

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA Forest Service / UNL Faculty Publications

U.S. Department of Agriculture: Forest Service --
National Agroforestry Center

2005

Seasonal Migration and Home Ranges of Female Elk in the Black Hills of South Dakota and Wyoming

Lakhdar Benkobi

Mark A. Rumble

Cynthia H. Stubblefield

R. Scott Gamo

Joshua J. Millspaugh

Follow this and additional works at: <http://digitalcommons.unl.edu/usdafsfacpub>



Part of the [Forest Sciences Commons](#)

Benkobi, Lakhdar; Rumble, Mark A.; Stubblefield, Cynthia H.; Gamo, R. Scott; and Millspaugh, Joshua J., "Seasonal Migration and Home Ranges of Female Elk in the Black Hills of South Dakota and Wyoming" (2005). *USDA Forest Service / UNL Faculty Publications*. 70.

<http://digitalcommons.unl.edu/usdafsfacpub/70>

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Forest Service -- National Agroforestry Center at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA Forest Service / UNL Faculty Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Seasonal Migration and Home Ranges of Female Elk in the Black Hills of South Dakota and Wyoming

LAKHDAR BENKOBI, MARK A. RUMBLE¹, CYNTHIA H. STUBBLEFIELD²,
R. SCOTT GAMO³, and JOSHUA J. MILLSPAUGH

Department of Forest, Rangeland, and Watershed Stewardship,
Colorado State University, Fort Collins, CO 80523 (LB)
USDA Forest Service, Rocky Mountain Research Station, Forest and Grassland
Research Laboratory, 1730 Samco Road, Rapid City, SD 57702 (MAR, CHS, RSG)
Department of Fisheries and Wildlife Sciences, 302 Anheuser Busch Natural
Resources Building, University of Missouri, Columbia, MO 65211 (JJM)

ABSTRACT -- Understanding the movement and dispersion patterns of elk (*Cervus elaphus*) on public lands and the underlying factors that affect each will facilitate elk management and help resolve conflicts between management that benefit elk and other uses of land resources. Consequently, there is a need to identify and examine the movement and dispersion patterns of elk in the Black Hills of South Dakota and Wyoming. Our study quantified seasonal movements, determined home ranges of female elk in two areas of the Black Hills, and examined underlying factors associated with each. Elk in the northern area did not demonstrate seasonal migration patterns. Rather, winter ranges in the northern area were contained mostly within the boundaries of the summer range. Elk in the southern area exhibited a north-south migration pattern that coincided with seasonal patterns of snowfall. These elk migrated to winter range in late November and returned to summer range in late April. Home ranges of elk in the southern area were larger ($P < 0.01$) than home ranges in the northern area. Landscape

¹Corresponding author. E-mail address: mrumble@fs.fed.us

²Current address: Department of Chemistry and Chemical Engineering, South Dakota School of Mines and Technology, 501 East Saint Joseph Street, Rapid City, SD 57701.

³Current address: Idaho Department of Fish and Game, 2885 North River Road, St. Anthony, ID 83445.

characteristics with marginally-significant correlations to elk home range area included road density ($P = 0.10$), and forage:cover ratio ($P = 0.08$); density of primary and secondary roads and average slope were significantly correlated with elk home range area ($P < 0.01$). Managers can use this information to develop strategies that meet population goals and reduce conflicts between management for elk and with other resources.

Key words: Black Hills, *Cervus elaphus*, elk, migration, seasonal ranges, South Dakota, Wyoming.

Understanding the movement and dispersion patterns of elk (*Cervus elaphus*) on public lands and the underlying factors that affect each will facilitate elk management and help resolve conflicts between management that benefit elk and other uses of land resources. Factors that influence movements, dispersion patterns, or home ranges of elk provide insights into potential causes of population changes and how these might influence management decisions. In the Black Hills, elk populations are higher than any time in the past century (unpublished report, South Dakota Department of Game, Fish and Parks, Rapid City, South Dakota), and conflicts between elk and other uses of land resources, such as livestock grazing, timber harvest, and mining have become increasingly common. Elk are valued highly for hunting and viewing, and maintenance of the population is of significant socio-economical concern to resource managers (Wisdom and Thomas 1996). More than 80% of the elk in South Dakota occur on public lands in the Black Hills (T. Benzon, South Dakota Department of Game, Fish and Parks, personal communication).

An animal's home range is the area traversed during food gathering, mating, and caring for young (Burt 1943). The size and geographic location of elk home ranges serve as a basis for monitoring behavior and evaluating elk habitat relationships (e.g., Millspaugh et al. 2000, 2004; Conner et al. 2001; Roloff et al. 2001). The extent and nature of wildlife movements and activities encapsulate the scale at which assessment of species should occur (Kernohan et al. 1998) and provide relevant information for analyzing management issues and making effective decisions.

Dispersion patterns of elk have been studied in national and state park landscapes of the southeastern Black Hills (Wydeven and Dahlgren 1985, Millspaugh 1999). However, land and resource management in these parks differs from that on National Forests. Elk populations in Wind Cave National Park (WCNP) and Custer State Park (CSP) are non-migratory (Varland 1978, Rice 1988, Millspaugh 1995) and movements are limited partially by fences bordering the parks. Hunting is permitted in the Black Hills National Forest and Custer State Park. To date, no studies have estimated home range or evaluated seasonal

movement patterns of elk in the Black Hills National Forest (BHNF). The objectives of our research included quantifying the timing and course of seasonal migrations, delineating seasonal ranges, estimating seasonal home range size, and evaluating the factors that influence migration and range extent for elk in the central and northern Black Hills of South Dakota and Wyoming.

STUDY AREA

The Black Hills extend approximately 198 km north to south and 99 km east to west, mostly in South Dakota, but include portions of eastern Wyoming. Elevations range from approximately 915 m in the eastern foothills to 2,207 m in a central granitic core and on the western uplifted plateau. The climate surrounding the Black Hills is continental with low winter and high summer temperatures. Winter temperatures vary with elevations and average from 5 to 6.7°C. January is the coldest month (1.8 to -11°C) while July and August are the warmest months (15 to 29°C). Annual precipitation ranges from 46 to 66 cm (Orr 1959) with June as the wettest month. Winter precipitation is greater in the northern and western portions.

Our study included northern and southern study areas (Fig. 1). The northern study area included that portion of the BHNF north of United States Highway 85 in Wyoming and South Dakota and the northern portion of the western uplifted Limestone Plateau. Elevation ranges from 2,100 m in the southern portion to less than 1,200 m at the northern boundary of the BHNF (Thilenius 1972). The northern half of the north study area contains steep canyons and drainages that feed several perennial streams. The southern study area also included the Limestone Plateau with elevations ranging from approximately 2,100 m in the north to 1,800 m in the south. Precipitation and snow depths decreased with the loss of elevation from approximately 56 to less than 50 cm in both study areas (Orr 1959). Both study areas were dominated by ponderosa pine (*Pinus ponderosa*). White spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*) occur in mesic sites and at high elevations on slopes with northerly aspects (Hoffman and Alexander 1987). Road density in the northern area was 2.51 km/km², while road density in the southern area was 2.13 km/km². These road densities could reduce the effectiveness of habitat by 70% (Lyon 1983).

The Manitoban subspecies of elk that existed in the Black Hills since the late Pleistocene (Sieg and Severson 1996) was eliminated (Bryant and Maser 1982). Rocky Mountain elk were introduced into the Black Hills from the Yellowstone region of Wyoming between 1912 and 1914 (Turner 1974). Estimated elk population in the northern area was increasing about 30% per year with an average ratio of 30 calves per 100 females; the estimated elk population in the southern area was increasing at about 20% per year with an average of 45 calves for 100 female elk



Figure 1. Map of South Dakota and location of the study area in the Black Hills.

(unpublished data, South Dakota Department of Game Fish and Parks, Rapid City, South Dakota). Elk were dispersed over both areas in small herds of approximately seven to ten animals.

METHODS

We studied elk movements and home ranges between August 1998 and October 2001. Initially, we captured elk on the summer range by net-gunning them from a helicopter. To maximize animal safety, we 1) limited the capture period from sunrise to 1200 hr, 2) discontinued capture if air temperature exceeded 29°C, 3) limited direct pursuit of elk to 5 minutes, 4) hobbled and blindfolded elk

immediately after capture, and 5) monitored rectal temperature and other signs of stress for elk (unpublished, Aviation operation plan for helicopter net-gunning, Rocky Mountain Research Station, Rapid City, South Dakota). Radio collars weighing approximately 600 g or GPS collars weighing approximately 1,600 g were placed on elk by using vinyl neck collars. Each transmitter was equipped with a head position activity sensor and mortality sensor that changed the pulse of the radio signal. Our goal was to have 25 female elk with radio collars in each study area. To maximize the probability that captured elk represented a random sample of the population, each study area was divided into quarters and five elk were captured in each quarter with five additional elk captured as opportunity presented in each study area. No more than two elk were captured from a single herd.

We located each radio-collared elk two to three times each month. During snow-free periods, we located elk by approaching them on foot with a hand-held two-element yagi antenna. Using a hand held GPS receiver, we attempted to obtain visual confirmation of the location and recorded the Universal Transverse Mercator (UTM) coordinates (North American Datum 1927, Zone 13). During winter, we located elk from a fixed-wing aircraft equipped with a directional two-element antenna attached to the wing strut on each side. When possible, we obtained visual confirmation of locations from aircraft and recorded locations with a GPS receiver as the aircraft passed over the observed animal(s). For elk with GPS collars, we randomly selected a GPS location between 0600 and 1800 hr at 16 day intervals from each animal to include with the locations from conventional radio telemetry for analyses.

We selected two subsets of the elk location data corresponding to summer (June to August) and winter (January to March). This division provided a starting point for the analyses and was based on field observations and preliminary examination of elk locations by using scatter plots of elk that were clearly on the summer or winter range. We used the classification and regression tree (CART) method (Breiman et al. 1984) in Answer Tree (SPSS Inc. 2001) to develop a dichotomous predictive model that delineated the boundary between summer and winter range from UTM's of locations and elevation. Using the results from the CART analysis, we developed a nonlinear regression model between Julian date and UTM northing and inserted the decision rule for UTM northing from CART into the nonlinear regression and solved for Julian date. This provided the predicted date that elk arrived on winter range. Finally, we tabulated the average Julian date that radio marked elk arrival on winter or summer range and compared these observed dates with those predicted dates in the nonlinear regression.

Volume of intersection (VOI) index (Seidel 1992, Millsbaugh et al. 2000) for 95% kernel use distributions of annual seasonal ranges in the northern and southern areas was used to compare the similarity among years of winter and summer ranges. Cumulative monthly snowfall and average daily snow depths for winter months were obtained from the climatological data for South Dakota

(National Oceanographic Administration 1998-2001). The GIS soils coverage was obtained from the Soil Conservation Service (1990).

We estimated the individual home range areas and the seasonal ranges (pooled locations) of female elk by using the 95% kernel use distribution (Hooge et al. 1999) with least squares cross-validation (Seaman et al. 1999) in ArcView 3.2 (Environmental Systems Research Institute, Inc. 1998). Locations within ± 2 SE of the average date elk arrived on winter or summer range were not included in estimates of seasonal ranges to eliminate locations that might have occurred during the migration period. Using the multiple response permutation tests (Mielke and Berry 2001), we tested for differences in average home range area between northern and southern areas.

As a post hoc analysis to examine factors associated with variation in home ranges of elk, we used GIS to obtain total road density, density of improved surface roads, cover:forage ratio, topographic roughness, and average slope within summer home ranges of individual elk. Total roads included all inventoried roads by the Black Hills National Forest; improved surface roads were gravel or paved and received greater than 7 vehicles per week of use. Cover was defined as white spruce or ponderosa pine with greater than 40% overstory canopy cover; forage was defined as ponderosa pine with less than 40% overstory canopy cover, aspen, or meadows. Topographic roughness was calculated as the standard deviation of the average elevation from 30 random points selected from a uniform distribution in each home range. These data were not distributed normally so we used Spearman's rank correlation to investigate associations of habitat characteristics with home range area of individual elk. We considered analyses significant at $P = 0.05$, but show actual P values to two significant digits for reader's interpretation.

RESULTS

During August 1998, we used a net gun fired from a helicopter to capture and radio collar 13 female elk in the northern study area and 21 females in the southern study area. During January 1999, we used a net-gun and helicopter to capture and radio collar 12 additional females in the northern study area and two females in the southern study area. In February 2000, we captured four additional female elk in the southern area with a net gun and helicopter, and in March-April 2001, we captured two female elk by using clover traps in the southern area. Elk captured in 2000 and 2001 were fitted with GPS telemetry collars. No animal mortality occurred from stress related to the capture process. We included 48 female elk (25 from northern and 23 from southern area) in our analyses of movements, from which we obtained 735 ($\bar{x} = 29$, $SD = 9$) elk locations from the northern area and 1046 ($\bar{x} = 45$, $SD = 17$) elk locations from the southern area.

Within the northern study area, the elk that were in South Dakota tended to move in a northeasterly direction during winter, but we could not quantify this through analyses. Elk in Wyoming were identified in the CART analyses as year-round residents and were a distinct herd from those elk in South Dakota. Thus, winter range of elk in the northern area was a portion of the summer range (Fig. 2). Elk in the southern area exhibited north to south migratory patterns between summer and winter ranges. The decision node from CART delineation of summer and winter range for the southern area was the UTM northing of 4870448. Despite a general decline in elevation from north to south, elevation was not included as a decision node. This delineation of summer and winter range had an 18% misclassification rate. The nonlinear regression of UTM northing on Julian date for elk in the southern area, ($\hat{Y} = 4847974 + 287.68$ (Julian date) - 0.67 (Julian date)², adjusted $r^2 = 0.45$, $P < 0.01$), intersected the 4870448 UTM northing on 21 November and 12 April (Fig. 3). Average dates that migratory elk crossed this delineation were 23 November (95% CI = 11 days) and 18 April (95% CI = 6.5 days). Snow accumulation for the southern area was recorded at a weather station 8 km east of the study area boundary. Snow accumulation at this station is lower than that in most of our study area (Orr 1959); consequently, it is only indicative of general patterns. The plot of snow depth intersected the predicted migration date during spring in early April when snow depths were approximately 18 cm (Fig. 3). During fall, snow depth plots intersected the predicted migration date in mid-November when snow depths were slightly more than 20 cm.

Volume of intersection indices (VOI) between annual summer ranges in both study areas were numerically higher than for the winter ranges (Table 1), indicating greater site fidelity in summer, although the distinction between summer and winter ranges was less in the northern area. The VOI for southern area summer ranges varied from 0.69 to 0.84, while the VOI for the northern area summer ranges varied from 0.47 to 0.79. The values of VOI, for the annual winter ranges of both northern and southern areas, declined between the successive years of our study. The greatest overlap between successive annual winter ranges was during 1998-1999 and 1999-2000. Values of VOI for winter ranges during 1998-1999 and 1999-2000 were 0.50 and 0.45 compared with 2000-2001, respectively.

The seasonal home range of elk in the northern area was 39% smaller ($n = 12$, $P < 0.01$) than the home range of elk in the southern area ($n = 18$) during the summer and 79% smaller during the winter ($P < 0.01$, Table 2). Twenty-nine of the animals with sufficient locations for calculating seasonal home ranges were contained within the GIS coverage. Larger summer home ranges of elk ($n = 29$) were correlated ($r = 0.56$, $P < 0.01$) with greater density of improved surface roads and with all roads ($r = 0.31$, $P = 0.10$). We did not explore the relations between winter home ranges and roads because we were unsure of the extent of vehicle and snowmobile use. These would have been influenced by snow depths and area closures during winter. Summer home range size of elk ($n = 29$) was negatively correlated ($r = -0.33$) with cover:forage ratio ($P = 0.08$) and average slope ($P < 0.01$).

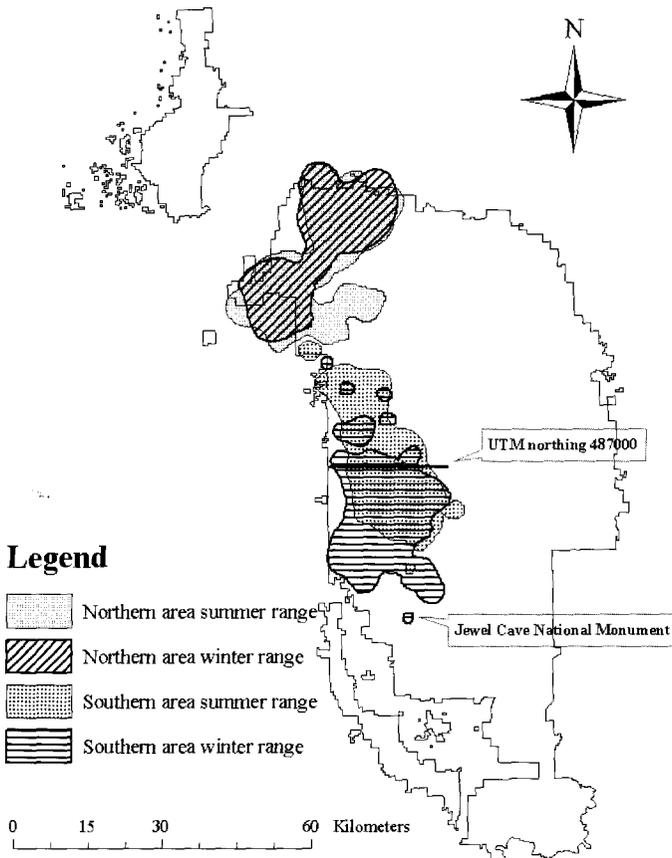


Figure 2. Composite 95% kernel summer and winter ranges for female elk in the northern and southern study areas of the Black Hills, South Dakota and Wyoming.

DISCUSSION

Seasonal movements by elk likely are stimulated by snow accumulation (Murie 1951, Adams 1982), but the direction of movement likely is influenced by forage quality and quantity. In our study, seasonal movements of elk in the southern study area were in a northerly to southerly direction. This migration path allowed elk to move to areas with less snow (Orr 1959), yet stay within areas of highly productive soils in the Black Hills (Bennett et al. 1987, Soil Conservation

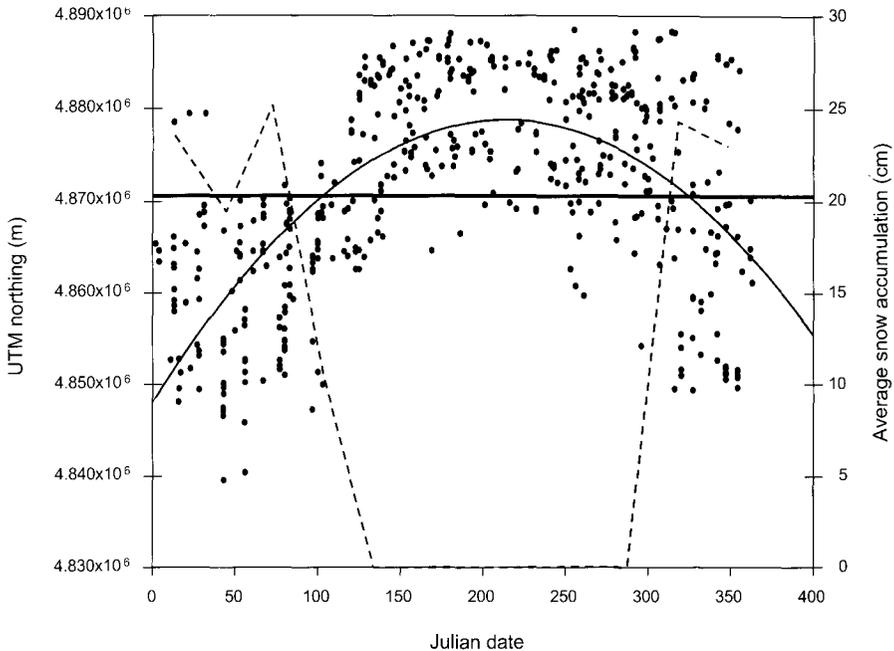


Figure 3. Nonlinear regression expressing average migration date for elk in the central Black Hills of South Dakota. Average monthly snowfall accumulation from a nearby weather station depicts the relation between migration date and snow accumulations (dashed line).

Service 1990). Snow increases the cost of movement by elk and covers forage that could be used by elk (Wickstrom et al. 1984). The migration by elk in the southern area coincided with snow accumulations of approximately 20 cm. Fifteen to 25 cm of snow initiated migration by elk from Yellowstone Park (Anderson 1954). If depth of snow were the only consideration affecting seasonal movements of elk, easterly or southwesterly migrations would result in shorter distances to areas of less snow in the Black Hills. Our regression model predicted that elk migrate to the winter range by late November. We attributed the variation in migration dates to the winter range in the southern area to annual variation in snow accumulation. During early November 2000, heavy snow accumulation on summer range of the southern area caused elk to migrate sooner.

Values of VOI between successive annual winter ranges in the northern and southern areas had similar patterns, but perhaps for different reasons. In the southern area, a late-summer wildfire in 2000 burned approximately 34,000 ha that

Table 1. Volume of intersection index (VOI) for summer and winter elk ranges from two areas of the Black Hills.

Comparison	VOI ¹
Northern area summer	
1999 with 2000	0.61
1999 with 2001	0.47
2000 with 2001	0.79
Average	0.62
Northern area winter	
1998-1999 with 1999-2000	0.77
1998-1999 with 2000-2001	0.53
1999-2000 with 2000-2001	0.42
Average	0.57
Southern area summer	
1999 with 2000	0.70
1999 with 2001	0.84
2000 with 2001	0.69
Average	0.74
Southern area winter	
1998-1999 with 1999-2000	0.72
1998-1999 with 2000-2001	0.50
1999-2000 with 2000-2001	0.45
Average	0.55

¹VOI index of 1.0 would indicate complete overlap in the area of use.

comprised approximately 65% the winter range of elk in the southern area the previous winters (unpublished data, Rocky Mountain Research Station, Rapid City, South Dakota). The timing of the fire, after the growing season, allowed little time for vegetation regrowth and forage quantity in the burn was limited the following winter. Although some elk were observed in the perimeter of the burn during the winter of 2000-2001 in the southern area, elk generally were displaced to the southwest and east of the burn area. In the northern area, annual elk winter ranges

Table 2. Estimated seasonal home ranges (km²) of female elk in the Limestone Plateau and northern Black Hills of South Dakota and Wyoming, 1998 to 2001¹.

Area	Season	Home Range (km ²)	
		$\bar{x} \pm SE$	Probability ²
Northern	Summer	99.7 \pm 4.2	< 0.01
Southern	Summer	163.2 \pm 6.0	
Northern	Winter	104.3 \pm 5.3	< 0.01
Southern	Winter	354.8 \pm 20.1	

¹n = 18 for southern area and n = 12 for northern area.

²Probability that the distributions of north and south home ranges are the same within a season, multiple response permutation procedure (Mielke and Berry 2001).

were contained within summer ranges and the area used depended, to a large degree, on the timing and duration of snow. Snowfall and accumulation patterns during winter 1998-1999 and 1999-2000 were more similar than winter 2000-2001. The snow that fell in November 2000 remained in the northern area until the latter part of the winter.

Inherent in the concept of a home range (e.g., Burt 1943) is that less energy is expended traversing smaller home ranges to meet the needs of the animal. Home ranges of mule deer (*Odocoileus hemionus*) are larger in areas where there is competition from or displacement by livestock (Kie et al. 1991, Loft et al. 1991). Thus, when comparisons are made within a species or among populations, smaller is better. High road densities reduce the effectiveness of habitat for elk (Lyon 1979, Rowland et al. 2004) because elk preferentially select areas away from roads (Rowland et al. 2000). Human disturbance increases elk movements (Cassierer et al. 1992, Conner et al. 2001) and alters dispersion patterns (Wertz et al. 1996, Millspaugh et al. 2000, Vieira et al. 2003) which results in larger home ranges. Larger summer home ranges were associated with total road density (although not significantly), but the strongest correlation was between improved surface roads and summer home range area. When we compared the home ranges from our study to those in Custer State Park, South Dakota, approximately 30 km southeast of our study, total road density appeared to influence home ranges of elk between the areas. Summer home ranges of elk in our study were 2.8 to 4.5 times larger than home ranges of elk in Custer State Park (CSP) (Millspaugh 1999). While the density of improved surface roads was similar between CSP and our study, our study had on average more than two times (2.3 km/km²) the total road density that occurred in CSP (0.9 km/km², Millspaugh 1999). However, travel off improved surface roads in

CSP is restricted, whereas in the BHNF, travel was permissible on and off road in our study area. There also are many unmapped roads in the Black Hills. Similarly, home ranges during winter in CSP were five to ten times smaller than in our study and snowmobiles are not allowed in CSP. The negative correlation of cover:forage ratio with home range area in our study was consistent with predicted effects of human disturbance on elk. Home ranges of elk in CSP were smaller than in our study, but CSP has less cover (45% grassland) than our study (12% grassland). Limited vehicle access reduced human disturbance to elk and reduced movements of Roosevelt elk (*C. e. roosevelti*) in southern Oregon Coast Range (Cole et al. 1997). Consequently, we surmise that human disturbance in our study area primarily was facilitated by roads, but that increased cover provides some buffer for elk in areas of high road density. Smaller home ranges in areas of steeper slopes might provide for topographic cover, but also might be a reflection of a negative correlation between road density and slope ($r = -0.55$, $P < 0.01$).

Elk movements and dispersion patterns can create conflicts if elk concentrate activities on lands that are in private ownership. Many of the private lands in the Black Hills are managed for livestock production. In the northern Black Hills, elk occasionally used private land north of the BHNF boundary. The greatest occurrence of elk on private lands was in the Wyoming portion of our northern study area, where elk were year round residents. We expected that elk would move between South Dakota and Wyoming or onto private lands north of the Black Hills, South Dakota because of disturbance during hunting seasons on public lands (e.g. Wertz et al. 1996, Conner et al. 2001, Vieira et al. 2003). However, there was little evidence of movements between South Dakota and Wyoming during our study. During winter, we noted concentrated elk use of the BHNF near the South Dakota Department of Game, Fish and Parks elk feed site along the northern study area boundary.

MANAGEMENT IMPLICATIONS

Our study showed that elk in the northern and southern areas were separate herds with occasional interchange in the northern portions of the Limestone Plateau. Elk in the Wyoming portion of our study were year-round residents and there were few occurrences of interstate movements of elk. Along the northern boundary of the BHNF, elk usually remained within the BHNF boundary and migratory patterns could not be quantified for this population of elk. Elk in the southern area migrated north to south between summer and winter ranges. Snow accumulation appeared to determine the timing of seasonal migrations and the extent of winter range. Because snow accumulation reduces forage availability and increases energy demands (Wickstrom et al. 1984), the ultimate factor determining arrival up on winter range probably was forage quantity. Consequently, during

years with deep snow accumulations in the northern area, elk might be displaced onto private land in the surrounding foothills. Knowing the migratory patterns and timing of the elk migrations should help wildlife managers develop harvest strategies to achieve goals for elk populations. Large habitat alterations, such as the Jasper fire can change elk ranges (Van Dyke et al. 1998), and the delineations of ranges identified in our paper might require re-examination in the next few years.

We suggest that roads are major predictors of habitat quality for elk across landscapes. Research clearly has shown that elk avoid roads (e.g., Rowland et al. 2004) and human disturbance (Wisdom et al. 2004). Elk show greater movements associated with human disturbance (Cole et al. 1997, Rumble et al. 2005), but they also need more space where there are more roads.

ACKNOWLEDGMENTS

Our study was supported by the United States Department of Agriculture Forest Service, Rocky Mountain Research Station (Study Plan No. 933, RMRS 98113 CC), in cooperation with Colorado State University (Agreement No. 00-JV-11221609), the Black Hills National Forest, South Dakota Department of Game, Fish and Parks (Study No. 7591, W-75 R-121), and the Rocky Mountain Elk Foundation. Field data were collected by L. Conroy, L. Flack, and M. Tarby. Earlier drafts of our manuscript were reviewed by F. Lindzey and J. Kie.

LITERATURE CITED

- Adams, A. W. 1982. Migration. Pp. 303-211 *in* Elk of North America: ecology and management (J. W. Thomas and D. E. Toweill, editors). Stackpole Books. Harrisburg, Pennsylvania.
- Anderson, C. C. 1954. Migration studies of Jackson Hole's elk herd. *Wyoming Wildlife* 18:26-34.
- Bennett, D. L., G. D. Lemme, and P. D. Evenson. 1987. Understory herbage production of major soils within the Black Hills of South Dakota. *Journal of Range Management* 40:166-170.
- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California.
- Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pp. 1-59 *in* Elk of North America: ecology and management (J. W. Thomas and D. E. Toweill, editors). Stackpole Books. Harrisburg, Pennsylvania.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.

- Cassirer, E. F., D. J. Freddy, and E. D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin* 20:375-381.
- Cole, E. K., M. D. Pope, and R. G. Antony. 1997. Effects of road management on movement and survival of Roosevelt elk. *Journal of Wildlife Management* 61:1115-1127.
- Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. *Journal of Wildlife Management* 65:926-940.
- Environmental Systems Research Institute, Inc. 1998. ArcView 3.2 Redlands, California.
- Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. Research Paper RM-276. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program. United States Geological Survey, Alaska Biological Science Center. <http://www.absc.usgs.gov/glba/gistools/intex.htm>. Date accessed: 10 January 2000.
- Kernohan, B. J., J. J. Millspaugh, J. A. Jenks, and D. E. Naugle. 1998. Use of an adaptive kernel home-range estimator in a GIS environment to calculate habitat use. *Journal of Environmental Management* 53:83-89.
- Kie, J. G., C. J. Evans, E. R. Loft, and J. W. Menke. 1991. Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55:665-674.
- Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55:16-26.
- Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry* 77:658-660.
- Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry* 81:592-595.
- Mielke, P. W. Jr., and K. J. Berry. 2001. Permutation methods: a distance function approach. Springer-Verlag, New York, New York.
- Millspaugh, J. J. 1995. Seasonal movements, habitat patterns and the effects of human disturbances on elk in Custer State Park, South Dakota. M.S. Thesis. South Dakota State University, Brookings.
- Millspaugh, J. J. 1999. Behavior and physiological responses of elk to human disturbances in the southern Black Hills, South Dakota. Ph. D. dissertation. University of Washington, Seattle.
- Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing. *Journal of Wildlife Management* 64:994-1003.

- Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2004. Herd organization of cow elk in Custer State Park, South Dakota. *Wildlife Society Bulletin*: 32:506-514.
- Murie, O. J. 1951. *The elk of North America*. The Stackpole Company, Harrisburg, Pennsylvania.
- National Oceanographic and Atmospheric Administration. 1998-2001. National Climatological Data Center. Asheville, North Carolina.
- Orr, H. K. 1959. Precipitation and streamflow in the Black Hills. Station Paper RM-44. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Rice, L. A. 1988. Evaluation of movements and habitat use of elk in the southern Black Hills, South Dakota, 1980-1986. Completion Rep. W-75-R-28 No. 7524. South Dakota Department of Game, Fish and Parks. Pierre, South Dakota.
- Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. *Journal of Wildlife Management* 65:899-914.
- Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672-684.
- Rowland, M. M., J. W. Wisdom, B. K. Johnson, and M. A. Penninger. 2004. Effects of roads on elk: implications for management in forested ecosystems. *Transactions of the North American Wildlife and Natural Resource Conference* 69: in press.
- Rumble, M. A., L. Benkobi, and R. S. Gamo. 2005. Elk responses to humans in a densely roaded area. *Intermountain Journal of Science* 11:10-24.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- Seidel, K. D. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. M.S. thesis. University of Washington, Seattle.
- Sieg, C. H., and K. E. Severson. 1996. Managing habitats for white-tailed deer in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming. General Technical Report RM-GTR-274. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Soil Conservation Service. 1990. Soil survey of Custer and Pennington Counties, Black Hills parts, South Dakota. United States Department of Agriculture, Soil Conservation Service in cooperation with the United States Department of Agriculture, Forest Service and South Dakota Agriculture Experiment Station, Washington, District of Columbia.
- SPSS Inc. 2001. *AnswerTree 3.0 user's guide*. SPSS Inc. Chicago, Illinois.

- Thilenius, J. F. 1972. Classification of deer habitat in the ponderosa pine forest of the Black Hills, South Dakota. Research Paper RM-91. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Turner, R. W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. Miscellaneous Publication Number 60. University of Kansas Printing Service, Lawrence, Kansas.
- Van Dyke, F. G., W. C. Klein, and S. T. Stewart. 1998. Long term range fidelity in Rocky Mountain elk. *Journal of Wildlife Management* 62:1020-1035.
- Varland, K. L. 1978. Herd organization and movements of elk in Wind Cave National Park, South Dakota. Pp. 215-253 *in* National Park Service Report Number 13. United States Department of Interior, National Park Service, Washington, District of Columbia.
- Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunters numbers and opening dates on elk movements. *Journal of Wildlife Management* 67:717-728
- Wertz, T. L., A. Blumton, L. E. Erikson, L. M. Kemp, and T. Thomas. 1996. Strategies to keep wildlife where you want them - do they work? Pp. 70-72 *in* Sharing common ground on western rangelands: proceedings of a livestock/big game symposium (K. E. Evans, compiler). General Technical Report INT-GTR-343. United States Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285-1301.
- Wisdom, M. J., H. K. Preisler, N. J. Cimon, B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. *Transactions of the North American Wildlife and Natural Resource Conference* 69: in press.
- Wisdom, M. J., and J. W. Thomas. 1996. Elk. Pp. 157-181 *in* Rangeland wildlife (P. R. Krausman, editor). Society for Range Management, Denver, Colorado.
- Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. *Journal of Wildlife Management* 49:805-813.

Received: 15 November 2004

Accepted: 22 October 2005

Associate Editor for Mammalogy: Brock R. McMillan