Am. Midl. Nat. 139:133-140

Summer Bed Sites of Elk (Cervus elaphus) in the Black Hills, South Dakota: Considerations for Thermal Cover Management

JOSHUA J. MILLSPAUGH¹

Wildlife Science Group, University of Washington, Box 352100, Seattle 98195

KENNETH J. RAEDEKE

Wildlife Science Group, University of Washington, Box 352100, Seattle 98195

GARY C. BRUNDIGE

Custer State Park, HC 83 Box 70, Custer, South Dakota 57730

AND

CHARLES C. WILLMOTT²

Department of Wildlife and Fisheries Sciences, South Dakota State University, Box 2140B, Brookings 57007

ABSTRACT.-We characterized 131 summer, diurnal bed sites of 26 elk (11 bulls and 15 cows) in Custer State Park, South Dakota, from 5 June-30 August 1994, 1995 and 1996. Overstory canopy closure, number and basal area of trees, percent litter and bare ground were greater (P < 0.05) at bed sites than at random plots. North aspects were selected (P < 0.05). Microsite air temperature and percent of grass were lower (P < 0.05) at bed sites than at random plots. Hiding cover, wind speed, percent of forbs, shrubs, rocks, and wood, slope percent, average tree dbh, elevation, distance to roads, distance to trails, and distance to water were not different between bed sites and random plots (P > 0.05). Trees were present at 128/131 (97.7%) of bed sites (0.01 ha square plot), but occurred on only 41.2% (54/131) of random plots. An average summer, diurnal elk bed site had basal area >12.4 m^2/ha , >110 trees/ha, >54% canopy closure on N aspects. Overstory canopy closure, tree basal area and microsite temperature correctly classified 86.2% of the observations, suggesting thermoregulatory factors influenced CSP elk use of summer, diurnal bed sites. Although elk are successful in some unforested areas despite the lack of suitable thermal cover, our data suggest that elk in the Black Hills prefer relief sites that provide thermal bed sites when available during the summer diurnal period. Management of appropriate thermal cover should be maintained in areas in which it exists.

INTRODUCTION

The importance and arrangement of thermal cover to elk (*Cervus elaphus*) has been discussed by several researchers (Black *et al.*, 1976; Thomas *et al.*, 1979; Peek *et al.*, 1982; Zahn, 1985; McCorquodale *et al.*, 1986; Merrill, 1987, 1991; Brown, 1994). Homeotherms such as elk must maintain a stable body temperature and use of thermal cover is one way elk balance heat gains and losses (Thomas *et al.*, 1979). Peek *et al.*, (1982) reported that in elk herds with access to adequate thermal cover, numbers fluctuate less and survival is higher during temperature extremes. However, the necessity of thermal cover by elk on summer range has been questioned (McCorquodale *et al.*, 1986; Merrill, 1987, 1991). McCorquodale *et al.*, (1986) and Merrill (1987) reported the presence of successful elk

¹ Corresponding author: e-mail, joshm@u.washington.edu; phone 206-685-2677

² Present address: Bighorn Institute, P.O. Box 262, Palm Desert, California 92261

populations despite the lack of suitable thermal cover in unforested environments. Increasing nocturnal activity, reduced diurnal activity, sweating and large home range sizes were behavioral adaptations to these heat-stressed environments (McCorquodale *et al.*, 1986; Merrill, 1987, 1991). Furthermore, Merrill's (1987, 1991) energy budgeting analyses indicate elk can maintain body temperatures despite high radiative heat gain in open habitats.

However, elk occupying open habitats incur greater thermoregulation costs than elk which have access to forest cover (Merrill, 1987). Although energy intake is high during the summer months, energetic costs associated with lactation and calf-rearing are also high. Additional metabolic costs of energy balances in areas without vegetative thermal cover could also be great. Important behavioral responses by elk in unvegetated areas (*e.g.*, Mount St. Helens) such as an increase in nocturnal activity may be successful only in areas where human disturbance is minimal and where abundant forage allows flexibility in foraging behavior (Merrill, 1991).

Although controversy exists over the necessity of summer thermal cover for elk, hiding cover is considered a critical component of elk habitat by reducing the frequency of human disturbances. Geist (1982) proposed that thermal cover needs of elk may be of secondary importance to an elk's hiding cover requirements. Therefore, knowledge of summer, diurnal microsite use by elk is important in determining both thermal and hiding cover needs.

In 1988 and 1990, about 40% of the forested habitat in Custer State Park (CSP), South Dakota, burned in wildfires representing a potentially significant impact on both thermal and hiding cover. Additionally, CSP has ca. 1.5 million visitors annually with peak use occurring in the summer diurnal period (Millspaugh, 1995). Therefore, we hypothesized that selected habitat variables during the summer diurnal period by CSP elk will be most associated with hiding cover, not thermal cover. This paper identifies important microsite characteristics of summer diurnal bed sites to elk in CSP, South Dakota.

STUDY AREA

Custer State Park encompasses 29,150 ha in the southern portion of the Black Hills region of western South Dakota. Temperatures average 27 C in the summer and -10 C in winter (Morgan, 1987). Elevations range from 1137 m in the E to 2083 m in the NW. Annual precipitation varies within the park from 472 mm to 638 mm.

Custer State Park features a wide variety of Black Hills topography ranging from forested mountains to prairies. Located in the central United States, CSP exhibits qualities of both eastern and western environments with respect to flora and fauna. The three general vegetation types that occur in the Black Hills are the coniferous forest, deciduous woodland and prairie grassland, all of which exist in CSP (Turner, 1974). Prairies dominate the SE part of the Park and ponderosa pine (*Pinus ponderosa*) dominates the forest community. Aspen (*Populus tremuloides*) and paper birch (*Betula papyifera*) are common in drainage areas. The Galena and Cicero Peak fires in 1988 and 1990, respectively, burned a total of 8500 ha within the Park, affecting about 40% of CSP's forest habitat. A 1.3 m woven wire fence topped by three strands of barbed wire surrounds the Park. Custer State Park is bordered by Wind Cave National Park to the S, private rangeland to the E and Black Hills National Forest to the N and W. Ungulate populations in CSP include ca. 1000 elk, 140–150 pronghorn antelope (*Antilocapra americana*), 125 mule deer (*Ocoileus hemionus*), 150 white-tailed deer (*O. virginianus*), 120–140 bighorn sheep (*Ovis canadensis*) and an overwintering population of approximately 950 buffalo (*Bison bison*).

METHODS

Capture.—Elk were trapped from 1 July to 30 August 1993 and 15 June to 29 July 1995 using one side-collapsible modified Clover trap similar to that reported by Thompson et al.

(1989) and eight "scissor" folding Clover traps (Sparrowe and Springer, 1970) baited with salt (Millspaugh *et al.*, 1994). Each captured adult elk was immobilized with a combination of Telazol® (Elkins-Sinn, Inc., Cherry Hill, N.J.) and xylazine hydrochloride (Millspaugh *et al.*, 1995) and fitted with a mortality sensing radio collar (Lotek Engineering, Inc., Ontario, Canada). Calves were released after being ear-tagged and sexed. Helicopter Wildlife Management (Salt Lake City, Utah) assisted in net-gunning elk on 6 August 1993 using a handheld or strut mounted net gun on a Hughes 500C helicopter. Each captured elk was fitted

Microsite characteristic measurement.—Each day from 5 June-30 August 1994, 1995 and 1996, one or two elk were randomly selected for visual verification of location from the ground for measurement of microsite characteristics. Visual observations were obtained by homing in on signals until the elk was seen. An attempt was made not to disturb the elk before a visual observation was made. We then induced movement of elk from their position to obtain microsite data.

with a mortality-sensing radio collar and released.

Ambient air temperature was recorded before the visual observation. At each elk location, the date, time, location (Universal Transverse Mercator coordinates), microsite air temperature (C), precipitation, percent cloud cover, wind speed, percent slope and aspect (N = $337.6^{\circ} - 22.5^{\circ}$; NE = $22.6^{\circ} - 67.5^{\circ}$; E = $67.6^{\circ} - 12.5^{\circ}$; SE = $112.6^{\circ} - 157.5^{\circ}$; S = $157.6^{\circ} - 202.5^{\circ}$; SW = $202.6^{\circ} - 247.5^{\circ}$; W = $247.6^{\circ} - 292.5^{\circ}$; and NW = $292.6^{\circ} - 337.5^{\circ}$) were recorded.

Understory characteristics of habitat were sampled using 20, 20 cm \times 50 cm plots (Daubenmire, 1959). Percent cover <1 m in height of grass, forb, shrub and ground cover of rock, litter, bare ground and wood was ocularly estimated to the nearest percent using four 5-m transects oriented in each compass quarter from the elk location. The upper corner of the plot frame was randomly placed to the left or right at 1-m intervals from the plot center along the transect.

Overstory habitat variables were recorded within a 0.01-ha plot centered at the position of each elk. Information recorded included tree basal area, overstory canopy closure, and cover type (dominant overstory tree species). All trees within the 0.01-ha plot were counted and their diameter was measured at breast height (dbh). A spherical densiometer was used to estimate overstory canopy closure from four readings placed at the elk location, one in each compass quarter. Horizontal obstruction (percent of cover cloth covered) was measured at 25, 50, 75 and 100 m in each compass quarter using a 2.25 m² checkered density board.

Elevation, distance to nearest road, distance to trails and distance to water were determined by overlaying elk locational data on maps within SPANS GIS (Spatial Analysis System, Geographic Information System, Tydac Technologies, Nepean, Ontario, Canada). All roads and trails in CSP were digitized from 1:24,000 USGS (United States Geological Survey) maps using TYDIG (Tydac Technologies Inc., Nepean, Ontario, Canada). Distances to roads, trails and water were divided into the following categories which have been shown to be important distances in identifying human impacts (Aune, 1981; Edge, 1982): <200 m, 201–400 m, 401–600 m, 601–800 m, 801–1000 m and >1000 m.

Microsite variables were also measured at randomly selected sites within the composite summer home range of CSP elk to represent microhabitat availability. Universal Transverse Mercator coordinates for random site locations were determined using a random number generator in program EXCEL and BASIC programming (Microsoft Corporation, Seattle, Wash.). All habitat variables measured at elk observation points were also recorded at random sites.

Statistical analyses.-Samples were pooled from bulls and cows each year if the two groups

Aspect	# bed sites	% bed sites	Bonferroni 95% CI	# random sites	% random sites	Jacob's D
N (337.6–22.5)	34	26.0	28.4-37.3*	14	9.1	0.886
NE (22.6–67.5)	22	16.8	2.1 - 29.7	17	18.2	
E (67.6–112.5)	15	11.5	0.7 - 26.5	19	18.2	
SE (112.6–157.5)	15	11.5	0-22.9	17	11.4	
S (157.6-202.5)	13	9.9	0-22.9	13	18.2	
SW (202.6-247.5)	7	5.3	0-16.3	16	6.8	
W (247.6–292.5)	8	6.1	0 - 16.3	15	11.4	
NW (292.6–337.5)	17	12.9	0-22.9	20	6.8	
Totals	131	100		131	100	

TABLE 1.—Number of occurrences of elk bed sites and random plots in aspect classes, June-August 1994, 1995, 1996

^a Indicates aspect used significantly greater than available (P < 0.05)

had equal variances (Zar, 1984). A Bartlett's test of homogeneity (SAS Institute, Inc., 1990) was used to test for differences by year. After pooling data from normally distributed data, we used a 2-group t-test (Zar, 1984) to compare mean microsite variables at elk locations and random sites to test the hypothesis that habitat characteristics did not differ between elk locations and random sites. If data were nonnormally distributed, we used separate variance 2-group t-tests.

Aspect was tested as categorical data using a chi-square goodness-of-fit test (Neu *et al.*, 1974; Byers *et al.*, 1984). If differences occurred between bed sites and random plots (P < 0.05), Bonferroni confidence intervals were used to indicate where use did not equal availability (Neu *et al.*, 1974; Byers *et al.*, 1984). Jacobs D test (Jacobs, 1974) was used to indicate the relative magnitude of selection or avoidance for significant Bonferroni confidence intervals.

Selection or avoidance for a distance category from a road or trail was defined as significantly greater use than expected. A chi-square test was used to test the hypothesis that distance category use occurred in proportion to availability. Analyses were considered significant at P < 0.05. Area analysis was performed within SPANS GIS for each road and trail to determine the expected number of observations within each distance category.

Stepwise discriminant function analysis (DFA) was used to identify variables contributing most to elk microsite use. Independent variables were included in the DFA if significant differences existed for the variable between elk microsites and random sites to minimize the effects of spurious results (Rextad *et al.*, 1988).

RESULTS

We located 44, 48 and 39 bed sites in 1994, 1995 and 1996, respectively, of 26 elk (11 bulls and 15 cows) in CSP. Our sample consisted of 1–3 bed sites for 10 elk and 4–6 bed sites for 16 elk. Bed sites were observed from 5 June–30 August from 0913 until 1849 h. No sex or yearly differences were detected (P < 0.05), so data were pooled across sexes and years.

Elk bedded at temperatures from 15 to 36 C. Ambient air temperature, recorded before homing on signal ($\bar{x} = 30.3$ C, se = 2.3, n = 131) was higher (t = -3.1, P = 0.03, n = 131) than at elk bed sites ($\bar{x} = 24.8$ C, se = 0.9, n = 131). Elk selected N facing slopes (chi-square = 15.14, 8 df, P < 0.05) (Table 1). Overstory canopy cover was greater (t = 4.81, P = 0.001, n = 131) at bed sites ($\bar{x} = 54\%$, se = 2.7, n = 131) than at random plots ($\bar{x} = 29\%$, se = 2.9, n = 131).

Hiding cover, wind speed, percent of forbs, shrubs, rocks, and wood, slope percent, average tree dbh, elevation, distance to roads, distance to trails and distance to water were similar between bed sites and random sites (P > 0.05). Basal area was higher (t = 8.42, P = 0.001, n = 131) at bed sites ($\bar{x} = 12.4 \text{ m}^2/\text{ha}$, se = 0.13, n = 131) than at random sites ($\bar{x} = 4.9 \text{ m}^2/\text{ha}$, se = 1.8, n = 131). Percent grass was lower (t = -6.01, P = 0.010, n = 131) at bed sites ($\bar{x} = 15.4$, se = 1.1, n = 131) than at random plots ($\bar{x} = 35.7$, se = 2.3, n = 131). There was more litter (t = 4.67, P = 0.004, n = 131) at bed sites ($\bar{x} = 57.2$, se = 2.4, n = 131) than at random sites ($\bar{x} = 35.1$, se = 1.5, n = 131). Percent bare ground was higher (t = 4.23, P = 0.03, n = 131) at elk bed sites ($\bar{x} = 3.9$, se = 0.7, n = 131) than at random sites ($\bar{x} = 2.6$, se = 0.2, n = 131). There were more trees (t = 10.17, P = 0.001, n = 131) at bed sites ($\bar{x} = 10.93$, se = 1.5, n = 131) than at random plots ($\bar{x} = 2.5$, se = 0.9, n = 131). Trees were present at 128/131 (97.7%) of bed sites (0.01 ha square plot) but occurred on only 41.2% (54/131) of random plots.

Microsite air temperature, tree basal area, overstory canopy closure, percent grass, litter, and bare ground were entered into the DFA based on univariate analyses. The number of trees was eliminated because it was correlated (r > 0.6) with overstory canopy closure. The most discriminating variables in the model were overstory canopy closure, microsite air temperature, and tree basal area, which correctly classified 86.2% of observations (F = 10.43, df = 1672). Standardized canonical discriminant function coefficients for elk bed sites vs. random sites were 0.801 for canopy closure, -0.525 for microsite temperature and 0.734 for basal area.

DISCUSSION

Our data support much of what has been previously documented regarding elk summer bed sites with a few noteworthy exceptions. Elevation and slope, two topographic variables which have been consistently reported to influence summer elk habitat use (Mackie, 1970; Marcum, 1975; Skovlin, 1982; Edge *et al.*, 1987), did not significantly influence summer elk bed site selection use in CSP. Generally, elk select higher elevations as summer progresses (Skovlin, 1982; Edge *et al.*, 1987). Selection of higher elevations in summer is generally attributed to differences in vegetation phenology and distribution (Skovlin, 1982). We believe the difference between vegetational phenology or distribution at different elevations within elk ranges in CSP is too limited to warrant elk selection of higher elevations.

Although not an important discriminating habitat variable in this study, CSP elk use of gentle slopes in summer is consistent with other elk herds. Elk selection of gentle slopes shows a degree of consistency among most elk herds (Skovlin, 1982) and has been reported to be among the most important variables in distinguishing elk summer habitat use (Edge et al., 1987). In Utah, Montana and Oregon, elk use was greatest on slopes <30% (Julander and Jeffrey, 1964; Zahn, 1974; Witmer and deCalesta, 1983). Selection of N-facing slopes by CSP elk may be because N slopes offer cooler moister microsites than other aspects (Skovlin, 1982). Julander and Jeffrey (1964), Bohne (1974) and Simmons (1974) all report elk selection of N or NE aspects in summer.

Because direct solar radiation can compound heat stress (Schmidt-Neilsen, 1964), we were not surprised at the importance canopy closure had on elk selection of summer, diurnal bed sites. Skovlin (1982) suggested that overstory canopy closure in forested environments may be the single most important feature in evaluating elk habitat and our data corroborate this report, at least during the summer diurnal period in CSP. Dense overstory canopy cover creates a relatively cool microclimate (Moen and Jacobsen, 1974) by reducing

direct solar radiation, helping elk conserve energy during warm summer days (Skovlin, 1982). Thermal loads on elk in more open areas are twice those in the shade (Zahn, 1985). In Montana (Marcum, 1975) and central Washington (Nelson and Burnell, 1976) elk selected sites containing 70 to 100% canopy closure. Brown (1994), working in the ponderosa pine/juniper forests of Arizona, reported elk made highest use of areas having >70% canopy closure. Thomas *et al.* (1979) and Leckenby (1984) report that good canopy cover is >70% and adequate canopy cover was between 50 to 70% for elk in Washington and Oregon. Our data suggest that CSP elk obtain thermal relief in sites containing >54% canopy closure.

Elk distributions may be influenced by human disturbances (Lyon and Ward, 1982). Distance to roads, trails and other human activities (*i.e.*, logging) have been shown to be important variables in elk habitat selection (Edge *et al.*, 1987). Custer State Park has an extensive road network with 341 km of roads and trails providing considerable access throughout much of the Park. However, our analyses indicate CSP elk bed sites were not influenced by distance to roads or trails. We attribute the lack of influence of the human uses evaluated to elk habituation to predictable disturbances such as road and trail use, and the existence of adequate topographic and vegetative cover near roads and trails.

We expected habitat variables associated with hiding cover, not thermal cover, would be most important to CSP elk during the summer diurnal period. Peak use by CSP's 1.5 million visitors occurs during the summer diurnal period (Millspaugh, 1995) and, although elk may become conditioned to human activity (Schultz and Bailey, 1979), CSP elk are extremely wary of people. Additionally, the wide variety of ecosystems North American elk occupy demonstrates their wide thermal tolerance capability. However, based on our DFA results, we believe that elk are selecting the most thermally neutral sites during the summer diurnal period. This study did not address the role of other variables such as topography, site selection on the slope or bedding direction with respect to wind direction which may be used for security, confounding the hiding vs. thermal cover issue.

In addition to selecting certain habitat components related to thermal factors, we believe bedding behavior was also an important aspect of behavioral thermoregulation for CSP elk. Bed site selection by CSP elk may have affected heat transfer not only by reducing the amount of solar radiation, but by using favorable understory substrates that may increase heat transfer (Merrill, 1987). Univariate analyses indicate CSP elk selected sites with exposed, bare ground, needle covered surfaces which could effectively increase conductive processes and reduce heat loads.

As some recent literature demonstrates (McCorquodale *et al.*, 1986; Merrill, 1987, 1991), elk thrive in areas despite the lack of thermal cover; however, we believe that in places which contain adequate thermal cover, elk are better able to cope with heat constraints and select sites that provide thermal relief. Management of appropriate thermal cover should be maintained in areas in which it exists. Specifically, our study demonstrates the importance of stands with basal area >12.4 m²/ha, >110 trees/ha, containing canopy closure >54% on northerly aspects. We believe these variables help mitigate heat loadings for CSP elk.

Acknowledgments.—J. Baldwin, D. Schlosser and R. Woods assisted with field operations. L. Bender, D. Garner, R. Gitzen and B. Kernohan provided helpful comments on the manuscript. Funding and logistical support was provided by Federal Aid to Wildlife Restoration Act (W-75-R; Study No. 7559) administered through the South Dakota Department of Game, Fish and Parks, Rocky Mountain Elk Foundation, University of Washington, South Dakota State University and Custer State Park.

LITERATURE CITED

- AUNE, K. E. 1981. Impacts of winter recreationsists on wildlife in a portion of Yellowstone National Park, Wyoming. M.S. Thesis, Montana State University, Bozeman. 110 p.
- BLACK, H., R. SCHERZINGER AND J. W. THOMAS. 1976. Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington, p. 11–31. In: S. R. Hieb (ed.). Proceedings of the elk logging-roads symposium, Moscow, Idaho.
- BOHNE, J. R. 1974. Food habits, seasonal distribution, and habitat utilization of elk in the South Fork of Fish Creek, Lolo National Forest, Montana. M.S. Thesis, University of Montana, Missoula. 197 p.
- BROWN, R. L. 1994. Effects of timber management practices on elk. Arizona Game and Fish Dep. Tech. Rep. 10, 71 p.

BYERS, C. R., R. K. STEINHORST AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage., 48:1050–1053.

- DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci., 33:43-64.
- EDGE, W. D. 1982. Distribution, habitat use and movements of elk in relation to roads and human disturbances in western Montana. M.S. Thesis, Univ. of Montana, Missoula. 98 p.
- ——, C. L. MARCUM AND S. L. OLSON-EDGE. 1987. Summer habitat selection by elk in western Montana: A multivariate approach. J. Wildl. Manage., 51:844–851.
- GEIST, V. 1982. Adaptive behavioral strategies, p. 219–277. In: J. W. Thomas and D. E. Toweill (eds.). Elk of North America. Stackpole Books. Harrisburg, Pa.
- JACOBS, J. 1974. Quantitative measurements of food selection. Oecologia, 14:413-417.
- JULANDER, O. AND D. E. JEFFREY. 1964. Deer, elk, and cattle range relations on summer range in Utah. Trans. N. Am. Wildl. Nat. Resour. Conf., 29:404-413.
- LECKENBY, D. A. 1984. Elk use and availability of cover and forage habitat components in the Blue Mountains, northeast Oregon 1976–1982. *Wildl. Res. Rep. No.* 14. Oregon Dep. Fish Wildl. 40 p.
- LYON, L. J. AND A. L. WARD. 1982. Elk and land management, p. 443–477. *In:* J. W. Thomas and D. E. Toweill (eds.). Elk of North America. Stackpole Books. Harrisburg, Pa.
- MACKIE, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. *Wildl. Monogr. No.* **20.** The Wildlife Society, Washington, D.C. 79 p.
- MARCUM, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph.D. Dissertation, University of Montana, Missoula. 188 p.
- McCORQUODALE, S. M., K. J. RAEDEKE AND R. D. TABER. 1986. Elk habitat use patterns in the shrubsteppe of Washington. J. Wildl. Manage., 50:664–669.
- MERRILL, E. H. 1987. Habitat ecology and population dynamics of Mount St. Helens elk. Ph.D. Dissertation, University of Washington, Seattle. 246 p.
- ------. 1991. Thermal constraints on use of cover types and activity time of elk. *Appl. Anim. Behav.* Sci., 29:251–267.
- MILLSPAUGH, J. J. 1995. Seasonal movements, habitat use and the effects of human disturbances on elk in Custer State Park, S.D. M.S. Thesis, South Dakota State University, Brookings, South Dakota. 166 p.
- ------, G. C. BRUNDIGE AND J. A. JENKS. 1994. Summer elk trapping in South Dakota. Prairie Nat., 26:125-129.
 - -, ----, C. L. TYNER AND D. A. HUSTEAD. 1995. Immobilization of Rocky Mountain elk with Telazol and xylazine hydrochloride and antagonism by yohimbine hydrochloride. J. Wildl. Dis., **31**:259-262.
- MOEN, A. N. AND F. L. JACOBSON. 1974. Changes in radiant temperature of animal surfaces with wind and radiation. J. Wildl. Manage., 38:366-368.
- MORGAN, C. C. 1987. Custer State Park: An area study. M.S. Thesis, South Dakota State University, Brookings. 67 p.
- MURIE, O. J. 1951. The elk of North America. Stackpole Books, Harrisburg, Pa. 376 p.
- NELSON, J. R. AND D. G. BURNELL. 1976. Elk-cattle competition in central Washington. p. 71–83. *In:* B. F. Roche. Range multiple use management. University of Idaho, Moscow.

- NEU, C. W., C. R. BYERS AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage., 38:541-545.
- PEEK, J. M., M. D. SCOTT, L. J. NELSON, D. J. PIERCE AND L. L. IRWIN. 1982. Role of cover in habitat management for big game in northwestern United States. Trans. N. Am. Wildl. Nat. Resour. Conf., 47:363-373.
- REXTAD, E. A., D. D. MILLER, C. H. FLATHER, E. M. ANDERSON, J. W. HUPP AND D. R. ANDERSON. 1988. Questionable multivariate statistical inference in wildlife habitat and community studies. J. Wildl. Manage., 52:794–798.
- SAS INSTITUTE, INC. 1990. SAS procedures guide, version 6, 3rd ed. SAS Institute Inc., Cary, North Carolina. 705 p.
- SCHMIDT-NIELSEN, K. 1964. Desert animals: physiological problems of heat and water. Oxford Clarendon Press, London, U.K. 299 p.
- SCHULTZ, R. D. AND J. A. BAILEY. 1979. Responses of National Park elk to human activity. J. Wildl. Manage., 42:91-100.
- SIMMONS, C. A. 1974. Seasonal range use and migration patterns of elk using various portions of the lower South Fork, Flathead River, winter range. Montana Dep. Fish and Game, Helena, Mont. Res. Proj. No. W-120-R-5 & 6. 99 p.
- SKOVLIN, J. M. 1982. Habitat requirements and evaluations, p. 369–413. In: J. W. Thomas and D. E. Toweill (eds.). Elk of North America. Stackpole Books. Harrisburg, Pa.
- SPARROWE, R. D. AND P. F. SPRINGER. 1970. Seasonal activity patterns of white-tailed deer in eastern South Dakota. J. Wildl. Manage., 34:420-431.
- THOMAS, J. W., H. BLACK, JR., R. J. SCHERZINGER AND R. J. PEDERSON. 1979. Deer and elk, p. 104–127. In: J. W. Thomas (ed.). Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Dep. Agric. Agric. Handb. No. 533. Washington, D.C.
- THOMPSON, M. J., R. E. HENDERSON, R. O. LEMKE AND B. A. STERLING. 1989. Evaluation of a collapsible clover trap for elk. *Wildl. Soc. Bull.*, 17:287–290.
- TURNER, R. W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. Univ. Kans. Misc. Publ. Mus. Nat. Hist. 178 p.
- WITMER, G. W. AND D. S. DECALESTA. 1983. Habitat use by female Roosevelt elk in the Oregon Coast Range. J. Wildl. Manage., 47:933–939.
- ZAHN, H. M. 1974. Seasonal movements of the Burdette Creek elk herd. Montana Fish and Game Dep., Helena. Job Comp. Rep. W-120-R-4. 70 p.
- ------. 1985. Use of thermal cover by elk in a western Washington summer range. Ph.D. Dissertation, University of Washington, Seattle. 175 p.
- ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ. 718 p.

SUBMITTED 16 DECEMBER 1996

Accepted 5 May 1997