solitary female-lamb pairs were preferred; however, we also attempted captures of lambs associated with small groups of females. Once animals bedded down, we noted the location of the animals in relation to topography and notable landmarks. Ideally, while attempting to avoid detection (e.g., by climbing up the opposite side of a ridge), 2 people approached the animals from above. When detection by the animals was imminent, we rapidly approached the animals' location causing the female to flee, and the lamb would hide or attempt to flee. We would conduct a short search or chase to capture the lamb.

Lamb handling and marking.–We physically restrained each captured lamb, blindfolded, and fitted the lamb with an expandable, 62-g VHF collar equipped with a 6-hr mortality switch (Model M4210; ATS) or an expandable, 83-g VHF collar equipped with a 2-hr mortality switch (MOD-305; Telonics Inc.). Additionally, sex, age, and weight data were collected from captured lambs. We monitored lamb survival after capture using telemetry to determine if lambs may have died or were abandoned as a result of our capture activities. We strived to keep handling time to <5 minutes.

Helicopter Capture

Net-gun.—We used 3 companies for helicopter capture work. Hawkins & Powers Aviation (Greybull, WY) captured lambs in Custer State Park and the Fra Cristobals Mountains. Helicopters by Oz (Marysvale, UT) also captured lambs in the Fra Cristobal Mountains, and Quiksilver Air, Inc. (Fairbanks, AK) attempted captures at Pikes Peak. The capture companies used a MD500D helicopter (MD Helicopters, Inc., Mesa, AZ) in South Dakota, and a MDHC500D in Colorado. In the Fra Cristobal Mountains, Helicopters by Oz used a Hughes 500 helicopter (Hughes Helicopters, Culver City, CA) and Hawkins & Powers Aviation used a Bell 206 JetRanger (Bell Helicopter Textron, Hurst, TX).

In Colorado, to minimize helicopter search time, we used radio-telemetry to locate groups of radiocollared females (n = 23), collared as part of a separate study. During capture activities in all study areas, the helicopter would approach a group of bighorn sheep containing lambs and gently haze animals into terrain suitable for capture. The gunner would then attempt to fire a 4 X 4-m nylon net with 10-cm mesh over the targeted lamb using either a hand-held or skid-mounted net-gun (CODA Enterprises, Inc., Mesa, AZ). Only 1 lamb was targeted, and females and lambs were not captured together. If a lamb was successfully netted, the helicopter would move >500 m away and land; capture personnel would immediately restrain the lamb via hobbles, collect biological samples of interest, and radiocollar the lamb using either a 68-g expandable neonate collar (M4210; ATS; Pikes Peak) or a 83-g expandable, breakaway MOD-305 transmitter on a CB-6 collar (Telonics Inc.; Custer State Park; Fra Cristobal Mountains). After a maximum of 5 minutes of hazing, we abandoned capture efforts of bighorn sheep that could not be hazed from or that moved into rugged terrain unsuitable for capture. We monitored all collared lambs post-capture to determine abandonment or capture-related mortality rates.

Hand-capture.—We used Helicopters by Oz with a Hughes 500 helicopter for all helicopter hand-captures. In addition to the pilot, 2 people were aboard the helicopter with doors removed. Radio contact was maintained between the pilot and capture crews on the ground. Ground crews attempted to visually locate female and lamb groups prior to capture. The helicopter was equipped with antennas and a receiver to locate radiocollared females known to have lambs. We attempted to gently haze sheep into accessible terrain, and limited our hazing and chase time to $\leq$5 minutes.

If a lamb became separated from a group and tried to hide against a sheer rock face or boulder, the capture crew exited the helicopter one at a time by stepping onto the skid, and jumped or stepped to the ground. The capture crew approached the lamb from 5–10 m in front of the cliff from different angles. When the lamb tried to flee, handlers attempted to manually restrain it. If a lamb was successfully captured, the helicopter would move >500 m away and land, and the lamb would be handled as described previously.

Animal handling was approved by the Institutional Animal Care and Use Committees at South Dakota State, New Mexico State Universities, Colorado Parks and

Wildlife and University of Washington (SDSU, Approval number 09-019A; NMSU, Approval number 2011-026, CPW, ACUC-04-2011; UW, ACUC 3165-01).

Cost Estimates

We estimated the yearly and average costs to capture and radiocollar a lamb in each of 2 years using our various lamb capture techniques. We recognize that capture costs will vary based on individual location and logistics. Our intent is for these estimates to serve as a basis of comparison only, and provide managers with a useful example of important cost considerations. We made several assumptions to permit cost estimation. First, we assumed annual female capture was necessary when capturing lambs from females fitted with VITs, but only necessary for the first year when capturing lambs from intensively monitored radiocollared females. For techniques requiring female capture, we used average capture success and survival rates of radiocollared females observed in our study to determine the average number of female captures needed to permit lamb capture during both years. Lastly, we assumed, if radiocollared females were not present in the study area, location of lambing areas were known well enough such that minimal time was spent searching for females with lambs. We estimated the costs of darting, drop-netting, and helicopter net-gunning females as follows: for darting females, we estimated the cost as $180/female representing mainly the cost of capture drugs (BAM) with the assumption that on average 1.5 darts are required to capture 1 female, and assumed the use of agency personnel; for drop-netting, we estimated the cost as $125/female which covers the cost of 10 technicians/day to conduct the capture (costs may be less if agency personnel were used in lieu of technicians); for helicopter net-gunning we estimated a cost of $700/female for helicopter time. For all capture techniques discussed above, there is an additional cost of approximately $225 for each VIT and for each radiocollar.

For capturing lambs, we estimated a cost of $700/lamb for helicopter net-gunning, and a cost of $900/lamb for helicopter hand-capture. The latter cost was higher because of the greater likelihood of unsuccessful capture attempts with helicopter hand-capture of lambs. Lastly, to estimate and compare the cost of monitoring radiocollared females fitted with VITs versus females without VITs and lacking detailed monitoring effort estimates, we used estimates provided by Bishop et al. (2007) for fawn capture. They found that 7 person-hours/captured fawn were required for does fitted with VITs versus 42 person-hours per fawn for females with failed VITs and females without VITs. These estimates seemed to provide a reasonable minimum estimate for lamb capture and provided a basis for comparison. We combined these effort estimates with an average cost of $20/hour (e.g., technician, vehicle mileage) to provide the total cost of monitoring radiocollared females. We did not include the salary of agency personnel for any of the capture techniques, but included a cost of $225/lamb for lamb radiocollars for all techniques.

RESULTS

Neonatal Capture

New Mexico: Peloncillo Mountains.—In early November 2011, 20 pregnant adult females were collared and fitted with VITs and translocated to the Peloncillo Mountains from the Fra Cristobal Mountains and New Mexico Department of Game and Fish’s Red Rock Captive Breeding Facility. Three females died prior to parturition; however, 1 of these females had prematurely expelled her VIT. Of the 17 females that survived to parturition, all produced viable lambs and 94% (*n* = 16) expelled their VITs ≤ 1 day of parturition. We captured lambs from 71% (*n* = 12) of the 17 surviving females with VITs, and observed no capture-related abandonment.

South Dakota: East-Central Black Hills.—We documented 96 (28 in 2010, 33 in 2011, and 35 in 2012) lambing events of collared females from May 2010 to June 2012 (Table 1). From February 2010 to March 2012 we deployed 62 VITs in collared females (Table 1). However, 2 females with VITs died shortly after capture for reasons apparently not associated with the transmitter or capture in 2011, and 1 additional female with a VIT was not monitored due to logistical error in 2012; thus, all 3 were censored from further VIT analyses. Number of females fitted with VITs as a percentage of total lambing events observed ranged from 82% (*n* = 23) in 2010 to 49% (*n* = 17) in 2012 (average = 62%, *n* = 51). Number of females retaining VITs to ≤ 1 day of parturition was 43 (73%, SD = 1.9%, range = 71%, [*n* = 12] – 74% [*n* = 17]; Table 2). When VITs were expelled prior to parturition, they were most often lost approximately 8 weeks post-insertion (range = 5 to 16 weeks, SD = 3 weeks).

Percentage of lambs captured (or where known fate was obtained; e.g., stillborns or lambs that died prior to collaring) from all radiocollared females, regardless of VIT status, ranged from 86% (24 of 28) in 2010 to 82% (27 of 33) in 2011 (Table 2). We captured slightly more lambs from females that retained VITs to ≤ 1 day to parturition (41 of 43; 95%) than those that were collared but not fitted with VITs (26 of 37; 70%) or from females that expelled VITs ≥1 day to parturition (13 of 16; 81%). We also observed 2 instances of lamb abandonment likely as a result of capture-related activities.

New Mexico: Fra Cristobal Mountains.—In November 1999, 16 adult females were captured and fitted with VHF collars (MOD-500, Telonics, Mesa, Arizona, USA) in the Fra Cristobal Mountains. Due to 2 subsequent mortalities, we had 14 radiocollared females in this herd in 2001, which we monitored for hand-capture without the use of VITs. We successfully captured 1 lamb by hand after monitoring a radiocollared female in 2000 to test the efficacy of this technique. We documented 24 lambing events (15 of collared females and 9 of uncollared females) from January to May 2001. We captured lambs from 29% (*n* = 4) of collared females and 22% (*n* = 2) of uncollared females, for a total of 6 neonate captures from January to March 2001.

Helicopter Capture

Colorado: Pikes Peak.—We attempted to capture bighorn sheep lambs from the Pikes Peak herd in June 2011, but were unsuccessful. Although we had multiple capture opportunities, our efforts in each case were thwarted by interference of golden eagles (*Aquila chrysaetos*). As we approached with the helicopter and hazed the bighorn sheep groups into an area suitable for capture, eagles that were perched on nearby rocks would fly from their perch and attack the lambs. In 2 instances, eagles successfully caught and killed lambs that we were pursuing. After locating all known groups of bighorn sheep in the area and noting eagle presence at all sites, we abandoned our capture efforts so as to not enable further predation by eagles.

New Mexico: Fra Cristobal Mountains.— We successfully captured bighorn sheep lambs from helicopters in the Fra Cristobal herd in 2001 and 2002. Lambing data for 2001 was presented above. One additional female mortality occurred in 2001. We observed 23 lambs (13 of collared females and 10 of uncollared females) from December 2001 to May 2002.

Helicopter capture operations were conducted on 16 March 2001 and 28 February 2002. On these dates, 11 and 15 lambs (9 of collared females, 2 of uncollared; 12 of collared, 3 of uncollared), respectively, were available for capture. Using the net-gun technique, we captured 36% (*n* = 4) of available lambs in 2001 (2 of collared females, 2 of uncollared) and 47% (*n* = 7) of available lambs in 2002 (5 of collared, 2 of uncollared females), for a total of 11 successful net-gun captures over 2 years. Additionally, in 2001 we captured 36% (*n* = 4) of available lambs (all lambs of radiocollared females) using the helicopter hand-capture technique. We captured every lamb possible before they moved to inaccessible areas.

In total, we captured 14 lambs in 2001, 8 using the helicopter techniques and 6 using intensive observation of radiocollared females in combination with ground-based capture of neonates. This represented the capture of 71% of lambs of radiocollared females, and 61% of total lambs detected during 2001. We captured a total of 7 lambs in 2002, which represents 39% of lambs born to radiocollared females and 30% of total lambs detected during 2002. Over 3 years, 22 lambs were captured in the Fra Cristobal population, and no capture-related mortalities or lamb abandonment was observed.

South Dakota: Custer State Park.— In July 1999, 3 lambs were collared out of 24 known lambs (13%) in the East End sub-herd, and 7 were collared out of 34 known lambs (21%) in the West End sub-herd. Differences in lambs captured in each sub-herd resulted from varying numbers of lambs found in accessible terrain. In July 2000, 6 lambs were collared in the East End sub-herd of 11 available lambs (54%) and 6 were collared in the West End sub-herd of 38 available lambs (16%). Thus, we captured a total of 22 lambs of 107 known lambs (21%) over the 2 years, and captured every lamb possible before they moved into inaccessible terrain. There were no capture related lamb mortalities in either year, although there was a single adult female mortality. This mortality occurred when the female was struck by one of the weights attached to the net while confronting the helicopter that was pursuing her lamb. No lamb abandonment was observed using this capture technique.

Cost estimates

We estimated the individual costs of each of the major aspects of each of the lamb capture techniques (Table 3). Based on the 2-year average cost estimates, the least expensive lamb capture technique was helicopter net-gunning of lambs, while the most expensive technique was capture of lambs of radiocollared females with VITs when females were captured via helicopter net-gunning (Table 4). We calculated 1.28 and 1.41 females would need to be captured annually and during the first year for radiocollared females with and without VITs, respectively, to capture 1 lamb during both years. This was based on an estimated annual survival rate of 93% with mortality focused during the winter, a lamb capture success rate of 80% from females with VITs and 69% from females without VITs (Table 4).

DISCUSSION

We described and evaluated 4 bighorn lamb-capture techniques. We were able to capture lambs using each technique; however, we captured the largest number of lambs using VITs in combination with radiocollared females. Helicopter net-gunning and hand-capture in conjunction with intensive monitoring of radiocollared females (i.e., no VITs) resulted in fewer captures. The fewest lambs were caught using helicopter hand-capture. Despite differences in the number of lambs captured with these techniques, we observed that each had strengths and weaknesses.

Neonatal Capture

Lamb capture using females with VITs.–Strengths of using VITs compared to the other capture techniques include: it was easier to document lambing events, leading to greater capture success; it reduces the need for daily visual observations on females for extended periods of time; it minimizes disturbance to females during the critical lambing period; it lowers observation costs because fewer personnel were needed to monitor females for lambing events; it provides more accurate estimates of parturition dates; it increases probability of documenting early age mortalities (e.g., stillborns); lamb captures can occur throughout the lambing season; and it permits identification of parturition sites. Drawbacks to the use of VITs include the following: it requires trained personnel and an ultrasound at capture; there are costs associated with female capture and VIT deployment; it may entail longer handling times during female captures if helicopters need to ferry animals to a processing location for VIT insertion; it requires repeated capture of females for multiple year studies; aerial monitoring of VITs may be required in areas with low road density or limited access (adding additional cost), and lambs must be neonates (<48 hrs old) for successful capture. Also, at locations or during periods of increased temperature or low cloud cover, VITs may emit the “undeployed” pulse rate after expulsion, leading to missed births.

Another potential difficulty associated with the use of VITs is expulsion of the VIT prior to parturition. We found that average VIT retention to parturition across the study areas (78%) was similar to studies that have used VITs in mule deer (Bishop et al. 2007, Tatman et al. 2011), but less than a concurrent study on elk (*Cervus canadensis*) in South Dakota (100% retention; B. Simpson, South Dakota State University, pers. communication). Additionally, 1 animal in New Mexico failed to shed its VIT until 5 days post-parturition, and 1 VIT in South Dakota failed due to mechanical or battery-related problems. Expulsion and failure would necessitate deployment of ≥ 20% more VITs to ensure an adequate sample of neonates was obtained in studies solely using VITs to capture lambs.

We experienced several other problems using VITs. The percentage of neonates successfully captured from females with VITs was similar across years in South Dakota (92%–100%), but was lower in New Mexico (71%). This discrepancy was likely because the Black Hills contains the highest road density of any western national forest (3.5 km/km^2; [USDA, 1997]). Consequently, of the 6 lambs we failed to capture (New Mexico = 4; South Dakota = 2), 2 were missed because females lambed in inaccessible terrain in New Mexico, which limited both our access and ability to monitor the radio signals of the VITs. We were unable to capture lambs for 3 reasons. First in New Mexico, 2 VITs indicated that the unit was not expelled because of increased temperature or low cloud cover. Thus, the capture crew missed the period when lambs lacked the mobility to escape hand capture; however, methodology changes (i.e., monitoring in the morning and evening) eliminated this problem later in the study. Second, we searched the area where we presumed the lamb was bedded, but simply failed to find it until the next day when it was too old for hand capture. Finally, we did not hear the VIT on the day the female lambed because she dispersed approximately 17 km overnight to an area not previously thought to be a lambing area. Based on our observations, it is imperative that VITs be monitored ≥1 times/day with ≥1 monitoring period early in the morning to decrease the chance of obtaining false negatives and ensure lambs lack the mobility to elude hand capture, particularly during periods of higher temperatures or low cloud cover. It is noteworthy that recent technological developments of VITs have led to the inclusion of a photosensor in addition to the standard temperature sensor, and this advancement has shown promise in reducing the problem of false negatives (Cherry et al. 2012).

Lamb capture using females without VITs.–The main strength of capturing lambs by intensively monitoring radiocollared females without VITs is that it eliminates the need for multiple captures for long-term studies because females can be followed for the life of their collars. This method also allows the capture of lambs throughout the lambing season, and eliminates the need for ultrasounds during capture to facilitate VIT insertion, which requires specialized equipment and increased animal handling time. However, difficulties of using this technique include: 1) it is challenging to determine parturition events; 2) it requires more intensive monitoring compared to females with VITs (i.e., visual observation of female with/without lamb); 3) it can only be used in areas accessible by foot; 4) it requires bighorn sheep to be reasonably approachable; and 5) it is only useful for capturing neonates.

One additional drawback to this methodology is that it has the potential to increase disturbance to females and lambs during critical times when lambs are most vulnerable. For example in South Dakota, we noted 2 potential instances of female abandonment that may have been related to trying to obtain visuals on radiocollared females. The first instance occurred as we attempted to obtain a visual location on a collared-only female while a separate female and lamb (that was collared the day before) were spotted walking down the same trail. When the female spotted the capture crew she ran off leaving the lamb. We monitored the female and lamb for several hours via telemetry until we suspected that she would not return as she had moved several kilometers from the lamb. We then captured the lamb and it was sent to a captive facility. The second incident was less obvious, but abandonment could have been the result of our actions. After collaring a lamb from a female with a VIT, we began approaching a second female in the same area not associated with a VIT. The female appeared to stay in the same general area as the newly collared lamb while we moved off over the hill toward the second female. However, the following day the female was not with the lamb and by the second day the lamb had died.

Helicopter Capture

Net-gun.–Strengths of the helicopter net-gun technique include the following: the option to capture in remote terrain not accessible by foot, the ability to capture lambs without intensively monitoring collared females and/or females with VITs, ability to capture lambs of uncollared females, fewer animals need to be captured (i.e., no females), potentially more control over sample size of lambs, and the capacity to capture lambs of varying ages (i.e., not just neonates) to administer various age-dependent treatments (e.g., vaccines). The main limitation of using helicopters for lamb capture is the difficulty in capturing lambs if the females move into heavily forested regions or areas inaccessible to helicopters (e.g., areas with strong winds or high elevation), particularly once they become accustomed to helicopter capture methods. This was the greatest drawback of this technique, and was the main factor limiting the number of lambs captured. Additional limitations include the following: the difficulty in locating an adequate number of lambs to meet sample size goals; particularly in regions with low bighorn densities; a greater risk of physical injury (e.g., being struck by a weight attached to the net); short duration for capture during the lambing season (i.e., only lambs alive while the helicopter is present are available for capture); potential disturbance to non-target animals due to helicopter over-flights; lack of cause-specific mortality data for early age mortalities or information on still-born lambs; lack of data on parturition sites; and the potential for predation of lambs during capture as witnessed in Colorado. It is important to note the impacts of predation are likely site-specific. For example, predation was not a concern in South Dakota or New Mexico where eagles were present and where they did not cause lamb mortality outside of capture activities, in contrast to Colorado. Although we were not able to compare eagle populations and their predation rates across our various study sites and capture years, it is possible that predation risk is related to golden eagle densities or to lambing synchronicity (i.e., higher in areas with shorter, more synchronized lambing seasons, and lower in areas with longer, more temporally distributed lambing seasons). Regardless of the underlying process, impacts of eagle predation may potentially be mitigated by capturing earlier in the lambing season prior to the formation of large nursery groups, or later in the year when the lambs are large enough to be less vulnerable to eagles. However, a greater understanding of the risk factors associated with eagle predation, and appropriate strategies to minimize the effects during helicopter capture operations remain areas for further investigation.

Hand-capture.–In addition to factors previously mentioned in association with the helicopter net-gun technique, the strengths of the helicopter hand-capture technique included the following: decreased risk of physical injury to lambs inherent in net-gunning (e.g., being struck by a weight, being captured in a net with an adult animal); and decreased risk to personnel from nets becoming entangled in helicopter rotors. The limitations of using helicopters for hand capturing lambs include the following: many helicopter models may lack the maneuverability necessary to accommodate personnel exiting the helicopter while hovering; terrain in some areas may preclude hand-capture attempts; this technique requires suitable terrain to "trap" the lamb while the handlers approach and attempt capture; multiple handlers are required for each lamb; it is generally more difficult than helicopter net-gunning, and pilots and handlers may lack experience to conduct this method safely.

Finally, a drawback shared by these helicopter capture techniques is the potential to increase disturbance to females and lambs during critical times when lambs are vulnerable. Bighorn sheep are susceptible to disturbance from helicopters, which may decrease foraging efficiency, increase flight distance, and elevate stress levels in target and non-target animals (Krausman et al. 1985, Miller and Smith 1985, Bleich et al. 1990, Stockwell et al. 1991, Jessup 1992). Thus, these potential effects of helicopter capture of wildlife should be critically evaluated and minimized, if possible, by wildlife professionals when employing these techniques.

Lamb survival and abandonment.–The only potential abandonment issues we observed were associated with hand-capture of neonatal lambs of intensively monitored radiocollared females, as previously described. We did not observe any lamb mortality or abandonment using any of the 3 remaining lamb-capture techniques. When using females fitted with VITs, we observed that 1 lamb was killed by a gray fox (*Urocyon cinereoargenteus*) 2 days after capture, and 1 lamb was killed by a golden eagle 4 days after capture; however, capture was not believed to have been a contributing factor. This was particularly evident in the first case where the dam was observed next to the killed lamb's carcass and she returned to it after the researcher left the site. It also is worth noting that over the course of this study the vast majority of females stayed relatively close to lambs that were collared, often remaining in sight. Although we did not record exact locations of females immediately following lamb capture, we did monitor their whereabouts and observed several fairly large movements. With the exception of the 2 incidents previously described, females returned to retrieve lambs soon after we left the area.

Cost estimates

We provided approximate cost estimates because actual cost estimates are largely site and/or herd-specific. This variability arises from, among other things, the feasibility and level of effort required for various female capture techniques, the location and terrain inhabited by the targeted herd, and approachability of animals within the herd. Therefore, we provide only general estimates to help managers identify and approximate potential costs to evaluate each lamb capture-technique. An important aspect to consider in addition to cost is the feasibility of achieving the desired sample size for each lamb-capture technique. We were not able to compare the feasibility of reaching sample size goals in our study because of the varying effort used with each lamb capture method. However, we believe that if only one lamb-capture technique is used, hand-capture of lambs from females with VITs is most likely to achieve larger sample sizes, while hand-capture of lambs using helicopters is the least likely.

MANAGEMENT IMPLICATIONS

It is likely that mangers may need to plan for and implement the use of multiple techniques to successfully achieve their objectives and reach desired sample sizes. Although bighorn sheep managers need to carefully evaluate the costs, impacts, benefits, and limitations of each of these various methods when choosing which lamb capture technique to employ, the ability to capture and radiocollar lambs removes many of the impediments to understanding factors influencing lamb recruitment. Specifically, the lamb-capture methods we describe provide a means for managers to investigate questions that were previously difficult or impossible to study in the absence of the ability to capture lambs. For example, managers can examine cause-specific mortality of bighorn sheep lambs; measure the rate of still-born births and abortions; and quantify the efficacy of disease treatments (e.g., vaccines) administered to the dam and/or lamb to improve lamb recruitment.

ACKNOWLEDGEMENTS

We thank Z. Holme, A. Keith, R. Swisher, B. Dreher, D. Ackley, S. Griffin, J. Broecher, B. Tycz, T. Berdan, J. Schmit, G. Brennan, B. Juarez, E. Rominger, T. Turnbull, J. Pitman, M. Gould, and M. Overstreet for their assistance on these studies and J. Kanta for logistical and technical support provided. We also acknowledge J. Olson and R. Small, in memoriam. Project funding and support was provided by Wild Sheep Foundation; South Dakota Game, Fish and Parks; New Mexico Department of Game and Fish; Houston Safari Club; New Mexico Chapter of The Wild Sheep Foundation; Colorado

Special Big Game Auction and Raffle funds; Boone and Crockett Wildlife Conservation Program; National Fish and Wildlife Foundation; New Mexico Ranch Properties Incorporated; Turner Endangered Species Fund; the University of Montana; and Safari Club International. South Dakota capture operations in the central Black Hills also were funded by Federal Aid to Wildlife Restoration (Study No. 7537) administered through South Dakota Game, Fish and Parks. We thank P. R. Krausman and 2 anonymous reviewers for constructive reviews of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Number of confirmed radiocollared females lambing, status of marked females, and VIT functionality in the Black Hills, South Dakota, 2010–2012.

		Females lambing by category		
Year	Total females lambing	Collared only females	Successful VITs	Failed VITs
2010	28	5 (18%)	17 (61%)	6 (21%)
2011	33	14 (42%)	14 (42%)	5 (15%)
2012[a]	35	18 (51%)	12 (34%)	5 (14%)
Total (%)	96	37 (39%)	43 (45%)	16 (17%)

[a] Due to logistical error 1 female with a VIT was censored from 2012.

Table 2. Total and female category of all captured bighorn lambs in the Black Hills, SD, 2010 – 2012.

		Lambs captured by female category[b]		
Year	Total lambs captured[a]	Collared only	Successful VITs	Unsuccessful VITs
2010	24 (86%)	3 (60%)	16 (94%)	5 (83%)
2011	27 (82%)	9 (64%)	14 (100%)	4 (80%)
2012 [c]	29 (83%)	14 (78%)	11 (92%)	4 (80%)
Sum (%)	80 (83%)	26 (70%)	41 (95%)	13 (81%)

[a] Percentage obtained from lambing marked females by year.

[b] Percentages obtained from lambing marked females for each category by year.

[c] Due to logistical error 1 female with a VIT and lamb was censored from 2012.

Table 3. Estimated per unit capture costs of technicians, equipment and helicopter expenses for capturing bighorn sheep lambs using 4 different lamb capture techniques: 1) hand-capture of lambs from radiocollared females fitted with vaginal implant transmitters, 2) hand-capture of lambs of intensively monitored radiocollared females, 3) helicopter net-gunning, and 4) hand-capture of lambs from helicopters.

	Female capture					Lamb capture		
Technique	Dart[a]	Drop-net	Helicopter	VITs	Collars	Monitoring[b,c]	Helicopter	Collars
Females with VITs	$180	$125	$700	$225	$ 225	$140	NA	$225
Females without VITs	$180	$125	$700	NA	$ 225	$840	NA	$225
Helicopter net-gunning	NA	NA	NA	NA	NA	NA	$700	$225
Helicopter hand-capture[d]	NA	NA	NA	NA	NA	NA	$900	$225

[a] Assumes on average 1.5 darts required to capture each female

[b] Assumes 7 hrs/lamb and $20/hr (based on Bishop et al. [2007])

[c] Assumes 42 hrs/lamb and $20/hr (based on Bishop et al. [2007])

[d] Assumes higher cost based on increased attempts to capture lamb

Table 4. Estimated average number of females required, yearly and average per lamb costs for capturing a bighorn sheep lamb each year of a 2-year study using 4 different capture techniques: 1) hand-capture of lambs from radiocollared females fitted with vaginal implant transmitters, 2) hand-capture of lambs of intensively monitored radiocollared females, 3) helicopter net-gunning, and 4) hand-capture of lambs from helicopters.

			Cost		
Technique	Female capture	Female numbers	Year 1	Year 2	Average
Females-VITs	dart	1.28[a,b]	$ 1,174	$ 1,174	$ 1,174
Females-VITs	drop-net	1.28[a,b]	$ 1,103	$ 1,103	$ 1,103
Females-VITs	helicopter	1.28[a,b]	$ 1,842	$ 1,842	$ 1,842
Females-no VITs	dart	1.41[b,c,d]	$ 1,635	$ 1,065	$ 1,350
Females-no VITs	drop-net	1.41[b,c,d]	$ 1,557	$ 1,065	$ 1,311
Females-no VITs	helicopter	1.41[b,c,d]	$ 2,366	$ 1,065	$ 1,716
Helicopter net-gunning	none	0	$ 925	$ 925	$ 925
Helicopter hand-capture	none	0	$ 1,125	$ 1,125	$ 1,125

[a] Assumes 80% of lambs captured from females with VITs

[b] Assumes 93% annual female survival rate with mortality occurring in winter months

[c] Assumes 69% of lambs captured from females without VITs

[d] Assumes no capture of females needed in second year, marked all in first year

CHAPTER 4: DISEASE AND PREDATION: SORTING OUT CAUSES OF A BIGHORN SHEEP (*OVIS CANADENSIS*) DECLINE

This chapter is being prepared for submission in PLoS One and was coauthored by Jonathan A. Jenks, Troy W. Grovenburg, and Robert W. Klaver.

Abstract: Estimating survival and documenting causes and timing of mortality events in neonate bighorn sheep (*Ovis canadensis*) improves understanding of population ecology and factors influencing recruitment. During 2010–2012, we captured and radiocollared 74 neonates in the Black Hills, South Dakota, of which 95% (70) died before 52 weeks of age. Pneumonia (36%) was the leading cause of mortality followed by predation (30%). We used known fate analysis in Program MARK to estimate weekly survival rates and investigate the influence of intrinsic variables on 52-week survival. Model $\{S_{1wk,\ 2\text{-}8wks,\ >8wks}\}$ had the lowest AIC_c (Akaike's Information Criterion corrected for small sample size) value, indicating that age (3-stage age-interval: 1 week, 2–8 weeks, and >8 weeks) best explained survival. Weekly survival estimates for 1 week, 2–8 weeks, and >8 weeks were 0.81 (95% CI = 0.70–0.88), 0.86 (95% CI = 0.81–0.90), and 0.94 (95% CI = 0.91–0.96), respectively. Overall probability of surviving 52 weeks was 0.02 (95% CI = 0.01–0.07). Of 70 documented mortalities, 21% occurred during the first week, 55% during weeks 2–8, and 23% occurred >8 weeks of age. We found pneumonia and predation were temporally heterogeneous with lambs most susceptible to predation during the first 2–3 weeks of life, while the greatest risk from pneumonia occurred from weeks 4–8. Our results indicated pneumonia was the major factor limiting recruitment followed by predation. Mortality from predation may have been partly compensatory to pneumonia and its effects were less pronounced as alternative prey became available. Given the high rates of pneumonia-caused mortality we observed, and the apparent lack of pneumonia-causing pathogens in bighorn populations in the western Black Hills, management activities should be geared towards eliminating contact between diseased and healthy populations.

Introduction

Bighorn sheep (*Ovis canadensis*) populations in North America have declined dramatically since European settlement [1]. These declines have been attributed to an array of environmental and demographic factors including: unregulated hunting, predation, habitat loss, and diseases [2,3]. While transplant efforts have proved effective in increasing overall bighorn numbers, many herds remain genetically and geographically isolated and often fail to recover to historical levels [4]. One of the major challenges currently facing managers attempting to restore these populations is low lamb recruitment.

In ungulates, juvenile survival is typically more variable than adult survival; thus, juvenile survival often has the greatest impact on population trajectories [5,6]. While numerous studies have used vaginal implant transmitters (VITs) or intensely-monitored females to radiocollar and examine neonate survival of elk (*Cervus elaphus*, [7]) and deer (*Odocoileus* sp., [8,9]), the steep and rugged terrain often used for lambing and rearing young [10] has precluded or severely limited this technique for neonate bighorn sheep [11]. Instead, most researchers have relied on visual observations of marked ewes for lambs at-heel, or lamb:ewe ratios in the herd [12–16]. Reliance on such metrics potentially allows reasonable assessments of overall recruitment into the population; however, it may obscure timing, causes of mortality, and may not reflect total mortality as such things as stillborn and early-age mortalities may be misconstrued as non-lambing events. Furthermore, it precludes the use of intrinsic variables (e.g., sex, weight) in survival analyses.

Documenting cause of mortality of juveniles is particularly important for bighorn sheep as many populations commonly experience pneumonia outbreaks that result in partial or complete die-offs [17,18]. These die-offs are typically followed by years of depressed lamb recruitment that hinder population recovery. Additionally, cougar (*Puma concolor*) predation on adults has been shown to contribute to some bighorn sheep population declines [19–22] with higher rates of predation occurring during declines in primary prey [23]. Predation by cougars also was the suspected cause of reduced lamb survival in the eastern Black Hills [24].

As in many other regions of the United States [25], native bighorn sheep were extirpated from the Black Hills, South Dakota, around the early 1900s [24] and western South Dakota around 1925 [26]. Reintroductions and transplants beginning in 1965 resulted in the establishment of 5 sub-herds in the Black Hills region. Beginning in 2006, surveys conducted annually by South Dakota Department of Game, Fish and Parks (SDGF&P) indicated significant declines in bighorn lamb recruitment in 3 sub-herds (i.e., Rapid Creek, Hill City, and Spring Creek) in the east-central Black Hills (SDGF&P, Rapid City, SD, unpublished data). Our objectives were to radiocollar neonate bighorn sheep to: 1) estimate survival and document cause-specific mortality of bighorn lambs in the eastern Black Hills, South Dakota and 2) determine the influence of intrinsic variables on neonate survival.

Materials and Methods

Study Area

The Black Hills are located in southwestern South Dakota and eastern Wyoming, USA. Topography of the area varied from steep ridges, rock outcrops, canyonlands, and gulches to upland prairie, rolling hills, and tablelands. Elevations ranged from 973 to 2,202 m above mean sea level (msl; [27]). Ponderosa pine (*Pinus ponderosa*) forest comprised 83% of the landscape [28]. Mixed grass prairie (5%), riparian (4%), aspen (*Populus tremuloides*)-mixed conifer forest (3%), and developed open space (2%) were other major land cover types present in our study area [28]. During our study, average annual precipitation in the project area was 53 cm. Mean temperatures ranged from a maximum of 28° C in July to a minimum of −10° C in January. Climate values were based on data collected at the Hill City, South Dakota weather station from 1981–2010 [29].

The study area for this project was located in the east-central portion of the Black Hills with bighorn sheep habitat encompassing an area of approximately 26,000 ha. Each herd maintained distinct wintering areas; however, we did observe some range overlap between Spring Creek and Rapid Creek ewes during the lambing season (Figure 1). Over the course of our study, no range overlap was observed between our study herds and that of other herds in the Black Hills. In 2010, breeding-age ewe population estimates were: Rapid Creek = 56, Spring Creek = 50, and Hill City = 10 (SDGF&P, Rapid City, SD, unpublished data). Estimated proportion of ewes collared by herd across years ranged from: Rapid Creek 25%–29% (2010–2012), Spring Creek 30%–42% (2010–2012), and Hill City 90%–100% (2011–2012). Previously, no all-age pneumonia outbreaks had been detected in these herds, although several lambs had tested positive for pneumonia prior to 2010 (S. Griffin, SDGF&P, Rapid City, SD, personal communication). There were no domestic sheep grazing allotments within the Black Hills National Forest; however, several small domestic sheep and goat flocks were kept on private lands within bighorn sheep use areas. Other ungulates in the study area included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), mountain goats (*Oreamnos americanus*), and elk. In addition to cougars, other potential predators of bighorn sheep included coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

Ewe Capture

We captured adult ewes using a drop-net baited with weed-free alfalfa hay or sheep were chemically immobilized (BAM; 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine) via dart rifle (Dan-Inject, Børkop, Denmark, EU). We estimated ewe age class (1 year, 2 years, 3 years, or ≥4 years) based on tooth replacement [30]. We evaluated pregnancy status of ewes via ultrasonography (Universal Ultrasound, Bedford Hills, NY, USA) at time of capture. We fitted pregnant ewes with M3930 VITs manufactured by Advanced Telemetry Systems (ATS; Isanti, MN) with a redesigned wing system and antenna length of 6 cm [31]. Ewes that were not pregnant or not checked for pregnancy at the time of capture were not fitted with VITs. Methods of VIT deployment followed Bishop et al. [31]. In addition to receiving VITs, all ewes were fitted with very high frequency (VHF) collars (M252OB or G2110D; ATS) that were uniquely marked to facilitate individual identification.

Lamb Capture Using Ewes with VITs

Prior to the lambing season, radiocollared ewes were monitored 1–3 times per week from the ground using hand-held directional antennas (Telonics, Inc., Mesa, AZ), or from a Cessna 182 airplane. We listened for possible VIT expulsion each time we located ewes. When we detected an expelled VIT prior to the lambing season, we retrieved it using ground telemetry, ascertained if the ewe had aborted the fetus on-site, and estimated date of expulsion as the mean date between the first mortality signal and the last active signal received.

During the lambing season in May and June, ewes with VITs were checked once daily to determine if the VIT had been expelled. If the radio signal indicated a VIT had been expelled and terrain permitted, personnel would use telemetry to locate the expelled VIT on foot and retrieve it. If the VIT was located at a birth site and the lamb was present, we attempted to hand-capture it. If the dam had moved away from the VIT or if a lamb was not located in the vicinity of the ewe, we searched the area surrounding the ewe's location and the VIT location, and if a lamb was located we attempted capture. In the event the VIT was prematurely expelled based on a lack of evidence of birthing activities at the VIT site and observation of the ewe without a lamb, we intensively monitored the individual ewe's behavior. If we subsequently established the ewe had lambed, we attempted to capture the lamb once it was observed.

Lamb Capture Using Ewes without VITs

We monitored radiocollared ewes without VITs on a near daily basis for movement patterns indicative of parturition and presence of newborn lambs via radio-telemetry and visual observation from a distance. When we detected a newborn lamb, we assessed its degree of mobility using observations of ambulatory movements. We attempted hand-capture from the ground if the lamb seemed sufficiently immobile and the terrain was accessible. We waited until animals bedded down before attempting capture. Solitary ewe-lamb pairs were preferred; however, we also attempted captures of lambs associated with small groups of ewes. Once animals bedded down, we noted location of the animals in relation to topography and notable landmarks. Ideally, while attempting to avoid detection (e.g., by climbing up the opposite side of a ridge), two people approached the animals from above. When detection by the animals was imminent, we rapidly approached the animals' location causing the ewe to flee, and the lamb would hide or attempt to flee at which time we attempted to capture the lamb.

Lamb Handling and Marking

We physically restrained each captured lamb, blindfolded, and fitted the lamb with an expandable, 62g VHF collar equipped with a 4-hr or 8-hr mortality switch (Model M4210; ATS). Additionally, we determined sex, age, and weight of captured lambs. We monitored lamb survival after capture using telemetry to determine if lambs had died or were abandoned as a result of our capture activities. We attempted to keep handling time to <5 minutes. All capture and handling procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists [32].

We monitored lambs and ewes daily for 60 days post-capture and 3–4 times/week thereafter from the ground using a receiver and hand-held directional antenna (Telonics, Inc.) or from a Cessna 182 airplane. When we detected a mortality signal, we immediately located the collar, and recorded evidence at the site of mortality to determine cause of death. If we could not determine cause of death in the field, we transported animals to the Washington Animal Disease Diagnostic Laboratory (WADDL) at Washington State University for further examination. We classified mortalities as predation based on observations at the mortality site including, bite marks, caching, plucking, blood, and consumption of carcass. To estimate survival and determine factors influencing lamb survival, we used the known fate model with the logit-link function in

Program MARK [33]. We estimated weekly survival for 52 weeks post capture. Intrinsic variables included capture year, sex, herd, mass at capture, age at capture, winter severity, cougar population estimate for the Black Hills, birth timing (early, peak, and late), and 4 age-intervals (Table 1).

Survival Analysis

We determined age of the lamb at capture on the basis of new hoof growth measurements and texture, umbilicus condition, behavioral characteristics such as mobility, the presence of afterbirth, and wet fur. We calculated winter severity by summing days with measurable snow accumulation with days that were $\leq -7^\circ$ C based on data obtained from Hill City (for Spring Creek and Hill City herds) and Rapid City (for Rapid Creek herd), South Dakota weather stations from 2009–2012 [29]. Cougar population estimates were based on mark/recapture and modeling of the Black Hills cougar population (J. A. Jenks, South Dakota State University, Brookings, SD, unpublished data). Stage-interval models were constructed to test hypotheses regarding lamb susceptibility to various sources of mortality (e.g., predation vs. pneumonia). For birth timing, we grouped neonates into 3 periods: peak born (date when 50% of known lambs were born ± 3 days), early (born >3 days before peak parturition date), and late (born >3 days after peak parturition date). We also considered 4 age-intervals: 1) a 2-stage model ($S_{1wk, >1wk}$) in which neonate survival varied from <1 week versus >1 week post birth, 2) a 3-stage model ($S_{1wk,2\text{-}4wks, >4wks}$) in which neonate survival varied among 1 week, 2–4 weeks, and >4 weeks post birth, 3) a 3-stage model ($S_{1wk, 2\text{-}8wks, >8wks}$) in which neonate survival varied among 1 week, 2–8 weeks, and >8 weeks post birth, and 4) a 4-

stage model ($S_{1wk,\ 2\text{-}4wks,\ 5\text{-}8wks,\ >8wks}$) in which neonate survival varied among 1 week, 2–4 weeks, 5–8 weeks, and >8 weeks post birth (Table 1).

We based *a priori* model construction on variables we considered biologically meaningful to neonate ecology and used Akaike's Information Criterion corrected for small sample size (AIC_c) to select models that best described the data. We compared AIC_c values to select the most parsimonious model and considered models differing by $\leq 2\ \Delta AIC_c$ from the selected model as potential alternatives [34]. We used Akaike weights (w_i) as an indication of support for each model. Because there is no current goodness-of-fit test statistic available for known fate models, we investigated model robustness by artificially inflating $\hat{c}$ (i.e., a model term representing overdispersion) from 1.0 to 3.0 (i.e., no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in Quasi-AIC_c ($QAIC_c$; [7,35]). Additionally, as some lambs were collared from the same ewe over multiple years, we performed a data-bootstrap analysis [36] in Program MARK to estimate overdispersion as a function of lamb maternity. Our bootstrap analysis was performed on our top ranked survival model and comprised 10,000 replicate datasets generated by resampling our data with replacement after removing lambs associated with each ewe across years.

We calculated a cumulative incidence function (CIF) to estimate cause-specific mortality related to pneumonia and predation to measure the contribution of each to survival rates [37]. We used the *wild 1* package [38] in Program R to calculate CIF for all individuals that survived ≥1 day. We used a log-rank test to evaluate whether observed differences between cumulative mortality curves differed between the 2 mortality factors using the *survival* package [39] in Program R. The test computes a χ^2

statistic for observed and expected mortality events during each time step and tests the null hypothesis of no difference between mortality curves.

Results

From February 2010 to April 2012, we captured and radiocollared 55 adult ewes (3 at 3 years of age; 52 at ≥4 years of age) and deployed 62 VITs [11]. From May 2010 to June 2012, we captured and radiocollared 77 neonates (25 in 2010, 25 in 2011, and 27 in 2012), 2 of which were from unmarked ewes (lamb capture by ewe VIT status summarized in Smith et al. [11]). Peak parturition occurred on 13 May 2010 (range = 2–31 May), 16 May 2011 (range = 4–26 May), and 16 May 2012 (range = 30 April–6 June). Of the 77 neonates radiocollared, 14 (18.2%) were born early, 40 (51.9%) were born during the peak period, and 23 (29.9%) were born late. Estimated age at capture ranged from <0.01 to 2 days and 54% of lambs were <1 day old at capture; mean age and weight at capture was 0.8 days (SE = 0.1, $n = 70$) and 4.7 kg (SE = 0.1, $n = 75$), respectively. We documented 72 mortalities from capture to 52 weeks post capture; 24 in 2010, 23 in 2011, and 25 in 2012. However, in 2012, 2 lambs died from possible capture-related activity and 1 lamb was transported to a captive facility following possible capture-related abandonment; thus, we censored them from survival analyses. Additionally, 1 lamb in 2010 was right-censored 163 days post capture after we determined the collar was no longer on the animal. In addition to the 70 mortalities of radiocollared lambs, we documented 5 mortalities of lambs <24hrs old; 3 stillborn, 1 predation, and 1 hypothermia. Because they were not collared, these animals also were excluded from survival analyses. Mean age at death was 42 days (SE = 5, $n = 70$).

From model results on survival analysis, we considered {$S_{1wk, 2\text{-}8wks, >8wks}$} as the best approximating model (w_i = 0.59). Remaining models were ≥2.00 ΔAIC_c units from this model, and the weight of evidence supporting this model was 1.4 times greater than all other models combined (Table 3). While 2 models, {$S_{1wk,2\text{-}4wks, 5\text{-}8wks, >8wks}$} and {$S_{birth\ timing}$}, were within ≤2.73 ΔAIC_c units from our top model, we excluded them for the following reasons; 1) survival estimates for weeks 2–4 (0.86, SE = 0.03) vs weeks 5–8 (0.86, SE = 0.03) from model {$S_{1wk,2\text{-}4wks, 5\text{-}8wks, >8wks}$} were not significantly different and were virtually identical to the 2–8 week survival estimate (0.86, SE = 0.02) obtained from model {$S_{1wk, 2\text{-}8wks, >8wks}$}, 2) given the lack of discrepancy between these 2 models, removal of model {$S_{1wk, 2\text{-}8wks, >8wks}$} resulted in weight of evidence supporting our top ranked model (w_i = 0.73) 2.7 times greater than all other models combined, and 3) the model {$S_{birth\ timing}$} 95% CI for the β estimate for early born lambs incorporated 0. Furthermore, model {$S_{1wk, 2\text{-}8wks, >8wks}$} had the lowest $QAIC_c$ when $\hat{c}$ = 2.0 (moderate dispersion; $QAIC_c$ wt = 0.34) and through $\hat{c}$ = 3.0 (extreme dispersion; $QAIC_c$ wt = 0.20). The β estimate and 95% confidence intervals for the intercept (default >8 weeks survival period; 2.78, 95% CI = 2.28 to 3.29), 1 week (−1.36, 95% CI = −2.11–−0.60), and 2–8 weeks age intervals (−0.96, 95% CI = −1.57–−0.36), indicated $\beta \neq 0$; thus, we considered survival was best explained by 3-stage age-intervals. Weekly survival estimates for 1 week, 2–8 weeks, and >8 weeks were 0.81 (95% CI = 0.70–0.88), 0.86 (95% CI = 0.81–0.90), and 0.94 (95% CI = 0.91–0.96), respectively; overall probability of surviving 52 weeks was 0.02 (95% CI = 0.01–0.07). Of 70 mortalities used in covariate models, 15 (21.4%) occurred during the first week, 39 (55.7%) during weeks 2–8, and 16 (22.9%) occurred >8 weeks of age. Results of data bootstrapping analyses provided limited evidence for overdispersion (i.e., limited sibling dependence) due to lambs being collared from the same female over multiple years ($\hat{c}$ = 1.23). Our estimate of $\hat{c}$ indicates sample variance was slightly underestimated; however, as we observed no change in our top ranked survival model after inflating $\hat{c}$ to 3.0, we believe multiple births from some ewes had little impact on our overall estimate of survival.

Pneumonia was the leading cause of mortality (35.7%, n = 25) followed by predation (30.0%, n = 21); we were unable to determine ultimate cause of death for 7 (10%) mortalities (Table 2). We verified cougar predation in 15 (71%) predation events, and suspected felid (cougar or bobcat) on 5 (24%) other occasions; canid (coyote or domestic dog [*C. lupus familiaris*]) was suspected in 1 (5%) instance. Additionally, we suspected pneumonia as the ultimate (6 unknowns) or proximate cause of death (1 predation event) in 7 other instances. In 6 cases, carcasses were too degraded for definitive diagnosis; however, carcasses were intact (i.e., no evidence of predation) and the mortalities occurred during peak times when lambs were most susceptible to the disease (Figure 2). Additionally, in one cougar-killed lamb we obtained sufficient tissue for analysis and pneumonia was detected.

The mortality curve from pneumonia was significantly different from predation (X^2 = 4.56, df = 1, P = 0.04), with average age of lambs succumbing to predation (35.5 days, SE = 8.9 days; median = 17.5 days) younger in age than those succumbing to pneumonia (60.3 days, SE = 9.8 days; median = 48.0 days). Risk of predation peaked around 21 days of age while pneumonia exhibited 2 peak periods, 28 and 49 days, before tapering off around day 84 (Figure 2). The CIF indicated the risk of mortality from predation (0.45, 95% CI = 0.30–0.58) was higher than for pneumonia (0.14, 95% CI =

0.02–0.25) during the first 21 days of life, while pneumonia (0.54, 95% CI = 0.39–0.68) was higher than predation (0.20, 95% CI = 0.05–0.34) for lambs surviving >21 days. Overall CIF for pneumonia and predation were 0.37 (95% CI = 0.25–0.48) and 0.30 (95% CI = 0.17–0.42), respectively.

Discussion

Nearly all lambs in the herds we studied died in their first year, and all but one died by the age of 2. Of 82 documented birthing events only 3 (4%) lambs survived to 1 year of age (2 in 2011 and 1 in 2012). However, both surviving lambs from 2011 ultimately died the following year; one was struck by a vehicle while migrating back to the lambing grounds at just over 1 year of age and the other was found dead of unknown causes at approximately 16 months of age. Based on our sample of 74 collared animals, recruitment averaged 0.04 (SD = 0.04) across years (2010 = 0.00, 2011 = 0.08, 2012 = 0.04) and was lower than previous regional estimates (range = 0.10–0.28; 2007–2009; SDGF&P, Rapid City, SD, unpublished data) but was within the range of recruitment observed in 9 populations of bighorn sheep in the Hells Canyon area of Idaho, Oregon, and Washington that displayed evidence of pneumonia epizootics ($\bar{x}$ = 0.17, SD = 0.11, range 0.39–0.00; [15]).

Similar to our study, Cassirer and Sinclair [15] determined that pneumonia (86%) was the leading known cause of lamb mortality. However, they relied on visual observations and documented only 1 (4%) predation event. Based on our observations, ewes that lost lambs as a result of predation were more likely to leave the area where the predation event occurred, while ewes that lost lambs as a result of other mortality events (e.g., pneumonia, starvation) were more likely to remain in the general vicinity. When attempting to retrieve lambs that died from causes other than predation, we routinely observed ewes in the same area as the recently deceased lamb; however, on only one occasion did we observe a ewe within sight of a lamb that was killed by a predator. As a consequence of observed ewe behavior, relying on visual observations would have led to an underestimate of mortality from predation. Furthermore, we documented 5 lamb mortalities prior to capture (e.g., they died ≤24 hrs old), and had we been relying solely on visual observations these events would most likely have been misconstrued as non-lambing events resulting in a lower assessment of overall lamb mortality. It is worth noting that despite having numerous ewes instrumented with VITs and attempting to obtain visual observations on ewes not instrumented with VITs on a near daily basis, we observed several instances where ewes had apparently given birth (e.g., presence of afterbirth on the animal) yet we were unable to find the lamb. Although of minimal importance in our study, with higher survival, these mortalities could contribute significantly to total estimates of survival.

Model selection results indicated that neonate survival was best explained by 3-stage age-intervals. Previous research examining neonate survival in deer [9] and elk [7] have identified similar 3-phase models as best explaining survival. However, their results were mainly attributed to different predator avoidance strategies (e.g., hiding vs. fleeing; [40]) typically exhibited in these species. Rather than a difference in life-history phases, we believe our results were more a reflection of the different mortality sources acting at distinct time periods on these populations. For instance, during the first week of life lambs were most likely to die of causes other than predation or pneumonia (e.g., handling, starvation, infection), while during the second and third weeks of life lambs experienced the greatest risk of mortality from predation, and at >3 weeks pneumonia was the leading cause of mortality (Figure 2). Gaillard et al. [5] noted that preweaning juvenile mortality typically occurs within 1 month of birth, yet, due to the presence of pneumonia, we observed no difference in survival from 2–8 weeks of life.

Summer pneumonia epizootics resulting in high rates of lamb mortality followed a similar pattern to those documented in other populations [15,41], with relatively few deaths occurring in the first few weeks. Lambs as young as 11 days died from pneumonia although the majority occurred ≥4 weeks of age (Figure 2). Cassirer and Sinclair [15] found that highest rates of pneumonia-related mortality occurred between 6–8 weeks post birth and suggested that morbidity may have coincided with the waning of passive immunity acquired from colostrum [42]. We found pneumonia-related mortality occurred slightly earlier, peaking from 4–7 weeks; however, we observed a definitive lull in mortality around week 5 (Figure 2). Lack of mortality at that time may simply be a result of sample size, or perhaps a function of the vigor in which the epizootic operated within each of the 3 herds. We did, however, find that birth weights of lambs that died of pneumonia ≤35 days old, were on average lighter (4.23 kg, SE = 0.14; *n* = 9) than lambs that died of pneumonia >35 days old (4.97 kg, SE = 0.10; *n* = 14) suggesting that heavier lambs lived longer.

Predation was our second leading cause of mortality with the greatest risk occurring primarily around 2–3 weeks of age. It is likely that decreased mobility during this time predisposed lambs to predation, although we suspect that changes in prey density also may explain some of the decreased risk at >3 weeks. For instance, birth peak for bighorn sheep was approximately 15 May across years, while the birth peak in the

Black Hills for mule deer was 7–14 June [43], for white-tailed deer it was 7–17 June [44], and for elk it was 28 May–4 June (Schmitz 2010, SDGF&P, unpublished data). If risk of predation was strictly a function of lamb mobility we would expect no difference in predation based on birth timing (e.g., early, peak, or late). However, if predation was a function of prey density we would expect a decrease in risk from early to late born lambs as other prey became available. Early, peak, and late born lambs represented 18% (*n* = 14), 52% (*n* = 40), and 30% (*n* = 23), respectively, of all documented mortality events; yet, they made up 29% (*n* = 6), 62% (*n* = 13), and 10% (*n* = 2), respectively, of predation events. The decreasing trend in relative predation risk we observed between birth periods, and the decreased susceptibility to predation after 3 weeks of life, indicates that prey density could influence neonate lamb risk of predation, and supports others (e.g.,[45]) who have hypothesized cougar predation on bighorn sheep is reduced when primary prey (deer; *Odocoileus spp*.) are more abundant.

Cassirer and Sinclair [15] noted a lack of lesions in predator-killed animals, no interaction between predation and disease-related mortality, and suggested that disease did not increase adult sheep vulnerability to predation. We, however, had evidence to the contrary in lambs. Although most predation events resulted in nearly the entire carcass being consumed, we were able to test one lamb that died at 81 days of age, and a second uncollared lamb that was found in the same cache pile. Both lambs were killed by a cougar the night before and laboratory (WADDL) results confirmed both had lesions consistent with bronchopneumonia. This was the only time we documented 2 lambs killed on the same evening by the same predator, and the fact that both were pneumonia positive suggests that disease can increase lamb vulnerability to predation. Additionally, the one lamb that died as a result of canid predation occurred when the lamb was approximately 158 days of age which, we assume, would have been sufficiently mobile to avoid canid predators had it been healthy. Yet, this lamb was observed 3 days prior to the mortality event and appeared gaunt and lethargic. Studies of domestic calves (*Bos taurus)* have indicated animals inoculated with *Mannheimia haemolytica* (one of the pathogens hypothesized to cause pneumonia in bighorn sheep) spent less time feeding and more time resting than control animals [46]. If these same behavioral characteristics were exhibited in bighorn lambs they would likely experience greater risk to predation.

Even though we considered only one model as best approximating survival, we did glean information from other models that was noteworthy. First, model {$S_{\text{age at capt}}$} 95% CI for the β estimate incorporated 0 (−0.16, 95% CI = −0.62–0.31) and the estimate suggested no positive relationship between age at capture and survival. Based on these results, it did not seem that capturing younger lambs during the first few hours of life, a time we hypothesized may be a critical bonding period, influenced survival. Additionally, model {$S_{\text{birth timing}}$} indicated that peak (0.90, 95% CI = 0.86–0.92) and early (0.93, 95% CI = 0.87–0.96) born lambs exhibited higher survival than late (0.78, 95% CI = 0.66–0.86) born lambs. As noted above, late born lambs were less likely to suffer mortality from predation, however, the opposite trend was observed for late born lambs dying of pneumonia. Late born lambs were 1.5 times (11 observed vs 7.1 expected) more likely to die of pneumonia than expected by chance, which was higher than for early (1.2; 6 observed vs 5 expected) or peak (0.6; 8 observed vs 12.9 expected) born lambs. This trend may simply be a function of late born lamb availability, as they were less likely to die of predation, or it could be a result of increased horizontal disease transmission. For example, lambs born early in the season would be present when sheep densities were at their lowest as most ewes had not given birth and remained on wintering grounds. Lambs born later in the year would arrive as sheep densities on the lambing grounds were at their highest. Assuming lamb immune systems are weakest during the first few weeks of life, late born lambs would have a much greater chance of coming into contact with other diseased animals, which could increase their chance of contracting the disease.

The sustained high levels of juvenile mortality we observed indicate these 3 populations are declining, primarily as a result of chronic pneumonia epizootics. Whether these pathogens are being maintained and transmitted among populations via bighorn sheep movements or from contact with domestic sheep and goats remains unclear. Over the course of our study we observed no range overlap between the Hill City and the other 2 sub-herds, and limited overlap during the lambing season between Rapid Creek and Spring Creek sub-herds (Figure 1). However, our sample of collared adults only included females, and it could be male movements, especially during the breeding season, could account for pathogen transmission. Conversely, bighorn sheep habitat in the Black Hills is made up of a matrix of public and private lands with several domestic sheep and goats present in areas adjacent to primary habitats or along known dispersal corridors. As effective buffers between domestics and bighorns have been identified as 20–40 km [47,48], the potential exists for all 3 herds to have contact with domestic sheep and goats, precipitating pneumonia-caused mortality.

Conclusions

We provide the first evaluation of the influence of intrinsic variables on neonate bighorn sheep survival and a quantitatively robust assessment of cause-specific mortality. Pneumonia was the major factor limiting recruitment followed by predation, although mortality from predation seemed to be partly compensatory to pneumonia and its effects were less pronounced as alternative prey became available. Given the politically untenable prospect of culling herds (J. Kanta, SDGF&P, personal communication), and the current lack of effective vaccines for wild bighorn sheep [16,49], it seems current declines in these 3 populations will likely go unabated. Future research assessing the role of male dispersal in perpetuating disease among populations, experimenting with vaccines that have shown promise in captive bighorns at reducing pneumonia-caused mortality [50], and quantifying the relationship between disease and predation at limiting bighorn sheep populations is warranted. Furthermore, given the high rates of pneumonia-caused mortality we observed, and the apparent lack of pneumonia-causing pathogens in bighorn populations in the western Black Hills (B. Parr, South Dakota State University, Brookings, SD, unpublished data), management activities should be geared towards eliminating contact between diseased and healthy populations.

ACKNOWLEDGMENTS

This project was funded by Federal Aid to Wildlife Restoration (Study No. 7537) administered through South Dakota Game, Fish and Parks. We thank S. Griffin, J. Broecher, B. Juarez, B. Tycz, L. Meduna., L. Dahl, J. Kanta, A. Lindbloom, T. Berdan, J. Schmit, and J. Felio for capture and monitoring assistance and F. Cassirer for helpful comments on our manuscript. Thanks also to the Civil Air Patrol and pilots L. Becht and

G. Kirk for assistance with flight time. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Figure 1. Bighorn sheep populations and locations of study populations in the Black Hills, South Dakota, USA, 2010–2012.

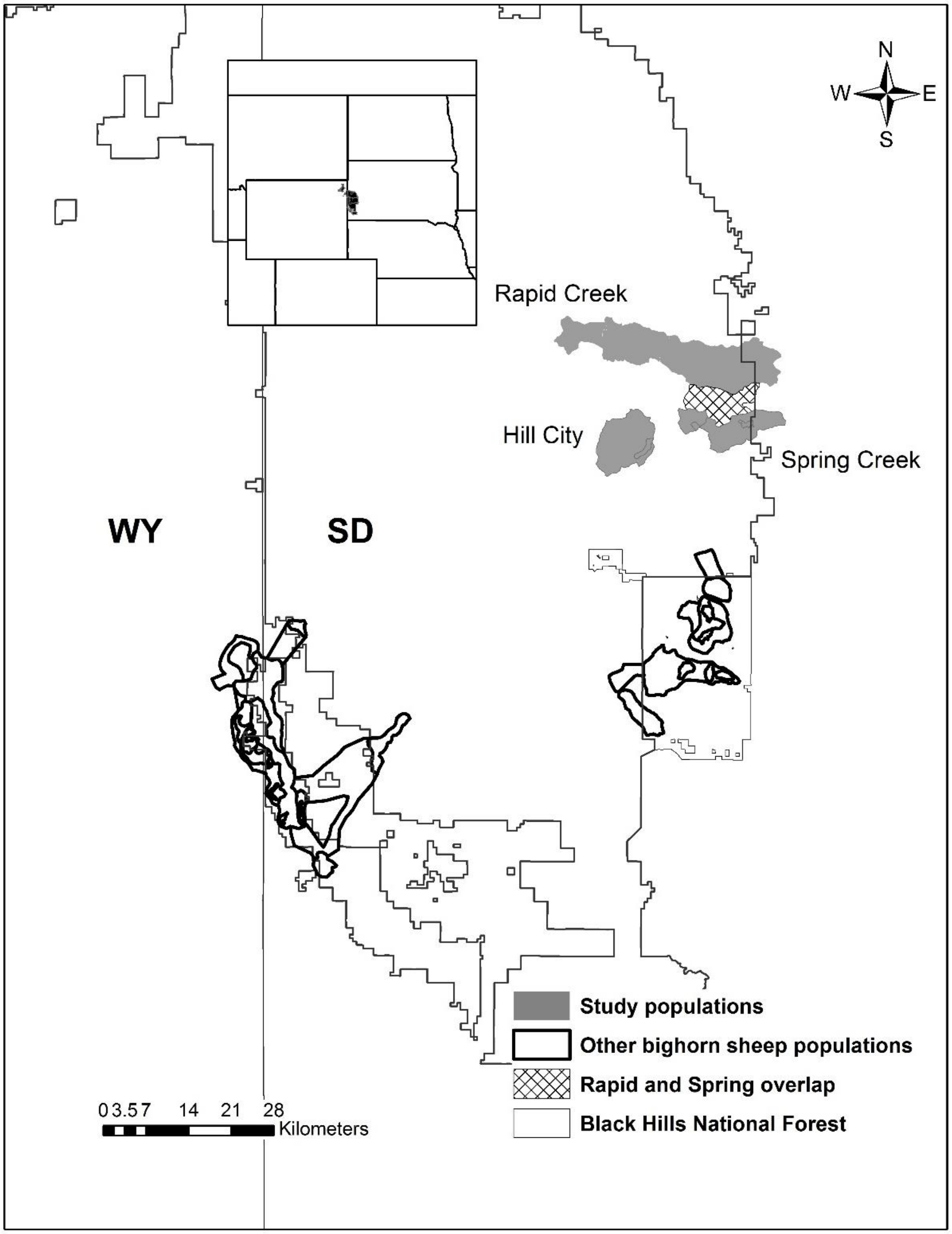
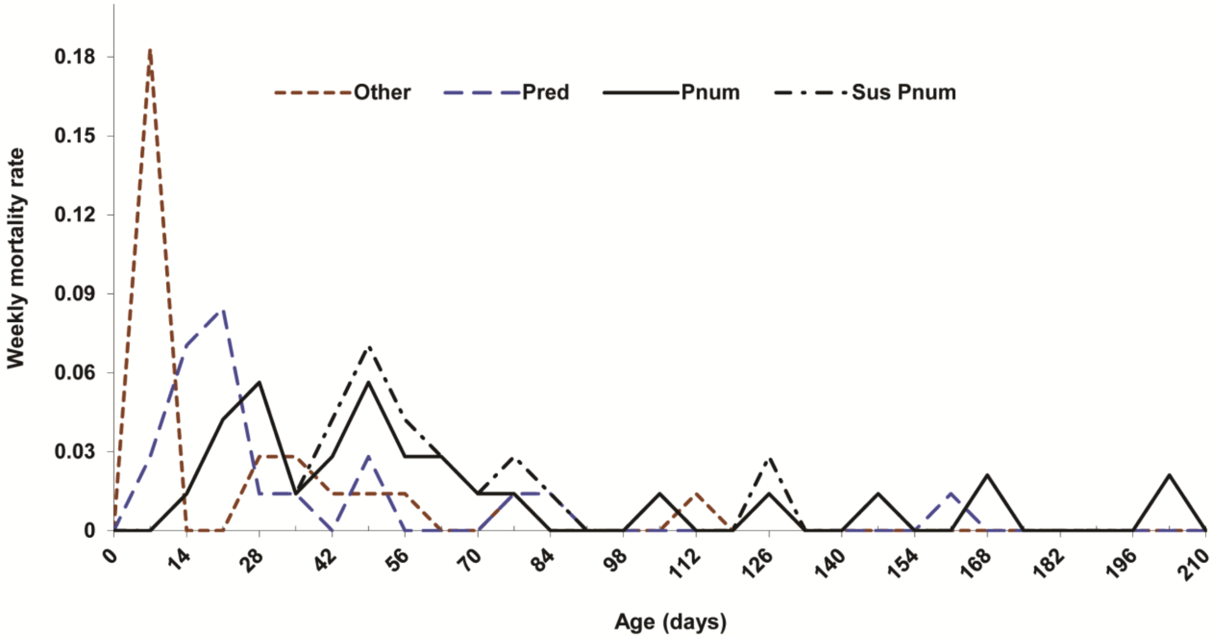


Figure 2. Average weekly mortality rate comparison for other[a], predation, pneumonia, and suspected pneumonia[b] mortality events of bighorn lambs in the Black Hills, South Dakota, USA, 2010–2012.



[a] Other includes all causes of mortality other than predation and pneumonia.
[b] Suspected pneumonia includes mortalities in which we assumed pneumonia was the ultimate or proximate cause of death in addition to confirmed pneumonia mortality events.

Table 1. A priori models constucted to determine the influence of intrinsic variables on bighorn sheep neonate survival in the Black Hills, South Dakota, USA, 2010–2012.

Model	*K*[a]	Description
$S_{constant}$	1	Survival was constant
$S_{vit\ status}$	2	Survival varied by whether ewe was vitted or non-vitted
$S_{age\ at\ capt}$	2	Survival varied by age at capture of neonates
S_{weight}	2	Survival varied by birth weight of neonates
$S_{birth\ timing}$[b]	3	Survival varied by birth timing (early, late, and peak)
S_{year}	3	Survival varied by year
$S_{winter\ severity}$	2	Survival varied by previous winter severity
$S_{cougar\ pop}$	2	Survival varied by estimated cougar population
S_{herd}	3	Survival varied by herd
S_{sex}	2	Survival varied by gender
$S_{1wk,\ >1wk}$	2	Survival varied by age in 2 stages
$S_{1wk,2\text{-}4wks,\ >4wks}$	3	Survival varied by age in 3 stages
$S_{1wk,\ 2\text{-}8wks,\ >8wks}$	3	Survival varied by age in 3 stages
$S_{1wk,2\text{-}4wks,\ 5\text{-}8wks,\ >8wks}$	4	Survival varied by age in 4 stages

[a] Number of parameters.

[b] Peak = date when 50% of known lambs were born +/- 3 days, early = born > 3 days before peak parturition date, and late = born > 3 days after peak parturition date.

Table 2. Cause-specific mortality of neonate bighorn sheep in the Black Hills, South Dakota, 2010–2012.

Cause-specific mortality	*n*	%
Pneumonia	25	35.7%
Predation	21	30.0%
Starved	8	11.4%
Unknown	7	10.1%
Ewe died	3	4.3%
Abandoned	1	1.4%
Contagious eczema (CE)	1	1.4%
Hypothermia	1	1.4%
Infection	1	1.4%
Underweight	1	1.4%
Vehicle	1	1.4%

Table 3. Top-ranked survival models of neonate bighorn sheep from birth to 52 weeks post capture in the Black Hills, South Dakota, USA, 2010–2012 when $\hat{c}$ (a model term representing overdispersion) was 1.0 (i.e., assumed no dispersion).

Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	Deviance
$\{S_{1wk,\ 2\text{-}8wks,\ >8wks}\}$	429.67	0.00	0.59	3	423.64
$\{S_{1wk,2\text{-}4wks,\ 5\text{-}8wks,\ >8wks}\}$	431.70	2.02	0.36	4	423.63
$\{S_{birth\ timing}\}$	432.40	2.73	0.26	3	426.36
$\{S_{1wk,2\text{-}4wks,\ >4wks}\}$	436.25	6.58	0.02	3	430.22

[a] Composition and description of models are listed in Table 1.

[b] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

[c] Difference in AIC_c relative to min. AIC.

[d] Akaike wt (Burnham and Anderson 2002).

[e] Number of parameters.

CHAPTER 5: SURVIVAL OF FEMALE BIGHORN SHEEP (*OVIS CANADENSIS*) IN THE BLACK HILLS, SOUTH DAKOTA

This chapter is being prepared for submission in the American Midland Naturalist and was coauthored by Troy W. Grovenburg, and Jonathan A. Jenks.

Abstract.— From 2010 to 2013, we estimated survival and cause-specific mortality of adult female bighorn sheep (*Ovis canadensis*) in the Black Hills, South Dakota, USA. We documented 21 mortalities with pneumonia (19%) and predation (19%) accounting for most known causes of mortality; 48% were unknown, however, we were able to conclude predation was not the ultimate cause of death. We used known fate analysis in Program MARK to estimate monthly survival; model $\{S_{\text{May–June}}\}$ was our best approximating model ($w_i = 0.83$) indicating survival differed between May–June and July–April periods. Monthly survival estimates for May–June were 0.95 (95% CI = 0.91–0.97) and 0.99 (95% CI = 0.98–0.99) for July–April periods, and overall annual survival was 0.81 (95% CI = 0.72–0.87). Because most mortalities resulted in whole carcasses (i.e., non-predation events), our results tend to indicate pneumonia may have a greater impact on these populations than we were able to confirm.

Introduction

Throughout North America, bighorn sheep (*Ovis canadensis*) have declined dramatically since European settlement (Buechner, 1960) due to an array of environmental and demographic factors (Singer *et al.*, 2001; Wehausen *et al.*, 2011). Restoration efforts aimed at restoring native populations have been mixed, with many populations experiencing repeated declines and extinctions (*e.g.*, Berger, 1990). These fluctuations have been mainly attributed to disease (Hobbs and Miller, 1992; Cassirer and Sinclair, 2007) or predation (Kamler *et al.* 2002; Rominger *et al.*, 2004). Pneumonia, typically *Pasturella* spp., has been particularly devastating across North America resulting in partial or complete dieoffs in numerous herds (*e.g.*, Cassirer *et al.* 1996; Jorgenson *et al.*, 1997), although some have found bighorn sheep to contain the pathogens without exhibiting clinical signs (Onderka and Wishart, 1988). These dieoffs are typically followed by years of depressed lamb recruitment which are often attributed to contact with domestic sheep (Singer *et al.*, 2000; Monello *et al.*, 2001). Cougar (*Puma concolor*) predation also has been implicated as the cause of bighorn declines (Hayes *et al*., 2000; Rominger *et al*., 2004), with several noting increased impacts during primary prey declines (Kamler *et al*., 2002; Rosas-Rosas *et al*., 2003). However, McKinney *et al*. (2006) found no influence of cougar abundance on bighorn predation and concluded that predation may be a function of learned behavior by individuals (*e.g.*, Ross *et al*., 1997).

Similar to other regions, native bighorn sheep were extirpated from the Black Hills in the early 1900s (South Dakota Department of Game, Fish and Parks, 2007) and western South Dakota around 1925 (Zimmerman, 2008). Transplants beginning in 1965 resulted in the establishment of 4 herds in the Black Hills region (South Dakota Game, Fish and Parks, 2013). Since 2006, annual surveys conducted by South Dakota Department of Game, Fish and Parks (SDGF&P) have indicated significant declines in lamb:ewe ratios as well as general population declines in the Rapid Creek herd in the east-central Black Hills. This population consists of 3 sub-herds; Rapid Creek, Spring Creek, and Hill City, and these declines tended to coincide with an overall increase in cougar abundance. Our objectives were to estimate survival and document cause-specific mortality in adult female bighorn sheep (hereafter ewes) within these 3 sub-herds.

Methods

STUDY AREA

The Black Hills are located in southwestern South Dakota and eastern Wyoming, USA. Topography of the area varied from steep ridges, rock outcrops, canyonlands, and gulches to upland prairie, rolling hills, and tablelands. Elevations ranged from 973 to 2,202 m above mean sea level (Froiland, 1990). Ponderosa pine (*Pinus ponderosa*) forest comprised 83% of the landscape (USGS 2013). Mixed grass prairie (5%), riparian (4%), aspen (*Populus tremuloides*)-mixed conifer forest (3%), and developed open space (2%) were other major land cover types present in our study area (USGS Gap Analysis Program, 2013). During our study, average annual precipitation in the project area was 53 cm. Mean temperatures ranged from a maximum of 28° C in July to a minimum of −10° C in January. Climate values were based on data collected at the Hill City, South Dakota weather station from 1981–2010 (National Oceanic and Atmospheric Administration [NOAA], 2013).

Our study area was located in the east-central portion of the Black Hills with bighorn sheep habitat encompassing an area of approximately 26,000 ha. Each herd (Rapid Creek, Spring Creek, Hill City) maintained distinct wintering areas; however, we did observe some range overlap between Spring Creek and Rapid Creek ewes during the lambing season (Figure 1). Over the course of our study, no range overlap was observed between our study herds and other herds (*e.g*, Custer State Park) in the Black Hills. In 2010, breeding-age ewe population estimates were: Rapid Creek = 56, Spring Creek = 50, and Hill City = 10 (SDGF&P, Rapid City, SD, unpublished data). Estimated proportion of ewes radiocollared by herd across years were: Rapid Creek 25%–29% (2010–2012), Spring Creek 30%–42% (2010–2012), and Hill City 90%–100% (2011–2012). Other ungulates in the study area included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), mountain goats (*Oreamnos americanus*), and elk

(*Cervus elaphus*). Potential predators of bighorn sheep included cougars, coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

CAPTURE AND MONITORING

We captured adult ewes using a drop-net baited with weed-free alfalfa hay or sheep were chemically immobilized (BAM; 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine) via dart rifle (Dan-Inject, Børkop, Denmark, EU). We estimated ewe age class (1 year, 2 years, 3 years, or ≥4 years) based on tooth replacement (Krausman and Bowyer, 2003). We evaluated pregnancy status of ewes via ultrasonography (Universal Ultrasound, Bedford Hills, NY, USA) at time of capture. We fitted pregnant ewes with M3930 VITs manufactured by Advanced Telemetry Systems (ATS; Isanti, MN) with a redesigned wing system and antenna length of 6 cm (Bishop *et al.*, 2011). Ewes that were not pregnant or not checked for pregnancy at the time of capture were not fitted with VITs. Methods of VIT deployment followed Bishop *et al.* (2011). In addition to receiving VITs, we fitted ewes with either very high frequency (VHF; M252OB, ATS; *n* = 50) or Global Positioning System (GPS; G2110D, ATS; *n* = 11) radio collars that were uniquely marked to facilitate individual identification, and equipped with an 8-hr mortality sensor. All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists (Sikes *et al.*, 2011).

During the lambing season (~ May – August) ewes were monitored daily from the ground using hand-held directional antennas (Telonics, Inc., Mesa, AS), or from a Cessna 182 (Cessna Aircraft, Co., Wichita, KS) airplane. Prior to the lambing season, ewes were monitored 1–3 times/week using similar protocols. When we detected a mortality signal, we immediately located the collar and recorded evidence at the site of mortality to determine cause of death. When possible, we collected sheep for evaluation at SDGF&P (Rapid City, SD), and sent tissue samples for gross and histological examination to Washington Animal Disease Diagnostic Laboratory (WADDL) at Washington State University (Pullman, WA, USA). When this was not feasible, we conducted field necropsies and collected tissue for examination at WADDL. When cause of death could not be definitively determined, we classified mortalities as unknown. We classified mortalities as predation based on observations at the mortality site including, bite marks, caching, plucking, blood, and consumption of the carcass.

SURVIVAL ANALYSIS

Records from radio-tracking surveys were converted to monthly encounter histories (White and Burnham, 1999) for each year ewes were monitored. We censored individuals if no locations were obtained in a given month and right-censored individuals when collars failed to transmit. Deaths were assigned to the month when date was known or mean date between the first mortality signal and the date the last active signal was obtained. To estimate survival and determine factors influencing ewe survival, we used a known fate model in Program MARK (White and Burnham, 1999) with the logit-link function. We used an a priori set of 11 candidate models to investigate the influence of temporal and individual covariates on ewe survival. Intrinsic variables included year, herd, winter severity, cougar population density for the Black Hills, pregnancy status, whether ewes received a VIT in a given year, and 3 temporal models (Table 1).

We calculated winter severity by summing days with measurable snow accumulation with days that were $\leq -7^{\circ}$ C based on data obtained from Hill City (Spring Creek and Hill City herds) and Rapid City (Rapid Creek herd), South Dakota weather stations from 2009–2012 (NOAA, 2013). Cougar population estimates were based on mark/recapture and modeling of the Black Hills cougar population (J. Jenks, South Dakota State University, Brookings, SD, unpublished data). Pregnancy status of each ewe was determined based on ultrasound results at time of capture, or observations of ewes with a lamb at-heel or other visual evidence the ewe had given birth (*e.g*., afterbirth present) for ewes that were not captured in a given year. We also incorporated temporal models that allowed survival to vary as a function of season (winter [Nov–April] vs. summer [May–Oct]), and 2 models where survival varied across the lambing season: 1) a 2-interval model $\{S_{\text{May – June}}\}$ in which survival varied from May–June vs the remainder of the year (July–April), and 2) a 2-interval model $\{S_{\text{June – July}}\}$ in which survival varied from June–July vs the remainder of the year (August–May; Table 2).

We based a priori model construction on variables we considered biologically meaningful on ewe ecology and used Akaike's Information Criterion corrected for small sample size (AIC_c) to select models that best described the data. We compared AIC_c values to select the most parsimonious model and considered models differing by ≤ 2 ΔAIC_c from the selected model as potential alternatives (Burnham and Anderson, 2002). We used Akaike's weights (w_i) as an indication of support for each model. Because there is no current goodness-of-fit test statistic available for known fate models, we investigated model robustness by artificially inflating $\hat{c}$ (i.e., a model term representing overdispersion) from 1.0 to 3.0 (i.e., no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in Quasi-AIC$_c$ (QAIC$_c$; Devrie *et al.*, 2003; Barber-Meyer *et al.*, 2008; Grovenburg *et al*. 2011).

RESULTS

We captured and radiocollared 55 adult ewes (3 = 3 years of age; 52 = ≥4 years of age) from 2010 to 2012 (ewe VIT status and number of ewes lambing across years summarized in Smith *et al.* 2014b), and documented 21 mortalities (Table 1). In cases where we could determine cause of death, predation and pneumonia were the leading cause of mortality (*n* = 4; 19.0%) followed by infection (*n* = 2; 9.5%), and vehicle (*n* =1; 4.8%); we were unable to determine ultimate cause of death for 10 (47.6%) mortalities. We attributed all known predation mortalities to cougars. Average confirmed pregnancy rates across years was 93.0% (range = 91.1%–96.6%).

From model results on survival analysis, we considered {S $_{\text{May – June}}$} as the best approximating model (w_i = 0.83). Remaining models were ≥2 ΔAIC$_c$ units from this model, and the weight of evidence supporting this model was 4.7 times greater than all other models combined (Table 2). Furthermore, model {S $_{\text{May – June}}$} had the lowest QAIC$_c$ when $\hat{c}$ = 2.0 (moderate dispersion; QAIC$_c$ wt = 0.50) and through $\hat{c}$ = 3.0 (extreme dispersion; QAIC$_c$ wt = 0.30). The β estimate and 95% confidence intervals for May–June (−1.45, 95% CI = −2.32 to −0.58) indicated $\beta \neq 0$; thus, we considered survival was best explained by 2-intervals. Monthly survival estimates for May–June were 0.95 (95% CI = 0.91–0.97), and 0.99 (95% CI = 0.98–0.99) for the July–April period; overall probability of surviving 12 months was 0.81 (95% CI = 0.72–0.87). Of the 21 mortalities documented 10 (48%) occurred during May–June and 11 (52%) occurred during the July–April period.

DISCUSSION

Annual survival of adult bighorn ewes was similar to survival rates reported elsewhere for populations not experiencing significant losses from predation (0.76–0.95%; Jorgenson *et al*., 1997; Kamler *et al*., 2002; Cassirer *et al*., 2007). Although we were unable to determine the ultimate cause of death for 10 (47.6%) ewes, carcasses were intact and we were able to conclude predation was not the cause of death. Festa-Bianchet *et al*. (2006) documented stochastic predation episodes in 3 populations of bighorn sheep in Alberta that led to population declines, and hypothesized that these events were the result of prey specialization in cougars. Predation patterns we observed tended to be more sporadic and not indicative of prey specialization. Of the 4 predation events we observed 3 occurred in 2011 and 1 in 2012. However, of the 3 that occurred in 2011, 2 were in Spring Creek and occurred 5 months apart, while the third predation event occurred in the Hill City herd. Nevertheless, we did observe a weak decreasing trend in annual survival correlated with predation events; 2010 exhibited the highest survival (0.83; 95% CI = 0.66–0.93) followed by 2012 (0.82; 95% CI = 0.71–0.89) and 2011 (0.78; 95% CI = 0.63–0.89), although model selection revealed little support ($w_i < 0.01$) for yearly effects.

We also failed to document any predation events in the Rapid Creek herd and speculate this pattern may be related to the migratory nature of this herd and the lack of spatial overlap with primary cougar habitat, especially in winter and early spring, a time when others have noted increased predation from cougars (Ross *et al*., 1997; Hayes *et al*., 2000; Cassirer and Sinclair, 2007). The Rapid Creek herd generally maintained wintering grounds in a relatively open area on the west side of Rapid City, and most ewes migrated west from 10 to 25 km to more rugged lambing grounds. These areas generally contained higher canopy cover and were more indicative of “typical” cougar habitat. However, the fact that they were only used for part of the year, and at a time when more vulnerable lambs were present, likely decreased risk of predation for ewes in this herd. In contrast, Spring Creek and Hill City herds typically inhabited the same general area throughout the year, with relatively small movements occurring during the lambing season.

Mortality from pneumonia also seemed somewhat sporadic with 1 event documented in 2010 (Spring Creek) and 2012 (Hill City), and 2 events in 2011 (Spring Creek). While we failed to detect significant differences in survival across years, Cassirer and Sinclair (2007) documented significantly lower survival in 9 populations of bighorn sheep in Hell’s Canyon, Idaho, Washington, and Oregon, during years when pneumonia was detected. Although speculative, we hypothesize that several unknown mortalities were pneumonia related and may have contributed more than estimated to overall mortality. For example, while we did not radiocollar adult males for our study, we observed 6 ram mortalities in the winter of 2010–2011 that we attributed to pneumonia based on gross examination, and Smith *et al*. (2014a) found pneumonia was the leading cause of mortality for lambs in the Black Hills during this time. Although adult-age and lamb die-offs from pneumonia are not necessarily linked (Cassirer and Sinclair, 2007), the fact that most mortalities resulted in whole carcasses (i.e., non-predation events) tends to indicate pneumonia may have a greater impact on these populations than we were able to confirm.

Model selection results indicated that ewe survival was best explained by a 2-interval model that allowed survival to vary from May–June vs the July–April period. The decreased survival during this time corresponded to peak parturition for ewes (~15 May; Smith *et al*., 2014a), and we were able to confirm 2 instances of ewes succumbing to infection that appeared directly related to parturition. Additionally, we documented 2 cases of pneumonia-related mortality, 1 mountain lion mortality, and 5 unknown causes during this time. Although we were unable to quantify parasite loads, Festa-Bianchet (1989) noted that lactating ewes had greater fecal counts of lungworms and seemed less resistant to parasites and pathogens than non-lactating ewes. Our results tend to support Festa-Bianchet's (1989) hypothesis that reproduction in bighorn sheep involves a fitness cost.

Unfortunately we were unable to determine ultimate cause of death for a significant portion of ewes in our study. Predation has been found to be a significant source of mortality for both native (Holl *et al*., 2004) and translocated-bighorn sheep (Rominger *et al*., 2004, Kamler *et al*., 2002), however, the fact that all unknown mortalities likely were not the result of predation, and given the low rates of bighorn sheep in cougar diets found in the Black Hills (0.6%; Smith *et al*., In Review; Chapter 1), suggests predation was not a significant source of mortality for adult ewes during our study. Rather, the pattern we observed is more indicative of disease, which also has been found to contribute to population declines associated with this species (Cassirer and Sinclair, 2007). The adult survival rates we report, in combination with the low rates of lamb recruitment documented in these herds (0.02%; Smith *et al*., 2014a), indicates these populations are declining. Future research assessing cause-specific mortality would benefit from greater monitoring and by decreasing mortality switches on radiocollars from 8 to 4 hours.

Acknowledgements.—We thank S. Griffin, J. Broecher, B. Juarez, B. Tycz, L. Meduna., L. Wiechman, J. Kanta, A. Lindbloom, T. Berdan, J. Schmit, and J. Felio for capture and monitoring assistance and D. Wilckens for helpful comments on earlier drafts. Thanks also to the Civil Air Patrol and pilots L. Becht and G. Kirk for assistance with flight time. Project funding and support was provided by the Wild Sheep Foundation and by Federal Aid to Wildlife Restoration (Study No. 7537) administered through South Dakota Department of Game, Fish and Parks.

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Table 1. A priori models constructed to determine influence of intrinsic variables on adult ewe bighorn sheep survival in the Black Hills, South Dakota, USA, 2010–2012.

Model	K^a	Description
$S_{constant}$	1	Survival was constant
S_{vit}	2	Survival varied by whether ewe was vitted or non-vitted
$S_{pregnant}$	2	Survival varied by whether ewe was pregnant or not
S_{winsev}	2	Survival varied as a function of previous winters severity
S_{coug}	2	Survival varied by cougar density
S_{Season}	2	Survival varied between summer (May–Oct) and winter (Nov–Apr)
$S_{June–July}$	2	Survival varied during “lactation” phase
$S_{May–Jun}$	2	Survival varied during birth phase
S_{herd}	3	Survival varied by herd
S_{year}	3	Survival varied by year
S_t	12	Survival varied by month

[a] Number of parameters

Table 2. Models of bighorn ewe survival in the Black Hills, South Dakota, USA, 2010–2012 when $\hat{c}$ (a model term representing overdispersion) was 1.0 (i.e., assumed no dispersion).

Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	Deviance
$\{S_{May–June}\}$	204.614	0	0.826	2	200.604
$\{S_{Season}\}$	209.146	4.532	0.086	2	205.136
$\{S_{June–July}\}$	211.118	6.504	0.032	2	207.108
$\{S_{constant}\}$	212.365	7.751	0.017	1	210.362
$\{S_{vit}\}$	213.063	8.449	0.012	2	209.053
$\{S_{pregnant}\}$	214.197	9.583	0.007	2	210.187
$\{S_{winsev}\}$	214.335	9.720	0.006	2	210.324
$\{S_{coug}\}$	214.350	9.736	0.006	2	210.340
$\{S_{herd}\}$	214.958	10.344	0.005	3	208.937
$\{S_{year}\}$	216.045	11.431	0.003	3	210.024
$\{S_t\}$	218.936	14.322	0.001	12	194.665

[a] Composition and description of models are listed in Table 1

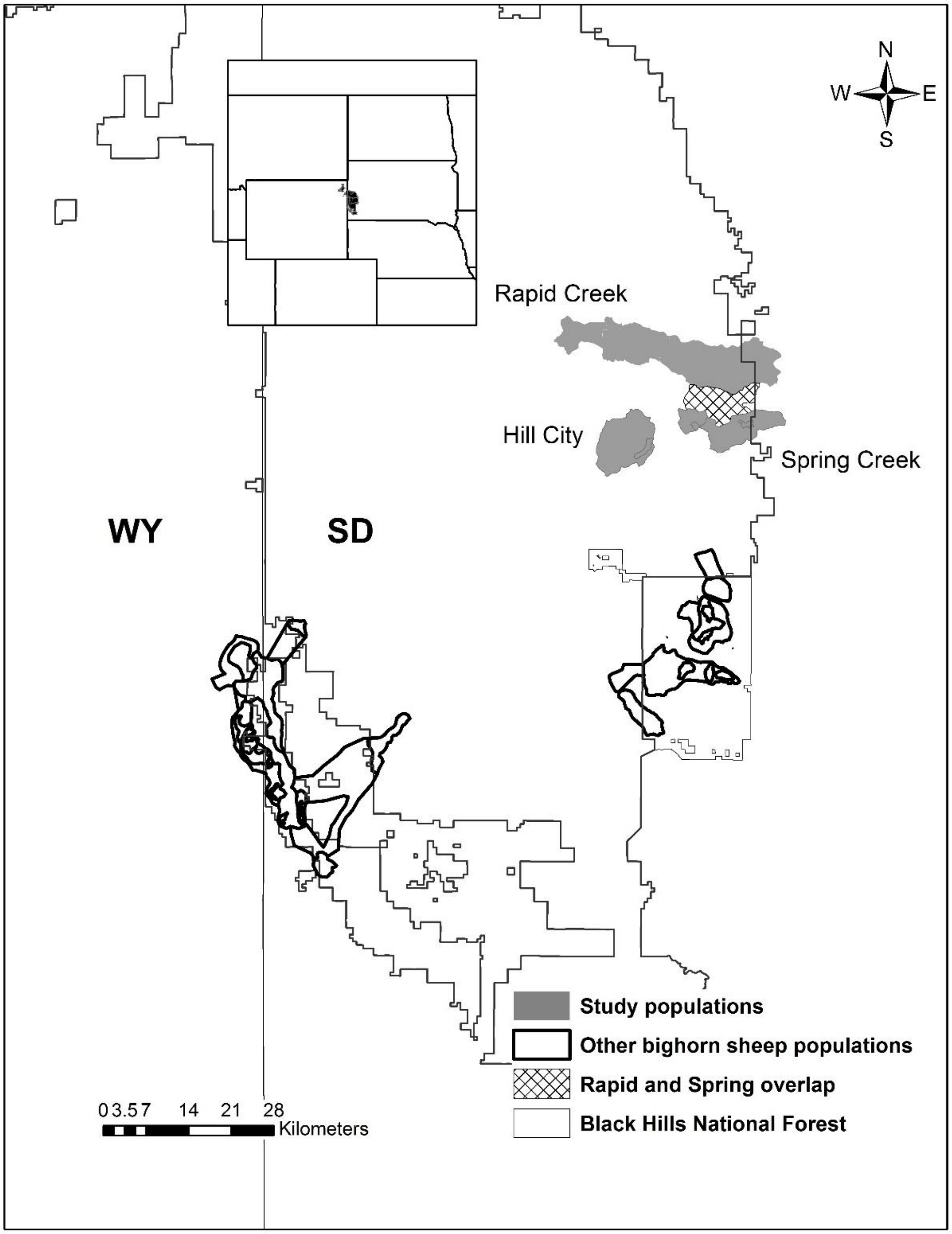
[b] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002)

[c] Difference in AIC_c relative to min AIC_c

[d] Akaike wt (Burnham and Anderson 2002)

[e] Number of parameters

Figure 1. Bighorn sheep populations and locations of study populations in the Black Hills, South Dakota, USA, 2010–2012.



CHAPTER 6: HABITAT SELECTION BY ADULT AND NEONATE BIGHORN SHEEP AT LOCAL AND LANDSCAPE SCALES

This chapter is being prepared for submission in the Journal of Wildlife Management and was coauthored by Troy W. Grovenburg, and Jonathan A. Jenks.

ABSTRACT Selection of parturition sites by wild ungulates involves trade-offs between maximizing forage quality/availability and minimizing predation risk. Previous studies documenting critical lambing habitat of bighorn sheep have relied on visual observations that can lead to biased results. From 2010–2012 we used vaginal implant transmitters (VITs) and intensely-monitored radiocollared ewes to: 1) accurately identify parturition events for bighorn sheep, 2) quantify habitat selection for parturition events at the macro- and microhabitat scales, and 3) quantify habitat selection of neonate lamb (≤24 hrs old) bed sites at the microhabitat scale in the Black Hills, South Dakota. Results of model-averaged generalized estimating equations revealed bighorn ewes selected for rugged terrain at both spatial scales, while at the macrohabitat scale ewes selected for areas that were close to perennial streams on south and west facing slopes and against anthropogenic disturbance. At the microhabitat scale, neonate lambs tended to select for greater cover and against north facing slopes. We hypothesize the patterns of selection we observed were related to predator-avoidance strategies and increased solar radiation. We also identified several parturition events outside of previously delineated lambing habitat and recommend mangers reassess areas defined by visual observations.

KEY WORDS bed site, bighorn sheep, birth site, Black Hills, generalized estimating equations (GEE), habitat selection, neonate, *Ovis canadensis*, parturition, vaginal implant transmitter (VIT)

INTRODUCTION

Selection of parturition sites by wild ungulates involves behaviors that can be influenced by their reproductive state as well as ecological conditions (Clutton-Brock et al. 1982, Festa-Bianchet 1988, Barbknecht 2011). Given these constraints, females likely make trade-offs between forage quality and predation risk (Berger 1991, Rachlow and Bowyer 1998) while simultaneously providing a favorable microclimate for neonates (Picton 1984, Bowyer et al. 1998). As neonate movements are often restricted during the first few weeks of life, ungulates are typically most vulnerable to predation during this time (Gailard et al. 2000, Raithel et al. 2007, Grovenburg et al. 2011*a*). Furthermore, human-induced disturbance also has been demonstrated to influence survival of neonates (Philips and Alldredge 2000, Singh et al. 2010). Thus, parturition sites should provide a means of predator avoidance (e.g., concealment; Van Moorter et al. 2009) and/or avoidance of anthropogenic disturbance.

Bighorn sheep (*Ovis canadensis*) are a well-studied species with considerable attention focused on seasonal habitat requirements (Fairbanks et al. 1987, Festa-Bianchet 1988, Bangs et al. 2005). Female bighorn sheep use steep and rugged terrain during lambing (Geist 1971, Shackleton 1999). Consequently, most studies have relied on visual observations of lambs at-heel, aerial observations, or a combination of visual observations with very high frequency (VHF) collars for delineating lambing habitat (e.g., Bleich et al. 1987, Etchberger and Krausman 1999, Bangs et al. 2005). However, reliance on such metrics may introduce bias towards areas of greater visibility or areas used by females after young are more mobile (Barbknecht 2008).

Despite increased use of vaginal implant transmitters (VITs) to capture and examine neonate survival of elk (*Cervus elaphus*; Barber-Meyer et al. 2008), deer (*Odocoileus* sp.; Bishop et al. 2007, Swanson et al. 2008), and bighorn sheep (Smith et al. 2014*a*), limited research has been conducted to identify or better quantify site-specific habitat characteristics at bighorn sheep parturition sites. Barbknecht et al. (2011) noted that <10 of 169 parturition sites identified using VITs occurred within previously delineated parturition range for elk in Wyoming. Given the more rugged terrain used by bighorn sheep for parturition, similar discrepancies are likely, potentially influencing management-related decisions.

The objectives of our study were to assess the effectiveness of using VITs, versus intensely-monitored radiocollared ewes, to document parturition sites of bighorn sheep in the Black Hills, South Dakota. Second, we assessed habitat selection for parturition events at 2 scales: 1) macrohabitat or study area and 2) microhabitat (≤150m from parturition sites); corresponding to Johnson's (1980) level II and III hierarchy, respectively. Third, because females choose the parturition site and neonates choose bed sites (Van Moorter et al. 2009), we also assessed neonate lamb (≤24 hrs old) bed site selection at the microhabitat scale.

STUDY AREA

The Black Hills are located in southwestern South Dakota and eastern Wyoming, USA. Topography of the area varied from steep ridges, rock outcrops, canyonlands, and gulches to upland prairie, rolling hills, and tablelands. Elevations ranged from 973 to 2,202 m above mean sea level (Froiland 1990). Ponderosa pine (*Pinus ponderosa*) forest comprised 83% of the landscape (USGS 2013). Mixed grass prairie (5%), riparian (4%), aspen (*Populus tremuloides*)-mixed conifer forest (3%), and developed open space (2%) were other major land cover types present in our study area (USGS Gap Analysis Program 2013). During our study, average annual precipitation in the project area was 53 cm. Mean temperatures ranged from a maximum of 28° C in July to a minimum of −10° C in January. Climate values were based on data collected at the Hill City, South Dakota weather station from 1981–2010 (National Oceanic and Atmospheric Administration [NOAA] 2013).

Our study area was located in the east-central portion of the Black Hills with bighorn sheep habitat encompassing an area of approximately 26,000 ha. Each herd (Rapid Creek, Spring Creek, and Hill City) maintained distinct wintering areas; however, we did observe some range overlap between Spring Creek and Rapid Creek ewes during the lambing season (Figure 1). Over the course of our study, no range overlap was observed between our study herds and other herds in the Black Hills. In 2010, breeding-age ewe population estimates were: Rapid Creek = 56, Spring Creek = 50, and Hill City = 10 (South Dakota Department of Game, Fish, and Parks, Rapid City, SD, unpublished data). Estimated proportion of ewes radiocollared by herd across years were: Rapid Creek 25%–29% (2010–2012), Spring Creek 30%–42% (2010–2012), and Hill City 90%–100% (2011–2012). Other ungulates in the study area included mule deer (*O. hemionus*), white-tailed deer (*O. virginianus*), mountain goats (*Oreamnos americanus*), and elk. Potential predators of bighorn sheep included cougars (*Puma concolor*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

METHODS

We captured adult ewes using a drop-net baited with weed-free alfalfa hay or sheep were chemically immobilized (BAM; 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine) via dart rifle (Dan-Inject, Børkop, Denmark, EU). We estimated ewe age class (1 year, 2 years, 3 years, or ≥4 years) based on tooth replacement (Krausman and Bowyer 2003). We evaluated pregnancy status of ewes via ultrasonography (Universal Ultrasound, Bedford Hills, NY) at time of capture. We fitted pregnant ewes with M3930 VITs manufactured by Advanced Telemetry Systems (ATS; Isanti, MN) with a redesigned wing system and antenna length of 6 cm (Bishop et al. 2011). Ewes that were not pregnant or not checked for pregnancy at the time of capture were not fitted with VITs. Methods of VIT deployment followed Bishop et al. (2011). In addition to receiving VITs, we fitted ewes with either very high frequency (VHF; M252OB, ATS; n = 50) or Global Positioning System (GPS; G2110D, ATS; n = 11) radio collars that were uniquely marked to facilitate individual identification. Lamb captures, and ewe and VIT monitoring, are summarized in Smith et al. (2014*b*). We identified parturition sites based on presence of placenta, lamb presence, observation of birth, or by site characteristics including a cleared area, moist soil, or characteristic odor (Barbknecht et al. 2011). All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Habitat Data Collection

To estimate available habitat, we generated herd-specific minimum convex polygons using the *adehabitatHR* package (Calenge 2006) in Program *R* (R Core Team 2014) using locations from GPS collared ewes and all lamb capture/birthing sites for each respective herd. We then generated 95% Brownian bridge movement models (BBMM; Horne et al. 2007) by herd from GPS collared ewes and buffered estimates of available habitat by 50% (700 m) of home range area to account for possible movements of VHF collared ewes. Because treating habitat use as a single point may increase bias (Rettie and McLoughlin 1999), we created 400-m buffers surrounding lamb capture sites, birth sites, and random points. The 400-m buffer corresponded to the average 1-week postpartum 100% BBMM area used (0.49 km^2) by GPS collared ewes. We generated all BBMM using the *BBMM* package (Nielson et al. 2013) in Program *R*.

Because we were using average weekly movements, we compared ewe parturition sites, as well as sites where lambs were captured at ≤24 hr of age, to available habitat at the macrohabitat scale using GIS technology. We created a landscape fragmentation layer for forested cover using the 2011 National Land Cover Database (Jin et al. 2013) and morphological image processing with The Landscape Fragmentation Tool (LFT v2.0) for ArcGIS available from the University of Connecticut Center for Land Use Education and Research (CLEAR). The types of fragmentation present in a specific land cover based on pixel-level patterns and classified fragmentation are core, perforated, edge, and patch based on edge width (Vogt et al. 2007, Wilson and Arnold 2009). Core habitat was interior pixels not degraded from the "edge effect" and was sub-classified as small (<101.17 ha), medium (101.17 ha – 202.34 ha), and large core (>202.34 ha) areas (Vogt et al. 2007, Wilson and Arnold 2009). Perforated habitat was comprised of pixels that made up the interior edge of small, non-target habitat areas within a core, such as a house built within the woods. Edge comprised the exterior periphery of core habitat tracts where they intersected non-target habitat areas (Vogt et al. 2007, Wilson and Arnold 2009). Patch represented small fragments of a habitat that were completely surrounded by non-target habitat areas (Vogt et al. 2007, Wilson and Arnold 2009). We reclassified land cover as 0 (non-targeted habitat) and 1 (forested habitat), set edge width to 100 m, and input the coverage into the Landscape Fragmentation Tool (Wilson and Arnold 2009). The resulting fragmentation layer provided a categorical index (0–6) indicating degree of forested fragmentation; lower values indicated greater fragmentation.

We then reclassified these layers as closed (1; values 4–6) or open (0; values 0–3) forest types.

We used a vector ruggedness measure (VRM) layer (Sasmal et al. 2013) that incorporated the heterogeneity of both slope and aspect (Sappington et al. 2007). The VRM used 30-m National Elevation Dataset (NED; Gesch et al. 2002) of merged individual tiles for a continuous layer for South Dakota and measured ruggedness using 3-dimensional dispersion of vectors normal to planar facets on a landscape (Sappington et al. 2007). The VRM ArcScript (ESRI Inc., Redlands, CA) decomposed unit vectors normal (orthogonal) to each grid cell into their x, y, and z components using the slope and aspect of each cell (Pincus 1956, Durant 1996, Sappington et al. 2007). The resultant vector was then calculated over a 3 × 3 neighborhood centered on each cell, using a moving-window. The magnitude of the resultant vector was then subtracted from 1, which resulted in a dimensionless ruggedness layer containing an index that ranged from 0 (flat) to 1 (most rugged; Hobson 1972, Sappington et al. 2007).

We quantified the influence of human population using housing density information derived from the U.S. Census 2010 TIGER data. We computed housing density (hectare per housing unit) by allocating housing units to 1-ha cells (Theobald 2005, Theobald et al. 2011). We quantified the influence of roads by creating a density function to account for the direct impact of road presence within a 30-m cell using U.S. Census TIGER 2010 data. We assigned human disturbance values of 10 (interstates and highways), 5 (secondary roads), 3 (local roads), and 1 (four-wheel drive roads) to each road type (Theobald 2010, Theobald et al. 2012). We used the focal statistics tool in ArcMap 10.0 (ESRI Inc., Redlands, CA) to calculate the average value for roads, ruggedness, housing, and forest fragmentation layers within the 400-m buffer for both selected and random sites.

We used the aspect spatial analyst tool in ArcMap to create aspect rasters from the NED. We separated aspect into 4 classes representing 90° increments centered on the 4 cardinal directions (Barbknecht et al. 2011). We created a perennial streams layer (class 4 and 5) derived from the Black Hills National Forest website, and used the near tool in ArcMap to calculate distance to secondary roads, highways, and streams from the centroid of all selected and random sites.

We collected microhabitat variables at birth sites, initial lamb capture locations where lambs were bedded and estimated to be ≤24-hrs old, and at paired random sites located ≤150 m from selected sites (bed or birth). We used the ≤150 m distance for random locations to ensure they were in similar habitats as selected sites. We estimated visual obstruction at each site using a 1-m^2 visual obstruction cloth (Kennedy 1992, DePerno et al. 2003). The cloth was separated into 2 sections, the bottom 50 squares (0.0–0.5 m) was considered representative of visual obstruction available to a bedded ewe/lamb (laying), and the top 50 squares (0.5–1.0 m) was considered representative of visual obstruction available to a standing ewe (standing; Bowyer 1986). The cloth was held perpendicular to the ground and four readings, one from each of the 4 cardinal directions, was made from a distance of 10 m from plot center and 1 m above ground level. If a square was ≥50% covered it was considered concealed and the number of squares concealed in each of the 2 sections represented the amount of visual obstruction available to a bedded and standing ewe/lamb, respectively. We also visually estimated the distance at which the visual obstruction cloth was 90% concealed in each of the 4 cardinal directions. We used the uphill and downhill as well as the average of the 4 visual obstruction percentages and distances for each location as potential covariates in models.

We used a 10-factor prism (Jim-Gem® Square Prisms: Forestry Suppliers, Inc., Jackson, MS) to estimate tree basal area (BA) at each selected and random site center (Sharpe et al. 1976) and classified sites as either young (DBH ≥12.7 cm) or shrub/sapling (<12.7 cm) based on USDA Forest Service criteria. We estimated tree canopy cover using a spherical densiometer (Geographic Resource Solutions, Arcata, CA) at selected and random site centers in each of the 4 cardinal directions. We also estimated average slope at each site using an inclinometer (Forestry Suppliers, Inc.) arranged in the 4 cardinal directions from the center point. Additionally, we estimated slope center at the birth/bed site and geometric center of random points. We attempted to collect microhabitat data within 30 days of the event or after lambs had moved from the area; however, due to the duration of the lambing season (~6 weeks; Smith et al. 2014*a*) this was not always feasible. Nevertheless, because we collected habitat data from selected and random sites at the same time of year, and the predominant vegetation was evergreen (i.e., ponderosa pine), we do not consider timing of data collection a significant source of bias.

Data Analysis

We performed all statistical analyses using SAS 9.3 (SAS Institute Inc., Cary, NC). We used logistic regression to test for relationships between presence/absence of a bed/birth site and independent variables. We used the generalized estimating equations (GEE) method to account for possible spatial and temporal correlation among outcome variables (i.e., individuals monitored for >1 year, and correlation within herds; Cui and Qian 2007, Pan 2001, Grovenburg et al. 2011*b*); repeated observations of an individual in a longitudinal study (i.e., outcome variable repeatedly measured on ≥2 occasions over time) were likely correlated because of the continuity of measurement over time (Burger et al. 2000, Cui and Qian 2007). The GEE method is an extension of the generalized linear model (Nelder and Wedderburn 1972) and enabled appropriate analysis of correlated data (Cui and Qian 2007).

We first tested for correlation between variables using Pearson's correction coefficient ($r \geq |0.7|$) and exchanged correlated variables within models. For example, we found standing and laying concealment were highly correlated; therefore, we used the standing estimates for birth sites and laying estimates for bed sites at the microhabitat scale. We generated 3 separate sets of models to assess site selection: 2 models for ewe parturition sites (macro- and microhabitat scales) and one for lamb bed site selection (microhabitat scale). Because we used average weekly movements for macrohabitat analysis, we included lamb capture sites where lambs were ≤24 hrs old in addition to parturition sites for analysis. We generated a priori models and used quasi-likelihood under the independence model criterion (QICu) for GEE to select models that best described the data (Cui and Qian 2007, SAS Institute Inc. 2012, Allison 2012). The fit statistic QICu is an approximation of QIC that is recommended as the GEE equivalent of the Akaike's information criterion (AIC) statistic for comparing models with different sets of predictor variables (Pan 2001, Allison 2012). The GEE method is based on quasi-likelihood theory (Wedderburn 1974) and not maximized-likelihood theory for independent observations (McCullagh and Nelder 1989). Consequently, model selection statistics such as AIC (Burnham and Anderson 2002) cannot be applied directly to the GEE method (Cui and Qian 2007, SAS Institute Inc 2012). When comparing models with QICu, the model with the smaller QICu statistic is preferred and is appropriate for selecting regression models; we considered models differing by ≤2 ΔQIC from the selected model as potential alternatives (Pan 2001, SAS Institute Inc 2012). To better determine the relative probability of a model, we calculated model weights (w_i) as an indication of support for each model and used a multimodel inference approach to average parameter estimates across competing models (Burnham and Anderson 2002).

RESULTS

From 2010–2012 we documented 71 unique sites (20 in 2010, 27 in 2011, and 24 in 2012) for inclusion in macrohabitat analyses (43 birth sites and 28 capture sites where lambs were ≤24 hrs old). Of the 43 birth sites documented, we located 29 (67%) from VITs. Additionally, because we were able to document bed and birth site locations for 19 lambs, we incorporated 47 lamb bed sites (15 in 2010, 16 in 2011, and 16 in 2012) in addition to the 43 birth sites (14 in 2010, 14 in 2011, and 15 in 2012) for microhabitat analyses. In cases where we could document unique bed and birth sites for lambs, bed sites were on average 32.3 m (range = 4.6–89.9 m) from birth sites.

At the macrohabitat scale, 3 models were within 2 ΔQICu (Table 1); thus, we used model averaged parameter estimates based on model weights. Beta coefficients that did not incorporate 0 indicated bighorn sheep parturition sites were more likely to be located in areas with higher ruggedness values, close to streams, and were less likely to be located in areas close to major roads, areas with high housing density, or on north and east facing slopes (Tables 2, 3). At the microhabitat scale for ewe parturition sites, 4 models were within 2 ΔQICu (Table 4); again, we used model averaged estimates. Center slope, slope, and north beta coefficients did not incorporate 0, indicating bighorn sheep selected for relatively flat areas within steep terrain and selected against north-facing slopes (Tables 5, 6). To evaluate model predictive power we classified scaled probability of use for parturition sites for our top-ranked models (Tables 1, 4). Overall, both models functioned well, predicting 77% of macro and 86% of micro sites containing probabilities >0.50.

Neonate lamb bed site selection included 3 models that were within 2 ΔQICu (Table 6); thus, we used model averaged parameter estimates. Similar to parturition sites, bed sites were more likely to be located in relatively flat areas within more rugged terrain with lambs selecting against north-facing slopes. However, lambs also tended to select for areas with greater downhill cover at 10 m and with less distance to 90% concealment in the uphill direction (Table 5, 7). Our top-ranked model predicted 81% of bed sites with probabilities >0.50.

DISCUSSION

The use of VITs proved an effective tool for locating bighorn sheep parturition sites. When we were able to document parturition sites, they were twice as likely to be from ewes that had successful VITs (defined as remaining in ewe until ≤1 day from parturition; Smith et al. [2014*b*]) rather than from intensely monitored radiocollared ewes. Overall, we were able to document parturition sites from 67% (29/43) of ewes that had successful VITs versus 26% (14/53; Smith et al. 2014*b*) for ewes that were not equipped with VITs or from ewes with failed VITs.

Bighorn sheep selected parturition sites that were located on steeper slopes and faced south and west at both the macro- and microhabitat scales. Ruggedness, or distance to escape terrain, has routinely been noted as an important component of habitat for mountain sheep and is used to minimize predation risk (Geist, 1971, Krausman and Leopold 1986, Bleich et al. 1997, Rachlow and Bowyer 1998, Bangs et al. 2005); cougars most often have been implicated as the major source of predation (e.g., Ross et al. 1997, Rominger et al. 2004). In fact, Berger (1991) reported higher frequency of lamb kills in flat or open terrain (71%) than in steep or rugged terrain (22%), and Festa-Bianchet (1988) reported bighorn sheep made trade-offs between risk of predation and foraging. Considering the relatively high rates of lamb predation in the Black Hills (30%; Smith et al. 2014*a*), selection for these more rugged areas would be expected.

At the macrohabitat scale, bighorn sheep also selected areas that were closer to streams, away from major roads, and areas with lower housing density. Whether ewes were actively selecting for areas that were farther from major roads with lower housing density specifically, or whether rugged areas are, by default, more likely to be located in these areas, is difficult to ascertain. However, we found no correlation between these variables, and Papouchis et al. (2001) found desert bighorn sheep (*O. canadensis nelsoni*) were influenced by distance to roads and that in some instances this represented a 15% decrease in use of potential suitable habitat. Our results tend to validate their assessment, as well as those of others (e.g., Zeigenfuss et al. 2000), that human disturbance can influence bighorn sheep behavior, and selection for parturition sites.

Bighorn sheep selection for areas near water has been somewhat equivocal, with some finding selection for areas closer to permanent water (Brundige and McCabe 1986) while others have found no selection (Bleich et al. 1997, Bangs et al. 2005) or distance to water increasing during the lambing season (DeCesare and Pletscher 2006). These findings could be related to bighorn sheep being able to meet their water demands through forage (Krausman and Etchberger 1995) or other non-perennial water sources. In our study, bighorn sheep selected for areas that were closer to perennial streams. Additionally, because water demands of lactating ewes would be expected to increase, and young lambs lack significant mobility, Smith et al. (1991) suggested water sources need to be within 675 m from desert bighorn lambing terrain. Our results revealed selected sites were on average 697 m (SD = 915 m) from perennial streams while random sites were on average 1,495 m (SD = 1,116 m) from streams.

At both the micro- and macrohabitat scales, aspect occurred in our top models and we consistently found a negative association with north and east facing slopes. Selection for south and west facing slopes may be related to solar radiation provided by these areas. Mean parturition date for lambs in our study was ~ 15 May across years (Smith et al. 2014*a*), and we routinely observed periods of snow or cold rains occurring during the lambing season. In 2010, we documented 5 lamb births following a fairly significant snowfall (~ 15 cm). Furthermore, in 2011, we observed one lamb mortality from apparent hypothermia (Smith et al. 2014*a*) after it was born during a particularly cold rain. Such events would tend to favor lambs born in areas with greater solar radiation. These areas also may provide greater available forage for ewes than north or east facing slopes, although we made no assessment of this in our study.

At the microhabitat scale, slope and center slope also were included in all our top-ranked models for both parturition and lamb bed sites. The fact that slope and ruggedness were significant at both spatial scales highlights how important escape terrain is for bighorn sheep. In contrast, the beta coefficient for center slope was negative, suggesting that not all rugged habitat may be suitable during this crucial time. Ewes and lambs consistently selected for more level areas within this rugged terrain demonstrating the importance of this feature during the first 48 hrs postpartum. We also found no strong definitive association indicating ewes were selecting for any type of concealment at the microhabitat scale. However, despite the fact that lamb bed sites were on average 32.3 m from parturition sites, we found neonate lambs were selecting for greater cover at 10 m in the downhill direction (62%) versus random sites (40%), while distance to 90% concealment in the uphill direction was lower for selected (16.4 m) than random sites (27.2 m). Selection for cover at a relatively close distance in the downhill direction would be more likely to reduce the risk of being spotted by a predator from the opposite ridge or valley floor, while the use of relatively flat areas within this rugged terrain likely negated the need for cover at such a fine scale in the uphill direction. For instance, most sites located on these “shelves” contained a relatively high rock embankment on the uphill side that functioned to block lambs until within a few meters. Smith et al. (2014*a*) found risk of predation for lambs was minimal during the first week post-partum, but increased during weeks 2–3 after lambs had become more mobile. Thus, selection for areas with this unique set of concealment is likely a predator-avoidance response.

MANAGEMENT IMPLICATIONS

The use of VITs provided an effective means for documenting timing and location of parturition events, and could provide researchers an opportunity to revisit or validate habitat requirements for parturient bighorn sheep. Accurate assessment of crucial lambing habitat and factors influencing selection for such areas is imperative for increasing effectiveness of management activities or restrictions that may be applied by managers. Our study revealed several parturition events that were outside of identified lambing habitat that were previously defined by visual observations or VHF-collared animals. Managers should consider redefining lambing habitat using VIT technology. Focusing management activities to areas with rugged terrain that has sufficient areas for parturition (i.e., shelves), especially on south and west facing slopes, reducing the amount of human disturbance (e.g., housing density), or protecting existing habitat away from such disturbance, would further increase parturition habitat.

ACKNOWLEDGEMENTS

We thank S. Griffin, J. Broecher, B. Juarez, B. Tycz, L. Meduna., L. Dahl, J. Kanta, A. Lindbloom, T. Berdan, J. Schmit, and J. Felio for capture and monitoring and D. Wilckens for helpful comments on early drafts of the manuscript. Thanks also to the Civil Air Patrol and pilots L. Becht and G. Kirk for assistance with flight time. Funding for this study was provided by Federal Aid to Wildlife Restoration administered by South Dakota Department of Game, Fish and Parks (Study No. 7537).

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Table 1. Logistic regression models using the generalized estimating equations (GEE) method for estimating macrohabitat at bighorn sheep parturition sites (*n* = 71) in the Black Hills, SD from 2010–2012.

Models[a]	K^b	QICu[c]	ΔQICu[d]	w_i^e
rug + dist_road + dist_strm + aspect	8	136.834	0.000	0.368
rug + aspect + dist_strm	7	137.925	1.090	0.213
rug + aspect	6	138.104	1.269	0.195
rug + aspect + dist_road	7	139.520	2.686	0.096
rug	2	140.642	3.808	0.055
housing + rug + road + forest_cover + dist_road + dist_strm + aspect	11	141.960	5.125	0.028
rug + road	3	142.252	5.418	0.024
rug + housing	3	142.616	5.781	0.020

[a] rug = average ruggedness value (0–1) within 400m radius of parturition or random sites, dist_road = distance to nearest road from parturition site or geometric center of random sites, dist_strm = distance to nearest perennial stream from parturition site or geometric center of random sites, aspect = 4 cardinal directions in relation to west, housing = average housing density within 400m radius of parturition or random sites, forest_cover = percentage of closed forest cover within 400m radius of parturition or random sites.
[b] Number of parameters.
[c] Quasi likelihood under the independence model criterion for GEE (Cui and Qian 2007).
[d] Difference in QICu relative to minimum QICu.
[e] QIC model weight.

Table 2. Model averaged parameter estimates and 95% confidence intervals for bighorn parturition site (*n* = 71) selection at the macrohabitat scale in the Black Hills, South Dakota, 2010–2012.

Parameter[a]	*β*	Lower (95% CI)	Upper (95% CI)
Intercept	−2.927	−3.620	−2.235
Rug	212.422	153.672	271.172
Dist_road	2.173×10^{-4}	-1.341×10^{-4}	-3.00×10^{-4}
Dist_stream	3.016×10^{-4}	-4.211×10^{-4}	-1.822×10^{-4}
North	−0.963	−1.771	−0.155
East	−1.150	−2.128	−0.171
South	0.430	−0.193	1.053
Housing	-2.268×10^{-5}	-4.180×10^{-5}	-3.563×10^{-6}
Road	−0.025	−0.222	0.172
Forest_cover	5.078×10^{-3}	−0.004	0.014

[a] rug = average ruggedness value (0–1) within 400m radius of parturition or random sites, dist_road = distance to nearest road from parturition site or geometric center of random sites, dist_strm = distance to nearest perennial stream from parturition site or geometric center of random sites, housing = average housing density within 400m radius of parturition or random sites, forest_cover = percentage of closed forest cover within 400m radius of parturition or random sites.

Table 3. Mean and standard deviation (SD) for habitat variables at bighorn sheep parturition or lamb capture sites (*n* = 47) and random sites (*n* = 47) at the macrohabitat scale in the Black Hills, South Dakota, 2010–2012.

Variable	Selected	SD	Random	SD
Housing (houses/ha)	47.33	53.95	160.90	532.45
Ruggedness	0.02	0.01	0.01	0.01
Roads (density value)	0.06	0.14	0.15	0.27
Forest core (%)	0.74	0.23	0.67	0.32
Dist. to road (m)	1491.66	816.62	1271.78	982.43
Dist. to stream (m)	697.21	915.23	1495.33	1116.24
North (proportion)	0.03		0.15	
East (proportion)	0.11		0.30	
South (proportion)	0.51		0.31	
West (proportion)	0.35		0.24	

Table 4. Top-ranked a priori logistic regression models using the generalized estimating equations (GEE) method for estimating microhabitat at bighorn sheep parturition sites (*n* = 43) in the Black Hills, SD from 2010–2012.

Models[a]	*k*[b]	QICu[c]	ΔQICu[d]	w_i[e]
censlope + aspect + dhdist + slope	8	99.812	0.000	0.280
censlope + aspect + slope	7	100.717	0.905	0.178
censlope + aspect + dhcover + dhdist + slope	9	101.147	1.335	0.144
censlope + aspect + uhdist + slope	8	101.362	1.550	0.129
censlope + aspect + dist + slope	8	102.087	2.275	0.090
censlope + aspect + uhcover + uhdist + slope	9	102.703	2.891	0.066
censlope + aspect + dhcover + dhdist + slope + cc + sa	11	103.327	3.515	0.048
censlope + aspect + cover + dist + slope	9	104.046	4.234	0.034
censlope + aspect + standing + dist + slope + cc + sa	11	105.635	5.823	0.015
censlope + aspect + uhcover + uhdist + slope + cc + sa	11	105.706	5.894	0.015
uhstanding + uhdist	4	115.588	15.776	0.000

[a] censlope = slope at center of selected or random site, aspect = the 4 cardinal directions in relation to west, dhdist = distance (m) in the downhill direction where cover board was estimated to be 90% concealed from site, slope = average slope in the 4 cardinal directions at 10m from, dhcover = percent of cover board concealed at 10m in the downhill direction from site, uhdist = distance in the uphill direction where cover board was estimated to be 90% concealed from site, dist = average distance in the 4 cardinal direction where cover board was estimated to be 90% concealed, uhcover = percent of cover board concealed at 10m in the uphill direction from site, cc = canopy cover at site, sa = stand age (1 = young; 0 = shrub/sapling) at site, and cover = average percent cover board concealed at 10m in the 4 cardinal directions.

[b] Number of parameters.

[c] Quasi likelihood under the independence model criterion for GEE (Cui and Qian 2007).

[d] Difference in QICu relative to minimum QICu.

[e] QIC model weight.

Table 5. Model averaged parameter estimates and 95% confidence intervals for bighorn lamb bed site (*n* = 47) and ewe parturition site (*n* = 43) selection at the microhabitat scale in the Black Hills, South Dakota, 2010–2012. Selected bed and birth sites compared to random locations at ≤150m from selected sites.

	Bed sites			Birth sites		
Parameter	*β*	Lower (95% CI)	Upper (95% CI)	*β*	Lower (95% CI)	Upper (95% CI)
Intercept	0.591	−1.272	2.454	−0.928	−2.320	0.463
Censlope	−0.131*	−0.176	−0.087	−0.070*	−0.105	−0.036
South	0.831	−0.301	1.964	1.289	−0.080	2.657
West	0.697	−0.405	1.799	0.794	−0.868	2.457
North	−3.297*	−4.825	−1.768	−0.510*	−2.625	1.604
Dhcover	0.875*	0.394	1.357	−0.071	−0.269	0.126
Dhdist	−0.006	−0.015	0.003	−0.009	−0.021	0.002
Slope	0.044*	0.005	0.083	0.035*	0.003	0.068
Uhcover	−0.187	−0.647	0.273	0.024	−0.069	0.118
Uhdist	−0.017*	−0.033	−0.002	−0.003	−0.009	0.004
CC	−0.187	−0.525	0.152	0.031	−0.080	0.143
SA	−0.008	−0.025	0.010	0.003	−0.002	0.008
Dist	0.000	−0.001	0.001	−0.001	−0.006	0.004
Cover	0.001	−0.009	0.012	0.016	−0.082	0.115

*Indicates 95% CI did not incorporate 0.

Table 6. Mean habitat variable values for bighorn sheep lamb bed sites (≤24 hrs old) (n = 47) and ewe parturition sites (n = 43) at the microhabitat scale in the Black Hills, South Dakota, 2010–2012.

Variables[a]	Birth sites	SD	Random	SD	Bed sites	SD	Random	SD
Center slope (degrees)	8.70	6.19	18.00	11.67	11.40	6.94	22.57	11.51
Uphill cover (%)	0.58	0.43	0.29	0.37	0.61	0.44	0.51	0.40
Uphill dist. (m)	17.15	14.48	27.93	15.44	16.39	11.91	27.23	16.21
Downhill cover (%)	0.43	0.41	0.33	0.35	0.62	0.39	0.40	0.36
Downhill dist. (m)	19.28	12.13	32.93	25.75	21.62	12.52	37.64	26.84
Dist. (m)	23.64	13.34	24.52	11.62	24.58	14.05	24.71	11.71
Cover (%)	0.45	0.26	0.33	0.26	0.52	0.29	0.51	0.25
Slope (degrees)	38.10	13.31	29.77	13.14	37.11	13.30	30.44	9.27
Canopy cover (%)	0.43	0.30	0.56	0.29	0.47	0.31	0.43	0.29
Stand age (dbh)	10.87	5.44	11.51	4.31	11.79	4.24	12.28	4.74
North (%)	0.02		0.16		0.02		0.28	
East (%)	0.05		0.35		0.11		0.17	
South (%)	0.60		0.09		0.45		0.34	
West (%)	0.33		0.40		0.43		0.21	

[a] Variables defined in Table 4.

Table 7. Top-ranked a priori logistic regression models using the generalized estimating equations (GEE) method for estimating microhabitat at neonate lamb (≤24 hrs old) bed sites (*n* = 47) in the Black Hills, SD from 2010–2012.

Models[a]	K[b]	*QICu*[c]	*ΔQICu*[d]	w_i[e]
censlope + aspect + dhcover + dhdist + slope	9	86.932	0.000	0.339
censlope + aspect + uhcover + uhdist + slope	9	87.531	0.599	0.251
censlope + aspect + dhcover + dhdist + slope + cc + sa	11	88.919	1.988	0.125
censlope + aspect + uhdist + slope	8	89.150	2.219	0.112
censlope + aspect + uhcover + uhdist + slope + cc + sa	11	90.265	3.333	0.064
censlope + aspect + dhdist + slope	8	91.039	4.107	0.043
censlope + aspect + slope	7	91.048	4.116	0.043
censlope + aspect + dist + slope	8	93.171	6.239	0.015
censlope + aspect + cover + dist + slope	9	95.049	8.117	0.006
censlope + aspect + cover + dist + slope + cc + sa	11	97.482	10.551	0.002
dhcover + dhdist	4	120.887	33.955	0.000

[a] censlope = slope at center of selected or random site, aspect = the 4 cardinal directions in relation to west, dhcover = percent of cover board concealed at 10m in the downhill direction from site, dhdist = distance (m) in the downhill direction where cover board was estimated to be 90% concealed from site, slope = average slope in the 4 cardinal directions at 10m from, uhcover = percent of cover board concealed at 10m in the uphill direction from site, uhdist = distance in the uphill direction where cover board was estimated to be 90% concealed from site, cc = canopy cover at site, sa = stand age (1 = young; 0 = shrub/sapling) at site, dist = average distance in the 4 cardinal direction where cover board was estimated to be 90% concealed, and cover = average percent cover board concealed at 10m in the 4 cardinal directions.

[b] Number of parameters.

[c] Quasi likelihood under the independence model criterion for GEE (Cui and Qian 2007).

[d] Difference in QICu relative to minimum QICu.

[e] w_i = model weight.

Figure 1. Bighorn sheep populations and locations of study populations in the Black Hills, South Dakota, USA, 2010–2012.