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Population Ecology of Rocky Mountain Elk in the Black Hills, South Dakota and Wyoming

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POPULATION ECOLOGY OF ROCKY MOUNTAIN ELK IN THE BLACK HILLS, SOUTH DAKOTA AND WYOMING

BY

BENJAMIN D. SIMPSON

A thesis submitted in partial fulfillment of the requirements for the

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2015

POPULATION ECOLOGY OF ROCKY MOUNTAIN ELK IN THE BLACK HILLS, SOUTH DAKOTA AND WYOMING

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries Science degree and as acceptable for meeting the thesis 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.

Jonathan A. Jenks, Ph.D.
Thesis Advisor Date

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Head, Department of Natural Resource Management Date

Dean, Graduate School Date

This thesis is dedicated to my grandfather, Lyman D. Currier

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ABSTRACT

POPULATION ECOLOGY OF ROCKY MOUNTAIN ELK IN THE BLACK HILLS, SOUTH DAKOTA AND WOMYING

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We conducted a 2-year (2012–2013) study of survival and cause–specific mortality using individually marked adult cow and neonate elk (*Cervus elaphus*) occupying the southwestern region of the Black Hills. We used known-fate analysis in Program MARK for survival analysis of adult cows and calves. We estimated survival and cause-specific mortality of 49 adult female elk over the 2 years of the study. Annual adult cow survival was 0.85 (95% CI = 0.72–0.87). We documented 12 mortalities with harvest (58.3%) and predation (16.6%) accounting for the majority of known mortalities. We captured and fit 71 neonates $\leq$10 days of age with expandable Very High Frequency (VHF) radiocollars during summer 2012 (n = 37) and 2013 (n = 34). Annual (12 month) survival of elk calves was 0.75 (95% CI = 0.61–0.84) while summer (20 weeks; 15 May–25 September) survival was 0.79 (95% CI = 0.68–0.88). Predation accounted for 87.5% of mortalities; remaining mortalities were from starvation (6.3%) and unknown (6. 3%) causes. We used Global Positioning System (GPS) collars to collect 167,707 locations to determine home range, movement ecology, and macro-scale resource selection of 48 adult cow elk. We documented elk using a variety of migration strategies (obligate migrator, resident, conditional migrator, disperser); the majority of the population (58%) was migratory. Spring migration distance travelled ranged from 2.45 km – 74.44 km (n = 42); fall migration distances ranged from 6.41km –

153.95 km (*n* = 46). We used 99% Brownian Bridge Movement Models to create seasonal and overall home ranges of adult cow elk. Mean overall home range size for conditional migrators was 249.28 km^2 (SE = 28.60, *n* = 7, range = 233.75), for obligate migrant elk it was 227.18 km^2 (SE = 13.94, *n* = 29, range = 346.83), and for resident elk it was 175.65 km^2 (SE = 22.75, *n* = 11, range = 216.04). We used discrete choice models to determine resource selection at the macro-habitat scale of collared adult elk using ArcMap 10.1 data. Adult cow elk selected for open grassland/herbaceous areas and early successional forest areas close to forested edges at higher elevations. Our study showed that elk populations have the ability to thrive within an ecosystem with healthy predator populations.

CHAPTER 1: CAUSE SPECIFIC-MORTALITY OF FEMALE ROCKY MOUNTAIN ELK (*Cervus elaphus*) IN THE BLACK HILLS, SOUTH DAKOTA, AND WYOMING

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

Cause Specific-Mortality of Female Rocky Mountain Elk (Cervus Elaphus) In the Black Hills, South Dakota, and Wyoming

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ABSTRACT.— Recent declines in population size and juvenile recruitment of elk (*Cervus elaphus*) in the Black Hills require information on factors affecting mortality and survival. We estimated survival and cause-specific mortality of 49 adult female elk (*Cervus elaphus*) in the Black Hills, South Dakota, and Wyoming, USA between 2012 and 2013. We documented 12 mortalities with harvest (58.3%) and predation (16.6%) accounting for the majority of known mortalities. We used known fate analysis in Program Mark to estimate annual survival; model $\{S_{\text{Fall/Harvest}}\}$ was our best approximating model ($w_i = 0.87$) indicating that survival differed between the Fall/Harvest season and the remainder of the year. Monthly survival estimates for Fall/Harvest were 0.97 (95% CI = 0.944–0.984) while survival for the remainder of the year was 0.99 (95% CI = 0.985–0.998) and overall annual survival was 0.85 (95% CI =

0.72–0.87). Our results indicate that hunter harvest was the leading cause of mortality with a limited effect of predation; intrinsic variables (*i.e.*, body weight, lactation status, and age) did not factor into our survival estimates.

INTRODUCTION

The Black Hills were once occupied by the Manitoban subspecies of elk (*Cervus elaphus manitobensis*; Bryant and Maser 1982). As Europeans began to colonize North America, elk were the most widely distributed deer on the continent with populations distributed from coast to coast and from Canada to the Gulf of Mexico (Murie 1951). As early explorers moved west into the open plains and Native Americans secured firearms, elk populations were greatly reduced and in some areas, extirpated (Bunnel 1997). Numbers were considered plentiful in the late 19th century yet the last elk was reportedly killed in the Black Hills in 1888 (Turner 1974). A reintroduction effort with Rocky Mountain elk (*Cervus elaphus nelsoni*), translocated from Yellowstone National Park to the Black Hills, began in 1911 and continued through 1920 (Turner 1974). This reintroduced population began with 200 animals and nearly 30 years later, in 1952, South Dakota had their first limited harvest season (Turner 1974). Elk numbers remained low until 1990 when the state transplanted 145 elk from Wind Cave National Park into the Black Hills National Forest (BHNF). As a consequence, in the mid 1990's into the mid 2000's, the elk population in the Black Hills increased to an all-time high (South Dakota Department of Game, Fish and Parks 2009). Hunters harvested 3,672 cow elk between 2003–2007, which resulted in a decline in elk populations for several years (South Dakota Department of Game, Fish and Parks 20009). Throughout these years, SDGFP conducted surveys to estimate cow/calf ratios, which averaged 49 calves/100 cows (South Dakota Department of Game, Fish and Parks 2015).

Elk are a highly desirable species for consumptive and non-consumptive use (Bunnel *et al.,* 2002). The southwestern portion of the Black Hills, which is comprised of Elk Hunting Unit 2, contains the largest number of elk in the region. This population has not been studied since the late 1990's (Benkobi 2005). Research conducted by the South Dakota Department of Game, Fish and Parks from 2007–2009 in the eastern region of the BHNF estimated that adult cow survival ranged from 0.56–0.68 (Schmitz 2011); hunter harvest was the leading cause of mortality (77%) across all three years of the study. Elk harvest reached a high of 553 harvested adult bulls and 898 adult cow elk in 2005; from 2002–2007 hunters in South Dakota harvested 4,172 antlerless elk (South Dakota Department of Game, Fish and Parks 2009). During those same years 94,977 applicants vied for 11,821 elk hunting licenses.

Understanding population dynamics of Rocky Mountain elk (*Cervus elaphus*) is enhanced by information on cause–specific mortality and survival rates (Sargeant and Oehler 2007). Elk have been studied throughout their range yet little is known about elk populations inhabiting the Black Hills National Forest (BHNF) and surrounding lands. South Dakota has seen an increase in elk populations inhabiting the Black Hills Region throughout the last two decades. Population estimates have ranged from 1,000 animals in 1988 (Rice 1988) to 4,600 in 2004 (Huxoll 2004); the 2013 aerial survey estimate was 5,100 elk (South Dakota Department of Game, Fish and Parks 2015).

With fluctuations in elk population estimates over the past 20 years and an increase in sportsman's concerns regarding elk populations and the effects that cougar (*Puma concolor*) predation may be having, there was a need for investigation into the population dynamics of the Black Hills elk herd. The objective of this project was to document cause–specific mortality and estimate survival of adult cow elk in the Black Hills of South Dakota.

METHODS

STUDY AREA

The Black Hills are an isolated, mountainous extension of the Rocky Mountains located in western South Dakota and northeastern Wyoming (Petersen 1984). Topography of the Black Hills varies extensively (Kennedy 1992). The mountains of the Black Hills are a maturely dissected domal uplift with a central crystalline core surrounded by steeply dipping sedimentary deposits (Hoffman and Alexander 1987). The Black Hills extend approximately 95 km east to west and 190 km north to south (Petersen 1984) covering an area of about 8,400 km^2 (Orr 1959, Turner 1974, Fecske *et al.,* 2002). Elevations range from 973–2,202 m above mean sea level. Seasonal temperature fluctuations in the Black Hills are typical of a continental climate (Orr 1959). Mean annual temperatures range from 5 to 9 °C with extremes of −40 to 44 °C. Mean annual precipitation is > 66 cm (Orr 1959). Yearly snowfall may exceed 254 cm at higher elevations (Thilenius 1972).

Our study focused on the southwestern region of the Black Hills National Forest in South Dakota extending into Wyoming (Figure 1). The western area of the BHNF is encompassed within Custer, Pennington, and Lawrence counties in South Dakota, and eastern Crook and Weston counties in Wyoming. The study area was comprised of large expanses of public land interspersed with small inholdings of private lands. The majority of private lands were located in the northwest portion of the study area in Wyoming. Dominant overstory vegetation of forested areas consisted of ponderosa pine (*Pinus ponderosa*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), interspersed with mountain juniper (*Juniperus scopulorum*) and mountain mahogany (*Cercocarpus montanus*) at low elevations in dry areas along southwestern fringes of our study area (Thilenius 1972, Severson and Thilenius 1976). Primary understory vegetation consisted of various forbs, grasses, and shrub species, including big bluestem (*Andropogon gerardii*), buffalograss (*Buchloe dactyloides*), Oregon grape (*Berberis repens*), bearberry (*Arctostaphylos uva-ursi*), snowberry (*Symphoricarpos occidentalis*), wild spirea (*Spiraea betuliforia*), and serviceberry (*Amelanchier alnifolia*; Thilenius 1972, Severson and Thilenius 1976, and Deperno *et al.,* 2000). Our study area was predominantly coniferous forest (66.4%) intermixed with grassland/herbaceous areas (15.3%) and areas of early successional forested stands (16.8%; NLCD; Jin *et al.,* 2013). The remaining landscape included small portions of deciduous forest (0.6%), mixed forest (0.2%), developed space (0.3%), hay/pasture lands (0.1%), and wetlands (0.1%). Private lands were located among forested stands and contained meadows, alfalfa (*Medicago sativa*)/hay fields, and limited row crop production.

In August of 2000, a large part of the southern study area was burned during the largest fire recorded in the Black Hills. The Jasper fire was a high-severity fire that started north of Highway 16, 4 km west of Jewel Cave National Monument and burned approximately 33,729 ha (83,500 acres; 7% of the BHNF and 10.4% of our study area; Jasper Fire Rapid Assessment, http://www.fs.fed.us/r2/blackhills/fire/history/jasper). The fire burned through a large portion of cow elk wintering range (Benkobi et al. 2005). LANDSAT data of the fire reported in the Jasper Fire Rapid Assessment, characterized the fire as highly variable leaving a mosaic across the landscape. Areas left unburned or with low intensity burns comprised 25% of the burn area. Moderate burns where crowns were entirely of nearly scorched comprised 48% of the burn. About 27% of the burn was high-intensity fire where trees were left completely void of needles (Lentile *et al.,* 2005).

Hunting seasons differed between South Dakota and Wyoming. The South Dakota archery only season occurred from 1 through 31 September and the rifle season occurred from 1 to 31 October with another two week antlerless rifle season from 1 to 15 December. Wyoming had a longer overall elk hunting season which spanned 15 August to 31 January in Hunt Area 117 and 1 September through 30 November in Hunt Area 1, with dates for legal methods of take (archery or rifle) varying within each hunt area during these timeframes. Hunt Area 1 contained the majority of BHNF in Wyoming.

Elk are found throughout the BHNF and occur sympatrically with white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and cattle (*Bos taurus*); the latter are permitted to graze in the national forest June through October. The primary predator of elk in the BHNF was the cougar; the forest also supported coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

CAPTURE AND MONITORING

We captured adult female elk during two separate capture periods; 3–6 March 2012 and 22–26 February 2013. Captures took place in the Jasper burn area north of

Highway 16 and west and north of Jewel Cave National Monument in the southwestern region of the BHNF. Elk were chemically immobilized (6 ml of Butophanol, 2 ml of Azaperone, and 3 ml of Medetomidine; Zoopharm, Windsor, CO, USA) via darts fired from a cartridge fired projector while pursuing elk in a helicopter (Quicksilver Co, CO, USA). Elk were darted with 3cc barbed darts (Pneu Dart, Williamsport, PA, USA) to ensure the immobilization drug was administered. Adult female elk were fitted with 1,150 g Global Positioning System (GPS)/Store on Board (*n* = 30, TGW–4600 Telonics Inc. Mesa, AZ, USA) and 825 g GPS/Iridium satellite collars (*n* = 10 G2110E Advanced Telemetry Systems, Isanti, MN, USA); collars also were fitted with very high frequency (VHF) beacons. Store on board collars were programmed to download locations every 2.5 hours throughout a 24 hour period beginning at 0100 h. Iridium collars were programmed to upload locations twice per day throughout the year at 0600 and 2000 h until the beginning of calving season (~ 1 May), at which time a location at 1200 h also was uploaded.

Elk were checked for pregnancy by rectal palpation (S. Lindsay, Fall River Veterinary Clinic, Hot Springs South Dakota, USA; Greer and Hawkins 1967). Pregnant cow elk were fitted with vaginal implant transmitters (VITs; M3960 Advanced Telemetry Systems, Isanti, MN, USA) using a fabricated polyvinyl chloride (PVC) applicator that was coated with lubricating jelly (Johnson *et al*., 2006). VIT information was used in a successive calf survival study (Simpson *et al*., 2015; unpublished data). We measured chest girth of cows that were not hobbled to estimate body mass for winter captures for both pregnant and non-pregnant animals (Cook *et al*., 2003). Cow elk mass was calculated from chest girth of elk that were captured in the early spring, either pregnant or not pregnant, and not hobbled using the equation of Cook *et al.,* (2003). We extracted a vestigial canine tooth from each animal during initial capture to determine age to the nearest year using cementum analysis (Hamlin *et al*., 2000; Matson's Laboratory, Milltown, MT, USA). We checked each cow to determine lactation status. Cows were classified as lactating if milk could be extracted from the teats. The presence of milk was an indication that a cow was nursing a calf, or had been nursing a calf within 3–11 days (Flook 1970, Fleet and Peaker 1978, Noble and Hurley 1999). We classified cows as non-lactating if no milk was present.

We collected approximately 20 ml of blood from each cow through the saphenous vein. Blood was then frozen the evening it was collected and kept frozen for up to 4 weeks at which time it was sent to a diagnostics lab (South Dakota State University Diagnostics Lab, Brookings, SD, USA) for disease testing. We tested serum for *Brucella abortus*, Type I and Type II bovine viral diarrhea, *Paratuberculosis*, *leptospirosis*, and epizootic hemorrhagic disease. Blood also was sent to BioPRYN$_{\text{wild}}$$^{©}$ to test for pregnancy. BioPRYN$_{\text{wild}}$$^{©}$ tests for the presence of protein B, which is produced in the placenta of cows (BioTracking, LLC, Moscow, Idaho, USA). We sent blood for these tests when palpation checks for pregnancy were questionable (BioTracking, LLC, Moscow Idaho, USA). All capture and handling procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 12–009A) and followed recommendations of the American Society of Mammalogists (Sikes *et al.,* 2011).

We used directional yagi antennas (Advanced Telemetry Systems, Isanti, MN, USA) from the ground, and a Cessna 182 to monitor live/dead signals of radio collared cow elk and VIT frequencies 3–5 times per week. Within 2 weeks of estimated parturition dates, and continuing through the entire calving season (May–September), we monitored cows on a daily basis until calves reached 60 days of age. When a mortality signal was detected, we immediately located the collar and recorded evidence at the site to determine cause of death. When adult cow mortalities were located, we searched the immediate area for signs (hair, scat, tracks, claw marks, disturbed vegetation, or portions of elk carcasses that were moved away from the main carcass) of predation or scavenging (Hornocker 1970). If sign at mortality sites indicated potential predation, we skinned the neck and face of elk to look for canine punctures, bite marks, or hemorrhaging. We verified cause of death from predation by observing predator specific wounds, concealment of the carcass, and/or consumption habits (Henne 1975, Wade and Bowns 1985). In South Dakota, harvested adult cow elk were required to be taken to a hunt check station. At that time we were able to meet with hunters, retrieve collars, and discuss the general location of the harvest site. Elk harvests in Wyoming were voluntarily reported by hunters, with harvest locations and collars provided to us.

SURVIVAL ANALYSIS

We used our data from radio-tracking surveys to develop monthly encounter histories (White and Burnham, 1999) for adult cow elk. Deaths were assigned to the particular month in which they were found. We used the known fate model in Program MARK (White and Burnham 1999) with the logit-link function to model potential factors influencing adult cow survival. We used a non-staggered entry design for our analyses because all cows were telemetered over a short (few days) time period during both capture seasons.

We used an *a priori* set of 11 candidate models to evaluate the influence of temporal and individual covariates on adult cow survival. Intrinsic variables included year (year), pregnancy status (pregnant), lactation status (lactating), chest girth (chestgirth), age at capture (age), and location during the harvest season (location). We also incorporated a constant (.) and time (t) dependent model into our survival analyses. We incorporated one temporal model that assessed variation in seasonal survival. We separated annual periods into 3 seasons; summer (1 May – 31 August), fall/harvest (1 September – 31 December), and winter (1 January – 30 April). We considered September–December as the harvest season because elk were available for harvest during that time in South Dakota and Wyoming. We based our *a priori* models on variables we considered to be biologically meaningful to adult cow elk 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 strongest model and considered models differing by ≤2 ΔAIC from the top model to be competitive model alternatives (Burnham and Anderson 2002). We used Akaike's weights (w_i) as a measure of support for each model.

RESULTS

We captured and radiocollared 49 adult cow elk between 2012 and 2013 (ages: 2–5 yr = 17, 5–10 yr = 24, 11–15 yr = 4, 16–20 yr = 4). In 2012, we captured 40 adult cows. In 2013, 35 of those cows were recaptured along with 9 newly captured adult cow elk. We documented 12 mortalities during the study. Mortalities were caused by hunter harvest (*n* = 7; 58.3%), predation (*n* = 2; 16.6%), starvation (*n* = 1; 8.3%), and injury (*n* = 1; 8.3%); we were unable to determine the cause of death for one cow elk (8.3%). Two adult cow elk tested positive for titers to epizootic hemorrhagic disease, and Type I and Type II bovine viral diarrhea virus, 3 cow elk tested positive for titers to only Type I bovine viral diarrhea virus, 1 adult cow tested positive for titers to both Type I and Type II bovine viral diarrhea virus, and 2 cows tested positive for titers to only Type II bovine viral diarrhea virus.

Two adult cows were censored during the second season of the project. One cow was censored after the second capture session as she was euthanized due to a capture–related injury; however, we were able to use locational data for this adult cow during the first year of the study. The second cow was censored during 2013 due to collar failure. All predation mortalities were a result of cougars. Pregnancy rates differed (2012 = 93%; 2013 = 66%; $P = 0.003$) between years. We deployed VITs during both capture periods ($n = 38$, 2012; $n = 33$, 2013). In 2012, we inserted a VIT into one cow that, after blood was analyzed for pregnancy, proved not to be pregnant. In 2013, 4 cows with VITs proved not to be pregnant based on blood tests. The number of cows that were lactating at the time of capture also differed ($n = 0$, 2012; $n = 10$, 2013; $P = 0.0012$) between years.

We observed similar mass of cow elk across years (229.68 kg, SE = 2.66 2012; 230.07 kg, SE = 2.10 in 2013, $P = 0.909$). We found mass was similar for pregnant and non-pregnant cows in 2012 (preg. = 228.79, SE = 2.70; non-preg. = 240.68, SE = 10.87, $P = 0.395$). We did, however, find a significant difference in body mass between pregnant and non-pregnant cows in 2013 (preg. = 234.89 SE = 1.96; non-preg = 219.75, SE = 3.75, $P = 0.002$).

From our model results on survival analysis, we considered {S $_{\text{fall/harvest}}$} as the best model to describe survival of cow elk (w_i = 0.87; Table 2). All remaining models were ≥2 ΔAIC_c units from our top model. The monthly survival estimate during the Fall/Harvest period was 0.97 (95% CI = 0.944 – 0.984), while survival for the remaining months of the year was 0.99 (95% CI = 0.985 – 0.998). Probability of adult cow elk surviving 12 months was 0.85 (95% CI = 0.758 – 0.914). Nine of the 12 (75%) confirmed mortalities occurred during the Fall/Harvest period. Of those 9 mortalities, 7 (77%) were from hunter harvest.

DISCUSSION

We documented high adult cow survival during the two years of our study in the Black Hills of South Dakota and Wyoming. Cause–specific mortality of adult cow elk in our study was in line with elk survival studies in other areas where elk were harvested (Unsworth *et al.,* 1993, Ballard *et al.,* 2000, Sargeant and Oehler 2007, Evans 2006, McCorquodale *et al.,* 2011); hunter–related mortality was commonly the leading cause of mortality for adult cow elk (Raedeke *et al.,* 2002). We documented two predation events over the 2 years of our study, both occurred in 2012 and both as a result of cougars. Fifty-eight percent (*n* = 7) of mortality was due to hunter harvest, which took place in either South Dakota (*n* = 2) or Wyoming (*n* = 5). We documented significant movements by elk from South Dakota to Wyoming throughout the study. Eleven and 12 cow elk spent ≥ 2 weeks in Wyoming during the hunting seasons in 2012 and 2013, respectively. In our survival analysis we considered the harvest season a period during which each of our collared cow elk were available for harvest. This resulted in the first month of the hunting season in Wyoming (August) being added to the summer temporal variable and the last month, (January), being included in the winter season.

Elk in the Blue Mountains of Washington documented lower survival for adult cows (80%) in an area with intense hunting pressure; yet, they noted a higher number of predation related mortalities (McCorquodale *et al.,* 2011). We observed an increase in survival from the previous study done in the central Black Hills from 2007–2009, which estimated that adult cow survival ranged from 0.56–0.68 (Schmitz 2011). Hunter harvest was the leading cause of mortality (77%) across all three years of this previous study. With the reduction in adult cow elk hunt tags during the time of our study, we expected as increase in survival.

Results of previous studies that assessed cause-specific mortality of elk populations noted low mortalities associated with predators. In Idaho, Unsworth *et al.,* (1993) estimated cow survival of 0.886 in an area with minimal hunting pressure. In Arizona, in an area with more intense hunting pressure, Ballard *et al.,* (2000) noted similar survival (i.e., 0.897). Survival of adult cow elk in a newly established population in North Dakota also was relatively high; they were able to estimate survival for a population during a time when the population was under low harvest pressure (0.99) and again when hunting pressure had increased (0.96; Sargeant and Oehler 2007). Research conducted in Yellowstone National Park calculated survival rates that ranged from 0.77–0.80 (Evans 2006). That population was exposed to hunting pressure when elk migrated outside of the Park; however, the Yellowstone Region had a diverse predator complex unlike most areas inhabited by elk. Elk in Yellowstone were affected by predation from wolves (*Canis lupus*), cougars, and bears (*Ursus arctos*, *U. americanus*; Evans 2006). In contrast, elk in the Black Hills were predated upon by cougars alone.

Age structure of harvested adult cow elk in our population was similar to that for a population in Wyoming (Wright *et al.,* 2006). Wright *et al.,* (2006) found the majority of harvested cows were <10 years of age while they noted that many adult cows >10 years were typically preyed upon by wolves (Wright et al. 2006). The majority of our adult cows (85%) were <10 years of age. Moreover, 86 percent of the adult cows that were harvested from our population were <10 years of age. The number of harvested cows that were <10 years could have a reproductive impact on the population as cows in their prime reproductive years are typically between 2–15 years of age (Wright et al. 2006). When prime aged females are harvested they are typically pregnant, which results in the immediate removal of 2 elk from the population (Wright et al. 2006). Harvest also removes the reproductive contribution of cow elk in the future (Wright et al. 2006). However, because elk in our study experienced little mortality other than hunter harvest and harvest rate was low, the population-level impact of harvest likely was not severe.

Pregnancy rate decreased from 93% in 2012 to 66% in 2013. Reduction in pregnancy rate was not a result of the age structure of our cows because 85% of our adult cow elk were prime–aged. We were, however, concerned that the low pregnancy rate in 2013 could have been the result of fitting adult cows with VITs during consecutive years. Johnson (2006) followed the same protocol with regard to deploying VITs and did not observe an effect on cow elk pregnancy rates or their ability to become pregnant the subsequent year. From 1998 and 2007, Cook et al. (2013) estimated pregnancy rates for adult cow elk across the western United States; rates ranged from 68–100%, which was similar to the range in pregnancy rates documented during our study. However, during late summer of 2012, South Dakota experienced the most severe drought in over 50 years with an average Palmer Drought Z Index (PDZI) of –2.16 (<2 = severe drought) compared to an average of 1.03 in 2011 and 1.42 in 2013 (both moderately moist; http://www.ncdc.noaa.gov/temp–and–precip/drought/historical–palmers.php). The PDZI estimates drought conditions monthly without taking into consideration precipitation measurements during the previous month, which accurately measures short-term drought (Karl, 1985). Four of the 12 months in 2012 were considered extreme drought months based on PDZI values (-2.75). Drought may have affected pregnancy of elk in 2013 via reduced fat stores due to a reduction in forage quality. A diminished adult female condition has been linked with a decrease in reproductive rates in other studies of elk and red deer (Thorne *et al*. 1976, Clutton-Brock *et al*., 1982; Singer *et al*., 1997; Cook 2000). Thus, the severe weather conditions in 2012 were most likely the cause of our low pregnancy rate (66%) during the second year of the study.

We also observed a higher number of lactating cow elk during the second capture period (February 2013). We suspect that this late lactation in cow elk could indicate that growth rates of calves may have been slow due to nutritional limitations caused by the drought and thus, calves were still relying on cows despite being nearly 9 months of age (Cook et al. 2013). Because of these environmental conditions, we considered lactation in our survival analysis as lactating females are typically in poorer body condition (Cook et al. 2013). Nevertheless, our $S_{\text{lactating}}$ model was not competitive with our top model (Table 2). We used chest girth to determine body mass as a primary condition index of the health of each cow elk (Cook *et al.,* 2013). Our hypothesis being that elk with higher body mass would have a higher chance of survival. Body mass, however, did not factor into our survival modeling as there was no significant relationship between body mass and survival of adult cow elk. Our seasonal model of survival ($S_{Fall/Harvest}$) was the best model for explaining survival of cow elk in the southwestern region of the Black Hills. During our study, we lost few adult cow elk overall and most elk mortalities were due to hunter harvest (four month period from 1 September to 31 December).

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Table 1. A priori models constructed to determine influence of intrinsic variables on adult cow elk survival in the Black Hills, South Dakota, USA, 2012–2013

Model	K[a]	Description
$S_{constant}$	1	Survival was constant
$S_{Fall/Harvest}$	2	Survival varied during harvest period
$S_{pregnant}$	2	Survival varied by whether cow was pregnant or now
$S_{lactating}$	2	Survival varied whether or not cow was lactating
$S_{locations}$	2	Survival varied if cow spent time in Wyoming during harvest
S_{year}	2	Survival varied by year
$S_{chestgirth}$	2	Survival varied by body mass
S_{age}	2	Survival varied by age
S_t	12	Survival varied by month

[a] Number of parameters

Table 2. Models of adult cow elk survival in the Black Hills, South Dakota, USA, 2012–2013

Model	AICc[b]	ΔAICc[c]	w_i[d]	K[e]	Deviance
$\{S_{Fall/Harvest}\}$	123.01	0	0.884	2	118.99
$\{S_{pregnant}\}$	129.29	6.278	0.038	2	125.27
$\{S_{constant}\}$	130.33	7.327	0.023	1	128.33
$\{S_{locations}\}$	131.31	8.306	0.014	2	127.30
$\{S_{age}\}$	131.41	8.399	0.013	2	127.39
$\{S_{lactating}\}$	132.11	9.107	0.009	2	128.10
$\{S_{year}\}$	132.12	9.118	0.009	2	128.11
$\{S_{chestgirth}\}$	132.27	9.259	0.009	2	128.25
$\{S_t\}$	137.39	14.385	0.001	12	113.05

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

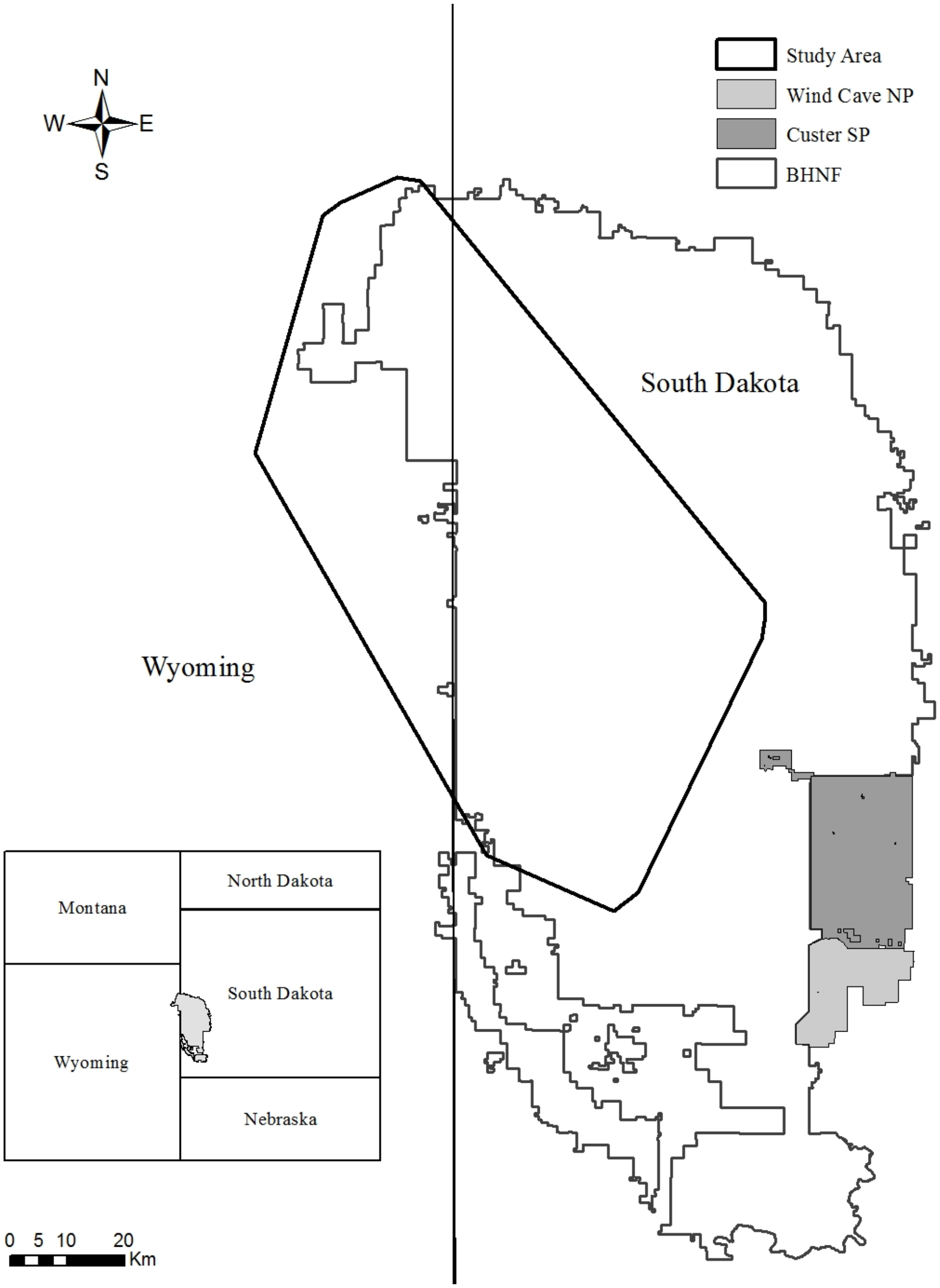
[b] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002)

[c] Difference in AICc relative to min AICc

[d] Akaike weight (Burnham and Anderson 2002)

[e] Number of parameters

Figure 1. Study area in the Black Hills National Forest, South Dakota 2012–2013.



CHAPTER 2: SURVIVAL AND CAUSE SPECIFIC MORTALITY OF NEONATE ELK IN A UNIQUE PREDATOR ENVIRONMENT IN THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING, USA.

This chapter is being prepared for submission in the Journal of Wildlife Management and was coauthored by Joshua B. Smith and Jonathan A. Jenks

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RH: Simpson et al. • Neonate Elk Survival and Cause-Specific Mortality

Survival and Cause Specific Mortality of Neonate Elk in a Unique Predator Environment in the Black Hills of South Dakota and Wyoming, USA.

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ABSTRACT We conducted a 2-year study of survival and cause-specific mortality of elk (*Cervus elaphus*) calves to determine the current status of elk occupying the southwestern region of the Black Hills. We captured and fit 71 neonates ≤10 days of age with expandable radiocollars during summer 2012 (n = 37) and 2013 (n = 34). Predation accounted for 87.5% of mortalities; remaining mortalities were from starvation (6.3%) and unknown causes (6.3%). Cougars (*Puma concolor)* accounted for all predation mortalities. We used known-fate analysis in Program MARK to estimate summer (15 May-25 Sep) and annual (12 month) survival for elk calves. The top model for summer survival was $\{S_{1-2wks,>2wks}\}$ indicating that mortality during 1-2 weeks of age and 3-20 weeks of age best explained survival; overall probability of surviving 20 weeks was 0.79 (95% CI = 0.68-0.88). For annual (12 month) survival, model $\{S_{birthweight}\}$ had the lowest AIC_c value indicating that birth weight of elk calves best explained survival as heavier born calves had a higher probability of survival. The overall probability that a calf survived to 12 months of age was 0.75 (95% CI = 0.61–0.84). Our results document high survival for neonate elk likely due to an ecosystem-specific predator guild and high alternative prey.

KEY WORDS Black Hills, cause-specific mortality, *Cervus elaphus,* Known-fate analysis, mortality, neonate, survival

INTRODUCTION

Juvenile recruitment and survival often exhibit the greatest impact on population dynamics as they are typically more variable than adult survival (Allee et al. 1949, Pimlott 1967, Gaillard et al. 2000, Raithal 2005, Raithal et al. 2007). Variation in juvenile survival has been linked to factors including, low birth mass (Guiness et al. 1978, Nelson and Woolf 1987, Keech et al. 2000, Ditchkoff et al. 2001, Jenkins and Barten 2005), birth timing (Clutton-Brock et al. 1987), disease (Smith et al. 2014), and predation (Harris et al. 2007); although determining their overall impact on a population is often difficult. In elk (*Cervus elaphus*), juvenile survival has been found to be more influential on population dynamics than adult female harvest (Raithel et al. 2007). Thus, estimates of elk calf survival and recruitment provide vital information on the status of a population.

Low birth mass has been documented to negatively affect survival; elk calves that are born lighter take longer to put on weight making them more susceptible to starvation during the winter (Cook et al. 2004), and potentially easier for predators to capture (Clutton-Brock et al. 1987). However, increased survival in neonates born during peak calving may be due to an abundance of other neonates on the landscape (Rutberg 1987). This increase in neonate density often coincides with cow and calf herds that benefit from the increased number of vigilant adult females (Wissel and Brandl 1988). In contrast, calves born early or late in the season are typically born when few neonates are on the landscape; however, early born calves often have the benefit of more time to put on body mass before late autumn-early winter (Cook et al. 2010). Early born calves, in some areas, have experienced higher probabilities of survival (Rearden 2005, Barber-Meyer et al 2008). When elk calves are 1–2 weeks of age they are typically hiding and inexperienced runners (Lent 1974), calves at 3–6 weeks of age have become better runners and are beginning to join nursery herds (Altmann 1952), and at 7–20 weeks of age calves have the ability to migrate or move significant distances with herds (Barber-Meyer et al. 2008).

Predation has been implicated as the primary factor limiting elk calf survival especially in areas with multiple predator species (Gasaway et al. 1992, Kunkel and Pletscher 1999). Elk calf survival in multi-prey systems has been well documented across the western United States (Griffin et al. 2011) especially with the reintroduction of wolves (*Canis lupus*) to the Greater Yellowstone Ecosystem (Barber-Meyer et al. 2008). While some have hypothesized that elk calf survival will decrease as the number of predator species on the landscape increases (Linnell et al. 1995), others have argued that mortality is compensatory due to interspecific competition and functional redundancy among predators (Caro and Stoner 2003, Griffin et al. 2011). Nevertheless, Griffin et al. (2011) found lower calf survival in ecosystems occupied with black (*Ursus americanus*) or grizzly (*U. arctos*) bears, wolves, coyotes (*Canis latrans*), and cougars (*Puma concolor*; Griffin et al. 2011).

Areas with newly populated elk in eastern North America, such as western Pennsylvania, do not have cougars on the landscape but do have black bears and coyotes and typically observe high calf survival (DeVivo et al. 2011). Similarly, in the Black Hills National Forest (BHNF) elk must contend with a myriad of predators, including cougars, coyotes, and bobcats (*Lynx rufus*); however, only cougars and coyotes are known to take elk calves in significant numbers. Cougars are known to specialize on deer (Rearden 2005, Smith et al. 2014). In central Idaho, Hornocker (1970) found that deer and elk comprised 70% of winter diets of cougars, and 75% of elk killed were ≤ 1.5 years old. Although deer were more abundant in that system, elk were the predominant prey item killed, which might suggest cougars selected for elk or that younger elk were more vulnerable to predation.

Although elk have been studied throughout their range, little is known about calf survival in populations inhabiting the BHNF and surrounding area (Wright et al. 2006). South Dakota has seen dramatic variations in elk populations throughout the last two decades; population estimates have ranged from 1,000 animals in 1988 (Rice 1988) to 4,600 in 2004 (Huxoll 2004), and the most current 2013 aerial survey estimate was 5,100 elk (South Dakota Department of Game, Fish and Parks 2015). Currently, there is concern among sportsman and the general public about elk calf populations in the BHNF, specifically regarding the number lost to predation. To better understand survival and recruitment of elk in the BHNF, we investigated cause-specific mortality, and evaluated the influence of intrinsic and temporal variables on elk calf survival.

STUDY AREA

The Black Hills are an isolated, mountainous extension of the Rocky Mountains located in western South Dakota and northeastern Wyoming (Petersen 1984). The Black Hills are a maturely dissected domal uplift with a central crystalline core surrounded by steeply dipping sedimentary deposits (Hoffman and Alexander 1987). The Black Hills extend approximately 95 km east to west and 190 km north to south (Petersen 1984) covering an area of about 8,400 km^2 (Orr 1959, Turner 1974, Fecske et al. 2002). Topography of the Black Hills varies extensively (Kennedy 1992). Elevation ranges from 973–2,202 m above mean sea level. Seasonal temperature fluctuations were typical of a continental climate (Orr 1959). Mean annual temperatures ranged from 5 to 9 °C with extremes of −40 to 44 °C.

Our study focused on the southwestern region of the BHNF in South Dakota extending into Wyoming (Figure 1). The western area of the BHNF was encompassed within Custer, Pennington, and Lawrence counties in South Dakota, and eastern Crook and Weston counties in Wyoming. The study area was comprised of large expanses of public land interspersed with small inholdings of private lands. The majority of private lands were located in the northwest portion of the study area in Wyoming. Dominant overstory vegetation of forested areas consisted of ponderosa pine (*Pinus ponderosa*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), and mountain mahogany (*Cercocarpus montanus*) at low elevations in dry areas along southwestern fringes of our study area (Thilenius 1972, Severson and Thilenius 1976). Primary understory vegetation consisted of various forbs, grasses, and shrub species, including big bluestem (*Andropogon gerardii*), buffalograss (*Buchloe dactyloides*), Oregon grape (*Berberis repens*), bearberry (*Arctostaphylos uva-ursi*), snowberry (*Symphoricarpos occidentalis*), wild spirea (*Spiraea betuliforia*), and serviceberry (*Amelanchier alnifolia*; Thilenius 1972, Severson, Thilenius 1976 and Deperno et al., 2000). Our study area was predominantly coniferous forest (66.4%) intermixed with grassland/herbaceous areas (15.3%), and areas of early successional forested stands (16.8%; National Land Cover Database (NLCD) 2011; Jin *et al.,* 2013). The remaining breakdown of the area included small portions of deciduous forest (0.6%), mixed forest (0.2%), developed space (0.3%), hay/pasture lands (0.1%), and wetlands (0.1%; NLCD 2011; Jin et al. 2013). Private lands were located among forested stands and contained meadows, alfalfa (*Medicago sativa*)/hay fields, and limited row crop production.

In August of 2000, a large portion of the southern study area was burned during the Jasper fire, the largest fire recorded in the Black Hills. The Jasper fire was a high-severity fire that started north of Highway 16, 4 km west of Jewel Cave National Monument; the fire burned approximately 33,729 ha (83,500 acres; 7% of the BHNF and 10.4% of our study area; Jasper Fire Rapid Assessment, http://www.fs.fed.us/r2/blackhills/fire/history/jasper). The fire burned through a large portion of cow elk wintering range. LANDSAT data for the fire reported in the Jasper Fire Rapid Assessment, characterized the fire as highly variable. Areas unburned or with low intensity burns comprised 25% of the burn area. Moderate burns where crowns were entirely of nearly scorched comprised 48% of the burn. About 27% of the burn was high-intensity fire where trees are left completely void of needles (Lentile et al. 2005).

Elk are found throughout the BHNF and occupy the ecosystem with white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and cattle (*Bos taurus*); the latter were grazed in the national forest through October. The primary predator of elk in the BHNF was the cougar; the forest also supported coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

METHODS

We captured adult female elk from 3–6 March 2012 and from 22–26 February 2013. All collared cows that were captured in 2012 and survived through the year (*n* = 35) were recaptured in 2013. We chemically immobilized (6 ml of Butophanol, 2ml of Azaperone, and 3 ml of Medetomidine; Zoopharm, Windsor, CO, USA) adult cow elk by darting them from a helicopter (Quicksilver Air, Inc., CO, USA). Elk were darted with 3cc barbed darts (Pneu Dart, Williamsport, PA) to ensure the immobilization drug was administered. In 2012, adult female elk were fitted with 1,150g Global Positioning System (GPS) Store–on–Board collars (*n* = 30, TGW–4600 Telonics Inc. Mesa, AZ, USA) or 825 g Iridium satellite collars (*n* = 10 G2110E Advanced Telemetry Systems, Isanti, MN, USA). Store–on–board collars were programmed to download locations every 2.5 hr throughout a 24–hour period beginning at 0100 hr. Iridium collars were programmed to upload locations twice/day throughout the year at 0600 and 2000 hr until the calving season (~ 1 May) was estimated to begin; during this season a location also was uploaded at 1200 hr.

Elk were checked for pregnancy by rectal palpation (S. Lindsay, Fall River Veterinary Clinic, Hot Springs South Dakota, USA; Greer and Hawkins 1967) as well as through blood samples using BioPRYN$_{\text{wild}}$$^{©}$ tests for the presence of protein B, which is produced in the placenta of cows (BioTracking, LLC, Moscow, Idaho, USA) when pregnancy status was in doubt. Pregnant cow elk were fitted with vaginal implant transmitters (VITs; M3960 Advanced Telemetry Systems, Isanti, MN, USA) using a fabricated polyvinyl chloride (PVC) applicator that was applied with lubricating jelly (Johnson et al. 2006). We measured chest girth to estimate body mass (Cook et al. 2003). We extracted a canine tooth to determine age through cementum analysis during each initial cow elk capture (Fancy 1980). We checked each cow to determine lactation status. Cows were considered lactating if milk could be extracted from the udder. The presence of milk was an indication that a cow was nursing a calf, or had been nursing a calf within 3–11 days (Flook 1970, Fleet and Peaker 1978, Noble and Hurley 1999). We classified cows as non-lactating if no milk was present.

We used expelled VITs from adult cow elk to locate elk calves. When the VIT signal changed to signify it had been expelled we would locate cows and search for calves on foot. We searched the area using a grid pattern to thoroughly cover the area. When VITs were located, we marked the location with a handheld GPS unit (Garmin USA, Wichita, KS, USA). We then searched that immediate area for a parturition site: areas with disturbed vegetation in a 1.2–m circular pattern often with bodily fluids, afterbirth, or sign that the cow consumed the placenta (Rearden et al. 2011). In addition to calves captured using VITs, we also searched by vehicle or on foot for solitary non-collared cows or herds of elk with young calves (i.e., random calves) or cows exhibiting behaviors that would indicate they had a calf (e.g., walking short distances while looking back at a particular area). If we suspected a cow had calved but did not visually observe the calf, we would search the area where we assumed the calf would be bedded. We continued searches for random calves throughout the calving season.

Once elk calves were captured, we blindfolded and hobbled animals for safe handling. Each calf was equipped with a 183 g expandable collar (M2220B; Advanced Telemetry Systems, Isanti, MN, USA), equipped with a 4–hr mortality sensor. During 2013, we added a heavy plastic sleeve to collars to avoid premature loss to barbed wire fences (Grovenburg et al. 2014, C. Lehman SDGFP, Custer, SD, pers. commun.). We determined sex and estimated age of calves captured from females with VITs using a combination of coat and ear wetness, hoof condition, condition of naval healing, tooth eruption, and overall size in comparison to characteristics of known–age calves (Johnson 1951). We measured (to the nearest 1 mm) overall body length from the tip of the nose to the last tail vertebrae and chest circumference directly behind the forelegs. Body length and chest girth were measured with a flexible metric tape. We attempted to obtain weights for each calf to the nearest kg using a small mesh net that would cinch at the top. We used that capture weight to calculate birth weight by taking the weight and estimated age at capture and subtracting the average weight gain of elk calves, 870 g d^{-1} (Hudson and Adamczewski 1990); weights of calves captured on the day they were born were assumed to be birth weights. All capture and handling procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 12–009A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Monitoring

We monitored elk calves daily for 20 weeks post-capture via aerial or ground telemetry. After 20 weeks, we monitored calves 3–5 times/week until mortality events or collars were separated from calves. When we received a mortality signal, we attempted to investigate the mortality event within 12 hours. Once a suspected mortality was located, we searched the immediate area for any sign of predation or scavenging. We looked for hair, scat, tracks, claw marks, disturbed vegetation, or parts of the carcass that were moved from the main carcass (Henne 1975; Wade and Browns 1982). We determined the cause of death by observing predator–specific wounds, concealment of the carcass, and consumption habits typically associated with specific predators (Henne 1975, Wade and Bowns 1985). If cause of death could not be determined in the field, we collected the entire carcass for necropsy at South Dakota Game, Fish and Parks (Rapid City, SD, USA).

Statistical Analysis

We used a Fischer's exact test to determine the proportional differences of lactating females and the sex ratio of calves between years. We conducted survival analyses for elk calves using known fate models with the logit-link function in Program MARK (White and Burnham 1999). Program MARK uses a modified Kaplan-Meier (1958) estimator as an option for censoring animals in analyses. We estimated summer survival (20 weeks post-marking; approx. May-Oct) using weekly intervals to model summer survival. We used a set of intrinsic variables for our survival analysis including capture year, capture age, sex, birth weight, and birth timing; variables were used to create life–stage–specific models to estimate weekly survival (Table 1). We developed our set of models based on data we collected during capture and review of similar elk calf survival studies conducted throughout the western United States (e.g., Barber-Meyer et al. 2008). We used a non-staggered entry design because all calves were captured within approximately 4 weeks and the purpose of our analysis was to determine survival probabilities at specific ages and life stages of elk calves. We included life–stage–specific models for summer survival based on existing literature that indicated survival differed for 1–2, 3–6, and 7–20 week age intervals (Altmann 1952, Lent 1974, Barber-Meyer et al. 2008).

We included a capture year model and a birth timing model using the median birth date for each year and calculating the absolute deviation in days from that date (Barber-Meyer et al. 2008). We also included 3, life–stage specific models: 1) a 2-stage model ($S_{1\text{–}2\text{wks},>2\text{wks}}$) where neonate survival differed for ≤2 weeks versus >2 weeks of age, 2) a 3-stage model ($S_{1\text{–}2\text{wks},\ 3\text{–}6\text{wks},\ 7\text{–}20\text{wks}}$) where neonate survival varied for ≤2 weeks, 3–6 weeks, and ≥7 weeks of age, and 3) a 2 stage model ($S_{1\text{–}6\text{wks},\ \geq 7\text{wks}}$) where neonate survival differed for 1–6 weeks and ≥7 weeks of age. We did not use body length or chest girth in our survival analyses because they were highly correlated ($r^2 = 0.77$, $p < 0.5$) with birth mass; birth mass was included in our models because it has been investigated in other calf survival studies (Singer et al. 1997, Oregon; Smith et al. 1998, Yellowstone; Rearden 2005, Oregon; Barber-Meyer 2008, Jackson, WY).

We also estimated annual (12 month; May – April) calf elk survival using monthly intervals. We used a staggered-entry design for survival analysis to determine calf survival throughout different seasonal periods in the first year of life. We included the same intrinsic variables for our annual survival analysis; capture year, sex, capture age, birth weight, birth timing (Table 2). We used one seasonal model ($S_{\text{Summer + Migration/Harvest + Winter}}$) where calf survival differed between summer (May–Aug), migration/harvest (Sep – Dec), and winter (Jan – Apr).

We based our a priori models on variables we considered to be biologically meaningful to calf elk 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 strongest model and considered models differing by ≤2 ΔAIC_c from the top model to be competitive model alternatives (Burnham and Anderson 2002). We used Akaike's weights (w_i) as a measure 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 (Devries et al. 2003, Barber-Meyer et al. 2008, Grovenburg et al. 2011) reflected in quasi–AIC_c (QAIC_c) values.

RESULTS

We captured and radiocollared 49 adult cow elk between 2012 and 2013 (2–5 yr = 17, 5–10 yr = 24, 11–15 yr = 4, 16–20 yr = 4) and deployed 71 VITS ($n = 38$ in 2012, $n = 33$ in 2013). In 2012, we captured 40 adult cows. In 2013, 35 cows were recaptured along with 9 uncollared elk. One cow in 2012 and 4 cows in 2013 with VITs were not pregnant. The number of cows that were lactating at the time of capture differed between years (Fisher's exact test; $p = 0.0012$; $n = 0$ in 2012; $n = 10$ in 2013, df = 1). From 15 May 2012 to 4 July 2013, we captured 71 neonates <9days of age (37 in 2012 and 34 in 2013), 13 of which were from unmarked cows (6 in 2012 and 7 in 2013). Of the 37 elk calves we captured in 2012, 20 were males and 17 were females. Of the 34 elk calves captured in 2013, 21 were males and 13 were females.

We found no difference between calf sex ratio between years ($p = 0.63$). Median birth date was 28 May (range = 17 May – 8 Aug) and 5 June (range = 15 May – 5 Jul) in 2012 and 2013, respectively. Estimated age at capture ranged from 0 (captured on day of birth) to 8 days; 75% of calves were captured at ≤ 2 days of age. To determine weights for calves where data were missing ($n = 4$), we took the mean weight for calves in that year for that particular age and sex and assigned the missing value with the mean weight. Mean estimated birth mass (EBM) for 2012 was 16.96 kg (SE = 2.8, $n = 37$); mean EBM for males was 17.44 kg (SE = 2.6, $n = 20$) and mean EBM for females was 16.39 kg (SE = 2.9, $n = 17$). By comparison, mean EBM in 2013 was 16.75 kg (SE = 2.8, $n = 34$), and mean EBM for males and females was 17.03 kg (SE = 2.9, $n = 21$) and 16.30 kg (SE = 2.7, $n = 13$), respectively.

We right-censored 26 collars (19, 2012; 4, 2013) because they were prematurely separated (e.g., caught on fences) from calves. In 2012, 11 calves retained collars ≥1 year; 20 calves retained collars in 2013. In 2012, elk calves that were censored due to collar loss retained collars for a mean of 79.3 days (SE = 8.5) while in 2013 mean collar retention was 129.75 days (SE = 9.63, $t_9 = -3.93$, $p = 0.002$). We captured 82% ($n = 58$) of elk calves with the use of VITs while the remaining 18% ($n = 13$) were randomly captured calves. Mean age at capture for elk calves captured with VITs was 1.5 (SE = 0.2) days whereas the average estimated age of randomly captured calves was 1.8 (SE = 0.5, $t_{14} = -2.93$, $p = 0.04$) days.

From model results for summer survival, we considered $\{S_{1–2wks,>2wks}\}$ as the best approximating model ($w_i = 0.51$; Table 4). The next closest model was 1.99 ΔAIC_c units from our top model. While the second model $\{S_{1–2wks,3–6wks,>7wks}\}$ was within 2 ΔAIC_c from our top model we excluded it from consideration because 1) survival estimates for weeks 3–6 (0.99, SE = 0.006) and ≥7 weeks (0.99, SE = 0.004) were not significantly different and nearly identical to one another, 2) due to the lack of discrepancy between these two models and as the deviance was the same as the top model with the addition of another parameter we removed the model $\{S_{1–2wks,3–6wks,>7wks}\}$, resulting in the weight of evidence for our top ranked model increasing to $w_i = 0.62$, which was 1.6 times greater than all other models. Additionally, model $\{S_{1–2wks,>2wks}\}$ had the lowest $QAIC_c$ when $\hat{c} = 2.0$ (moderate dispersion; $QAIC_c$ $w_i = 0.28$) and through $\hat{c} = 3.0$ (extreme dispersion; $QAIC_c$ $w_i = 0.21$). Model $\{S_{1–2wks,>2wks}\}$ also was our only model in which β estimates did not include zero (1–2 weeks; 4.74, 95% CI = 4.04–5.43; and >2 weeks; −1.46, 95% CI =−2.59 –−0.33); thus, we considered survival best explained by this 2 life–stage interval model. Weekly survival estimates were 0.96 (95% CI = 0.916 – 0.985) for 1–2 weeks and 0.99 (95% CI = 0.983 – 0.995) for calves >2 weeks while probability of surviving 20 weeks was 0.79 (95% CI = 0.68 – 0.88). Of the 16 mortalities used in covariate models, 6 (38.0%) occurred during the first two weeks 1 (6.3%) from 3–6 weeks, 6 (38.0%) from 7–20 weeks, and 3 (19.0%) after 20 weeks of age.

From model results for annual survival we considered $\{S_{birthweight}\}$ as the best approximating model ($w_i = 0.45$; Table 5). One other model $\{S_{sex+bdDev+birthweight}\}$ was within 1.40 ΔAIC_c; however, 2 of the β estimates incorporated 0; sex (0.92, 95% CI = −0.19–2.03), and birth timing (0.005, 95% CI =−0.03–0.04). The deviance was similar for the two models ($\{S_{\text{birthweight}}\}$ = 125.89, $\{S_{\text{sex+bdDev+birthweight}}\}$ = 123.24). Additionally, model $\{S_{\text{birthweight}}\}$ had the lowest $QAIC_c$ when $\hat{c} = 2.0$ (moderate dispersion; $QAIC_c\ w_i$ = 0.29) and through $\hat{c} = 3.0$ (extreme dispersion; $QAIC_c\ w_i$ = 0.22). Overall annual survival was 0.75 (95% CI = 0.56–0.84).

We documented 12 mortalities from capture to 20 weeks and 4 additional mortalities to 52 weeks; 7 in 2012 and 9 in 2013. Predation was the leading cause of mortality (Table 3; 81%, *n* = 13). Mean age at death was 64.4 days of age (SE = 63.7). In 2012, all of the elk calf mortalities were from cougars. In 2013, 5 mortalities (67%) were a result of cougars, 1 (11%) mortality was from starvation due to possible abandonment, 1 (11%) from vehicle collision, and 1 (11%) of unknown cause (Table 5).

DISCUSSION

Our study covered a large portion of the BHNF (~35%) with calving areas dispersed throughout the area. Thus, our survival estimates were reasonable values of neonate elk survival in the region. Elk calves in the western Black Hills exhibited relatively high summer survival in comparison to other western populations, yet, survival was lower than in 2 studies conducted in the eastern United States (Bender et al. 2002, DeVivo et al. 2011). In our study, calves exhibited decreased survival during the first two weeks of life; survival was relatively constant for the remaining 18 weeks. This was in contrast to elk calf survival in northern Yellowstone Region, where survival was lowest from 7–20 weeks of age (Barber-Meyer et al. 2008). In our study, calf survival was lowest during the 1–2 week of age period and higher from 3–20 weeks of age. We noted the greatest number of calf elk mortalities as a result of predation in the shortest duration of time at ≤2 weeks of age. We also noted 6 predation events from 7–20 weeks of age. In contrast to other studies, we did not document any mortalities from coyotes, although previous research in this region found high coyote mortalities (71%) on adult white-tailed deer (Deperno et al. 2000). In contrast, Barber-Meyer et al. (2008) documented 7–9% coyote mortality of elk calves from 1987–1990 in the Yellowstone National Park ecosystem, which may have resulted from increased coyote pack size after the reintroduction of wolves (Merkle et al. 2009).

While predation was the most significant source of mortality in our study, we observed high survival. Our summer survival rates for elk calves where more in line with those of eastern elk populations. Predation is the leading cause of neonate elk mortality in North America (Schlegal 1976, Singer et al 1997) with bears often accounting for the highest number of predation events. Barber-Meyer et al. (2008) found that between 2003–2005 bears killed more elk on the northern range of Yellowstone National Park than wolves, coyotes, and cougars combined. Furthermore, predation by black bears accounted for 92% of elk calf mortalities in North Carolina (Murrow et al. 2009). The mean age of elk calves killed by cougars in our study was 122.7 days, which was comparable to other elk calf studies that found cougars predating on elk calves. In comparison, Barber–Meyer et al. (2008) found that the average age of elk calves killed by cougar, was 107 days.

Differences in the predator guilds do not seem to be the only factor influencing elk calf survival. Areas exhibiting high elk calf survival may have higher densities of alternative prey. In the BHNF, South Dakota Department of Game, Fish and Parks estimates deer populations at 39,300 (95% CI = 30,300–48,300; K. Cudmore, SDGFP, Rapid City, SD, pers. commun.) white-tailed deer and 8,700 (95% CI = 5,700–11,800;

South Dakota Department of Game, Fish and Parks 2015) mule deer in the forest. Smith et al. (2014) found deer made up 83% of cougar diets.

The time period where elk calves are the only neonate available in this area is relatively short (15 May – 1 June; Jansen et al. 2012). Approximately one month after the start of elk calving, prey density in the BHNF increases (Jansen et al. 2012). Median birth date for other ungulates in the BHNF occur 1–2 weeks after that of elk; mule deer peak from 7–14 June (Schmitz 2010) and white-tailed deer peak from 7–17 June (Schmitz 2006). Smith et al. (2014) found a similar pattern with bighorn sheep (*Ovis canadensis*) in the BHNF as predation on bighorn lambs began to decrease after 2–3 weeks of age, which coincided with the increase in other ungulate prey on the landscape.

We observed a decrease in predation after two weeks; yet, predation increased again in September when calves were ~3 months old and extremely mobile. Mortality at this age is most likely due the biology of prey and density of predators on the landscape rather than prey densities. Elk calves are susceptible to predation during the first two weeks of life, as they are solitary and in their hider phase. They are possibly being taken opportunistically by cougars that happen upon them (Lent 1974). As they age and join nursery groups they are protected by herd numbers and minimal movement which may increase their susceptibility to predation (Altmann 1952). As calves age, become more mobile and the migration period begins they are moving in an area of cougars who are ambush predators (Barber-Meyer et al. 2008).

Birth weight was the most important variable affecting annual survival in calf elk in our study; higher calf weights were associated with a higher chance of survival to 12 months of age. The mean EBM for elk calves in our study (17.23 kg, SE = 0.43) was considerably higher than populations of elk in eastern North America, such as Pennsylvania (16.4 kg and 13.7 kg; DeVivo et al. 2011) and Kentucky (16.4 kg and 15.2 kg; Seward 2003) as well as for free–ranging elk in western United States (range = 14.8–16.8 kg; Rush 1932, Johnson 1951, Schlegal 1976, Smith et al. 1997, Raithel 2005, Barber Meyer et al. 2008). Only Rearden et al. (2005) found higher birth mass in male and female calves (21.7 kg and 19.4 kg, respectively) in western Oregon. The high survival in elk calves we documented could be an indication of excellent body condition of cow elk (Clutton–Brock et al. 1987, Bender et al. 1997) in the BHNF. Cow elk in good body condition tend to produce healthier calves with higher body mass that ultimately leads to quicker development and reduced risk to predation (Thorne et al. 1976, Bender et al. 2002).

Open grasslands comprised 37% of our study area, and forage quality has likely improved in recent years in response to increased tree harvest to combat mountain pine beetle (*Dendroctonus ponderosae*; USDA Forest Service 2005) infestation which covers 168,300 ha of the BHNF, and the Jasper burn, which occurred in 2001. Previous studies on adult cows in the central BHNF showed average to above average percent ingesta–free body fat (Cook et al. 2013). Studies of calf survival in moose (*Alces americanus*) have shown birth mass as an important factor related to calf survival as heavier calves were better suited to handle winter (Cederlund et al. 1991). Studies on captive elk in western Wyoming found elk calves with birth weights >16 kg had a 90% chance of surviving to 4 weeks of age, while calves born <11.5 kg had <50% chance of survival (Thorne et al. 1976). Similarly, Smith et al. (2006) found a significant correlation between elk calf birth mass and survival in Wyoming. In contrast, DeVivo et al. (2011) found low birth mass did not affect calf survival in Pennsylvania; however, they had no mortality events during the duration of their study. The explanation for their high survival was due to high densities of white-tailed deer. We found high calf survival under conditions with both high densities of alternate prey sources and high birth weights supporting good forage quality in the BHNF. These results occurred despite the low pregnancy rates we found in 2013, which was most likely a result of extreme drought the year before as forage quality has been found to directly affect pregnancy rates in ungulates (Hebblewhite and Merrill 2011) The high collar loss we experienced in 2012 was most often the result of collars tearing off elk calves after becoming entangled in barbed-wire fences. Of the 19 (51% of our collars were lost) collars lost, we located 16 (84%) hanging from a fence or on the ground directly under a fence. In 2013, we altered the design on our calf collars by adding a heavy rubber sleeve over the entire collar. Consequently, we experienced a 38% decrease in collar loss. There is evidence that some calves that lost their collars may have survived. During adult cow elk captures in February 2013, 10 cows were still lactating at that time indicating that they were still feeding calves or were feeding calves within the previous 3–11 days (Flook 1970, Fleet and Peaker 1978, Noble and Hurley 1999), which supported our hypothesis that some calves that were right-censored because of lost collars were still alive.

MANAGEMENT IMPLICATIONS

Our findings are relevant to wildlife managers in an area of Black Hills National Forest where little was known on neonatal elk survival. We demonstrated that predation from cougars was the leading cause of mortality; nevertheless, we documented that elk calf survival can be high even when associated with a predator system that includes cougars, coyotes, and to a lesser extent, bobcats. We documented high estimated birth mass in our calves alluding to good forage conditions. However, there may be concern for elk recruitment after events of extreme drought when adult cow elk pregnancy rates may be affected and the number of elk calves in the population may be reduced.

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Table 1. A priori models constructed to determine the influence of intrinsic variables on 20 week neonate Rocky Mountain elk (*Cervus elaphus*) survival in the Black Hills, South Dakota and Wyoming USA, 2012–2013.

Model	K^a	Description
$S_{constant}$	1	Survival was constant
S_{time}	1	Survival varied over time
$S_{BirthWeight}$	2	Survival varied by birth weight of neonates
$S_{BirthTiming}^b$	2	Survival varied by birth timing (median birth date)
S_{sex}	2	Survival varied by sex of neonates
S_{age}	2	Survival varied by age at capture of neonates
S_{year}	2	Survival varied by year
$S_{1–2wks,>2wks}$	2	Survival varied by age in 2 stages
$S_{1–2wks,3–6wks,>7wks}$	3	Survival varied by age in 3 stages
$S_{1–6wks,>7wks}$	2	Survival varied by age in 2 stages

Table 2. A priori models constructed to determine the influence of intrinsic variables on annual neonate Rocky Mountain elk (*Cervus elaphus*) survival in the Black Hills, South Dakota and Wyoming, USA, 2012–2013.

Model	K^a	Description
$S_{constant}$	1	Survival was constant
S_{time}	1	Survival varied over time
$S_{BirthWeight}$	2	Survival varied by birth weight of neonates
$S_{BirthTiming}^{b}$	2	Survival varied by birth timing (median birth date)
S_{sex}	2	Survival varied by sex of neonates
S_{age}	2	Survival varied by age at capture of neonates
S_{year}	2	Survival varied by year
$S_{summer+Migration/Harvest+Winter}$	3	Survival varied by season

Table 3. Cause-specific mortality of neonate Rocky Mountain elk (*Cervus* elaphus) in the Black Hills, South Dakota and Wyoming, USA, 2012–2013.

Cause-specific mortality	*n*	%
Predation	12	75%
Unknown predation	1	6%
Starvation	1	6%
Vehicle	1	6%
Unknown	1	6%

Table 4. Top-ranked survival models of neonate Rocky Mountain elk (*Cervus elaphus*) from birth to 20 weeks post-capture in the Black Hills, South Dakota and Wyoming, USA, 2012–2013 when ĉ (a model term representing overdispersion) was 1.0 (i.e., assumed no dispersion).

Model[a]	AICc[b]	ΔAICc[c]	w_i[d]	K[e]	Deviance
$\{S_{1\text{–}2wks,>2wks}\}$	138.89	0.00	0.50	2	134.88
$\{S_{1\text{–}2wks,3\text{–}6wks,>7wks}\}$	140.88	1.99	0.19	3	134.86
$\{S_{Constant}\}$	142.27	3.38	0.09	1	140.27
$\{S_{1\text{–}6wks,>7wks}\}$	143.59	4.70	0.05	2	139.58
$\{S_{BirthWeight}\}$	143.94	5.05	0.04	2	139.93
$\{S_{Sex}\}$	144.17	5.28	0.04	2	140.16
$\{S_{Age}\}$	144.28	5.39	0.03	2	140.26
$\{S_{Year}\}$*}	144.28	5.39	0.03	2	140.27

[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.

Table 5. Top-ranked survival models of neonate Rocky Mountain elk (*Cervus elaphus*) from birth to 12 months post-capture in the Black Hills, South Dakota and Wyoming, USA, 2012–2013 when ĉ (a model term representing overdispersion) was 1.0 (i.e., assumed no dispersion).

Model[a]	AICc[b]	Δ AICc[c]	w_i[d]	K[e]	Deviance
$\{S_{BirthWeight}\}$	129.91	0.00	0.45	2	125.89
$\{S_{Sex+BirthTiming+BirthWeight}\}$	131.31	1.40	0.22	4	123.24
$\{S_{Sex}\}$	133.06	3.15	0.09	2	129.04
$\{S_{Winter}\}$	133.62	3.71	0.07	2	129.60
$\{S_{Constant}\}$	133.99	4.08	0.06	1	131.98
$\{S_{Summer +Migration/Harvest+Winter}\}$	134.68	4.77	0.04	3	128.63
$\{S_{BirthTiming}\}$	135.96	6.05	0.02	2	131.94
$\{S_{Year}\}$	135.98	6.07	0.02	2	131.96
$\{S_{Age}\}$	135.99	6.08	0.02	2	131.97
$\{S_{Time}\}$	145.43	15.52	0.00	16	112.46

[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.

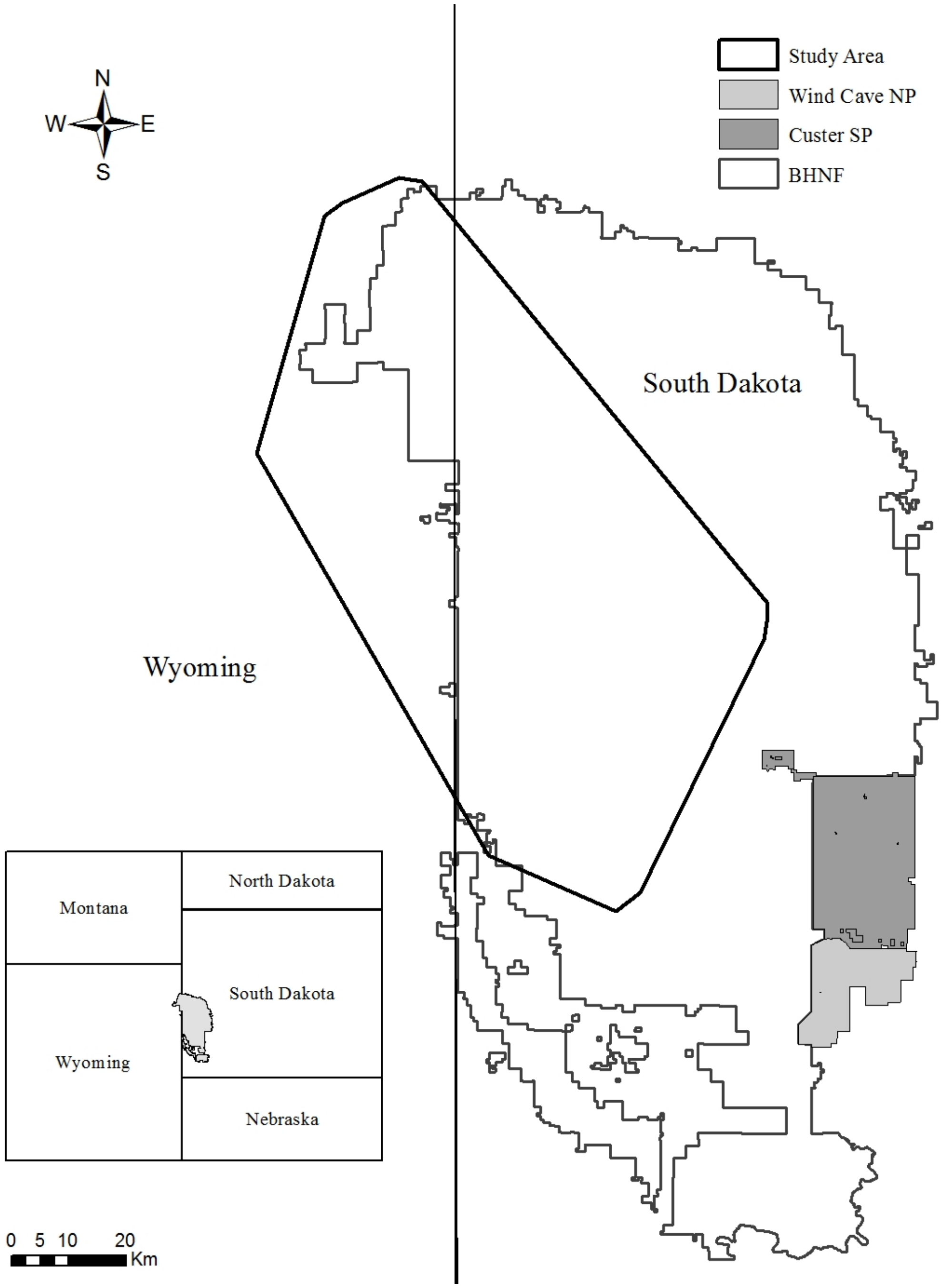
[d] Akaike wt. (Burnham and Anderson 2002).

[e] Number of parameters.

Table 6. Comparison of elk calf survival rates among elk populations throughout North America.

Area	Summer	Winter	Annual	Source
Eastern Populations				
Kentucky			0.77	Seward 2003
Michigan	0.90	0.97	0.87	Bender et al. 2002
Pennsylvania	0.92	0.90	0.82	DeVivo et al. 2011
Pennsylvania			0.71	Cogan 1999
North Carolina			0.59	Murrow et al. 2009
Western Populations				
California	0.85			Howell et al. 2002
Northcentral Idaho	0.18–1.00			White et al. 2010
Northcentral Idaho	0.00–0.84		0.06–0.83	Zager et al. 2005
Northcentral Idaho	0.32			Schlegel 1976
Montana		0.82–0.86		Knight 1970
Northern Yellowstone	0.65	0.72	0.43	Singer et al. 1997
Northern Yellowstone	0.29	0.90	0.22	Barber-Meyer et al. 2008
Northwestern Wyoming	0.84	0.84	0.58	Smith & Anderson 1998
Northwestern Wyoming		0.26–0.69		Sauer & Boyce 1983
Southeastern Washington			0.47	Myers 1999
South Dakota	0.79	0.96	0.75	Our study

Figure 1. Study area in the Black Hills National Forest, South Dakota and Wyoming, USA 2012–2013.



CHAPTER 3: HOME RANGE AND MOVEMENT ECOLOGY OF ADULT COW ELK IN THE BLACK HILLS, SOUTH DAKOTA AND WYOMING

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RH: Simpson et al. • Home Range and Movement Ecology

Home Range and Movement Ecology of Adult Cow Elk in the Black Hills, South Dakota and Wyoming

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ABSTRACT We studied seasonal movements and home range ecology of individually marked adult cow elk (*Cervus elaphus*) in the Black Hills, South Dakota and Wyoming, USA from 2012 to 2013. We captured and fit 49 adult cow elk with Global Positioning System (GPS) collars during 2 winter (Feb 2012 and Mar 2013) capture periods. We documented that elk in this region use a variety of movement strategies (migrant, resident, conditional migrators, dispersers); the majority of the population (58%) was migratory. Despite this migratory behavior, we found no difference in elevation and habitats between winter and summer ranges. Migrant elk could be separated into two distinct groups (Wyoming, Deerfield) relative to summer ranges. Spring migration distance travelled ranged from 2.45 km – 74.44 km *(n* = 42); fall migration distances ranged from 6.41 km – 153.95km (*n* = 46). We used 99% Brownian Bridge Movement Models to create seasonal and overall home ranges of adult cow elk. Mean overall home range size for conditional migrators was 249.28 km^2 (SE = 28.60, *n* = 7, range = 233.75), for migrant elk it was 227.18 km^2 (SE = 13.94, *n* = 29, range = 346.83), and for resident elk it was 175.65 km^2 (SE = 22.75, *n* = 11, range = 216.04). The large number of locations we were able to collect with the use of GPS collars and the BBMM home range analysis allowed us to accurately illustrate home range size and location as well as seasonal elk movements. We evaluated a dominantly migrant adult cow elk population with home ranges covering large areas of the Black Hills. Our results highlight a unique migratory elk herd within a forest–dominated landscape that had yet to be studied comprehensively.

KEY WORDS Black Hills**,** Brownian Bridge Movement Models (BBMM), home range, conditional, migrant, migration, resident, South Dakota, Wyoming

INTRODUCTION

Variation in migratory behavior has been documented in various ungulates such as caribou (*Rangifer tarandus*; Bergerud et al, 1990), elk (*Cervus elaphus*; Mordantini and Hudson 1989, Woods 1991), moose (*Alces alces*; Ball et al. 2001), mule deer (*Odocoileus hemoinus*; Kufeld et al. 1989, Nicholson et al. 1997), pronghorn (*Antilocapra americana*; Hoskinson and Tester 1980), and white-tailed deer (*O. virginianus*; Nelson and Mech 1991). Migration allows animals to move to areas that are favorable to their long-term fitness through enhanced reproduction success (Dingle 1996, Hebblewhite 2008). However, migration strategies can differ due to demographic class, the quality of the environment, or social cues (Alerstam et al. 2003, Hebblewhite and Merrill 2007, Sakuragi et al. 2003, Sutherland 1998).

Seasonal movements are common in elk and have been documented in regions where they travel from low elevation wintering areas to higher elevation summer ranges in response to seasonal changes in climate and forage availability (Irwin 2002). Depending on conditions, not all elk in a population migrate; some may move short distances, some make multiple trips between seasonal ranges, while others travel directly from summer to winter ranges (McCullough 1969, Martinka 1969). Adult cow elk are known to exhibit site fidelity between seasons and years (Craighead et al. 1972, Rudd et al. 1983, Edge and Marcum 1985, Edge et al. 1986, Smith and Robbins 1994), often these are behaviors in which calves learn from their mothers (Van Dyke et al. 1998). Few elk are known to disperse from populations (Edge et al. 1986).

Home range size (i.e., the area an animal occupies) is directly related to the movement patterns and the distribution of the population (Anderson et al. 2005). Animals make movement decisions that optimize the chance of survival (White et al. 2010). There is a balance between movement to avoid predation and finding suitable forage while minimizing thermal stresses and retaining social contacts (White et al. 2010). Elk must meet their energetic needs and the distances they travel are dependent on the abundance and location of forage (Frair et al. 2005). If poor forage results in larger home ranges then winter elk home ranges will in all likelihood be larger than summer home ranges as winter weather can reduce the availability (Wickstrom et al 1984) and quality of forage (Albon and Langvatn 1992). Variation between forested areas and open grasslands, available to cervids, creates edge, which is important to elk (Kie et al. 2002).

Environmental factors, namely habitats related to forage and cover (Hobbs et al. 1981) affect home range size of elk. Frair et al. (2005) found that broad scale movements were directly related to open forest patches while large forest patches limited elk movement. Large patches result in a tradeoff between foraging opportunities and predation risks (Frair et al. 2005). Cook et al. (1998) suggested that cover is not considered a significant factor for improving the energetic status of elk and instead is utilized for available forage and predator avoidance. Thus, energy requirements of elk, as well as forage abundance, quality, and distribution across habitats, have direct effects on seasonal home ranges size (Mace et al. 1984).

The purpose of our study was to define seasonal home ranges and migration ecology of elk occupying the southwestern region of the Black Hills of South Dakota and Wyoming. Our goal was to determine if elk were utilizing distinct migration strategies. Benkobi et al. (2005) evaluated migration of elk in the central region of the Black Hills, which provided basic migration information. With an elk population in the Black Hills believed to be expanding there was a need for detailed information on migration ecology. Ultimately, this project will help to answer ecological questions concerning regional use and carrying capacity of a previously unstudied population of elk.

STUDY AREA

The Black Hills are an isolated, mountainous extension of the Rocky Mountains located in western South Dakota and northeastern Wyoming (Petersen 1984). The mountains of the Black Hills are a maturely dissected domal uplift with a central crystalline core surrounded by steeply dipping sedimentary deposits (Hoffman and Alexander 1987).

Topography of the Black Hills varies extensively (Kennedy 1992). The Black Hills extend approximately 95 km east to west and 190 km north to south (Petersen 1984) covering an area of about 8,400 km^2 (Orr 1959, Turner 1974, Fecske et al. 2002). Elevation ranges from 973−2,202 m above mean sea level. Seasonal temperature fluctuations in the Black Hills are typical of a continental climate (Orr 1959). Mean annual temperatures range from 5 to 9 °C with extremes of−40 to 44 °C. Mean annual precipitation is > 66 cm (Orr 1959). Yearly snowfall may exceed 254 cm at higher elevations (Thilenius 1972).

Our study focused on the southwestern region of the BHNF in South Dakota extending into Wyoming (Figure 1). The western area of the BHNF is encompassed within Custer, Pennington, and Lawrence counties in South Dakota, and eastern Crook and Weston counties in Wyoming. The study area was comprised of large expanses of public land interspersed with small inholdings of private lands. The majority of private lands were located in the northwest portion of the study area in Wyoming. Dominant overstory vegetation of forested areas consisted of ponderosa pine (*Pinus ponderosa*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), interspersed with mountain juniper (*Juniperus scopulorum*), and mountain mahogany (*Cercocarpus montanus*) at low elevations in dry areas along southwestern fringes of our study area (Thilenius 1972, Severson and Thilenius 1976). Primary understory vegetation consisted of various forbs, grasses, and shrub species, including big bluestem (*Andropogon gerardii*), buffalograss (*Buchloe dactyloides*), and Oregon grape (*Berberis repens*; Thilenius 1972, Severson and Thilenius 1976). Our study area was predominantly coniferous forest (66.4%) intermixed with grassland/herbaceous areas (15.3%) and areas of early successional stands (16.8%) (National Land Cover Database (NLCD); Jin et al. 2013). The remaining breakdown of the area included small patches of deciduous forest (0.6%), mixed forest (0.2%), developed space (0.3%), hay/pasture lands (0.1%), and wetlands (0.1%). Private lands contained more meadows, alfalfa (*Medicago sativa*)/hay fields, and limited row crop production and were juxtaposed among forested stands.

A large part of the study area was burned during the Jasper Fire in 2000, which was a high-severity fire that burned approximately 33,729 hectares (83,500 acres; 7% of the BHNF and 10.4% of our study area; Jasper Fire Rapid Assessment, http://www.fs.fed.us/r2/blackhills/fire/history/jasper), of interior forest from August until official containment was declared in September 2000. LANDSAT data for the fire reported in the Jasper Fire Rapid Assessment, characterized it as highly variable. Areas left unburned or with low intensity burns comprised 25% of the burn area. Moderate burns where crowns were entirely or nearly scorched comprised 48% of the burn. About 27% of the burn was high-intensity fire where trees were left completely void of needles (Lentile et al. 2005).

METHODS

Elk capture events took place in the Jasper burn area north of Highway 16 and west and north of Jewel Cave National Monument in the southwestern region of the BHNF. We captured <6 elk per group and distributed captures throughout the study area (Figure 1). Elk were chemically immobilized (6 ml of Butophanol, 2 ml of Azaperone, and 3 ml of Medetomidine; Zoopharm, Windsor, CO, USA) via darts fired from a cartridge fired projector while pursuing elk in a helicopter (Quicksilver Co, CO, USA). Elk were darted with 3cc barbed darts (Pneu Dart, Williamsport, PA, USA) to ensure the immobilization drugs were administered.

Adult female elk were fitted with 1,150g Global Positioning System (GPS)/Store on Board (*n* = 30, TGW-4600-2 Telonics Inc. Mesa, AZ, USA) and 825 g GPS/Iridium satellite collars (*n* = 10 G2110E Advanced Telemetry Systems, Isanti, MN, USA). Store on board collars were programmed to download locations every 2.5 hr throughout 24 hr periods beginning at 0100 hr. Collars were set to attempt a GPS fix for 180 seconds at each scheduled fix time and store location information in the collar housing unit. Locations were then manually downloaded in the field during a recapture period in 2013 and again when collars were collected after remote release from animals in January 2014. Collars were programmed with a 4 hr mortality signal. Iridium collars were programmed to upload locations twice per day throughout the year at 0600 and 2000 hr until calving season was estimated to begin (~ 1 May), at which time a location at 1200 hr was added to the download schedule. Iridium collars were set to attempt a GPS fix for 180 seconds at each scheduled fix time (ATS “forest” setting), then transmit those coordinates via satellite every 24 hr to an automated email system. These collars were programmed with a 4 hr mortality signal but were changed to 6 hr when we began to have issues with false mortality signals.

Captured elk were checked for pregnancy by rectal palpation conducted by a veterinarian (S. Lindsay, Fall River Veterinary Clinic, Hot Springs South Dakota, USA; Greer and Hawkins 1967). Pregnant cow elk were fitted with vaginal implant transmitters (VITs M3960; Advanced Telemetry Systems, Isanti, MN, USA) using a fabricated polyvinyl chloride (PVC) applicator that was coated with lubricating jelly

(Johnson et al. 2006). We extracted a canine tooth to determine age using cementum analysis during each initial cow elk capture (Fancy 1980). We collected approximately 20ml of blood from each cow through the saphenous vein. Blood was sent to BioPRYN$_{\text{wild}}^{\copyright}$ to test for pregnancy. BioPRYN$_{\text{wild}}^{\copyright}$ tests for the presence of protein B, which is produced in the placenta (BioTracking, LLC, Moscow, Idaho, USA). We transferred blood to the laboratory (BioTracking, LLC, Moscow Idaho, USA) for testing when palpation checks for pregnancy were questionable. All capture and handling procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 12-009A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Home Range Analysis

We first determined if elk were migratory or non-migratory by examining cow elk locations and running a K-means cluster analysis (Systat Software Inc., Chicago, Illinois, USA; Boulanger et al. 2006) to evaluate grouping of locations. We set clusters to $n = 3$ for these analyses to ensure distinct seasonal ranges were included. If cluster analyses showed significant seasonal separation of x and y coordinates with nonoverlapping ranges and animals had high fidelity to winter range, we classified elk as migrants (Cagnacci et al. 2011). When elk had distinct clusters of summer locations that were separate from winter locations yet the elk made considerable movements between summer and winter ranges, we classified these elk as conditional migrators (Jones et al. 2014). If clusters were not significant indicating that seasonal ranges overlapped and elk did not exhibit seasonal movement events, they were classified as residents (Jones et al. 2014). We classified elk as dispersers if they left the winter range where captured and did not return the following year (Jones et al. 2014). For our migratory elk, we used location clusters to determine the extent of summer and winter home ranges. We calculated migration timing by identifying the date at which a cow elk made a directed movement away from one seasonal range and did not return. If an animal left a seasonal range and moved into another range but returned again, the final movement out of a seasonal range was considered the migration date (Jones et al. 2014).

We calculated 99% home ranges using Brownian Bridge Movement Models using the computer package BBMM (Neilson et al. 2013) in Program R (R Core Team 2013). We used all successful locations for each elk to estimate overall home range; summer and winter (~November-March) locations were used to estimate seasonal home ranges. We were not concerned with missing observations or fix-rate biases because 96% of GPS fix attempts were successful. Nevertheless, we used a maximum time-lag of 200 minutes for store–on–board collars and 1500 minutes for Iridium collars to exclude consecutive locations from BBMM estimates. We used an estimated location error of <15m because 99% of GPS locations were three dimensional (3-D) fixes and tests on ATS collars have shown low positional error (Di Orio et al. 2003).

To determine migration distance, we isolated locations associated with migration; we then selected the last point of the previously occupied seasonal range and the first point of the alternative seasonal range entered for each migration season. We used the points to line tool in ArcMap 10 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to estimate the distance traveled for each elk during each migration event. We used the same migration line to calculate migration direction. We measured azimuths at the start, middle, and end of each of these migration lines and calculated the mean of the three azimuths to determine migration direction for each elk from circular statistics using Program Oriana 4 (Kovach Computing Services, Anglesey, Wales, UK).

We then took the mean of each elk migration direction during spring and fall to determine seasonal migration direction. To determine particular migration corridors that migrant cow elk were using, we selected all migration–specific locations from each migrant elk, placed them over a World Terrain Base Map in ArcMap10 (Environmental Systems Research Institute, Inc., Redlands, CA, USA), and then placed a 11–km wide polygon over the region of the study area where a majority of the migration locations were observed during field activities. We determined the mean elevation for seasonal locations for the winter range as well as summer range for migrating elk using an elevation layer for the Black Hills available in ArcMap 10 (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

Data Analysis

We used Program R (R Core Team, 2013) and SYSTAT 13.0 (Systat Software Inc., Chicago, Illinois, USA) to conduct statistical analyses. We used paired t-tests to compare home range sizes by year and pregnancy status, and seasonal migration distances between years of each migration group. We used t-tests to compare overall home range size between seasons and seasonal migration distances between migration groups. We used a Bonferroni correction to maintain the experiment-wide alpha level when using multiple statistical tests. We used analysis of variance (ANOVA) to compare home range size by migration type and a Tukey’s HSD test to determine differences in pair-wise comparisons.

RESULTS

We captured adult female elk ≥2 years of age during two separate capture periods; 3–6 March 2012 and 22–26 February 2013. In 2012, we captured 40 adult cows. In 2013, 35 of those cows were recaptured along with 9 newly captured adult cow elk. Mean age of captured elk was 7.4 years (SE = 0.61; ages: 2–5 yr = 17, 5–10 yr = 24, 11–15 yr = 4, 16–20 yr = 4). Pregnancy rate differed (2012 = 93%; 2013 = 66%; $p = 0.003$) between years. We deployed VITs during both capture periods ($n = 38$, 2012; $n = 33$, 2013). In 2012, we inserted a VIT into one cow that, after blood was analyzed for pregnancy, proved not to be pregnant. In 2013, 4 cows with VITs proved not to be pregnant. One elk was removed from home range analyses because it was lost to predation 49 days after collaring in 2012. In 2013, 2 elk were removed from analyses. One elk had a significant foot injury at capture (non-capture related) and was treated with antibiotic to aid in recovery; thus, information from 2012, only, was used in analysis. This elk survived through the summer period but her movements were atypical. A second elk was removed from analyses because of capture related mortality during the second capture period; we were able to use a full year of data in analyses. A total of 167,707 locations (Iridium, n = 15,602, Store-on-board n = 152,105) was collected over the course of our study. We documented the migration status for 48 elk through the duration of our study; 28 migrant elk (20, 2012–2013; 5 in 2012, 3 in 2013), 11 resident elk (6, 2012–2013; 3 in 2012, 3 in 2013), 6 conditional migrators (5, 2012–2013; 1 in 2013). We also documented 3 dispersers; one elk dispersed to the northern end of the study area immediately after the first winter capture. The next remained in the southern end of the study area for a full summer and winter season before dispersing to Wyoming for the remainder of the study.

We considered the last elk a disperser as it followed a similar migration pattern until the last winter of the study in 2013 and did not return to the original wintering area.

The mean overall home range size was 227.87 km^2 (SE = 22.44, *n* = 6, range = 140.00), 223.95 (SE = 14.05, *n* = 28, range = 346.84), and 175.65 (SE = 22.75, *n* = 11, range = 216.04) for conditional migrators, migrants, and residents, respectively. The overall mean migration date for 2012-2013 for migrant elk during spring was 11 April (SE = 2.88); the mean fall migration date for migrant elk was 24 October (SE = 8.09). We calculated a total 164 home ranges using all successful locations; 33 were for elk with 2 complete years (2012–2013) of locations. We calculated 48 annual home ranges (mean = 219 km^2, SE = 11, range = 346.84), 39 summer home ranges in 2012 (mean = 109.91 km^2, SE = 6.94, range = 182.74), and 42 summer home ranges in 2013 (mean = 119.81 km^2, SE = 11.05, range = 241.3). We calculated 35 complete winter home ranges (mean = 115.34 km^2, SE = 8.9, range = 242.75).

We did not observe differences between the overall home range sizes among migration types ($F_{2,42}$ = 1.90, p = 0.16; Table 2). We did not detect differences between summer (2012 and 2013) and winter home ranges ($F_{2,98}$ = 0.23, p = 0.79; Table 2) or between seasonal ranges by migration types ($F_{2,98}$= 1.93, p = 0.11). We did, however, observe a difference in seasonal home range size between migration types ($F_{4,98}$ = 19.16, p = 0.01) seasonal home range size was similar between conditional and resident elk (p = 0.96, 95% CI =−33.33–41.43) but differed between migrant and conditional migrators (p = 0.001, 95% CI =−89.29–−25.49) and between resident and migrant elk (p = 0.001, 95% CI = 33.74–89.13).

Mean summer home range size of pregnant and nonpregant cow elk was 113.83 km^2 (SE = 13.39, *n* = 12) and 127.74 km^2 (SE = 21. 68, *n* =12; t =−0.77, *P* = 0.46), respectively; home range size of cow elk did not differ (t_{32} =−0.77, *P* = 0.45) based on pregnancy status. A total of 33 elk survived throughout the study. We compared summer 2012 and 2013 home ranges of these elk; mean home range size in 2012 was 104.80 km^2 (SE = 8.19, *n* = 33, range = 182.73) and in 2013 it was 115.10 km^2 (SE = 12.51, *n* = 33, range = 239.62); estimates did not differ (t_{32} =−0.29, *p* = 0.77) between years. We also ran an independent t-test between home range size of resident and conditional migrating elk to ascertain if the drought year in 2012 affected summer home range size. Summer home ranges in 2012 and 2013 were similar (t_{32} = 1.21, *p* = 0.25).

We observed two distinct migration groups during our study. One group (Wyoming group) moved northwest from winter range into and along the Wyoming border (*n* = 16) while the second group (Deerfield group) migrated in a northeasterly direction to the Deerfield Lake area in the central Black Hills (*n* = 9: Figure 2). Mean elevation for the summer range occupied by the Wyoming group was 1,919.21 m (SE = 1.71; range = 1,145.29–2,153.68 m, *n* = 5,816) while the elevation for the Deerfield group was 1,824.06 m (SE = 1.23; range = 1,649.18–2,149.79 m, *n* = 3,163). Mean elevation for the wintering area occupied by all elk during the study was 1,825.5 m (SE = 1.14; range =1,429.19–2,108.03 m, *n* = 8,224), which was similar (t_{8497} =−0.86, *p* = 0.19) to the summer range of the Deerfield group but differed (t_{10626} = 45.61, $p < 0.002$) from the summer range of the Wyoming group.

The mean migration date for the Wyoming group during spring 2012 was 29 March (SE = 4.1, *n* = 16; Table 1) and they traveled for an average of 6 days (SE = 0.9, *n*

= 16) between ranges. The mean migration date for spring 2013 for the Wyoming group was 1 May (SE = 3.1, $n = 15$) and the average time traveled between ranges was 3 days (SE = 0.4, $n = 15$). In spring, the mean number of travel days between ranges differed between years for the Wyoming group of adult cow elk ($t_{30} = 3.03$, $p = 0.006$).

The mean spring 2012 migration date for the Deerfield group was 6 April (SE = 3.8, $n = 9$) and mean time traveled between ranges was 4 days (SE = 1.2, $n = 9$). During spring 2013, Deerfield elk began migration on 10 April (SE = 3.5, $n = 9$) and the mean time traveled was 3 days (SE = 0.2, $n = 9$). Spring migration time traveled between ranges did not differ ($t_{17} = -0.20$, $p = 0.84$) between years.

The mean migration date for the Wyoming group during fall 2012 was 22 November (SE = 5.9, $n = 14$) and the average time traveled between ranges was 11 days (SE = 3.4, $n = 14$). The mean departure date for fall 2013 was 28 October (SE = 6.9, n = 12) and the Wyoming group travelled an average of 7 days (SE = 2.3, $n = 12$) between ranges. We found no difference ($t_{25} = 0.99$, $p = 0.33$) in the number of days traveled during fall migration between years for the Wyoming group. The mean migration departure date during fall 2012 for the Deerfield group was 28 October (SE = 6.9, $n = 8$) and they traveled for an average of 32 days (SE = 3.3, $n = 8$) between ranges. Whereas, the mean departure date for Deerfield elk in fall 2013 was 10 October (SE = 3.5, $n = 8$) and these elk traveled for 3 days (SE = 0.2) between ranges. The time traveled for fall migration differed ($t_{15} = 8.24$, $p = 0.001$) between years.

The mean migration distance traveled for the Wyoming group during spring 2012 was 28.02 km (SE = 4.25, $n = 16$, range = 62.64); for spring 2013 it was 17.92 km (SE =

1.62, *n* = 15, range = 22.18). The mean migration distance traveled for the Wyoming group during fall 2012 was 51.93 km (SE = 12.32, *n* = 14, range = 147.54) and for fall 2013 was 28.82 km (SE = 8.17, *n* = 12, range = 97.57). Mean distance traveled was similar between years for spring ($t_{11} = 1.32, p = 0.21$) and fall ($t_9 = 1.8, P = 0.10$) migrations for the Wyoming migration group.

The mean migration distance traveled for the Deerfield group during spring 2012 was 19.58 km (SE = 5.28, *n* = 9, range = 55.95); for spring 2013 it was 21.33 km (SE = 4.63, *n* = 9, range = 47.39). The mean distance traveled during fall 2012 for the Deerfield group was 99.58 km (SE = 12.76, *n* = 8, range 114.77); during fall 2013 it was 19.32 km (SE = 2.46, *n* = 8, range = 22.05). Mean distance traveled for the Deerfield group in spring was similar ($t_7 = -0.64, p = 0.55$) across years; however, the distances traveled during fall differed ($t_6 = 8.14, p = 0.0002$) between years. Mean migration distance did not differ between migration groups during spring 2012 ($t_{23} = -1.22, p = 0.23$) and 2013 ($t_{22} = 0.83, p = 0.42$). We did, however, document a difference in distance traveled between the Wyoming and Deerfield migration groups in fall 2012 ($t_{20} = 2.51, p = 0.02$) but not in fall 2013 ($t_{18} = -0.92, p = 0.37$).

Mean migration direction for the Wyoming group during spring 2012 was 340.09° (SE = 8.29°) whereas the mean direction for spring 2013 was 351.83° (SE = 10.87°). The mean fall 2012 migration direction for the Wyoming group was 161.59° (SE = 6.77°); for fall 2013 it was 168.57° (SE = 12.32°). Mean migration direction for the Deerfield group during spring 2012 was 21.47° (SE = 16.28°); during spring 2013 it was 48.17° (SE = 14.78). Mean migration direction for the Deerfield group during the fall 2012 migration period was 223.30° (SE = 36.02°) and during the fall 2013 it was 196.00°.

DISCUSSION

We collected ecological information on an elk population that has been studied little since its reintroduction nearly 100 years ago. The large number of locations we were able to collect with the use of GPS collars and the BBMM home range analysis allowed us to accurately illustrate home range size and locations as well as seasonal elk movements. We identified a unique population of elk utilizing three migration strategies; the majority of our elk were migrators. We also documented elk that switched migration strategies between years.

Elk populations with multiple migration strategies have been documented in other regions of North America. Portions of the Jackson elk herd have varying migration strategies (Boyce 1991) as well as those in Banff National Park, Canada (Hebblewhite and Merrill 2007). Typically, migrant elk in other populations migrate to areas of higher elevations during the summer season following green up of forage (Albon and Langvatn 1992, Parker et al. 2009). Although we found a statistical difference in elevations between the winter range and the summer range of Wyoming elk; a difference of 93.71 m shows there was no biological difference between the two. Furthermore, habitat throughout our study area was dominated by evergreen forests. Nonetheless, in Wyoming we saw a higher proportion of open areas compared to South Dakota. Open spaces in Wyoming were confined to areas outside of the BHNF while in South Dakota, open areas were located in a few large sections (i.e., Jasper burn) surrounded by considerable expanses of ponderosa pine forests. The concentration of open areas in Wyoming could be attracting the larger group of migrant elk that occupied the summer range of the Wyoming group considering the importance of habitat heterogeneity for adult cow elk (Boyce et al. 2003). The winter range that migrant elk leave in the Jasper burn area is typically first to green up and seasonal summer areas are often covered in snow when elk arrive.

We documented high site fidelity of migrant elk, which has been seen in other elk populations in mountainous areas in North America (McCullough 1985, Morgantini 1989, Woods 1991). We documented 1 adult cow elk that dispersed soon after being collared and 2 that dispersed after utilizing the same migration strategy for at least 2 consecutive seasons. The elk that dispersed set up a resident home range in the north end of the study area along the South Dakota and Wyoming border. This elk was 2 years old at capture and successfully raised a calf in the two summers she was collared. One elk that switched migration strategies also was 2 years old at capture and spent the first year of the study as a resident elk in the south end of the study area. During the early summer of 2013, that elk moved over 70 km northwest and remained there for the majority of the final year of the study. Although, as the winter season progressed, this elk moved south but did not completely return the initial capture area. Smith et al. (2001) found that dispersal occurs mostly in cow elk before they reach 3 years of age. The second adult elk was a 9 year old at capture and she did not return to the same winter range from the previous year. She did return early in the migration season after a severe snow but returned to Wyoming until the end of the study. Other studies also have documented elk switching migration strategies (Woods 1991) but little is known as to why these changes occur. These cows may have dispersed due to a growing elk population and high survival in the Black Hills, as has been seen in other populations (Van Dyke et al. 1998).

Our spring migration dates were similar to those (12 April) documented for elk in this region in the late 1990's; although, fall migration dates were a month earlier (23 November; Benkobi et al. 2005). Our migration dates were similar to other elk herds in North America including the Jackson Hole elk herd (spring migration April and May, fall migration October-November; Smith and Robbins 1994) the North Yellowstone elk herd (spring migration April and May; Craighead et al. 1972), the Blackfoot-Clearwater elk herd in Montana (April and May; Hurley 1994), and the White River Plateau elk herd in Colorado (April and May; Boyd 1970), as well as fall migration dates for the Absaroka-Yellowstone elk herd (November; Rudd et al. 1983), Banff National Park elk herd (September-November; Morgantini and Hudson 1988), and the northern Yellowstone elk herd (12 – 23 October; White et al. 2009). We also observed similar mean overall migration distances compared to other elk herds in the west; Absaroka-Yellowstone (48.3 km; Rudd et al. 1983), North Fork Salmon River, Idaho and Montana (40.5 km; Grkovic 1976), and western Wyoming (35.4−54.6 km; Jones et al. 2014). Nevertheless, elk in the Black Hills represent one of the few migratory elk herds where summer and winter range elevation was relatively constant.

Migrating elk spend the majority of the year on summer ranges, which are snow covered when they arrive and begin accumulating snow before they leave for summer range. During October 2013, a major snow event (>30cm) occurred during which, elk from both migration groups returned to the wintering area. The storm resulted in 65% of migrant elk from the Wyoming group, returning to winter range and remaining there until the end of October. Of the Deerfield group, 88% left immediately after the storm ended and remained on the winter range, however; one elk left the summer range only to return a week later and subsequently remained on summer range until 5 November. Of the Wyoming group, 50% left summer range after the storm and remained on winter range, 4 elk from that group left summer range only to return ~2 weeks later and subsequently migrated to winter range from 26 October – 22 November. Two elk from the Wyoming group left their designated summer range but did not move all the way to the winter range though these elk occupied the southernmost edge of the area occupied by the Wyoming group and did not travel far to complete their migrations. Snow depths commonly effect migration in elk populations in Washington (Mitchell and Lauckhart 1948), Wyoming (Anderson 1958, Rudd et al. 1983, Boyce 1989), Montana (Lovass 1970, Picton and Picton 1975) and Idaho (Leege and Hickey 1977, Brown 1985). Snow depths between 15 to 25 cm initiated migrations of elk in Yellowstone National Park (Anderson 1954). We observed elk in the southwestern Black Hills traveling to summer ranges when snow depths were above 60 cm suggesting that depth was not the primary factor initiating migration.

Comparing home range size for the elk herd in the southwestern Black Hills with those of other elk herds is difficult because of the varying analyses used to calculate home ranges. Our study collected a large number of elk locations using GPS technology, which allowed us to create home ranges using BBMM methodology. This method uses large numbers of locations and thus, allowed us to accurately predict the chance of an animal being in the described location (Kie et al. 2010). Using BBMM to calculate home ranges omits the subjectivity that smoothing parameters cause in other analyses (Horne et al. 2007). BBMM takes into account the serial correlation of GPS locations and provides a model of landscape movements using Brownian motion to estimate the paths traveled between successive GPS locations while determining the probability of an individual being in an area (Horne et al. 2007). Estimation of movement paths allows the BBMM to identify travel pathways used by individuals and withhold areas of avoidance from home range estimates (Horne et al. 2007). These characteristics of the BBMM provide enhanced understanding of animal movements. Estimating home range size using other analyses (e.g., convex polygon) results in the inclusion of areas within the home range contours that may not be occupied by the animal especially when home ranges are irregularly shaped (Walter et al. 2011). This can lead to an over estimation of home range size (Wilckens 2014).

When we compared home ranges of elk in our study to the estimates of those of elk previously studied in this region, previous estimates were greater than for elk in our study (Benkobi et al. 2005). The previous study used a fraction of the locations collected in our study and a kernel use distribution to calculate home ranges (Benkobi et al. 2005). Studies on elk in Wisconsin, Alberta, and Yellowstone estimated summer home range sizes of 52.96 km^2, 21.34 km^2, and 134 km^2, respectively, and winter home range sizes of 101.04 km^2, 28.41 km^2, and 179.74 km^2, respectively (Anderson et al. 2005). Home range size for elk populations in Wisconsin and Alberta were related to forage biomass and a high percentage of forest cover (Anderson et al. 2005).

We documented similar summer and winter home range size, which is not typical. Anderson et al. (2005) in their study of elk in Yellowstone, Alberta, and Wisconsin noted larger winter than summer ranges. Winter home ranges are larger when resources are scarce, the quality of forage is decreased, and often forage is covered with snow (Wickstrom et al. 1984, Albon and Langvatn 1992). The Jasper burn, which occurred in 2000 and consisted of large open areas, may be the reason for elk in our study occupying smaller winter home ranges. All of our elk were captured in the Jasper Burn area and 98% of those elk wintered there the following year. This high site fidelity shows the importance of the burned area to elk. The open nature and lower amounts of precipitation seen in the area of the burn (Brown and Cook 2005) allowed for large areas to be windswept and void of snow, which provided elk easy access to forage. There also were patches of forested cover found throughout the burn that provided cover for elk during winter.

The two distinct migration groups (Wyoming and Deerfield) observed during our study had different summer home ranges yet they used a similar migration corridor (Figure 3). In our analysis, we estimated migration direction based on the final seasonal movement cow elk made from one seasonal range to another. When we compared migration corridors used by the two groups we noted similarities. Both groups of elk migrated from seasonal home ranges using a large draw that runs north-south along the Wyoming-South Dakota border. Sawyer et al. (2009) observed similar behavior in mule deer in Wyoming, as a large proportion of animals were using the same migration route segments. They hypothesized that these migratory patterns were influenced by behavior and energy constraints (Sawyer et al 2009). Also, migrating in groups along a familiar pathway also may be advantageous relative to avoiding predators and thus, increasing the probability of survival (Nelson and Mech 1981).

Migration between South Dakota and Wyoming was not observed in a previous study conducted on elk in this region of the Black Hills (Benkobi 2005). However, the elk collared during that study were not captured in the same area as our captures. During our study, 17 adult cow elk spent >21 days in Wyoming. The mean time that elk remained in Wyoming was 215 days, which occurred primarily during the summer. One elk that dispersed moved to an area north of where she was captured along the border of South Dakota and Wyoming; she spent a total of 254 days in Wyoming. These Wyoming elk spent an average of 52 days in Wyoming, which overlapped with the Wyoming hunting season. We did not see movement out of summer areas in Wyoming in response to hunting risk, which was documented in the northern Yellowstone region (White et al. 2009) where elk delayed movements into areas with hunting pressure.

A reasonable hypothesis for the migration pattern exhibited by elk in the southwestern Black Hills is that these cows learned to migrate from their mothers; this hypothesis was first presented for elk by Murie (1951). McCullough (1985) also suggested that young animals develop patterns of home range use and migration timing through the association with other elk, including their mothers. Elk in this region were extirpated in the late 1880’s and repopulated with elk from Yellowstone National Park; those elk were translocated from a population of migratory elk (White et al. 2010). It is not known if the migration pattern documented for these elk was affected by learned behavior from the Yellowstone Region or was developed post–release in the Black Hills.

MANAGEMENT IMPLICATIONS

Knowledge of cow elk movement timing and movement patterns as well as home range size allows managers to make decisions in a multi-use National Forest. Small winter home ranges indicate the importance of large open areas intermixed with patches of forested cover to winter habitats of elk. The management strategy for this herd may need to be altered as 71% of our elk lost to hunter harvest were harvested in Wyoming; all of which wintered in South Dakota. SDGFP conducts elk population surveys during the winter (South Dakota Department of Game, Fish and Parks 2015). Elk in the Black Hills also inhabit areas with other ungulates as well as domestic cattle. Knowing where these elk are moving and the regions they are occupying throughout the year will aid in distribution of grazing allotments. Migrant elk were localized within one major, 6 km wide, migration corridor. We calculated 78% of spring migration locations and 92% or fall migration locations within this corridor. With the identification of a specific migration corridor, efforts can be localized to these areas to maximize the potential of protected areas. Also, the state is in the process of reevaluating their elk management plan (South Dakota Department of Game, Fish and Parks 2015) and this study will provide information related to the amount of habitat the Black Hills may require to support an elk population of this size.

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Table 1: Migration timing and the number of days traveled for two groups of migrant elk in the Black Hills, South Dakota and Wyoming, USA, 2012 – 2013.

Mig. Group	*Season*	*Mean Departure Date*	*Mean Travel Days*
Wyoming	Spring 2012	3/29 (± 4.1)	6 (± 0.9)
	Fall 2012	11/22 (± 5.9)	11 (± 3.4)
	Spring 2013	5/1 (± 3.1)	3 (± 0.4)
	Fall 2013	10/28 (± 6.9)	7 (± 2.3)
Deerfield	Spring 2012	4/6 (± 3.8)	4 (± 1.2)
	Fall 2012	10/28 (± 4.6)	32 (± 3.3)
	Spring 2013	4/10 (± 4.6)	4 (± 0.9)
	Fall 2013	10/10 (± 3.5)	3 (± 0.2)

Table 2: Overall and seasonal mean home range size of adult cow elk based on Brownian Bridge Movement Model, home range analysis in the Black Hills, South Dakota and Wyoming, USA. 2012 –2013.

	Home Range Size		
Type	Overall	Summer	Winter
Migrant (*n* = 28)	223.95 (SE = 14.05)	83.69 (SE = 5.21)	100.66 (SE = 11.49)
Conditional (*n* = 6)	227.87 (SE = 22.44)	150.37 (SE = 19.39)	154.81 (SE = 27.70)
Resident (*n* = 11)	175.65 (SE = 22.75)	160.29 (SE = 13.97)	126.74 (SE = 16.10)
Disperser (*n* = 3)	314.06 (SE = 37.88)	201.34 (SE = 17.65)	145.88 (SE = 31.43)

Figure 1. Study area in the Black Hills National Forest, South Dakota 2012–2013.

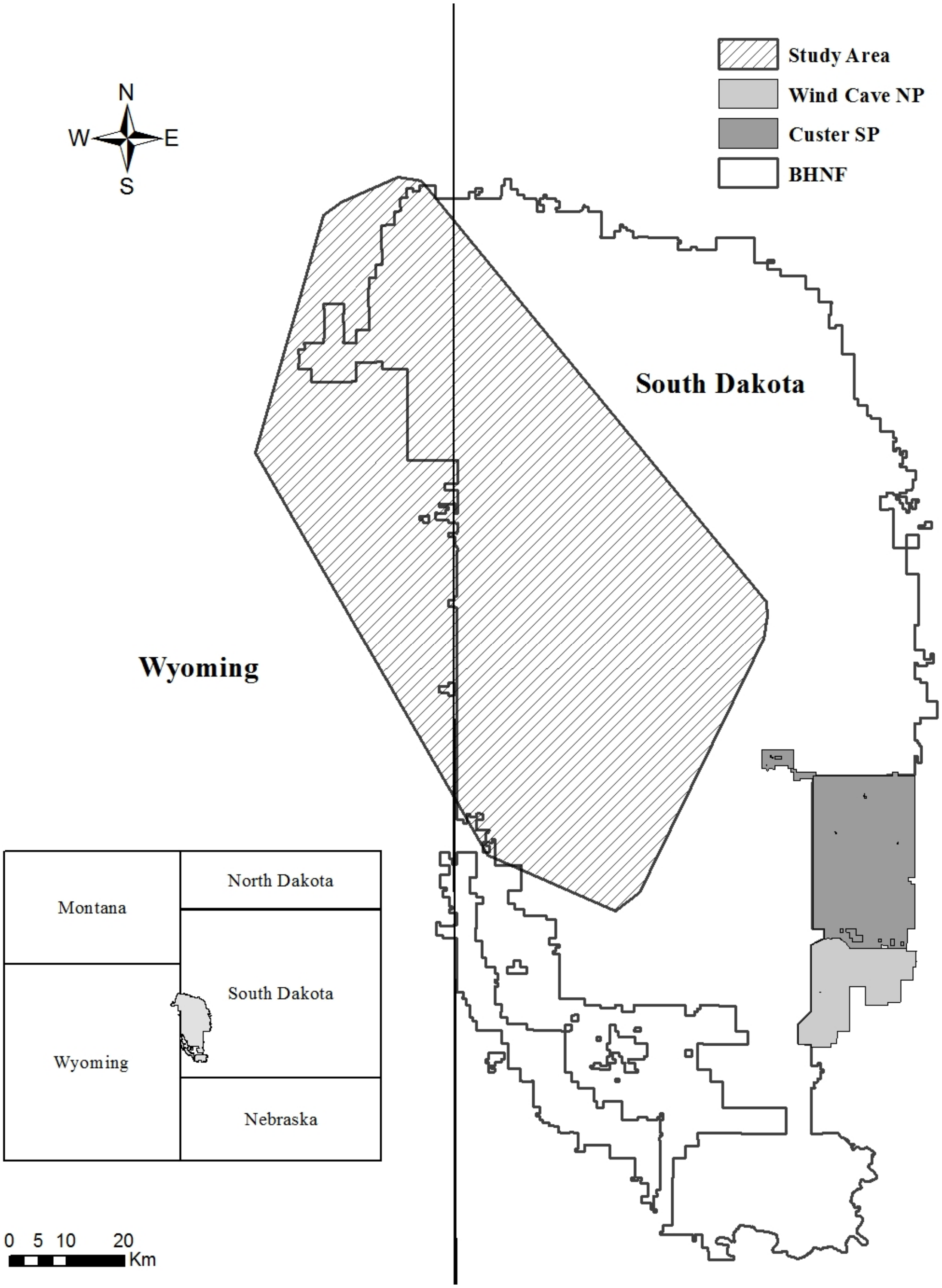
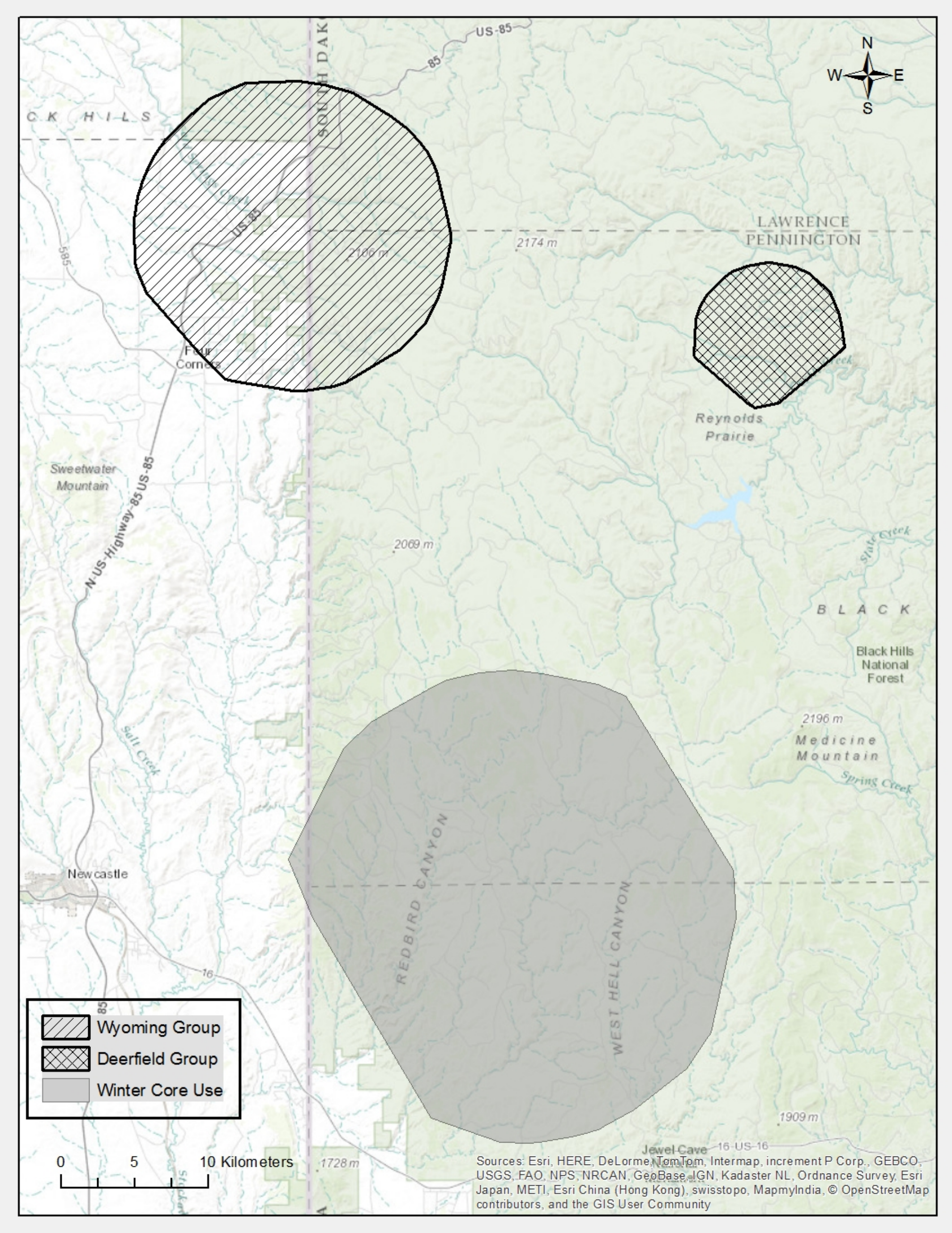
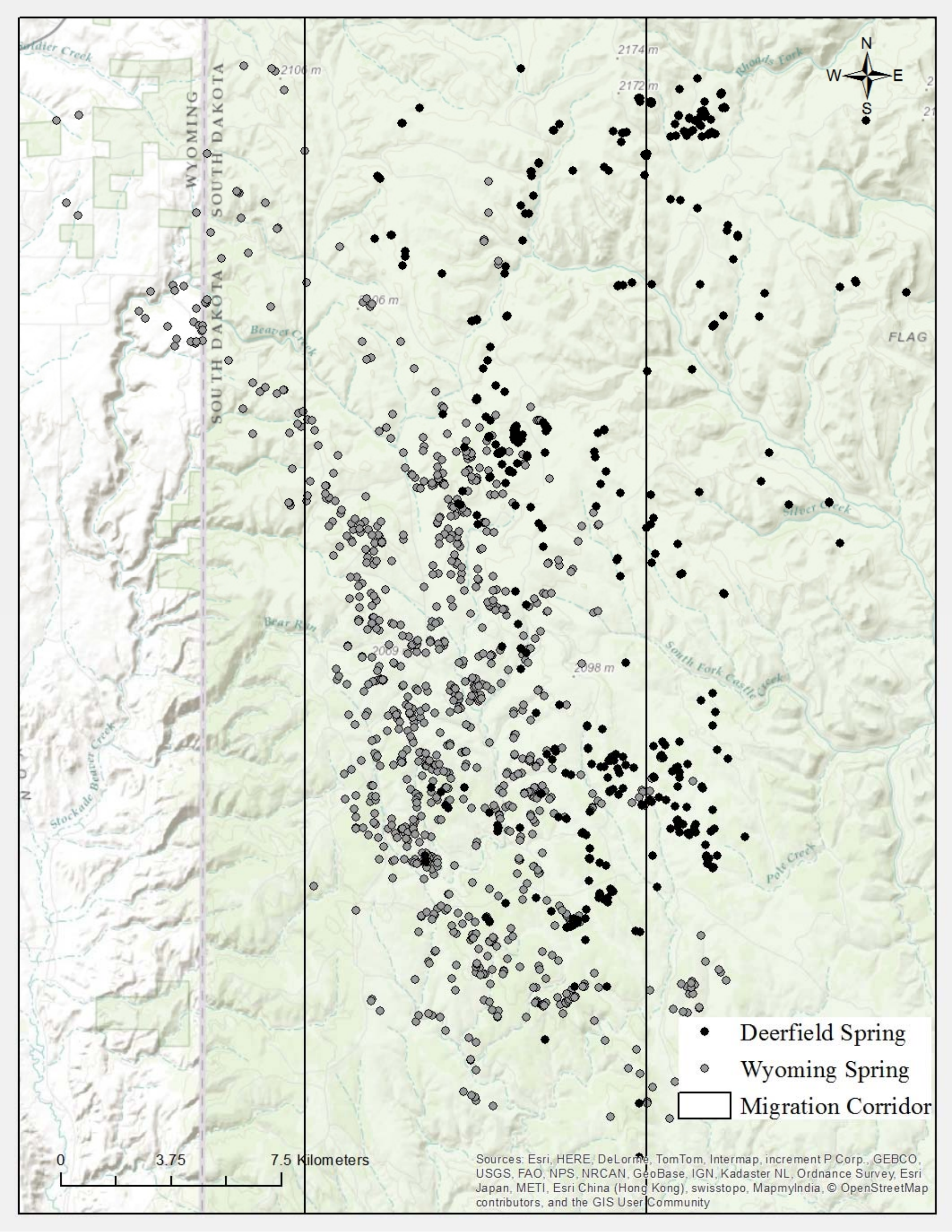


Figure 2: Distinct adult cow elk migration groups documented in the Black Hills, South Dakota and Wyoming, USA. 2012 – 2013.



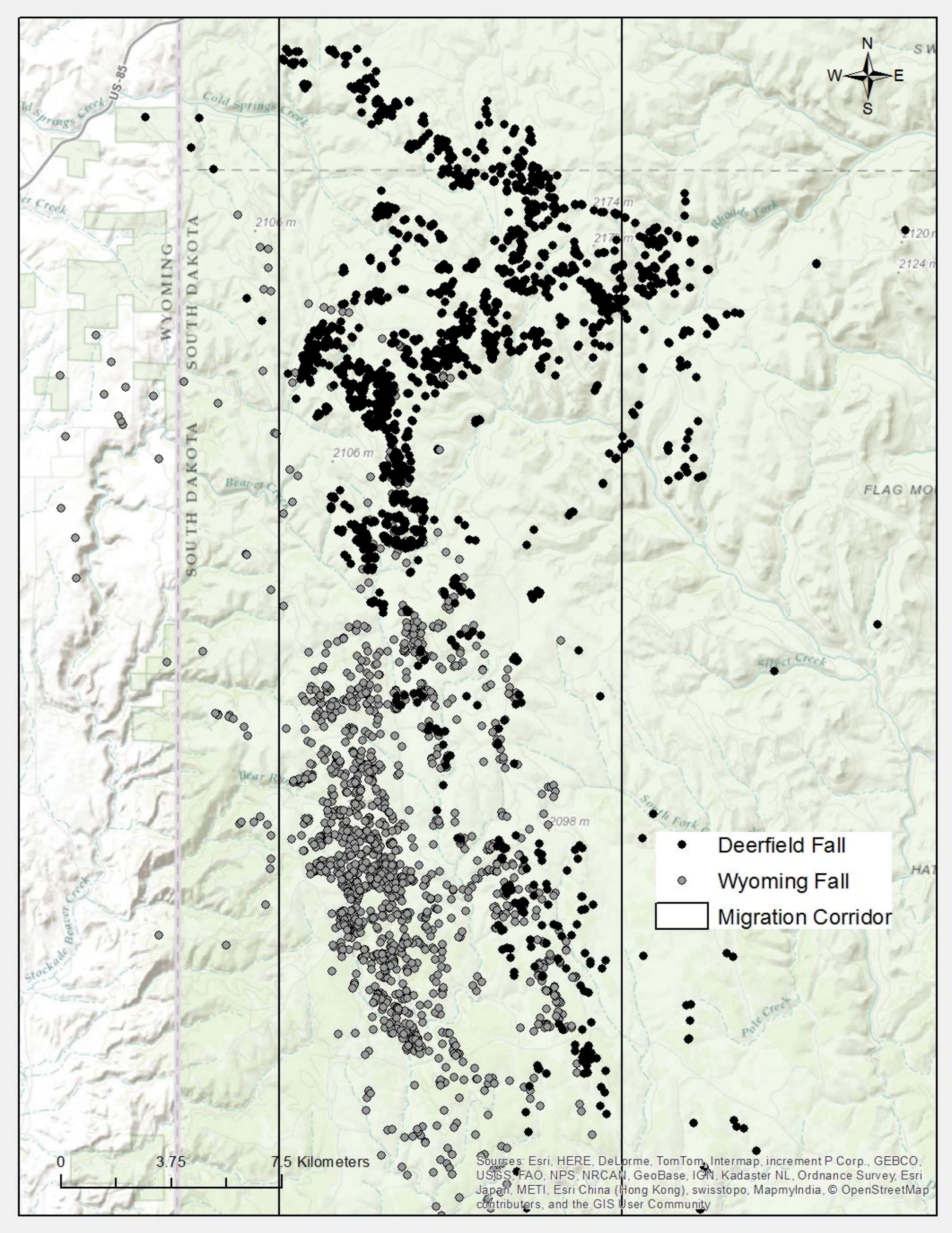
Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3: Spring migration locations for adult cow elk from both Wyoming and Deerfield migration groups. Migration corridor shows shared migration route of the two groups in the Black Hills, South Dakota and Wyoming, USA. 2012 –2013.



Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3: Fall migration locations for adult cow elk from both Wyoming and Deerfield migration groups. Migration corridor shows shared migration route of the two groups in the Black Hills, South Dakota and Wyoming, USA. 2012 –2013.



Sources: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

CHAPTER 4: RESOURCE SELECTION BY ADULT COW ELK AT THE LANDSCAPE SCALE

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

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RH: Simpson et al. • Neonate Elk Survival and Cause-Specific Mortality

Resource Selection by Adult Cow Elk at the Landscape Scale

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ABSTRACT Information regarding resource selection of adult cow elk (*Cervus elaphus*) is critical to management decisions in a multi-use forest. With landscape alteration including logging, fire, fire suppression, and grazing occurring in the Black Hills National Forest there is a need for information regarding resource selection of elk. Our goal was to provide knowledge of habitats elk were selecting to provide information to wildlife managers to aid in decisions on population goals and carrying capacity based on present habitat availability. We completed a 2–year study (2012–2013) to understand the habitat selection and resource choices adult cow elk were making in a forest dominated landscape. We captured and fit 49 adult cow elk with Global Positioning System (GPS) collars during 2 winter (February 2012 and March 2013) capture periods. We collected

167, 707 GPS locations then selected 1 daily random location (*n* = 25,947), for individual adult cow elk, to create discrete choice sets to use in discrete choice multinomial models to evaluate resource selection of elk at the macro-habitat scale. We compared 18 models comprising a selection of habitat variables including: land cover, distance to forested cover, distance to open areas, distance to edge, canopy cover, elevation, slope, and aspect. Adult cow elk selected for grasslands dominated by herbaceous vegetation as well as early successional forest. Elk also selected for areas near forested cover and points at higher elevations based on the best approximating model that accounted for 100% of model weight. We hypothesize that the patterns of resource selection we observed were due to elk selecting for habitats that were uniformly distributed across the landscape.

KEY WORDS adult cow elk, bootstrap, *Cervus elaphus,* discrete choice analysis, resource selection, validation

INTRODUCTION

The increase in human encroachment into historic elk (*Cervus elaphus*) habitats has resulted in greater demands on shared resources and requires an understanding using sound science for developing management decisions. Historically, elk ranged across North America exhibiting their wide habitat tolerance and adaptability; currently they inhabit the expansive region of inland mountains and plains as well as western coastal habitats (Slovkin et al. 2002). Human expansion caused drastic declines in elk populations and required reintroduction efforts to restore many populations including those inhabiting in the Black Hills National Forest (BHNF; Turner 1974).

Elk habitat use can be affected by topography, weather, cover, and forage (Hobbs and Hanley 1990). Elk occupy forest edges during both the summer and winter for protection from predators, to satisfy forage needs, and to a lesser extent for thermal cover (Cook et al. 1998). They also select for topographical and vegetative cover types to provide physical and thermal cover during calving (Barbknecht et al. 2011). Elk select slopes with minimal steepness, with south-facing aspects (Irwin and Peek 1983, Slovkin et al. 2002, Stubblefield et al. 2006), and they often select areas at higher elevations during summer seasons to use suitable forage, and lower elevations during winter to avoid heavy snow (McCullough 1985, Boyce 1991, Irwin et al. 2002**).** Currently, elk in the west are found in coniferous forests associated with mountains, foothills, or canyon rangelands (Skovlin et al. 2002).

Elk compete with grazing cattle and other ungulates on landscapes that were once maintained by common wildfires (Skovlin et al. 2002). Fire created a patch-like mosaic of open habitat preferred by elk. Post-fire succession provided substantial forage and cover for elk in subsequent years until increased canopy reduced understory vegetation. With increased fire control, coniferous stands became the dominant land cover (Arnold 1950). Fire frequency and average fire intensities have decreased in pine forests across North America over the last century (Covington and Moore 1994). Historically, low intensity surface fires burned every 10–30 years in the Black Hills (Brown and Sieg 1996). Logging has ultimately replaced fires in effectively creating mosaic patches, creating areas of secondary succession resulting in a mix of ecotones and forage producing areas (Skovlin et al. 1999). These areas can provide quality forage for populations of elk within these early successional forested stages (Cook et al. 2013).

A significant threat to elk across the west and a considerable limiting factor to populations is a region–wide decline in availability of early successional habitats (Sporting Conservation Council 2008). These early seral habitats are vital to productive ungulate populations (Cook et al. 2013). Several western elk populations saw dramatic increases in populations after large scale disturbances yet those populations are currently in decline as forest succession has advanced (Cook et al. 2013). When early successional habitats decline, increased competition can ensue due to reduction in available forage, especially during limiting seasons (Jenks and Leslie 2011). In the Black Hills system, potential competitors of elk include mule deer (*Odocoileus hemoinus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), and domestic cattle (*Bos taurus*).

The majority of the elk in the southwestern Black Hills are migratory with summer and winter areas having little change in elevation and minimal change in dominant land cover characteristics. The goal of our study was to access resource selection at the macrohabitat scale for elk in the Black Hills of South Dakota and Wyoming. We examined habitat selection over a two–year period and chose locations over a 24-hr period to evaluate overall selection preferences of adult cow elk. We hypothesized that adult cow elk were selecting for forested edges for thermal cover, forage, and protection from predators. We expected that elk also utilize these forested edges due to their location in relation to open grassland areas as well as for early successional forests. Grassland areas as well as early successional forests provide patches of high forage biomass in the Black Hills; forage biomass is directly related to the proportion of meadows on the landscape and meadow complexity (Stubblefield et al. 2005).

STUDY AREA

The Black Hills are an isolated, mountainous extension of the Rocky Mountains located in western South Dakota and northeastern Wyoming (Petersen 1984). Topography of the Black Hills varies extensively (Kennedy 1992). The mountains of the Black Hills are a maturely dissected domal uplift with a central crystalline core surrounded by steeply dipping sedimentary deposits (Hoffman and Alexander 1987). The Black Hills extend approximately 95 km east to west and 190 km north to south (Petersen 1984) covering an area of about 8,400 km^2 (Orr 1959, Turner 1974, Fecske et al. 2002). Elevations range from 973-2,202 m above mean sea level. Seasonal temperature fluctuations in the Black Hills are typical of a continental climate (Orr 1959). Mean annual temperatures range from 5 to 9 °C with extremes of−40 to 44 °C. Mean annual precipitation is > 66 cm (Orr 1959). Yearly snowfall may exceed 254 cm at higher elevations (Thilenius 1972).

Our study focused on the southwestern region of the Black Hills National Forest (BHNF) in South Dakota extending into Wyoming (Figure 1). The western area of the BHNF is encompassed within Custer, Pennington, and Lawrence counties in South Dakota, and eastern Crook and Weston counties in Wyoming. The study area is comprised of large expanses of public land interspersed with small inholdings of private lands. The majority of private lands were located in the northwest portion of the study area in Wyoming. Dominant overstory vegetation of forested areas consisted of ponderosa pine (*Pinus ponderosa*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), interspersed with mountain juniper (*Juniperus scopulorum*) and mountain mahogany (*Cercocarpus montanus*) at low elevations in dry areas along southwestern fringes of our study area (Thilenius 1972, Severson and Thilenius 1976). Primary understory vegetation consisted of various forbs, grasses, and shrub species, including big bluestem (*Andropogon gerardii*), buffalograss (*Buchloe dactyloides*), and Oregon grape (*Berberis repens*; Thilenius 1972, Severson and Thilenius 1976). Our study area was predominantly coniferous forest (66.4%) intermixed with grassland/herbaceous areas (15.3%) and areas of early successional stands (16.8%) (National Land Cover Database (NLCD); Jin et al. 2013). The remaining breakdown was small portions of deciduous forest (0.6%), mixed forest (0.2%), developed space (0.3%), hay/pasture lands (0.1%), and wetlands (0.1%). Private lands contained more meadows, alfalfa (*Medicago sativa*)/hay fields, and limited row crop production among forested stands.

A large part of the study area was burned during the Jasper Fire in 2000. The Jasper fire was a high-severity fire that burned approximately 33,729 hectares (83,500 acres; 7% of the BHNF and 10.4% of our study area; Jasper Fire Rapid Assessment, http://www.fs.fed.us/r2/blackhills/fire/history/jasper), of interior forest from August until official containment was declared in September 2000. LANDSAT data of the fire reported in the Jasper Fire Rapid Assessment, characterized the fire as highly variable. Areas left unburned or with low intensity burns comprised 25% of the burn area. Moderate burns where crowns were entirely or nearly scorched comprised 48% of the burn. About 27% of the burn was high-intensity fire where trees were left completely void of needles (Lentile et al. 2005).

METHODS

Captures took place in the Jasper burn area north of Highway 16 and west and north of Jewel Cave National Monument in the southwestern region of the BHNF. We captured

<6 elk per group and captured elk from groups distributed throughout the capture area to ensure a robust sample. Elk were chemically immobilized (6 ml of Butophanol, 2 ml of Azaperone, and 3 ml of Medetomidine; Zoopharm, Windsor, CO, USA) via darts fired from a cartridge fired projector while pursuing elk in a helicopter (Quicksilver Co, CO, USA). Elk were darted with 3cc barbed darts (Pneu Dart, Williamsport, PA) to ensure the immobilization drugs were administered.

Adult female elk were fitted with 1,150 g Global Positioning System (GPS)/Store on Board (*n* = 30, TGW-4600-2 Telonics Inc. Mesa, AZ, USA) and 825 g GPS/Iridium satellite collars (*n* = 10 G2110E Advanced Telemetry Systems, Isanti, MN, USA). Store on board collars were programmed to download locations every 2.5 hours throughout a 24 hr period beginning at 0100 hr. Collars were set to attempt a GPS fix for 180 seconds at each scheduled fix time and store location information in the collar housing unit. Locations were then manually downloaded in the field during a recapture period in 2013 and again when collars were collected after remote release from the animal in January 2014. Iridium collars were programmed to upload locations twice per day throughout the year at 0600 hr and 2000 hr until calving season was estimated to begin (~ 1 May), at which time a location at 1200 hr was added. Iridium collars were set to attempt a GPS fix for 180 seconds at each scheduled fix time (ATS “forest” setting), then transmit those coordinates via satellite every 24 hr to an automated email system. These collars were programmed with a 4 hr mortality signal, which was later changed to 6 hr due to intermittent errors of mortality switches. It was determined that, during specific times of the year (i.e., winter) elk would often be immobile for nearly 4 hours, resulting in false mortality signals. The change to 6 hr alleviated the issue.

Elk were checked for pregnancy by rectal palpation (S. Lindsay, Fall River Veterinary Clinic, Hot Springs South Dakota, USA; Greer and Hawkins 1967). Pregnant cow elk were fitted with vaginal implant transmitters (VITs; M3960, Advanced Telemetry Systems, Isanti, MN, USA) using a fabricated polyvinyl chloride (PVC) applicator that was applied with lubricating jelly (Johnson et al. 2006). We extracted a canine tooth to determine age through cementum analysis during each initial cow elk capture (Fancy 1980). All capture and handling procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 12-009A) and followed recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Habitat Data Collection

We used ArcMap 10.1 (ESRI Inc., Redlands, CA, USA) to extract data on selected habitat variables from GIS coverages to estimate resource selection of adult cow elk. All data were collected on a macrohabitat scale to predict habitat use on a large scale in the BHNF. Universal Transverse Mercator locations were downloaded from adult cow elk collars and imported into ArcGIS 10.1. Each point was set to a 30 x 30 m cell for data collection. We created a land cover layer using the 2011 National Land Cover Database (Jin et al. 2013) for South Dakota and Wyoming. The land cover layer was originally separated into 14 habitat types; we combined all developed areas into one category and all wetland types into one category resulting in 10 cover types (grassland, evergreen forest, shrub/scrub, deciduous, wetlands, mixed forest, pasture/hay, developed, barren, and crops) available for our use in analyses.

We first selected a random daily (24–hr period) location for each collared elk in the study to ensure all points were independent of one another. We calculated the average daily movements of all elk to determine a buffer size which would include areas in which an adult cow elk could reach within 1 day of travel in relation to the known location. We created a buffer around each known location to decrease the chance for bias (Rettie and McLoughlin 1999); to ensure adequate representation of habitats available to elk within buffers. We generated 4 random points, within each buffer, for comparison to known locations using ArcMap 10.1.

We reclassified land cover as 0 (non-forested) and 1 (forested) to calculate the distance, in meters, to cover, to open areas, and to edge. We used the Euclidian distance tool in ArcMap 10.1 (ESRI Inc., Redlands, CA, USA) for all distance measurements. Distance to cover was measured as the distance to a forested area. Distance to open was measured as the distance that locations were to open grassland or shrub areas. The distance to edge was measured as the distance that any location in relation to a forested edge.

We used a 30-m National Elevation Dataset (NED; Gesch et al. 2002) to measure elevation for all locations. We then used the same dataset and the aspect spatial analyst tool in ArcMap to create an aspect raster coverage. We separated aspect into 8 classes (north, 337.6° – 22.5°; northeast, 22.6° – 67.5°; east, 67.6° – 112.5°; southeast, 112.6° – 157.6°; south, 157.6° – 202.5°; southwest, 202.6° – 247.5°; west, 247.6° – 292.5°; and northwest, 292.6° – 337.5°; Cooper et al. 1999). We used that same NED and the slope spatial analyst tool in ArcMap to create a slope raster coverage (slope in degrees; 0° – 90°).

We used a road layer from the USGS National Transportation Dataset (NTD; 2012) for Wyoming and South Dakota. We quantified the influence of roads on adult cow elk resource selection by measuring the distance in meters, elk locations were from 4 road types; RC1 (decommission/closed), RC2 (two-track/primitive), RC3 (moderate traffic/secondary),and RC4 (heavy traffic/primary). We used the United States Forest Service stream layer for the Black Hills National Forest watershed from the BHNF website and used the near tool in ArcMap to measure distance, in meters, to streams.

We measured canopy cover as a continuous percentage variable (0–100%) using the NLCD 2011 United States Forest Service Tree Canopy Layer. We first determined if elk were migratory or residents by examining cow elk locations and running a K-means cluster analysis in SYSTAT 11.0 (Systat Software Inc., Chicago, Illinois, USA; Boulanger et al. 2006). We set each cluster analysis to 3 clusters. If home ranges showed distinct separation and nonoverlapping seasonal ranges in clusters and animals returned to the same winter range we classified elk as migrants (Cagnacci et al. 2011). When elk home ranges had distinct clusters of summer locations that were separate from winter locations yet the elk made considerable movements between summer and winter ranges we considered these elk to be conditional migrators. If clusters showed no separation and seasonal ranges overlapped without a seasonal movement event, then elk were classified as residents (Jones et al. 2014). We classified elk as dispersers if they left the winter range in which they were captured and did not return the following year. For our migratory elk, we used the clusters to separate locations in summer and in winter. We used the average dates of migration to seasonal home ranges of migrant cow elk to determine seasons for non-migratory elk. We tested all variables for correlation ($r > |0.7|$) and selected the most useful covariates using a Pearson correlation matrix.

We created 75% fixed kernel ranges in Program R (R Core Team 2013) for summer and winter ranges for adult cow elk. To quantify and compare the habitat variability across summer ranges for each migration type and the winter core use area for all cow elk we clipped the NLCD layer around each kernel range using ArcMap 10.1. When then calculated the percentages of major cover types in each fixed kernel polygon.

We used discrete choice multinomial logit models to determine resource selection of adult cow elk using PROC MDC (Allison 2012; SAS Institute, Inc. 2010). The true value of the intercept term plays no role in determining conditional probabilities of positive outcomes because of the conditioning involved in the logit. Therefore, conditional models have no intercept term (Hosmer and Lemeshow 2013, Duchesne et al. 2010, SAS Institute, Inc. 2010). We compared 18 models using Akaike's Information Criterion (AIC). We considered models differing by ≤ 2 ΔAIC from the model with the lowest AIC as potential alternative models (Burnham and Anderson 2002), and we used Akaike weights (w_i) as an indication of support for each model (Burnham and Anderson 2002). Any model that was ≤ 2 ΔAIC from the top model with ≥ 1 parameter more than that top model and that had the same maximized log-likelihood was removed from consideration in the analysis (Burnham and Anderson 2002). We assessed our top model based on Mcfadden's rho-squared values and considered models with rho-square values between 0.2 and 0.4 to be good predictors of selection (Tabachnick and Fidell 1996).

As elk are a herd species, we performed a data-bootstrap analysis (Bishop et al. 2008) to reduce autocorrelation as a function of elk proximity and to generate more robust standard errors. Our bootstrap analysis was performed on each model and was comprised of 10,000 replicate datasets generated by resampling our data with replacement after randomly removing individual elk. We ran a validation test to test the accuracy of our top model. We randomly chose 60% of the locations in the initial analysis and then used the remaining 40% to test our results. The validation test estimated the probability that our known location was the choice location based on our top model. We calculated a McFadden's Rho-squared statistic for the top model to measure model performance. McFadden's Rho-squared is intended to mimic r-squared values but tend to be lower (McFadden 1974). Hensher and Johnson (1981) state that McFadden's Rho-squared values between 0.2 and 0.4 should be considered highly satisfactory

RESULTS

We captured adult female elk ≥2 years of age during two separate capture periods; 3–6 March 2012 and 22–26 February 2013. We captured and radio-collared 49 adult cow elk between 2012 and 2013 (ages: 17= 2–5; 24= 5–10; 4= 11–15; 4= 16–20). In 2012, we captured 40 adult cows. In 2013, 35 of those cows were recaptured along with 9 newly captured adult cow elk. One elk was removed from analyses because it was lost to predation early in the study. Between the two collar types (Iridium, *n* = 15,602, Store-on-board *n* = 152,105) used during the project we collected 167,707 total locations. Mean daily movement for all cow elk throughout the duration of the study was 1.4 km/day. We documented the migration status for 48 elk through the duration of our study; 28 migrant elk (20, 2012–2013; 5 in 2012, 3 in 2013), 11 resident elk (6, 2012–2013; 3 in 2012, 3 in 2013), 6 conditional migrators (5, 2012–2013; 1 in 2013). We also had 3 dispersers, one elk that dispersed immediately after the first winter capture and the remaining two elk dispersed after spending a full summer and winter season in the same area. We used 25,947 GPS locations and created 103,788 random locations for use in our analysis. The majority of locations were located in 3 habitat types (evergreen forest, grassland/herbaceous, shrub/scrub). The largest number of locations (59%, n = 15,313) were in evergreen forests; locations also were in grassland/herbaceous (21.8%, n = 5,662), and shrub/scrub (18.6%, n = 4,825) habitats (Figure 2). The remaining 0.06% of locations were dispersed among the remaining 7 land cover types (developed, 0.25%; barren, 0.04%; deciduous forest, 0.57%; mixed forest, 0.19%; pasture/hay, 0.13%; crops, 0.04%; wetlands, 0.05%; Table 1). We found no correlation between any covariates; therefore, we were able to use all of them in our models.

Results of our analysis indicated that only one model (land_cover + dist_cover + elev; w_i = 1.00; Table 2) best estimated resource selection of adult cow elk. Parameter estimates (Table 4) and logistic odds ratios (Table 5) indicated that elk selected specific land cover types. The odds ratio was 1.72 (95% CI = 1.553 – 1.899) for grassland/herbaceous areas and was 1.45 (95% CI = 1.309 – 1.611) for shrub/scrub, which indicated that elk selected for the two land cover types. Elk selected for higher elevations but the odds ratio was small (odds ratio = 1.002, 95% CI = 1.002 – 1.004) likely due to little change in elevation across the study area. Our results indicated that elk were selecting locations that were closer to cover than random locations (odds ratio = 0.99, 95% CI = 0.998 – 0.999). The fit test of our top model (land_cover + dist_cover +

elev) showed support for the model (rho-squared = 0.317; Table 6). Results from our data bootstrapping analysis resulted in minimal changes to the standard errors in parameter estimates for the significant variables in our top model (Table 4). Bootstrap analysis did not significantly change the odds ratios for the significant variables in our top model; the 95% CI's, however, did change slightly for grassland/herbaceous (95% CI = 1.542 – 1.912), and shrub/scrub (95% CI = 1.304 – 1.617; Table 5). The bootstrap analysis also increased the rho-squared (0.321) value for our fit test (Table 6).

DISCUSSION

We estimated resource selection for 2 years during 2 seasons (summer and winter) for elk exhibiting 3 movement patterns (migrant, resident, and conditional migrant) in the BHNF in South Dakota and Wyoming. With the use of GPS collars, we were able to use a large number of locations to estimate resource selection. The best approximating model from a selection of habitat variables based on elk ecology carried all of the model weight. Adult cow elk in our study selected for open meadow areas dominated by herbaceous vegetation and early successional forest areas. Elk were selecting locations in these open areas close to forested cover at higher elevations.

Potential for adult cow elk overlap resulting in autocorrelation in our analysis was an initial concern. Our concerns were alleviated as a result of the number of cow elk in our sample and the large sample size of known locations used in our analysis. Alldredge and Ratti (1992) pointed out in their comparison of statistical techniques the advantages of having numerous animals observed and a large number of observations per animal. The number of known locations per animal in our study ranged from 217 – 670 depending on the length of time an animal was collared. We also, randomly selected one location per day for each elk to reduce correlation of the locations as elk herd overlap will vary between seasons (Millspaugh et al. 2004). To further limit effects of autocorrelation of the locations of our adult cow elk, we ran a bootstrap analysis using the biased corrected method where the bias was the difference between the original model coefficients and the bootstrapped coefficients. After running 10,000 iterations with replacement, we documented similar parameter estimates as the original model coefficients, which indicated that elk locations used in our analysis were minimally biased relative to their association with other elk locations.

Our top model also included elevation; yet, the odds ratio was 1.002 likely because elevation changes in our study area were gradual and forested areas were typically along marginally higher ridges. Commonly, elk will migrate to higher elevations as snow melts to follow spring green-up (Sweeney 1975). Elk in our study typically began to migrate in early spring before significant snow melt began at those elevations (29 March – 1 May) but their seasonal summer ranges would be established as new vegetation began to emerge. Mean elevation for the summer range occupied by the Wyoming group was 1,919.21 m (SE = 1.81) while the elevation for the Deerfield group was 1,824.06 m (SE = 1.23). Mean elevation for the wintering area occupied by all elk during the study was 1,825.5 m (SE = 1.14). The difference in elevation between known locations and random locations was 2.7 m. Our results were interesting in that land cover, distance to cover, and elevation was the only model that carried any weight in our analysis. As elevation changes did not differ between seasons, results indicated that elk were selecting areas of slightly higher elevation throughout their ranges.

Resource selection of elk in our study may be explained, in part, by the limited diversity in land cover types in our study area. Evergreen forests, dominated by ponderosa pine made up 66% of our study area while shrub/scrub and grassland/herbaceous cover types comprised 16.8 and 15%, respectively, of the area (Figure 2). The remaining 3% was comprised of small amounts of the remaining cover types (Table 5). To further quantify habitat variability across the study area we used the 75% fixed kernel ranges around each elk migration type (migrant, conditional migrator) with separate kernel ranges for the Wyoming group and the Deerfield group as well as the core winter range (Figures 3–7). We found that each range had similar percentages of habitats with evergreen forests dominating each range. The winter range contained the most variation with equal percentages of each land cover type (Figure 2).

Late season fires eliminate forage in the areas that are burned reducing forage for the subsequent winter (Pearson et al. 1995). Nevertheless, forage quality is improved in subsequent years (Hobbs and Spowart 1984, Coppock and Detling 1986). Forest succession post fire may result in an increase the number of shrub species and early successional forest on the landscape (Harniss and Murray 1973, Gruell 1980, Griffin and Friedel 1984, West and Hassan 1985, Noste and Bushey 1987). Stands that survive the burn leave patches of mature trees that increase the overall heterogeneity of the area and provide suitable habitat for elk (Stubblefield et al. 2006).

In 2000, the Jasper fire transformed a large portion of the southern Black Hills into a mix of open grassland and forested habitat in which the elk in our study spent the winter season. This area was often windswept and devoid of snow, which allowed elk to access forage. Elk in Yellowstone National Park utilized areas that were burned for forage because of increased herbaceous understory resulting from reduced canopy cover (Turner et al. 1999). Yellowstone elk continued to use these burned areas long after the fire (12 to 14 years; Mao et al. 2005), which is a similar time frame to elk use of the Jasper burn. In addition to open areas there also were patches of habitat represented by forested ridges where elk would seek shelter during harsh winter weather. Historically, elk inhabiting the central Black Hills would migrate to this area prior to the burn (Benkobi et al 2008). Therefore, the burn improved a large portion of the Black Hills relative to elk; currently this area supports one of the largest wintering elk herds (~3,000) in the Black Hills (South Dakota Department of Game, Fish and Parks 2015).

In addition to the Jasper Fire, subsequent small fires and increased tree harvest to combat mountain pine beetle (*Dendroctonus ponderosae*) damage have increased open areas throughout the BHNF (USDA Forest Service 2005). The juxtaposition of open stands with forested cover positively affect elk as it increases edge habitat, which allows herds to reduce their need for travel to meet forage requirements (Thomas et al. 1979, Hanley 1983, Irwin and Peek 1983, Edge et al. 1987). These open areas along forest edges represent high diversity habitats and are an important component of elk habitat. Winn (1976) found that elk selected for areas near forest edges because the frequency of plant species and herbage biomass within the edge was two times greater than 46 m into the meadow and biomass continued to decline farther into the meadow. Leckenby (1984) noted that elk in the Blue Mountains of Oregon selected open areas within 300 m of a forested edge. We found elk selected for locations within 100 m of a forested edge. We documented this behavior in our study as cows were focused near forest edges around areas of varying stratification. Rice (1988) documented elk in the BHNF would seldom move farther than 90 m from forested edges during spring, summer, and fall. These behaviors changed significantly during the winter as elk were found farther (0.4 km) into open areas (Rice 1988). We did not find these differences as the mean distance to cover during the spring, summer, fall in our study was greater than distances found during the winter.

Canopy cover did not factor into our model selection but previous studies of elk found it was a significant factor to elk habitat selection because they utilize forested areas for thermal cover as well as protection from predators and human disturbance (Peek et al. 1982). Stubblefield et al. (2005) observed that elk selected for canopy cover ≤40%. Although canopy cover was not significant in our model, elk were found in forested areas with a mean canopy cover of about 41%.

Resource selection of elk did not differ between seasons, years, or based on migration status. Typically, elk migrate to areas of higher elevations during the summer season following green up of nutritious forage (Albon and Langvatn 1992, Parker et al. 2009). In the Black Hills, however, we found no difference in seasonal habitat selection or any changes in elevation shifts between summer and winter seasonal ranges. Thus, we studied a population utilizing different migration strategies with high fidelity to seasonal ranges. Thirty-five percent of adult cow elk remained in the same area for both summer and winter seasons; thus, forage was likely uniform throughout the study area. Stubblefield et al. (2005) suggested that elk will select for areas with the highest forage potential.

Leege et al. (1975) documented elk selected for slopes of 20°− 40° for bedding and feeding sites while elk in our study were typically found on slopes of >7°. This finding in addition to the differences in elevation, provided evidence that elk were focusing on ridge-tops during times of foraging and loafing. Visual observations of elk collected during our study found elk on forested ridge-tops in the summer and open ridge-tops in the winter. We also did not document elk selecting a particular aspect direction; elk often select south facing slopes during the winter season to take advantage of solar radiation; these areas are often the first to be free of snow (Slovkin et al. 2002).

Cow elk did not avoid roads as has been observed with other elk herds (Sheehy and Vavra 1996, Benkobi et al. 2004, Rumble and Gamo 2011, Stubblefield et al. 2005). Locations of cow elk in our study averaged 297.6 m from primitive roads, which were the most frequent road type (58% of all roads) in the southwestern Black Hills. Furthermore, elk averaged 2,365.9 m from decommissioned roads, 1,654 m from secondary roads, and 2,639 m from primary roads. Mean distances from each road type for known locations were similar to distances to random locations. Previous studies in the BHNF found elk were selecting against areas near roads at distances of >260 m (Stubblefield et al. 2005, Rumble and Gamo 2011). Locations of adult cow elk during our study fell within this range of distances yet previous studies collected habitat data for elk during daytime hours. In our study, we evaluated habitat selection over a 24–hr period.

Johnson et al. (2000) found elk avoided roads based on vehicle traffic. We were unable to collect traffic data within the BHNF but we suspect that our study area saw minimal traffic due to the remoteness of the southwestern Black Hills. Road avoidance was related to the amount of road activity for elk in the central Black Hills (Stubblefield et al. 2005). Millspaugh (1999) also found that roads did not influence elk; elk in Custer State Park would change their behavior based on road traffic and during periods of increased human use. During the evening when human use was low, elk used habitats nearer to roads at increased rates (Millspaugh 1999). In the BHNF, many of the meadows have roads bisecting them or have roads in close proximity. During the night when there was minimal traffic, elk were actively foraging in these meadow areas.

MANAGEMENT IMPLICATIONS

Adult cow elk in the Black Hills selected for open grasslands and early successional forested areas in close proximity to forested cover. These areas were located at slightly higher elevations represented by ridge tops throughout the study area. Habitat modifications that improve these habitat types, such as current logging operation occurring to remove trees killed by the mountain pine beetle throughout the BHNF could be beneficial to population sustainability. Small fires that may occur periodically in the BHNF will also open up the canopy layer and increase forage. Further investigation of microhabitat use by elk, which would quantify resource selection at this finer scale, is warranted.

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Table 1: Cover type and description from 2011 National Land Cover Database (NLCD; Jin et al. 2013) land cover layer used in resource selection for adult cow elk in the Black Hills, South Dakota and Wyoming, USA, 2012–2013.

Cover Type (% of Study Area)	Description
Grassland/Herbaceous	graminoid or herbaceous vegetation, no intensive management, utilized for grazing.
Evergreen Forest	tree > 5 m tall, >75% of tree species maintain leaves all year.
Shrub/Scrub	shrubs < 5 m tall, includes early successional young trees.
Deciduous Forest	trees > 5 m tall, >75% of tree species shed foliage.
Wetland	soil or substrate is periodically saturated with or covered with water.
Mixed Forest	trees > 5 m, neither deciduous nor evergreen species are >75% total cover.
Pasture Hay	> 20% grasses, legumes, or grass-legume.
Developed	areas of constructed materials.
Barren Land	bedrock, desert, pavement, scarps, talus, slides < 15 vegetation.
Cultivated Crops	> 20% annual crops, i.e. corn, soybeans, vegetables, orchards, vineyards.

Table 2: Discrete choice models to quantify adult cow elk resource selection in the Black Hills National Forest, South Dakota and Wyoming, USA, 2012-2013.

Models[a]	K[b]	AIC[c]	ΔAIC[d]	w_i[e]
land_cover + dist_cover + elev	12	31680.00	0.00	1.00
land_cover + dist_cover	11	31742.00	62.00	0.00
land_cover + dist_open	11	31874.00	194.00	0.00
canopy_cover	1	31910.00	230.00	0.00
canopy_cover + migration	4	31922.00	242.00	0.00
canopy_cover + season	4	31922.00	242.00	0.00
season + dist_open + dist_cover + dist_edge	9	31964.00	284.00	0.00
slope + aspect	9	31992.00	312.00	0.00
slope + aspect + season	12	32000.00	320.00	0.00
RC1 + RC2 + RC3 + RC4	4	32160.00	480.00	0.00
RC1 + RC2 + RC3 + RC4 + migration	7	32172.00	492.00	0.00
RC1 + RC2 + RC3 + RC4 + season	7	32172.00	492.00	0.00
year + elev	4	32188.00	508.00	0.00
season + elev	4	32188.00	508.00	0.00
elev + migration	4	32190.00	510.00	0.00
stream + migration	4	32192.00	512.00	0.00
season	3	32200.00	520.00	0.00
year	3	32200.00	520.00	0.00

[a] land_cover = distinct habitat types (evergreen forest, grassland herbaceous, shrub/scrub, developed, barren, deciduous forest, mixed forest, pasture/hay, crops, and wetlands derived from 2011 NLCD layer, dist_cover = distance to nearest forested area from geometric center of known and random locations, elev = elevation at known and random locations, dist_open = distance to an open/non-forested area from geometric center of known and random locations, canopy_cover = % (0–100) of canopy clover at each known and random location, migration = migration type of adult cow elk (migrant, resident, conditional), season = designated season location was taken (summer 2012, winter, summer 2013), slope = slope at center of known and random locations, aspect = 8 intercardinal directions, RC1= distance to nearest decommissioned road, RC2 = distance to nearest two-track/primitive road, RC3 = distance to nearest moderately travelled/secondary road, RC4 = distance to heavily travelled/primary roads, stream = distance to the nearest stream from known and random locations.

[b] Number of parameters.

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

[d] Difference in AIC relative to minimum AIC.

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

Table 3: Mean and standard deviation (SD) for habitat variables at Rocky Mountain cow elk known sites and random sites at the macrohabitat scale.

Variable	Locations	SD	Random	SD
Distance to Roads				
RC1 (decommissioned)	2621.91	1161.14	2596.98	1699.94
RC2 (primitive)	287.45	260.94	277.99	269.75
RC3 (secondary)	1834.46	1193.18	1784.17	1226.75
RC4 (primary)	2531.94	1743.82	2529.08	1778.92
Distance to Streams	315.68	254.55	293.73	252.39
Canopy Cover (%)	36.37	33.47	39.01	33.17
Elevation (m)	1894.70	122.89	1891.40	125.49
Slope (degrees)	6.89	4.39	7.31	4.94
Aspect (Proportion)				
North	0.08		0.09	
Northeast	0.10		0.11	
East	0.12		0.12	
Southeast	0.11		0.10	
South	0.16		0.13	
Southwest	0.21		0.19	
West	0.14		0.16	
Northwest	0.08		0.09	
Land cover (Proportion)				
Evergreen	0.58955		0.64285	
Grassland/Herbaceous	0.21799		0.18051	
Shrub/Scrub	0.18576		0.17001	
Deciduous	0.00354		0.00282	
Wetland	0.00054		0.00090	
Mixed Forest	0.00046		0.00052	
Pasture/Hay	0.00031		0.00029	
Developed	0.00058		0.00186	
Barren Land	0.00012		0.00003	
Crops	0.00012		0.00017	
Distance to Open	69.98	175.16	65.44	173.04
Distance to Cover	107.45	145.11	116.06	146.85
Distance to Edge	177.43	191.58	181.49	190.58

Table 4: Parameter estimates (β), standard errors, and significance tests from the top–ranked conditional logistic regression model and bootstrap analysis to determine adult cow elk resource selection in the Black Hills National Forest, South Dakota and Wyoming, USA, 2012–2013.

Parameter[a]	Bootstrap β	Bootstrap SE	Bootstrap *t*–value	Bootstrap *P*-value
Grassland/Herbaceous	0.54	0.05	10.56	< 0.0001
Evergreen Forest	0.04	2.12	0.07	0.91
Shrub/Scrub	0.37	0.05	7.05	< 0.0001
Deciduous Forest	0.33	0.28	1.22	0.22
Wetland	-1.76	1.04	-1.73	0.08
Mixed Forest	-1.31	1.05	-1.26	0.21
Pasture Hay	0.07	1.14	0.06	0.95
Developed	-0.76	0.54	-1.40	0.16
Barren Land	-9.69	32.79	-0.06	0.93
Cultivated Crops	12.49	28.88	0.08	0.91
Distance_Cover	-0.001	0.0002	-6.37	< 0.0001
Elevation	0.003	0.0005	5.74	< 0.0001

[a] Distance_Cover = distance to nearest forested area from geometric center of known and random locations.

Table 5: Odds ratio (95% confidence interval) from original model and bootstrap analysis for significant habitat variables in discrete choice models predicting adult cow elk resource selection in the Black Hills National Forest, South Dakota and Wyoming, USA, 2012 – 2013.

Variable	Bootstrap Odds Ratio[a]	Bootstrap 95% CI
Grassland/Herbaceous	1.717	1.542– 1.912
Shrub/Scrub	1.452	1.304– 1.617
Distance_Cover	0.999	1.999– 0.999
Elevation	1.003	1.002– 1.004

[a] Odds ratios >1 indicate positive relationship; <1 indicate negative relationship.

Table 6: Validation test results of known locations and randomly generated locations in discrete choice analysis predicting adult cow elk resource selection in the Black Hills National Forest, South Dakota and Wyoming, USA, 2012 – 2013.

Decision[a]	Bootstrap Mean Probability[b]	Bootstrap SE	Bootstrap *n*
1	0.64	0.020	10379
2	0.03	0.001	10379
3	0.07	0.001	10379
4	0.10	0.010	10379
5	0.15	0.010	10379

[a] 1 represents the known elk locations, 2–5 represents the randomly generated locations.
[b] It is expected that the mean probability estimate will be 1 based on predicted probabilities for all

Figure 1. Study area in the Black Hills National Forest, South Dakota 2012–2013.

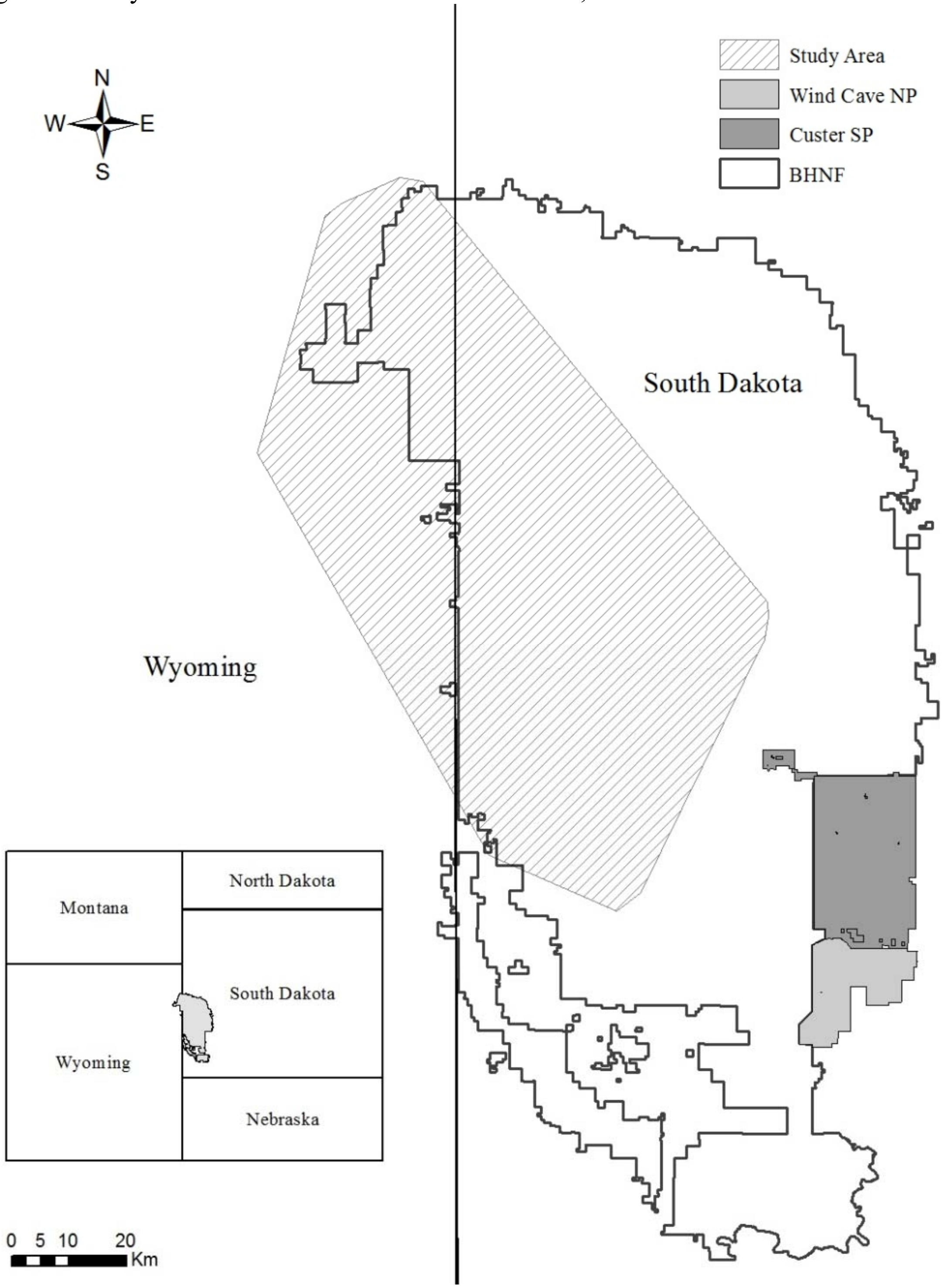


Figure 2: Dominant land cover map of our study area in the Black Hills National Forest, South Dakota and Wyoming

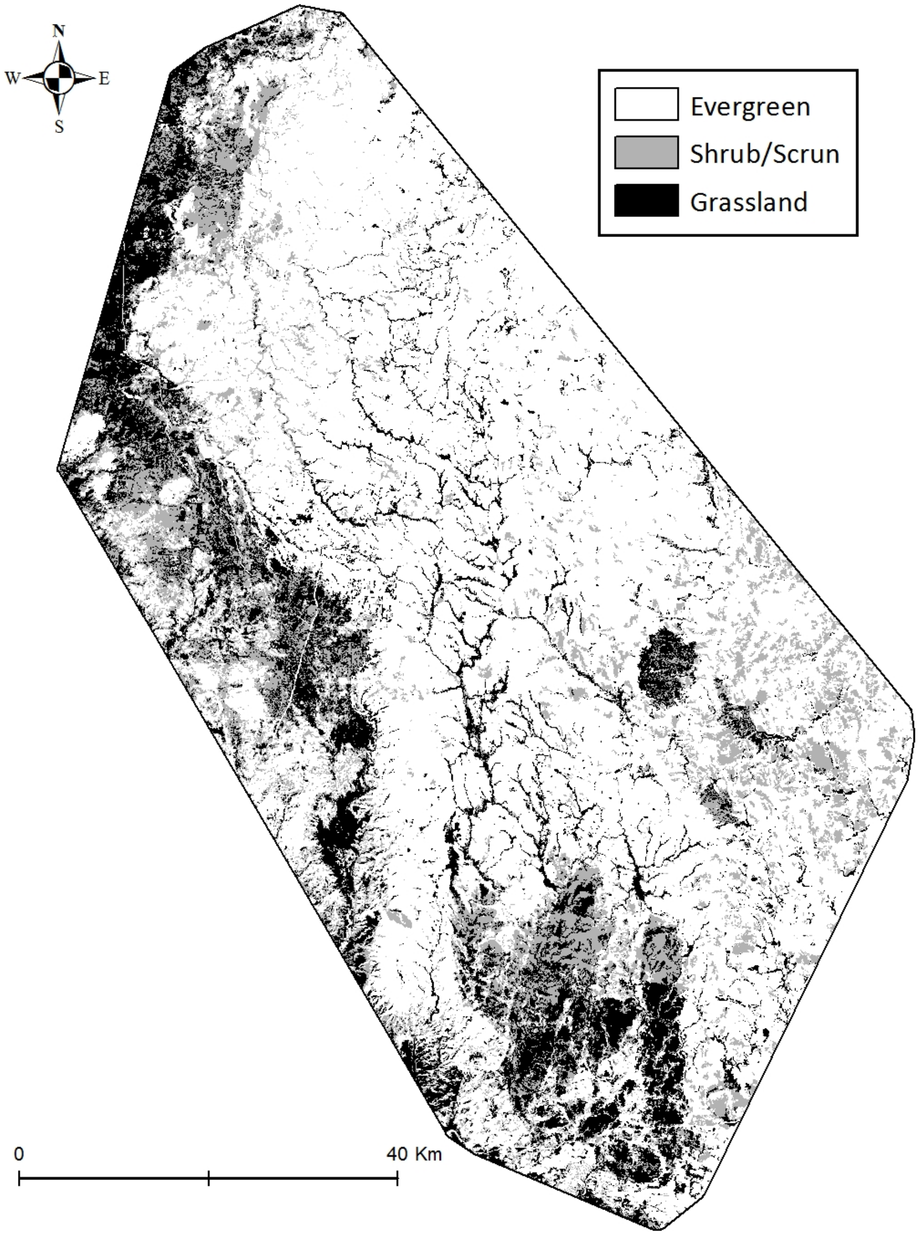


Figure 3: Dominant land cover map of the Wyoming migration group of migrant adult cow elk in the Black Hills National Forest, South Dakota and Wyoming

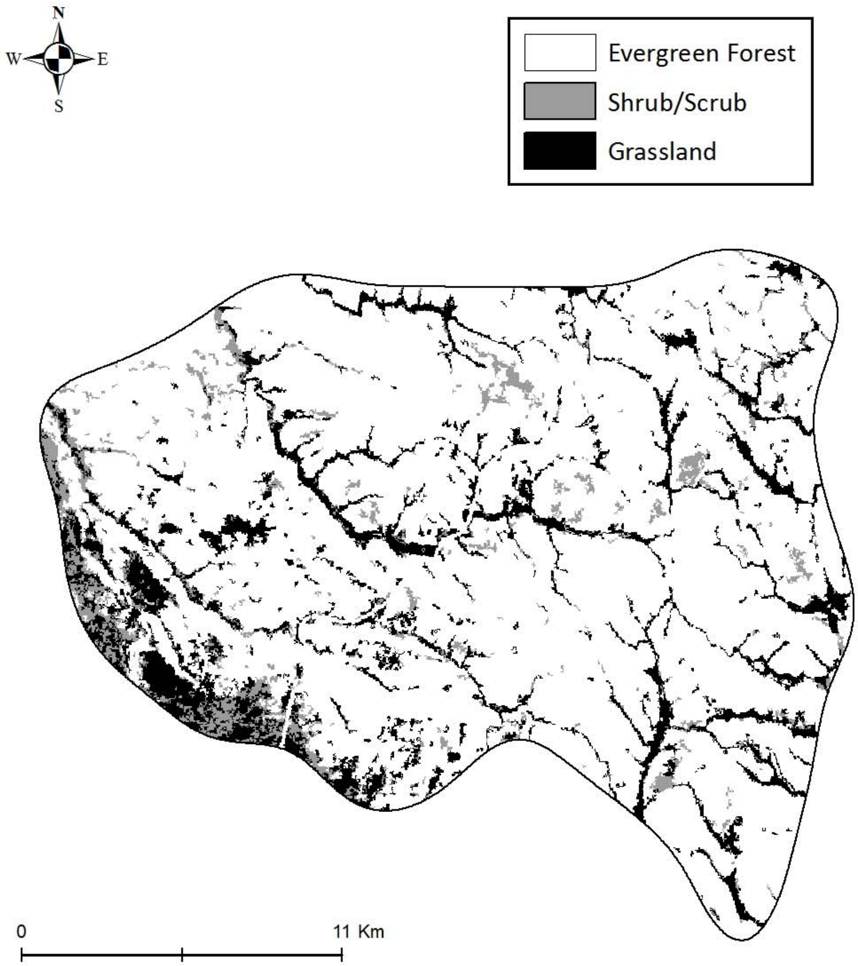


Figure 4: Dominant land cover map of the Deerfield migration group of migrant adult cow elk in the Black Hills National Forest, South Dakota and Wyoming

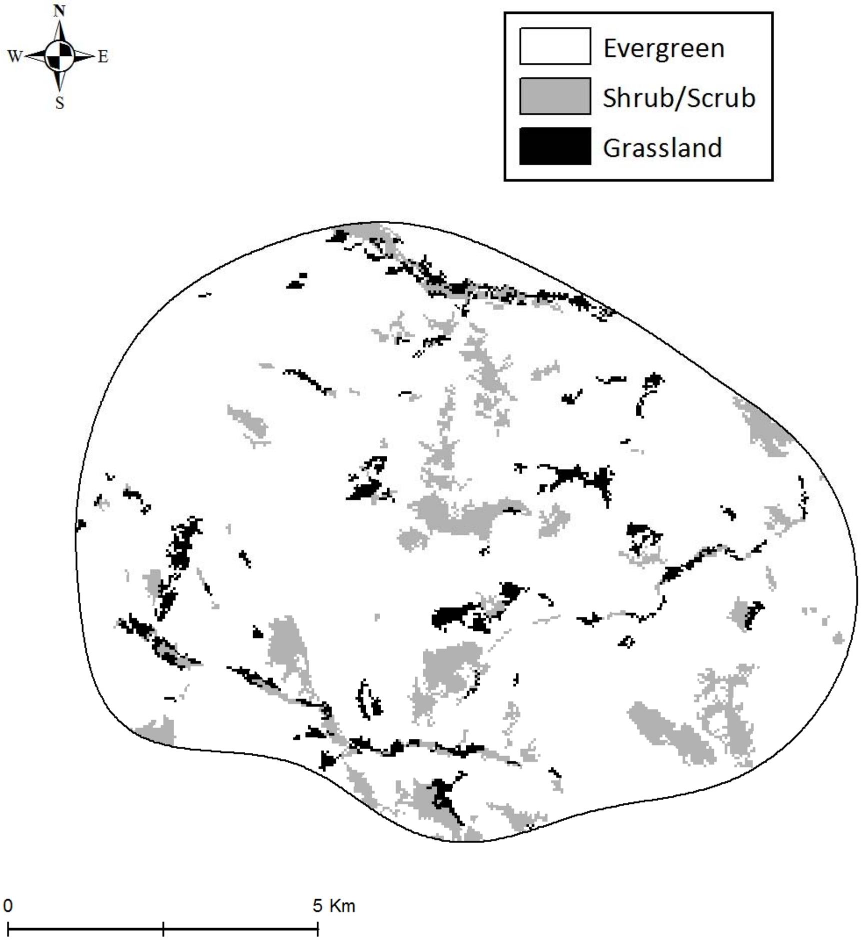


Figure 5: Dominant land cover map of conditional migrant adult cow elk in the Black Hills National Forest, South Dakota and Wyoming

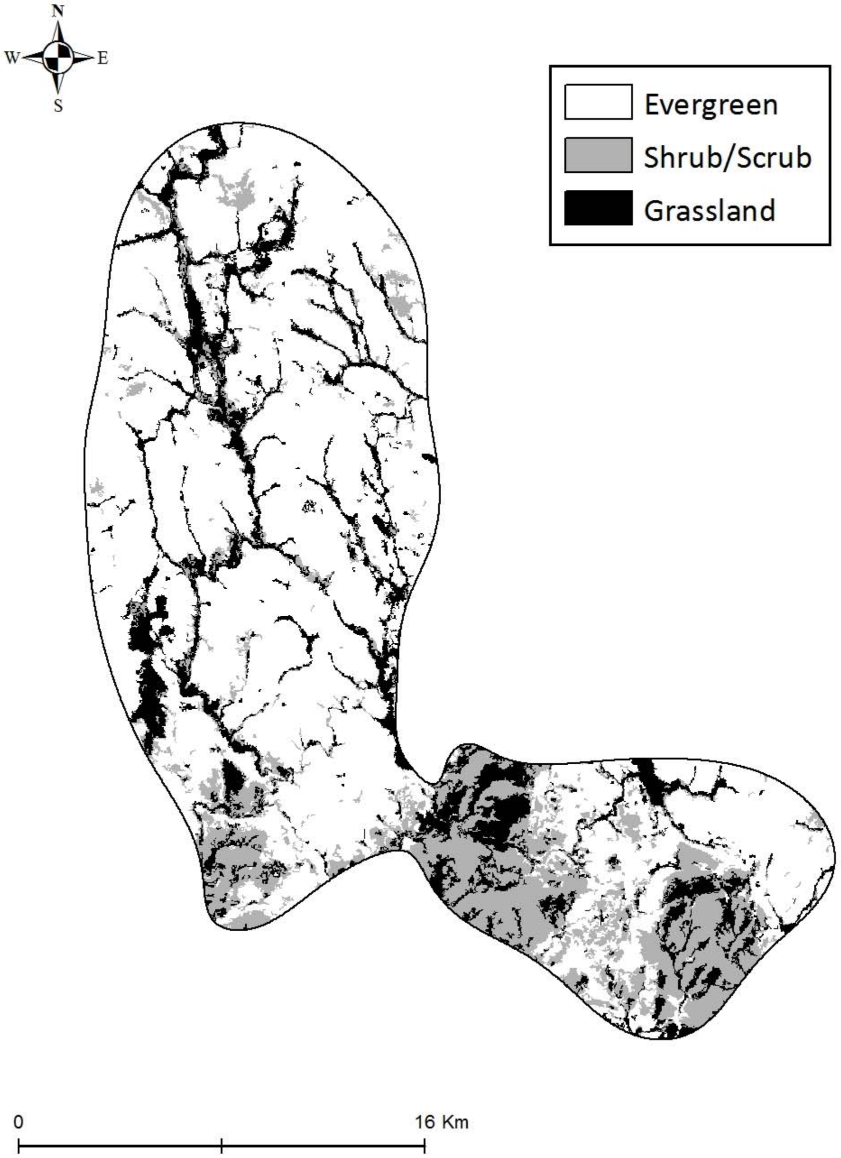


Figure 6: Dominant land cover map of resident adult cow elk in the Black Hills National Forest, South Dakota and Wyoming

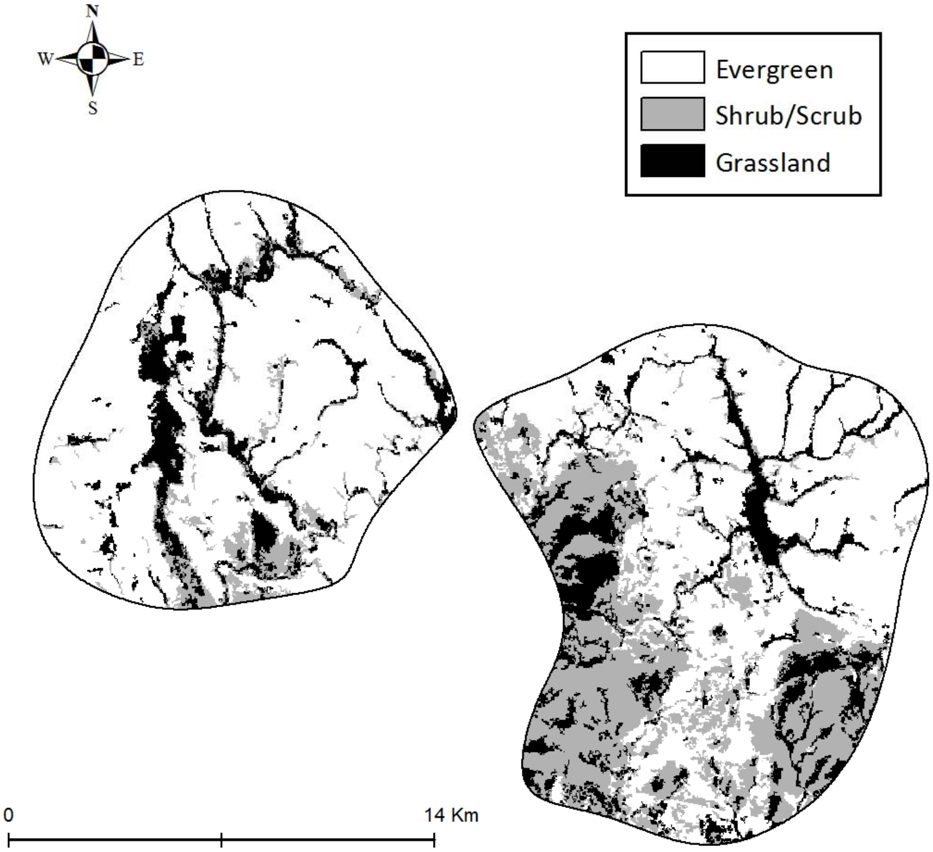
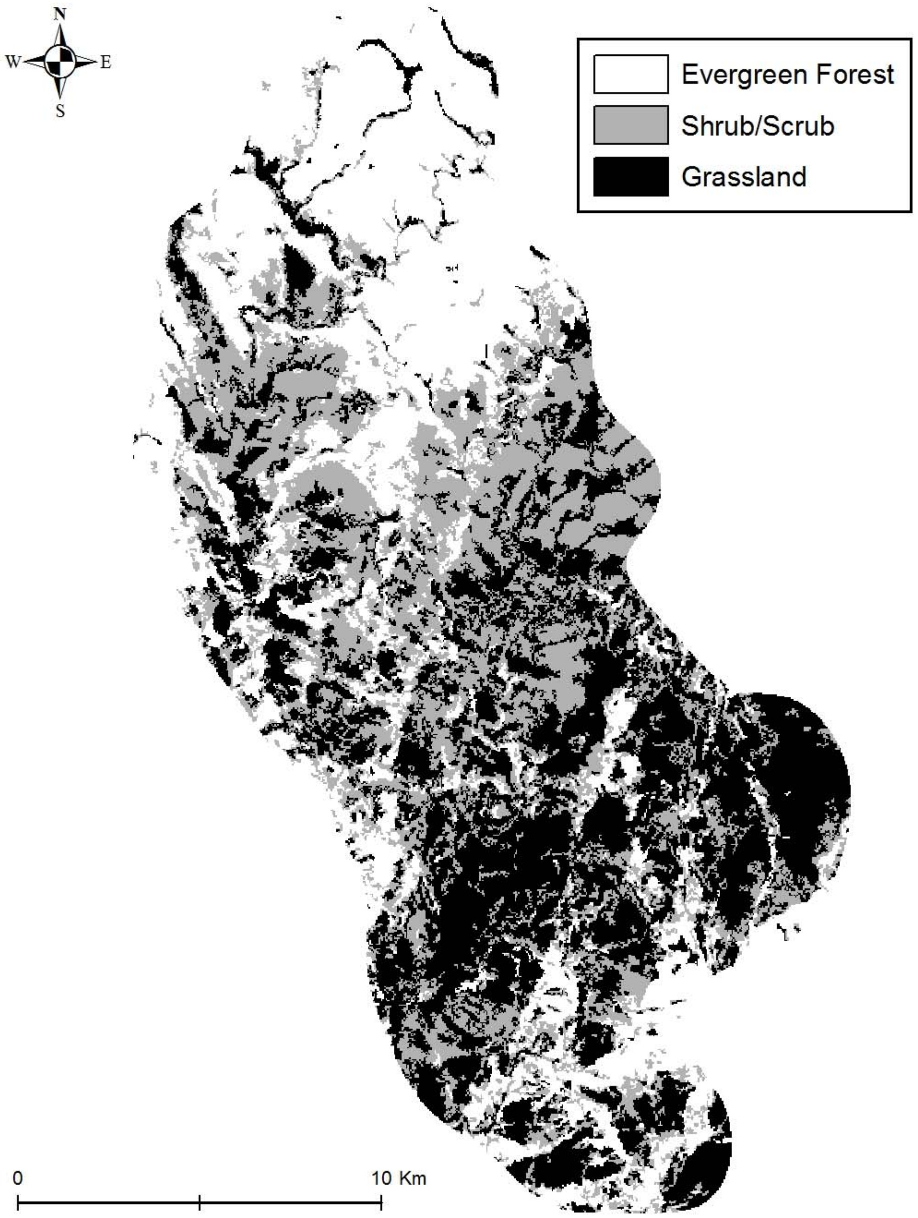


Figure 7: Dominant land cover map of the winter core use area for adult cow elk in the Black Hills National Forest, South Dakota and Wyoming



APPENDIX A

SUMMARY OF ADULT COW ELK (Cervus elaphus) AND NEONATE ELK CAPTURE DATA FROM 2012–2013

BENJAMIN D. SIMPSON

2015

Table A–1. Capture data and the number of days spent in South Dakota and Wyoming during harvest season for radiocollared adult cow elk (*Cervus elaphus*) in the Black Hills South Dakota, March 2012.

Frequency	Date	Capture Age	Mortality Date	Cause of Mortality	Lactating	Mass (kg)[1]	Pregnant	VIT	SD Hunt Days[2]	WY Hunt Days[3]
155.013	3/4/2012	8	—	—	N	238.82	Y	Y	76	0
155.024	3/5/2012	9	10/16/2012	Harvest	N	233.23	Y	Y	1	61
155.033	3/3/2012	8	—	—	N	229.65	Y	Y	76	0
155.044	3/4/2012	9	—	—	N	227.64	Y	Y	76	0
155.054	3/5/2012	2	—	—	N	233.23	Y	Y	31	19
155.064	3/5/2012	5	4/23/2012	Predation	N	222.06	Y	Y	0	0
155.075	3/5/2012	7	—	—	N	250.00	Y	Y	76	0
155.085	3/3/2012	8	—	—	N	252.79	Y	Y	75	1
155.094	3/5/2012	2	—	—	N	222.06	Y	Y	20	74
155.100	3/5/2012	3	—	—	N	244.41	Y	Y	76	0
155.104	3/5/2012	—	—	—	N	227.64	Y	Y	0	112
155.110	3/6/2012	7	—	—	N	202.50	Y	Y	76	0
155.120	3/6/2012	5	—	—	N	250.00	Y	Y	76	0
155.130	3/5/2012	9	—	—	N	222.06	Y	Y	45	40
155.140	3/6/2012	8	—	—	N	252.79	Y	Y	76	0
155.150	3/6/2012	4	6/7/2012	Predation	N	208.09	Y	Y	0	0
155.260	3/5/2012	2	—	—	N	194.12	Y	Y	76	0
155.280	3/5/2012	12	—	—	N	224.85	Y	Y	20	73
155.290	3/5/2012	6	—	—	N	244.41	Y	Y	76	0

Table A–1 cont.

155.310	3/6/2012	4	—	—	N	230.44	Y	Y	74	2
155.320	3/5/2012	2	—	—	N	210.88	Y	Y	74	0
155.330	3/5/2012	15	—	—	N	233.23	Y	Y	76	0
155.340	3/5/2012	9	—	—	N	229.65	Y	Y	76	0
155.360	3/5/2012	7	—	—	N	208.09	Y	Y	76	0
155.370	3/5/2012	8	—	—	N	210.88	Y	Y	51	42
155.380	3/4/2012	17	—	—	N	241.61	Y	Y	71	8
155.390	3/5/2012	4	11/24/2012	Harvest	N	238.82	Y	Y	0	102
155.410	3/5/2012	5	—	—	N	222.06	Y	Y	76	0
155.420	3/5/2012	18	—	—	N	241.61	Y	Y	62	24
155.430	3/3/2012	8	—	—	N	272.35	Y	Y	76	0
155.440	3/5/2012	6	10/4/2012	Harvest	N	252.79	N	Y	34	0
155.450	3/6/2012	4	—	—	N	210.88	Y	Y	76	0
155.460	3/4/2012	17	—	—	N	219.26	N	N	76	0
155.470	3/3/2012	4	—	—	N	229.65	Y	Y	76	0
155.480	3/5/2012	2	—	—	N	210.88	Y	Y	76	0
155.490	3/6/2012	7	—	—	N	208.09	Y	Y	58	18
155.510	3/6/2012	6	—	—	N	230.44	Y	Y	75	1
155.520	3/3/2012	4	—	—	N	238.82	Y	Y	76	0
155.530	3/3/2012	11	—	—	N	216.47	Y	Y	76	0
155.540	3/4/2012	17	—	—	N	250.00	N	N	76	1

Table A–2. Capture data and the number of days spent in South Dakota and Wyoming during harvest season for radiocollared adult cow elk (*Cervus elaphus*) in the Black Hills South Dakota, February 2013.

Frequency[a]	Date	Capture Age	Mortality Date	Cause of Mortality	Lactating	Mass (kg)[1]	Pregnant	VIT	SD Hunt Days[2]	WY Hunt Days[3]
155.033	2/23/2013	9	—	—	Y	220.37	N	N	76	0
155.013	2/24/2013	9	—	—	Y	227.64	Y	Y	75	1
155.044	2/24/2013	10	—	—	Y	218.57	N	N	76	0
155.054	2/25/2013	3	—	—	N	236.03	Y	Y	33	58
155.075	2/24/2013	8	—	—	N	247.20	Y	Y	76	0
155.085	2/24/2013	9	—	—	N	258.38	Y	Y	76	0
155.094	2/22/2013	3	12/7/2013	Harvest	Y	218.57	N	N	24	60
155.100	2/23/2013	4	—	—	Y	209.12	N	N	76	0
155.104	2/25/2013		—	—	N	230.44	Y	Y	38	79
155.110	2/23/2013	8	—	—	N	236.03	Y	Y	76	0
155.120	2/23/2013	6	—	—	N	204.40	N	N	76	0
155.130	2/23/2013	10	—	—	Y	216.21	N	Y	38	68
155.140	2/22/2013	9	—	—	N	250.00	Y	Y	0	0
155.260	2/23/2013	3	—	—	Y	241.61	N	Y	0	93
155.280	2/23/2013	13	—	—	N	222.06	Y	Y	39	54
155.290	2/23/2013	7	—	—	Y	236.03	Y	Y	76	0
155.310	2/23/2013	5	—	—	N	219.26	Y	Y	64	23
155.320	2/23/2013	3	8/28/2013	Cap. Mortality	N	255.58	Y	Y	75	1
155.330	2/23/2013	16	9/4/2013	Harvest	N	227.64	N	N	3	0
155.340	2/23/2013	10	—	—	Y	227.64	Y	Y	76	0

Table A–2 cont.

155.360	2/23/2013	8	—	—	N	222.06	Y	Y	76	0
155.370	2/24/2013	9	12/7/2013	Harvest	N	224.85	Y	Y	39	75
155.380	2/23/2013	18	—	—	N	250.00	N	Y	63	13
155.410	2/23/2013	6	—	—	N	204.40	N	N	76	0
155.420	2/24/2013	19	8/27/2013	Starvation	N	206.76	N	Y	0	0
155.430	2/24/2013	9	—	—	N	250.00	Y	Y	76	0
155.440	2/25/2013	9	—	—	N	236.03	Y	Y	76	1
155.450	2/23/2013	5	—	—	N	219.26	N	N	76	0
155.460	2/24/2013	18	—	—	N	233.23	Y	Y	76	0
155.470	2/23/2013	5	—	—	N	222.06	Y	Y	76	0
155.480	2/24/2013	3	—	—	N	222.06	Y	Y	76	0
155.490	2/23/2013	8	—	—	N	233.23	Y	Y	41	51
155.510	2/23/2013	7	—	—	N	224.85	Y	Y	68	8
155.520	2/23/2013	5	—	—	N	238.82	1	Y	76	0
155.530	2/24/2013	12	—	—	Y	204.40	N	N	76	0
155.540	2/24/2013	18	11/25/2013	Injury	N	235.12	N	N	60	18
155.024b	2/24/2013	5	—	—	N	233.23	Y	Y	76	0
155.065b	2/24/2013	6	—	—	N	241.61	Y	Y	33	72
155.150b	2/24/2013	7	—	—	N	241.61	Y	Y	76	0
155.220b	2/24/2013	10	—	—	N	238.82	Y	Y	76	0
155.300b	2/24/2013	8	—	—	N	250.00	Y	Y	76	0
155.320b	2/23/2013	8	—	—	N	232.57	Y	Y	0	0
155.390b	2/24/2013	4	9/28/2013	Harvest	N	219.26	Y	Y	27	1
155.400b	2/24/2013	13	9/29/2013	Unknown	N	236.03	Y	Y	29	0

[a] Frequency ending in (b; n = 9) were initial captures, remaining frequencies were recaptures (n = 35)

Table A–3. Capture data for neonate elk (Cervus elaphus) in the Black Hills, South Dakota and Wyoming, USA. 2012.

Calf	Capture Date	Birth Date	Year	Capture Age	Sex	Birth Weight(kg)[1]	Capture Weight(kg)	Censor/Mort Date	Cause of Censor/Mort
154.527	5/23	5/21	2012	2	F	16.40	18.14	8/18/2012	Lost Collar
154.552	6/1	6/1	2012	0	M	17.29	17.29	9/3/2012	Lost Collar
154.562	6/6	6/4	2012	1	F	16.00	16.87	—	—
154.581	5/29	5/26	2012	3	F	15.14	17.75	8/13/2012	Lost Collar
154.592	6/1	5/31	2012	1	M	19.45	20.32	—	—
154.612	5/18	5/17	2012	1	M	12.46	13.33	7/17/2012	Lost Collar
154.630	6/6	6/4	2012	2	M	20.94	22.68	9/14/2012	Lost Collar
154.651	5/21	5/17	2012	4	F	18.63	22.11	5/27/2012	Predation
155.601	7/1	6/30	2012	1	F	9.17	10.04	9/21/2012	Predation
155.620	5/27	5/25	2012	1	M	17.27	18.14	—	—
155.642	6/3	6/3	2012	0	M	22.68	22.68	8/3/2012	Lost Collar
155.661	6/4	6/4	2012	0	F	16.74	16.74	7/7/2012	Lost Collar
155.670	6/1	5/28	2012	4	F	19.20	22.68	7/23/2012	Predation
155.681	6/19	6/17	2012	2	M	13.23	14.97	8/1/2012	Lost Collar
155.691	6/3	5/31	2012	3	M	19.16	21.77	—	—
155.702	5/23	5/22	2012	1	M	15.50	16.37	—	—
155.742	5/31	5/31	2012	0	M	20.41	20.41	8/12/2012	Lost Collar
155.751	8/14	8/8	2012	6	F	20.12	25.34	—	—
155.771	5/28	5/26	2012	2	F	16.86	18.60	7/30/2012	Lost Collar
155.782	5/19	5/17	2012	2	M	16.29	18.03	—	—
155.791	6/4	5/31	2012	4	F	19.20	22.68	10/15/2012	Lost Collar

Table A–3 cont.

155.801	6/14	6/13	2012	1	M	15.73	16.60	8/7/2012	Lost Collar
155.812	5/22	5/20	2012	2	F	12.38	14.12	9/22/2012	Predation
155.821	5/21	5/20	2012	1	F	14.64	15.51	9/19/2012	Lost Collar
155.832	5/30	5/26	2012	4	F	19.20	22.68	6/5/2012	Lost Collar
155.852	6/20	6/19	2012	1	M	16.37	17.24	—	—
155.862	6/15	6/13	2012	2	M	20.94	22.68	8/9/2012	Lost Collar
155.872	5/28	5/25	2012	3	M	15.53	18.14	—	—
155.882	6/1	6/1	2012	1	M	15.73	16.60	—	—
155.892	5/26	5/25	2012	1	M	17.73	18.60	9/14/2012	Lost Collar
155.902	5/20	5/17	2012	3	F	17.88	20.49	10/28/2012	Lost Collar
155.917	6/22	6/22	2012	0	F	17.12	17.12	10/3/2012	Lost Collar
155.922	5/29	5/28	2012	1	M	17.73	18.60	6/12/2012	Predation
155.941	5/25	5/23	2012	2	M	17.76	19.50	6/2/2012	Predation
155.961	6/5	6/4	2012	1	F	17.55	18.42	8/16/2012	Lost Collar
155.971	5/28	5/25	2012	3	F	12.40	15.01	11/19/2012	Predation
155.982	5/24	5/22	2012	2	M	16.54	18.28	—	—

[1] Capture weight used to determine a birth weight by taking the weight and estimated age at capture and subtracting the average weight gain of elk calves, 870 g d^{-1} (Hudson and Adamczewski 1990)

Table A–4. Capture data for neonate elk (Cervus elaphus) in the Black Hills, South Dakota and Wyoming, USA. 2013.

Calf[1]	Capture Date	Birth Date	Year	Capture Age	Sex	Birth Weight(kg)[2]	Capture Weight(kg)	Censor/Mort Date	Cause of Censor/Mort
154.532	6/24	6/24	2013	0	M	44.28	20.09	—	—
154.551	5/18	5/17	2013	1	M	30.55	14.73	5/24/2013	Lion
154.551b	6/17	6/15	2013	2	M	37.16	18.60	—	—
154.582	6/6	6/5	2013	0	F	30.48	13.83	—	—
154.621	6/6	6/6	2013	0	M	41.79	18.96	11/5/2013	Lost Collar
154.632	6/18	6/13	2013	5	F	47.69	25.99	10/2/2013	Lost Collar
154.641	5/22	5/21	2013	1	M	40.47	19.23	—	—
154.652	6/2	6/2	2013	0	F	36.59	16.60	—	—
155.611	5/23	5/22	2013	1	M	37.07	17.69	—	—
155.632	5/31	5/28	2013	3	M	40.33	20.91	—	—
155.652	6/2	5/31	2013	2	M	30.15	15.42	—	—
155.662	6/20	6/20	2013	0	F	36.78	16.69	—	—
155.672	6/19	6/12	2013	7	M	46.00	26.96	—	—
155.682	6/2	6/1	2013	1	M	39.76	18.91	9/9/2013	Unknown Pred.
155.711	6/20	6/18	2013	2	M	38.06	19.01	—	—
155.722	5/23	5/22	2013	1	M	32.88	15.79	9/20/2013	Lost Collar
155.743	6/4	6/4	2013	0	M	31.69	14.38	—	—
155.772	6/5	6/5	2013	0	F	30.48	13.83	1/31/2014	Unknown
155.793	5/18	5/15	2013	3	F	32.44	17.33	—	—
155.802	5/30	5/28	2013	2	M	18.56	10.16	5/7/2014	Year Old
155.813	5/19	5/19	2013	0	M	36.59	16.60	—	—
155.822	6/18	6/15	2013	3	F	44.74	22.91	—	—

Table A–4 cont.

155.832	5/26	5/24	2013	2	M	40.36	20.05	6/1/2013	Starvation
155.832b	6/17	6/9	2013	8	M	49.04	29.21	—	—
155.843	6/2	6/1	2013	1	M	40.77	19.37	9/17/2013	Lost Collar
155.863	6/8	6/7	2013	1	M	39.76	18.91	6/25/2013	Lion
155.863b	7/5	7/4	2013	1	F	32.58	15.65	7/16/2013	Lion
155.892	6/8	6/7	2013	1	F	39.17	18.64	—	—
155.912	6/26	6/25	2013	1	F	26.18	12.75	—	—
155.932	6/1	5/30	2013	2	F	34.36	17.33	8/4/2013	Lion
155.941	6/2	6/1	2013	0	F	38.68	17.55	—	—
155.952	6/12	6/10	2013	2	M	36.85	18.46	9/16/2013	Lion
155.962	6/12	6/11	2013	1	M	36.08	17.24	—	—
155.972	6/18	6/13	2013	5	F	36.89	21.09	12/25/2013	Vehicle

[1] Calf frequency preceded by (b, n = 3) were redeployed during the same capture season

[2] Capture weight used to determine a birth weight by taking the weight and estimated age at capture and subtracting the average weight gain of elk calves, 870 g d^{-1} (Hudson and Adamczewski 1990)