Research Article

Landscape-Scale Attributes of Elk Centers of Activity in the Central Black Hills of South Dakota

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Abstract

We researched the environmental attributes (n = 28) associated with elk (n = 50) summer range (1 May–30 Sep) in the central Black Hills of South Dakota, USA, during 1998–2001. We defined high-use areas or centers of activity as landscapes underlying large concentrations of elk locations resulting from the shared fidelity of independently moving animals to specific regions on summer range. We divided the study area into 3-km grid cells to represent the distance elk travel in a 24-hour period. We computed mean elevation and slope, proportion and configuration of overstory canopy cover, proportion and configuration of dominant vegetation type, estimated biomass, road density, traffic rate, and amount of habitat not dissected by improved surface roads for each cell. We used a combination of multiple stepwise regression and likelihood ratio tests to develop spatially adjusted models with total number of elk locations per cell as the dependent variable. Environmental attributes varied in their significance based on their availability to different elk subpopulations. Collectively, the number of elk locations was positively associated (model $r^2 = 0.50$, $P < 0.001$) with elevation, proportion of non–road-dissected habitat, shape complexity of meadows, proportion of forest stands with ≤40% overstory canopy cover, and proportion of aspen (Populus tremuloides). Elk were responsive to a landscape structure emphasizing forage potential, and their selection was based on the composition and pattern of both biotic and abiotic variables. Defining the characteristics of high-use areas allows management to manipulate landscapes so as to contain more of the habitats preferred by elk. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1060–1069; 2006)

Key words

Black Hills National Forest, Cervus elaphus*, dissected habitat, elk, habitat selection, high-use areas, landscape metrics, landscape-scale, road pattern.*

Studies of a variety of species have shown that animals use some areas in their home range more frequently than others (Van Ballenberghe and Peek 1971, Dixon and Chapman 1980, Springer 1982, Samuel et al. 1985). The manner in which a large ungulate such as elk select home ranges and exploit resources within home ranges is critical to management, especially on multiple-use public lands (Lyon and Jensen 1980).

During the last decade, management of federally administered lands outside of national parks in the United States has shifted from multiple-use management emphasizing resource exploitation to ecosystem management emphasizing conservation of biodiversity and compatible human uses (Dombeck 1996, Thomas and Dombeck 1996). National forest plans include prioritizing the management of species of local concern. Elk (*Cervus elaphus*) are a species of local concern throughout the western United States due to their high social and economic value (Brooks et al. 1991, Bolon 1994, Canfield et al. 1999). Elk also interact directly or indirectly with domestic species and other wildlife, increasing the possibility for conflict and competition. Knowledge of elk distribution in the context of landscape attributes is an important asset for managing elk populations and their habitat needs on multiple-use public lands. Although existence of, and fidelity to, specific areas have been described for elk (Craighead et al. 1973, Edge and Marcum 1985, Burcham et al. 1998, Van Dyke et al. 1998), relatively few

descriptions of these high-use landscapes have included an assessment of their spatial and aspatial elements and the influence of abiotic variables.

Our objective was to determine how environmental characteristics of the landscape are related to use intensity by elk. We examined habitat selection patterns during a period of high energetic demand in which female elk rear calves, male elk grow antlers and prepare for breeding (Clutton-Brock 1982, Canfield 1999), and during which livestock and human activity is high in the area used by our study elk population.

Study Area

The Black Hills encompasses approximately 15,540 km^2 of mostly ponderosa pine (*Pinus ponderosa*) forest in western South Dakota and eastern Wyoming, USA. Most of the Black Hills is forested (92%) with interspersed meadows and small valleys. Ponderosa pine is considered the dominant climax forest type (84%), with snowberry (*Symphoricarpos* spp.), kinnikinnick (*Arctostaphylos uva-ursi*), and juniper (*Juniperus communis*) as common understory species (Hoffman and Alexander 1987). Quaking aspen (*Populus tremuloides*) comprises 4% of the Black Hills National Forest (BHNF) as a climax vegetation type with paper birch (*Betula papyrifera*) or as an earlier sere to pine and white spruce (*Picea glauca*). White spruce (2% of the BHNF) is primarily found on north-facing slopes and at higher elevations (Hoffman and Alexander 1987). Elevations range from approximately 915 to 2,207 m. Mean annual precipitation ranges from approximately 46 to 66 cm (Orr 1959). January is typically the coldest month, with

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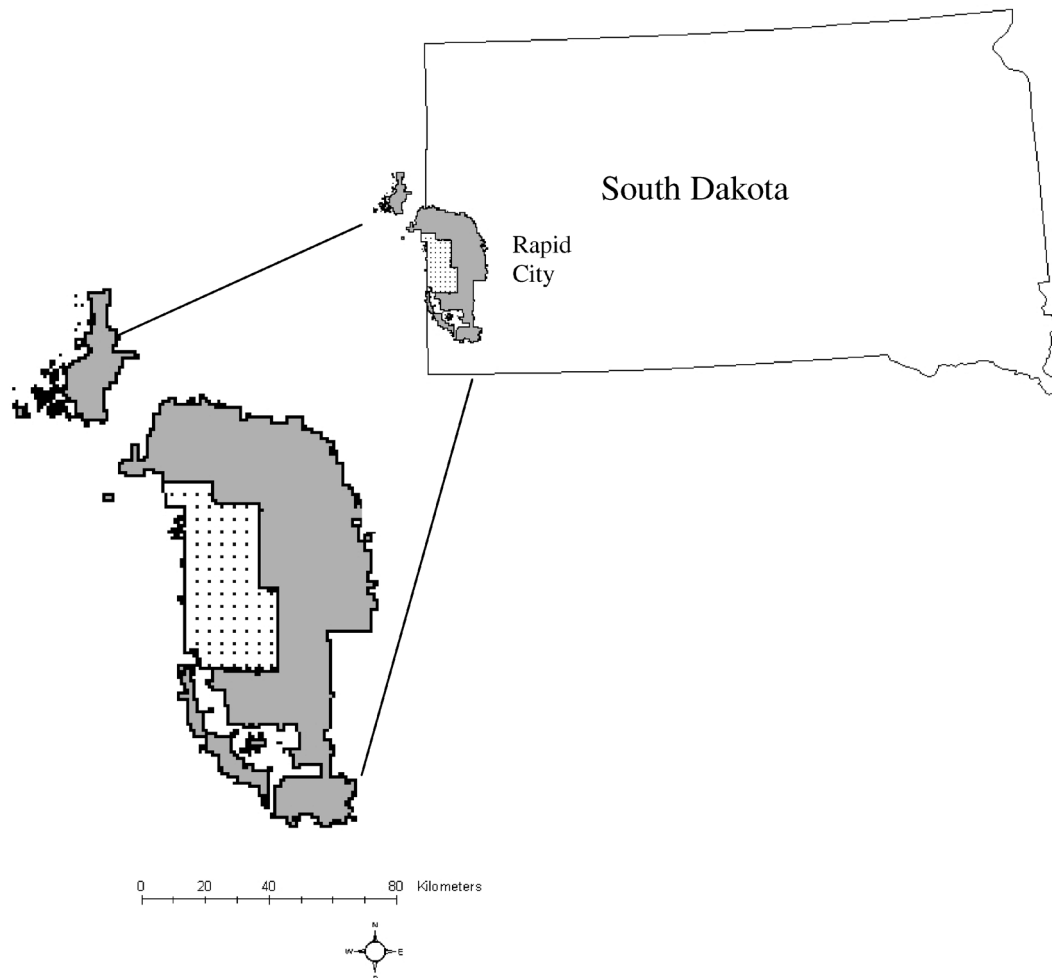
Figure 1. Black Hills National Forest (shaded) and central Black Hills elk study area (speckled) located in western South Dakota, USA, 1998–2001. Data are projected in North American Datum 1927 Universal Transverse Mercator Zone 13N.

mean temperature extremes of 1.8 to −11°C. July and August are the warmest months with mean temperature extremes of 15 to 29°C. Our study area was located on the Limestone Plateau of the Black Hills, which ran adjacent to the Wyoming–South Dakota border (Fig. 1). The BHNF supports a large elk population of approximately 5,000 to 6,000 animals.

Methods

Capture and Telemetry

We captured 21 female and 15 male elk in August 1998, 2 females and 4 males in January 1999, and 3 females and 5 males in February 2000 with helicopter-deployed capture nets. We blind-folded captured elk, monitored them for body temperature, and fitted them with very high frequency (VHF; 41) or Global Positioning System (GPS; 9) radiotelemetry collars and released them (Animal Care and Use Guidelines, American Society of Mammalogists 1987, Aviation plan for helicopter net-gunning, USDA Rocky Mountain Research Station, unpublished report). To ensure samples of radiocollared elk had geographic distributions representative of the study area population, we divided the study area into quadrants, and we sampled animals equally from each quadrant, with no more than 2 animals from the same herd. With the aid of a 2-element yagi antenna, we systematically

located individual elk approximately 2–4 times per month from the ground. We ascribed locations Universal Transverse Mercator (UTM) coordinates using a GPS. We collected observations used between 1 May and 30 September 1998–2001.

Data Analyses

Fidelity.—We selected animals with ≥3 years of data for analyses of site fidelity; this included 20 females and 5 males. We tested the assumption that elk frequented the same landscapes year after year using multiresponse permutation procedures (Mielke and Berry 2002). This test is robust, with no assumptions about the shape of the underlying distribution and sample sizes for each year (White and Garrott 1990). Our null hypothesis was that 2 or more sets, in this case, years, of elk locations came from a common probability distribution (White and Garrott 1990). We set significance for the fidelity test a priori at $\alpha < 0.05$.

Independence.—We tested the assumption that high-use landscapes were the result of selection by independently moving animals. We selected 3 pairs of female elk, which were radiocollared across all 4 summers of the study, occupied different zones of the study area, and had the greatest number of co-occurrences than any other pair of radiocollared animals. We then used Cole's (1949) coefficient of association tests to check for individual independence; animals that co-occur <50% of the time

were considered independent (Knight 1970, Varland et al. 1978, Clutton-Brock et al. 1982).

Cell variables.—We divided the study area into 3-km grid cells. A grid provided the advantage of viewing the study area as a set of cells containing large-scale habitat characteristics believed to be the most influential to elk. Three kilometers has been reported as the average distance traveled over a 24-hour period by elk during the summer months (Craighead 1973, Clutton-Brock et al. 1982), and this was supported with data from elk with GPS-equipped radiocollars in our study area (USDA Rocky Mountain Research Station, unpublished report). We defined these 3-km cells as landscape (Forman and Godron 1986, Urban et al. 1987) units with attributes representative of what an elk had available each day (e.g., Clark et al. 1993, Apps et al. 2001). Cells truncated by the BHNF (west) or study area boundaries (north, south, east) were retained in the analyses if their area was at least 450 ha, or half of a complete cell.

We estimated 28 independent variables for each grid cell using Geographic Information System (GIS); we selected these variables based on their reference in published research and their seeming importance to our study elk (Table 1). We estimated vegetation and topography variables from the BHNF resource inventory system database and a digital elevation model of the BHNF. Variables included proportion of the 4 major vegetation types (Table 1), proportion of forest overstory canopy cover categories (Table 1; Buttery and Gillam 1983), proportion of open or nonforested cover (meadows plus early seral stages), largest contiguous patch of forest cover, area of cover to area of forage ratio, number of unique stand types—a combination of vegetation type, overstory canopy cover, and diameter at breast height category (seedling/pole, mature, and old growth; Buttery and Gillam 1983), total number of stands, average and range of slope, average elevation, number of water sources, and biomass of herbaceous vegetation. We considered forested stands with >40% overstory canopy cover as cover, and we considered meadows, early seral stages, and forested stands with ≤40% overstory canopy cover as forage (Thomas et al. 1979) for the cover to forage ratio calculation. We estimated the herbaceous understory biomass (kg/ha) of each unique stand type from 300 random field sites (60 × 60 m transects) using a stratified design. We estimated the average herbaceous biomass for each site with clippings from 4 0.50-m radius circular frames. We combined site estimates within the same stand type and averaged (trimmed mean) them for an overall estimate of herbaceous biomass per stand type. We then extrapolated these estimates to the cells based on the area of each unique stand type contained within. Landscape measures of shape complexity (area-weighted mean shape index), distance between patches (mean nearest neighbor), and interspersion (interspersion-juxtaposition index) were computed for each overstory canopy class and vegetation type within a cell using Patch Analyst (Elkie et al. 1999), a FRAGSTATS (McGarigal and Marks 1995)-derived extension for ArcView (Environmental Systems Research Institute 2001).

Our road variables included density of all roads, density of improved surface roads (gravel and paved), estimated vehicles per day on improved surface roads, and area of the largest piece of land remaining after dissection by improved surface roads. Improved surface roads included roads classified as primary and secondary by

Table 1. Independent variables considered for analysis in cell-scale models of habitat use by elk in the central Black Hills, South Dakota, USA, 1998–2001.

Variable	Description
Roads	
Traffic rate	Average number of vehicle trips per day
Intact habitat	Proportion of cell not transected by an improved road
Overall road density	Density of all roads (km/km^2)
Improved road density	Density of gravel and paved roads (km/km^2)
Topography	
Elevation	Mean elevation
Slope mean	Mean slope
Slope range	Range of slope (max. − min.)
Vegetation	
Overstory canopy cover	
	Proportion of overstory canopy cover ≤40%
	Proportion of overstory canopy cover 41–70%
	Proportion of overstory canopy cover >70%
	Proportion of open cover – meadows and early seral stages
Cover	Proportion of cell composed by contiguous cover (>40%)
Cov/For	Area ratio of cover patches (>40%) to forage patches (≤40%)
Vegetation type	
Pine	Proportion of pine
Aspen	Proportion of aspen
Spruce	Proportion of spruce
Meadow	Proportion of meadow
Vegetation classes[a]	Number of distinct vegetation classes
Total stands[b]	Total number of stands or patches within the cell
Other	
Water[c]	Number of water sources – stock dams, springs
Biomass	Estimated biomass (kg/ha) of herbaceous vegetation
Precipitation	Mean annual rainfall
Landscape metrics (for the following 2 classes)	
Overstory canopy cover (open, ≤40%, 41–70%, >70%)	
Vegetation type (pine, aspen, spruce, meadows)	
Interspersion-Juxtaposition Index[d]	
Mean Nearest Neighbor[e]	
Area Weighted Mean Patch Shape Index[f]	

[a] Vegetation class is a combination of vegetation type, overstory canopy cover, and structural stage.
[b] Patches or stands of the same type could be counted more than once as long as not adjacent or dissolvable in a Geographic Information System.
[c] Streams or creeks within elk occupied cells are ephemeral.
[d] Measure of interspersion of each class across the cell.
[e] Measure of patch isolation from other patches in the same class.
[f] Area weighted measure determines patch shape complexity independent of patch size.

the BHNF. We calculated all road variables except vehicles per day with a GIS road coverage developed for the BHNF.

To test our assumption that improved roads vary in traffic rate and thus in their effects on elk distribution, we recorded the number of vehicles per day traveling on improved surface roads with road counters. We recorded traffic daily between 0900 and 1200 hours for a minimum of 7 days during the summers of 2000 and 2001. We used daily readings to estimate an average number of trips per day for each improved surface road; we obtained cell
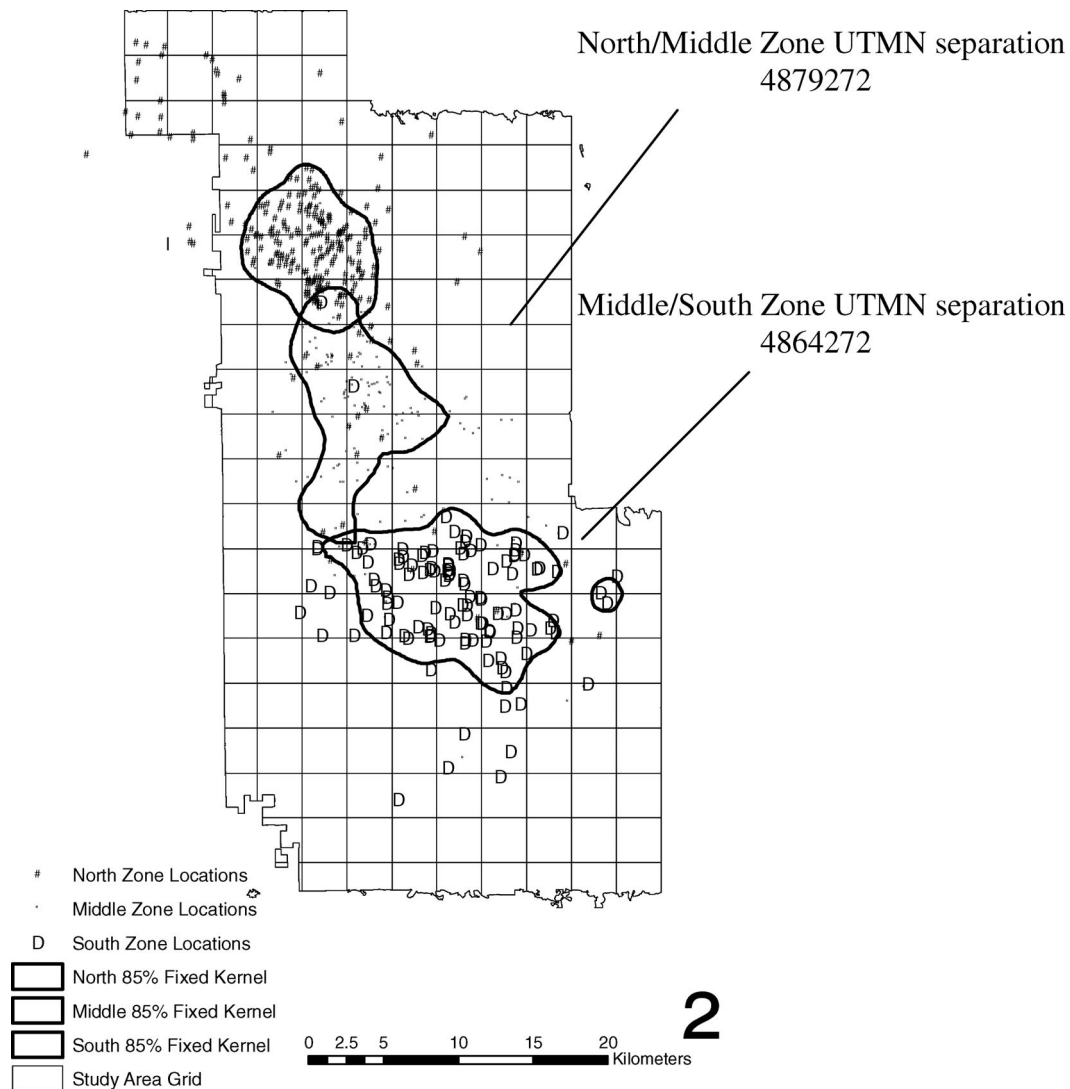
Figure 2. The 1998–2001 distribution of radiocollared elk across the 3-km grid study area (shaded) with the 85% fixed kernel utilization distributions used to define (from top to bottom) the north, middle, and south subpopulations and study zones. Data are projected in North American Datum 1927 Universal Transverse Mercator Zone 13N.

values by averaging these estimates for all improved roads within the cell. We corrected for inflated values of traffic resulting from the duel axles of trucks on 2 major logging routes in the following manner: we observed both roads for 4 hours, and we recorded the number of logging truck passes, we then doubled this value to estimate the number of trucks traveling on each road per day (8-hr period). We then subtracted the estimates from the day's total reading for each road to adjust for the doubling. Within each cell, we digitized the largest piece of intact land, or that not dissected by an improved surface road, and converted it to a proportion of the total cell area. We used climate data (National Oceanic Atmospheric Administration 1998–2001) from several stations in the Black Hills to interpolate a surface coverage of average annual precipitation for each cell.

Our preliminary field observations, verified with GIS plots, indicated that elk partitioned themselves into 3 distinctive groups or subpopulations after migration from winter range. We were interested in the environmental variables underlying concentrations of elk locations across the spatial extent of the study area and how climatic, edaphic, and topographic variations (Orr 1959) might influence the composition, spatial distribution, and productivity of vegetation underlying each subpopulation. Therefore, we assessed elk distribution at 2 spatial scales: across the study area and within each of the areas surrounding the different subpopulations. These divisions are henceforth referred to as the north, middle, and south zones. To research the independent variables affecting elk distribution at a subpopulation level and work within the same cell-based analysis, we used the following steps to divide the study area into zones: 1) We combined locations of individual elk with more than 20 locations (multiple years of data) occurring in the same zone of the study area, 2) we developed (Hooge et al. 1999) fixed-kernel estimates (Worton 1989, Seaman and Powell 1996) of the 85% utilization distribution (Seaman et al. 1999) with least squares cross-validation (Bowman 1985) for the 3 composite or subpopulations, and 3) we drew boundaries (UTM northings) so that each zone contained the majority of locations of the resident animals (Fig. 2). We separated the middle and south zones below the top of the

south 85% fixed kernel. Although some locations of south zone animals were misplaced in the middle zone, more locations of middle zone animals were retained within their resident zone than if we had separated the 2 zones above the south kernel. We subsequently added locations of remaining elk, including those from the 9 GPS-collared animals ($N = 84$), with ≤ 1 year of data to the analysis. To avoid dominance by GPS animals, we randomly selected a daytime (0600–1800) location every 7–14 days from each GPS animal data set to match the sampling protocol of the VHF collared elk.

We developed stepwise multiple regression models for the 3 zones and study area to explore elk location density as a function of environmental variables. We chose number of elk locations per cell as our dependent variable as it accounted for an individual animal's fidelity (return trips) to the landscape. We used pairwise correlations (Pearson) and variance inflation factors to test for bivariate correlations and collinearity amongst variables. We considered a variance inflation factor (VIF) above 10 indicative of a serious collinearity problem (Neter et al. 1989). We excluded highly correlated variables ($r \geq 0.50$) from the models by including only one of each pair of correlated variables. We tested homoscedasticity and normality using univariate procedures (residual plots, Shapiro-Wilk's statistic); we log-transformed the dependent variable if normality assumptions were violated. Significance level for variable entry into the models was $P \leq 0.10$. We assessed stability of the selection for individual variables and combinations of variables in stepwise regression models using a bootstrap technique in which we drew 1,000 bootstrap samples with replacement from the data. We estimated a stepwise regression model for each bootstrap sample, and we tabulated the frequency of each explanatory variable (satisfying the stepwise entry and retention criteria) and variable subset across the bootstrap samples (Draper and Smith 1981, Burnham and Anderson 2002).

We used effect size and standardized beta coefficients for 2 additional perspectives regarding the interpretation of models. The unique effect size of individual model variables as characterized in a power analysis (Cohen 1988) gives perspective to the P values, and is basically a scaled partial r-squared. Standardized model beta coefficients (Afifi and Clark 1990) remove the effect of scale and provide a pragmatic look at the numerical effect of the various variables on model predictions.

We were interested in the level of use of available habitats. Since we were unable to discern whether empty cells represented unavailable landscapes or sampling error, we omitted cells with no recorded locations from our analyses. We observed substantial overlap in range use between male and female elk and a repertoire of behaviors during observations of individual animals. Therefore, we did not distinguish locations by sex or behavior at this large spatial scale. We used variograms to determine the presence and degree of spatial correlation in residuals from regression models. If residuals were spatially correlated, we modified the regression model variance structure to estimate the variance between any 2 observations as a function of the spatial distance between the observations. We specified a spherical spatial covariance structure using the TYPE option of the REPEATED statement of the SAS MIXED procedure (SAS Institute 2001). We used a

likelihood ratio test to assess model goodness-of-fit with and without the spatial correlation component and to develop final models (Littell et al. 1996). For each model, we compared the -2 residual log likelihood value pre- and post-spatial adjustment against a χ^2 distribution with 1 degree of freedom ($\alpha \leq 0.05$) to determine the presence of spatial autocorrelation. Also, if the spatial adjustment resulted in a loss of significance ($P \geq 0.10$) in any of the variables, we consequently removed them from the final model. The SAS REG procedure was used to estimate standard regression models, and the MIXED procedure was used to add a spatial correlation component to models initially estimated in REG (SAS Institute 2001).

Variable levels as a function of use.—We wanted to further our research on the habitat characteristics of elk high-use landscapes by comparing the distribution of independent variables as a function of use intensity. Paralleling methods described by North and Reynolds (1996), we developed a frequency histogram of the number of elk locations contained within each grid cell. Histogram display was then categorized into use-levels based on the natural clumping patterns in the frequency distribution. We then examined the mean, minimum, and maximum values as well as the frequency distribution of each independent variable associated with the different categories of elk use with PROC MEANS and PROC CHART (SAS Institute 2001). We repeated these methods for the study area and for the north, middle, and south zone.

Results

Fidelity and Independence
We obtained 733 locations while elk were on summer range (i.e., 1 May–Sep 30). Sixty-six percent of the locations (485) were direct visual observations from the ground, and the remaining 25% were locations within 50–200 m accuracy. Only 1 out of 25 elk differed significantly ($P < 0.001$) in the area used for its summer range. Coefficient of association tests indicated elk were independent in their locations. Maximum associations were 3% for the north zone, 25% for the middle zone, and 8% for the south zone.

Cell Variables
Maximum VIF in the regression models was 1.48 ($\overline{x} = 1.23$) indicating collinearity was not an issue of concern in our analyses. The degree of effect size for individual variables in all models closely corresponded to the rank order of importance observed with the standardized beta coefficients. We listed beta coefficients (raw and standardized) and partial r-squares for all predictor variables (Table 2); however, we limited our reporting and discussion to the standardized beta coefficients.

We dropped biomass and precipitation from the models, as neither were significant predictors of numbers of elk locations. Although both variables were inexorably tied to available forage, we suspected their release from the habitat models was primarily due to the crudeness of their estimates. In the case of precipitation, the scale at which we estimated the annual mean was not as resolute as any of the other variables and potentially not distinguishable across individual cells within a zone. The readings that were interpolated came primarily from stations on the periphery of the study area and thus did not accurately reflect the internal cell to cell variation. Biomass was significantly correlated

Table 2. Habitat attributes associated with elk centers of activity in the central Black Hills, South Dakota, USA, during 1998–2001 based on stepwise multiple regression models. Model r^2 = adjusted variance explained by model.

Variable	Mean	SD	Coefficient	SE	Partial r^2	P value	Standardized coefficient
North zone 29[a]							
Intercept			−17.81	4.97			
≤40% OCC[b]	0.35	0.13	25.15	11.07	0.24	0.03	0.30
Meadows	0.11	0.06	95.15	31.52	0.21	0.005	0.38
Aspen	0.12	0.14	41.43	14.91	0.12	0.01	0.39
Spruce	0.15	0.19	32.76	11.34	0.06	0.008	0.42
Model r^2				0.59			
Middle zone 30							
Intercept			−0.18	0.43			
Meadow shape[c]	2.35	0.87	0.38	0.15	0.31	0.02	0.33
Aspen	0.05	0.04	10.97	2.84	0.18	<0.001	0.44
≤40% OCC	0.46	0.24	1.80	0.58	0.13	0.005	0.44
Traffic volume	30.00	24.00	−0.009	0.005	0.04	0.10	0.22
Model r^2				0.61			
South zone 36							
Intercept			−9.23	1.65			
Elevation	1,930	121	0.004	<0.001	0.47	<0.001	0.49
Intact habitat[d]	0.76	0.17	2.08	0.54	0.12	0.002	0.36
Meadow shape	2.24	0.80	0.47	0.13	0.11	0.006	0.38
Road density	3.62	0.81	−0.22	0.12	0.03	0.07	−0.18
Model r^2				0.69			
Study area[e] 95							
Intercept			−7.57	1.56			
Elevation	1,981	106	0.003	0.001	0.27	<0.001	0.34
Meadow shape	2.86	1.26	0.18	0.07	0.09	<0.001	0.21
Intact habitat	0.71	0.22	1.52	0.38	0.06	<0.001	0.31
≤40% OCC	0.38	0.22	1.39	0.39	0.05	0.005	0.29
Aspen	0.05	0.09	3.02	0.98	0.05	0.002	0.26
Model r^2				0.50			

[a] Number of grid cells used in the analyses.
[b] OCC is overstory canopy cover.
[c] Meadow shape refers to the area weighted mean patch shape index; values can range from 1 (patches are square or circular) to >1 depending on shape complexity.
[d] Intact habitat is the largest amount (proportion) of land not dissected by an improved road.
[e] Dependent variable (number of elk locations per cell) was log transformed for the study area and the middle and south zones.

with proportion of meadows, meadow complexity, and sometimes proportion of aspen, all of which were superior independent variables.

The study area regression model indicated elk use was positively associated with higher elevation, meadows with increased shape complexity, presence of aspen, overstory canopy cover ≤40%, and more intact habitat (i.e., land not dissected by an improved surface road; Table 2). Based on standardized beta weights, elevation made the most important contribution to number of elk locations followed by proportion of intact habitat. Elevation explains 1.25 to over 2.5 times as much of the variance ($beta_1^2$/$beta_2^2$) in location count as does the other model variables. Intact habitat accounted for almost 1.25 times as much of the variance in number of elk locations as the third ranked variable. All model variables were individually selected in ≥94% of the bootstrap models, which was consistent with stepwise entry and retention criteria of $\alpha = 0.10$. The variable subset of elevation, meadow shape complexity, aspen, overstory canopy cover ≤40%, and intact habitat had a 74% occurrence in bootstrap models. Spatial correlation was present in the study area model ($N = 93$, $\chi^2 = 26.7$, $P < 0.001$) and extended for a range of 4,276 m. All variables retained significance after the

spatial adjustment and thus were retained in the model. In the north zone, vegetation types secondary to ponderosa pine and overstory canopy cover ≤40% explained most of the variance in quantity of elk locations (Table 2). Model output indicated elk use was associated with greater proportions of spruce, meadow, and aspen vegetation and landscapes with greater proportions of overstory canopy cover ≤40%. Standardized beta coefficients for the different vegetation types indicated an almost equal contribution to the number of elk locations. As individual variables, spruce and meadows occurred in 90% of the bootstrap models, and aspen and overstory canopy cover ≤40% occurred in 80% and 60%, respectively. In group models, the variable subset of spruce, meadows, aspen, and overstory canopy cover ≤40% were present in 50% of the bootstrap models.

Another comparable regression model, more parsimonious but less commonsense biologically, was developed for the north area ($r^2 = 0.60$). In this second model, elk locations were associated with lower proportions of pine (partial $r^2 = 0.50$) and overstory canopy cover 41–70% (partial $r^2 = 0.10$). The model described the same phenomenon as the 4-variable model, as there was an inverse relationship between pine and the other vegetation types and

Table 3. Characteristics of predictor variables associated with landscapes receiving high or low-use by elk in the central Black Hills, South Dakota, USA, 1998–2001.

	Mean				Min.		Max.	
Variable	High	SE	Low	SE	High	Low	High	Low
North zone 9/15[a]								
≤40% OCC[b]	0.45	0.07	0.24	0.04	0.22	0.06	0.80	0.52
Meadows	0.13	0.02	0.08	0.01	0.05	0.01	0.21	0.17
Aspen	0.17	0.17	0.09	0.03	0.00	0.00	0.52	0.33
Spruce	0.27	0.07	0.07	0.04	0.01	0.00	0.57	0.55
Pine	0.44	0.05	0.72	0.04	0.22	0.38	0.80	0.93
Middle zone 11/16								
Meadow shape	3.41	0.23	2.40	0.18	1.94	1.23	4.78	4.37
Aspen	0.04	0.02	0.01	0.004	0.00	0.00	0.22	0.04
≤40% OCC	0.61	0.05	0.37	0.06	0.16	0.03	0.79	0.86
Traffic volume	21.45	5.69	32.67	6.29	1.00	1.00	53.00	77.00
South zone 10/20								
Elevation	2,033	23.63	1,862	25.34	1,881	1,593	2,111	2,020
Intact habitat	0.83	0.05	0.74	0.04	0.63	0.36	1.00	1.00
Meadow shape	2.90	0.23	1.82	0.14	1.83	0.00	4.27	2.99
Road density	3.46	0.25	3.82	0.19	2.36	2.11	4.80	5.55
Study area 27/40								
Elevation	2,040	10.07	1,919	18.14	1,881	1,593	2,122	2,111
Meadow shape	3.33	0.17	2.40	0.24	1.62	1.00	7.96	5.82
Intact habitat	0.76	0.04	0.64	0.03	0.38	0.23	1.00	1.00
≤40% OCC	0.50	0.04	0.29	0.03	0.09	0.03	0.81	0.86
Aspen	0.07	0.02	0.03	0.01	0.00	0.00	0.52	0.33

[a] Ratio of the number of high-use cells, those with ≥12 locations, to number of low-use cells, those with ≤3 elk locations.
[b] OCC represents overstory canopy cover.

between the 2 overstory canopy cover classes (≤40% and 41–70%) in the north zone. No spatial correlation was detected in north zone models ($P > 0.95$). In the middle zone, elk were associated with landscapes that had increased meadow shape complexity and greater proportions of aspen and overstory canopy cover ≤40% (Table 2). Elk were also negatively associated with landscapes that had increased traffic volume. Aspen and overstory canopy cover ≤40% were equal in rank order of importance according to standardized beta coefficients. Meadow shape complexity and overstory canopy cover ≤40% occurred as individual variables in >90% of the bootstrap models. Individually, aspen and traffic volume occurred in 87% and 56% of the bootstrap models. In group models, the variable subset of meadow shape complexity, overstory canopy cover ≤40%, aspen, and traffic volume co-occurred in 45% of the models. No spatial correlation was detected in the middle zone model ($0.50 < P < 0.75$). In the south zone, the regression model accounted for nearly 70% of the variability in quantity of elk locations; with the majority of variance explained by elevation ($r^2 = 0.47$). Elevation accounted for 1.5 to 7 times as much variance in the number of elk locations as the other model variables. Elk were associated with landscapes that had a higher elevation, more intact habitat, increased meadow shape complexity, and a lower overall road density (Table 2). Elevation, meadow shape complexity, and intact habitat occurred in 100% of the bootstrap models as individual variables, while overall road density occurred in 80%. In group models, elevation, meadow shape complexity, intact habitat, and overall road density occurred in 80% of the bootstrap models. No spatial correlation was detected in the south zone model based on

the likelihood ratio test ($0.25 < P < 0.50$); a range of 1,361 m was reported; however, this distance is less than half the spatial extent of a cell or the analysis unit.

We limited our examination of the range and frequency distribution of independent variables to 2-layers (Table 3). A *moderate* category is somewhat subjective, and since our goal was a constructive description of the high-use landscapes, we concentrated our comparisons between cells with ≥12 locations, which we classified as landscapes with high-use, and cells with ≤3 locations, which were classified as low-use landscapes. There were 288 elk locations in the north zone, and the count ranged from 1 to 50 locations per cell ($\bar{x} = 9.97$, SE = 0.82). There were 250 elk locations in the middle zone; the count also ranged from 1 to 50 locations per cell ($\bar{x} = 8.62$, SE = 0.55). In the south zone, there were 195 locations, ranging from 1 to 20 locations per cell ($\bar{x} = 5.39$, SE = 0.35).

Discussion

Consistent with other range use analyses (Hershey and Leege 1982, Irwin and Peek 1983, Edge and Marcum 1985, McCorquodale 2003), elk in our study demonstrated a fidelity to their summer ranges. Because of their tendency to behave as habitat specialists elk may be more affected by habitat modification than habitat generalists and species with more behavioral plasticity (Nupp and Swihart 2000). Locations from individual animals were sufficiently separated in time and associations between study animals minimal (not statistically significant) thus the elk locations obtained in this study represented a temporally and spatially independent sample (Millspaugh et al. 1998). We believe

repeated use of the same landscapes by multiple and independently moving elk represents a convergence on selected resources and thus reflects the quality of habitats in that landscape.

Although we stratified our study area to account for variations in resource availability, dispersion, and correlation structure, we observed a consistency in the attributes of high-use landscapes across zones. In general, elk concentrated in landscapes that emphasized forage potential. We suspected elk use of higher elevations was related to forage potential via precipitation. General precipitation patterns in the Black Hills differed along elevation and latitudinal gradients; northern locations and higher elevations received more precipitation than southern locations and lower elevations (Orr 1959). The upper elevations of the study area also aligned with the Stovho Soil Complex. This particular soil type was reported to be one of the most productive in the Black Hills (Bennett et al. 1987). Consequently, soil type and the associated productivity may be one of the major abiotic factors in the large-scale distribution of elk in this geographic region.

Where available, elk concentrated in landscapes containing other vegetation types than the predominant ponderosa pine (Orr 1959). Elk were selecting habitats with a more diverse forest. We attributed the association of elk with aspen to the superior forage potential offered by this vegetation type. Aspen stands were second only to meadows in herbaceous cover and biomass in the BHNF (Hoffman and Alexander 1987; USDA Rocky Mountain Research Station, unpublished data). Aspen stands also provided forage of high nutritional value to elk (Nelson and Leege 1982, Canon et al. 1987) and were a favorite food source (Barnett and Stohlgren 2001). Meadows were also integral to elk high-use areas, but specifically those with increased shape complexity. We realize values for this parameter are difficult to visualize and thus compare; however intricately shaped meadows have received more use (Hanley 1983) presumably because their curvilinearity (Forman and Moore 1992) increases the probability these open stands juxtapose with cover patches. Elk have responded to cover and forage patch juxtaposition by increasing their movements across patch types and concentrating their activities in the edges between these two resources (Thomas et al. 1979, Hanley 1983, Irwin and Peek 1983, Edge et al. 1987). Meadows that are complex in shape offer a source of forage but not at the expense of a loss in cover. Elk use of landscapes in the north zone was influenced by proportion of meadows rather than their shape complexity. We suspect this is because meadows in the north zone are all complex in shape and primarily adjoin with stands of white spruce, a vegetation type providing significant cover (USDA Rocky Mountain Research Station, unpublished data). Elk high-use landscapes were dominated by the more open overstory ($\leq$40%), which in almost all cases was distributed across proportions $\geq$0.45. We observed that landscape use dropped significantly when overstory canopy cover increased. This was also true for the south zone; elk did not concentrate in landscapes with greater overstory canopy cover in spite of demonstrable road effects. Although stands with greater overstory cover have been previously reported as ideal cover for elk (Thomas et al. 1979), there is an inverse relationship between overstory canopy cover and understory production (Uresk and Severson 1989).

Our research supplemented that of previous studies, demon-strating elk avoid areas near roads open to motorized vehicles (Perry and Overly 1977, Morgantini and Hudson 1979, Thomas et al. 1979, Irwin and Peek 1983, Lyon 1983) and areas with a high rate of traffic (Wisdom 1998, Wisdom et al. 2004). The BHNF contains a lot of roads. Minimum road density (2.11 km/km^2, 3.38 mi/mi^2) surpasses levels of concern expressed for elk in other geographic regions (Lyon 1983, Wisdom et al. 1986, Lyon and Canfield 1991). The densities we reported are for open roads. None of the existing roads in our study area were closed during the summer. These open and abundant roads can exact short-term energetic costs as well as long-term reductions in quality habitat (Canfield et al. 1999). We have no clear explanation of why roads influenced only some elk distributions, or why some road effects were more influential than others. We suspected variations in the effects of roads on the different elk distributions were due to variations in vegetation and topography. Although our results indicated elk concentrate in landscapes that emphasize forage production, the importance of cover as a mitigating factor on road effects cannot be overlooked. Complexity of the terrain and type and amount of forest cover has helped define the amount of security from human disturbance and use of habitats (Edge and Marcum 1991). Our estimates of daily traffic were coarse. However, we believe the values we obtained reliably separated or distinguished roads with the greatest use. Averaging traffic rates for the roads within a cell provided an estimate of how much motor vehicle use was in that landscape unit. Elk in the middle zone were situated between 4 major access roads and variations in traffic volume on improved roads in this zone have affected their distribution. Sixty-four percent of high-use landscapes averaged $\leq$10 vehicles per day, whereas most (67%) low-use landscapes averaged $\geq$30 vehicles per day. No high-use landscape had >55 vehicles per day, where almost a quarter (22%) of the low-use landscapes averaged $\geq$70 motor vehicles a day.

The majority of elk habitat effectiveness studies examine each road type individually with results suggesting tertiary roads have less of an effect on elk use of habitat than improved surface roads (Millspaugh 1995, Wisdom 1998, Benkobi et al. 2004). However, in the south zone, the only zone in which road density was a significant model variable, cumulative road density rather than density of improved roads influenced elk distribution. Where improved roads exerted their greatest influence in our study was in their pattern across the landscape (Rowland et al. 2000). Elk responded positively to landscapes not dissected by improved roads. Elk were concentrated on landscapes that possessed a minimum proportion of 0.65 of continuous open space. Within each landscape unit, this potentially resulted in a 1,000 m distance buffer between elk and the nearest improved road. Although this value was reduced when landscapes were assessed across the study area, larger proportions of intact habitat were still more frequent compared to landscapes of lesser use.

We based our estimate of elk use on number of locations within a cell and did not focus on the quantity of locations within individual stands or stand types. It is possible for elk to have avoided sections of the cellular landscape or not have used all stands equally. However due to their mobility and our bias for diurnal locations, we assumed that all habitat components of the landscape defined its quality and use by elk. The models we

selected (Table 2) had the greatest overall regression coefficients, frequency in bootstrap models (individual and group), and were the most significant biologically. We acknowledge the relationship between habitat attributes and elk use is seldom linear. More (or less) is not always better. Beyond a certain point, even with collinearity checks in place, the continued increase in one variable limits the presence or extent of one or more other variables. There are also environmental constraints. Elevation, one of the best predictor variables in our study, did not continue past 2,200 m. And somewhere between the maximum elevation at which we observed elk and this upper limit, drastic increases in slope and loss of cover render the surrounding habitat unavailable. Therefore, we indicated the range of values observed for the environmental correlates significantly linked to landscapes intensively used by elk.

Management Implications

Management for elk in commercial forests such as the BHNF may require alterations to established forestry practices. In some forests an elk's need for cover may be secondary to that of forage. Collectively, this means management for elk should include a shift from relatively closed stands of commercial timber (e.g., ponderosa pine) to more open forested stands consisting of other vegetation types.

Although road density and road pattern are not equivalent, the best way to provide and preserve quality habitat without prior knowledge of elk distributions is to reduce open road densities. A reduction in density will also reduce the impact of other road effects. As knowledge of elk distributions increases, forethought can be used to control the placement or obliteration of roads in the proximity of elk centers of activity. We suggest making landscapes available where elk have the potential to distance themselves >500 m on all sides from an improved road.

Acknowledgments

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