

Resource Selection by Elk at Two Spatial Scales in the Black Hills, South Dakota

MARK A. RUMBLE¹ AND R. SCOTT GAMO²

Forest and Grassland Research Laboratory, US Forest Service, Rocky Mountain Research Station, 8221 South Highway 16, Rapid City, SD 57702, USA (MAR, RSG)

ABSTRACT Understanding resource selection by elk (*Cervus elaphus*) at multiple spatial scales may provide information that will help resolve the increasing number of resource conflicts involving elk. We quantified vegetation at 412 sites where the precise location of elk was known by direct observation and 509 random sites in the Black Hills of South Dakota during 1998–2001. We obtained stand level variables from geographic information system coverages for a 250 m buffer around elk and random sites. We used classification and regression trees to simultaneously evaluate environmental thresholds of resources selected by feeding and bedded elk at the site and stand spatial scales. Length of roads (≤ 11.4 m) within 250 m differentiated elk feeding and bed sites from random sites. Only 24% of random sites were misclassified based on this criterion. Ninety-two percent of sites selected by bedded elk had little or no occurrence of the open forest shrub (western snowberry [*Symphoricarpos occidentalis*]) demonstrating general selection of medium to dense forest while elk were bedded. Whereas, 82% of elk feeding sites and 95% of the random sites with ≤ 11.4 m or roads at the first node (a dichotomous split in the decision tree) had $>2\%$ cover of western snowberry. Feeding sites of elk not classified based on snowberry cover occurred in grassland and open forest vegetation types while random sites mostly occurred in pole-size forest with $>40\%$ overstory canopy cover and mature forest stands $>70\%$ overstory canopy cover. Overall, the estimated error of the classification and regression tree model was approximately 15%, with less clear separation occurring in the second and third nodes of the tree. Site characteristics were more important than stand characteristics determining sites selected by elk.

KEY WORDS Black Hills, classification and regression trees, elk habitat, resource selection, roads, South Dakota

The goal of wildlife habitat research is to identify the preferences (e.g., Thomas and Taylor 1990) and requirements of animals which can then be incorporated into management plans to improve wildlife habitats and populations. Elk (*Cervus elaphus*) range over large areas (Clutton-Brock et al. 1982, Benkobi et al. 2005, Stubblefield et al. 2006) and habitat research has increasingly focused on landscapes and analyses across multiple spatial scales (Jones and Hudson 2002, Boyce et al. 2003, Anderson et al. 2005, Frair et al. 2005, Visscher and Merrill 2009). The hierarchical nature of habitat selection (Johnson 1980) provides a useful framework from which to describe elk habitat selection at multiple spatial scales and it is likely that elk select habitats simultaneously at multiple spatial scales (Boyce et al. 2003, Anderson et al. 2005).

We investigated resource selection of an expanding elk herd in a ponderosa pine (*Pinus ponderosa*) dominated ecosystem at two spatial scales. Specifically, our study occurred in an ecosystem in which one forest type occupied $>80\%$ of the landscape and also contained the highest road density (3.2 km/km^2) of any western national forest (1996 Land and Resource Management Plan, Black Hills National Forest, Custer, South Dakota, USA). Road densities in most studies evaluating effects of roads on elk were conducted in areas with $<1.3 \text{ km/km}^2$ (Lyon 1983, Rowland et al. 2000). We simultaneously evaluated hypotheses of elk habitat selection at 2 spatial scales in an ecosystem with 2–3 times as many roads as previous studies. Given the pervasive

literature describing negative effects of roads on elk habitat (Lyon 1983, 1984, Rowland et al. 2000), we hypothesized that roads would negatively affect elk habitat selection, though the spatial scale at which it would occur was uncertain. Because elk select sites with specific characteristics for forage and bedding (Millspaugh et al. 1998, Jones and Hudson 2002), we also hypothesized that vegetative conditions at sites would be more important determinants of elk site selection than surrounding stand level variables. Homogeneity of this landscape and its composition allowed us to evaluate these hypotheses without interactions among variables often found in more variable ecosystems.

STUDY AREA

The Black Hills is a coniferous forest ecosystem extending 198 km north to south and 99 km east to west surrounded by prairies of western South Dakota and eastern Wyoming. Elevations ranged from 915 m in the eastern foothills to 2,207 m in a central granitic core and on the western uplifted Limestone Plateau. The climate was continental and characterized by cold winters and hot summers, averaging 6° C in winter and 22° C in summer (Orr 1959). Precipitation ranged from 46 to 66 cm (Orr 1959), most of which occurred between April and August. Winter precipitation was greater in the northern and western portions. Precipitation and snow depths decreased with the

¹ Corresponding author email address: mrumble@fs.fed.us

² Present address: Wyoming Game and Fish Department, Cheyenne, Wyoming 82006, USA

loss of elevation in the northern and southern Black Hills (Orr 1959).

Our research occurred in the west-central to northwestern portions of the Black Hills (Fig. 1). Elevation ranged from approximately 2,100 m in central portion of our study area and declined to 1,200 m at the northern edge of the Black Hills and 1,800 m at the southern edge of the study area (Thilenius 1972). Steep canyons and drainages were characteristic of the forest as elevation descended to the surrounding prairie of the Great Plains.

Ponderosa pine forest comprised 78% of the forested landscape with white spruce (*Picea glauca*), and quaking aspen (*Populus tremuloides*) comprising 7% and 4%, respectively in mesic sites and higher elevation northerly aspects (Hoffman and Alexander 1987). Grasslands comprised approximately 10% of the area. Road density in the north was 2.51 km/km², while road density in the south was 2.13 km/km².

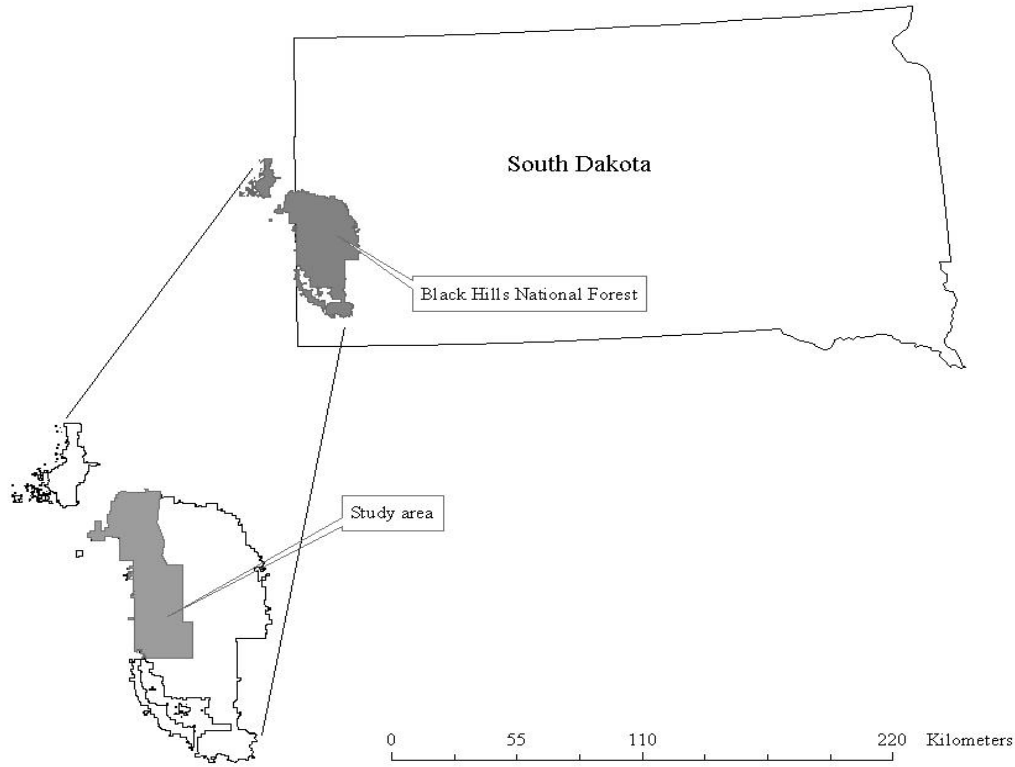


Figure 1. Elk study area in the Black Hills of South Dakota, 1998–2001.

METHODS

Capture Methods and Telemetry

We partitioned our study area into north and south units and further divided each of these into 4 subunits. Seasonal migratory patterns of this elk population were unknown when we initiated the study. Therefore, we captured elk across a large area to ensure sampling of different subherds. We captured and radiocollared elk using a helicopter and netgun during August 1998 and January–March 1998–2000 (Webb et al. 2008, Jacques et al. 2009), and clover traps during late winter 2001 (McCullough 1975, Thompson et al. 1989). Radiocollars (600 g; Telonics Inc., Mesa, Arizona, USA) equipped with activity and mortality sensors that

switched to mortality mode after the transmitter remained motionless for ≥ 6 hr were placed on each captured elk. We equipped 4 female elk with global positioning system (GPS) receivers (Telonics Inc.) weighing approximately 1,600 g that also had very high frequency (VHF) transmitters. Our protocol allowed for capture of 5 females in each subunit and 5 females at random. We captured male elk opportunistically in the south subunit, and ≤ 2 elk from a single group of animals. To maximize animal safety during capture events, we 1) limited the capture period from sunrise to 1200 hr, 2) discontinued daily 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 watched for panting as indicators of stress for elk

(unpublished, Aviation operation plan for helicopter net-gunning, Rocky Mountain Research Station, Rapid City, South Dakota, USA).

We used VHF radiotelemetry to determine sites used by elk for feeding and bedding. Between August 1998 and October 2001, we located each radiocollared elk 2–3 times each month. During snow-free periods, we approached radiocollared elk on foot with a hand-held two-element yagi antenna (Telonics Inc.) and attempted to obtain visual confirmation of foraging or bedding sites. During winter, we located elk from a fixed-wing Cessna 172/182 aircraft equipped with directional two-element antennas attached to the wing struts. When possible, we obtained visual confirmation of bedding or feeding sites from aircraft and recorded sites as the aircraft passed over observed animal(s). We recorded Universal Transverse Mercator (UTM) coordinates (North American Datum 1927, Zone 13) using a hand-held GPS receiver for each site and recorded activity (feeding or bedded) of radiocollared animals facilitated by the head-position activity sensor in the radio transmitter. We recorded occurrence of multiple radiocollared individuals in a herd as a single site.

Vegetation Characteristics of Elk Sites

The Black Hills National Forest is delineated into land units (stands) approximately 4–32 ha in size. We classified vegetation stands using a hierarchical scheme of vegetation type, structural stage, and overstory canopy cover categories (vegetation structural stages) previously described by Buttery and Gillam (1983). Vegetation types included grasslands, aspen, ponderosa pine and white spruce. Structural stages are visualized as seral stages of forest vegetation (Buttery and Gillam 1983) and our study included grass/forb, seedling/shrub, sapling/pole (2.5–22.8 cm diameter-at-breast-height [dbh]), mature (>22.8–41 cm dbh), and old-growth (>41 cm). We divided sapling/pole and mature tree stages into 3 overstory canopy cover categories of 0–40%, >40–70% and >70% (e.g., Buttery and Gillam 1983). We obtained these data from an existing Black Hills National Forest geographic information system (GIS) and subsequently updated this coverage to include private lands. We assigned vegetation structural stages to private land based on interpretation of 1:24,000 air photographs and digital orthoquads.

We overlaid UTM coordinates of individual elk on the GIS coverage to determine the vegetation structural stage in vegetation stands where elk occurred. We computed the average nearest neighbor distance among elk locations and used 50% of that distance as a buffer radius (250-m) that we intersected with the vegetation structural stage GIS coverage to describe vegetation structural stages surrounding vegetation sites. We also intersected 250 m buffers with the GIS road coverage and summed the length of primary, secondary, primitive and total roads.

Within 1 week of visually locating radiocollared elk, we collected vegetation data at each elk site. At each site, we established 2, 60-m perpendicular transects centered over the site of the observed animal. We randomly assigned transect orientation and recorded aspect as the down-hill direction into 1 of 8 categories that represented increments of 22.5° from standard 45° directions. We estimated percent slope using a clinometer. We recorded forest characteristics at the animal location using a variable radius plot determined from a 10-factor prism (Sharpe et al. 1976) for trees ≥15.2 cm dbh and a 5.03 m fixed-radius plot for trees <15.2 cm dbh. We recorded species and dbh of all live trees and calculated tree density, basal area, and average dbh from these data. We estimated downed woody debris at each site from photo guides developed in the Black Hills (Photo series for quantifying forest residues in the Black Hills, USDA Forest Service, Rocky Mountain Region, AFM 831, 1982). We estimated overstory canopy cover using a convex spherical densiometer (Griffing 1985, Nuttle 1997) at the center point and 30 m away on each transect ($n = 5$). Along these transects, we estimated percent vegetative cover in 0.1 m² quadrats (Daubenmire 1959) at 2-m intervals ($n = 60$) for total cover; categories of grasses, forbs and shrubs; and shrub species. We tabulated all stems < 2.54 cm dbh and < 2 m tall in 2, 1 × 30 m belt plots along each transect. At the intersection of the transects we placed a 1-(tall) × 2-(wide) m vinyl cover cloth with 40 alternating black and white 25 × 25 cm squares approximately 70 cm above the ground. We tallied the number of squares that were not visible at 61 m and the distance at which only 4 squares were visible in 4 directions along a line projected from the transects and quantified security cover as percent of a standing elk obscured at 61 m (e.g., Thomas et al. 1979).

We also quantified vegetation at random sites from July–September 1999–2001. We selected random sites using a stratified random sampling design with vegetation structural stages as the strata (Table 1). Each year, we randomly selected 5–10 polygons for each stratum of the GIS vegetation coverage without replacement to ensure a broad distribution of random points across the study area. We created a 50-m grid in GIS for the selected stands and randomly selected one grid point in a stand. We located grid points in the field with a hand-held GPS unit. We considered private lands within the study area as separate stratum at the outset. We excluded obvious errors in the assignments of vegetation structural stages during field measurements and subsequently selected alternative stand and random sites with similar vegetation structural stages as replacement sites.

Data Analyses

For all analyses, we weighted data from random sites to account for deviations from proportional sampling using the following formula: $wgt = n_r * p_i/n_i$ where n_r is total number

of random sites, p_i is the proportion of the study area of the i_{th} strata and n_i is the number of sites in the i_{th} strata. We used hierarchical cluster analysis and principal component

analysis (SPSS 2001) independently to reduce the number of variables for further analyses.

Table 1. Vegetation classification and sample sizes (n) used for stratified random sampling of study area for evaluating elk resource selection in the Black Hills of South Dakota, 1998–2001¹.

Vegetation type	Structural stage	Overstory canopy cover	n
Grassland	NA	NA	44
Shrubland	NA	NA	10
Aspen	Seedling/shrub	NA	24
Aspen	Sapling/pole	0–40%	27
Aspen	Sapling/pole	41–70%	22
Aspen	Sapling/pole	>70%	28
Aspen	Mature	0–40%	17
Aspen	Mature	41–70%	19
Aspen	Mature	>70%	22
Ponderosa pine	Grass/forb	NA	10
Ponderosa pine	Seedling/shrub	NA	21
Ponderosa pine	Sapling/pole	0–40%	29
Ponderosa pine	Sapling/pole	41–70%	24
Ponderosa pine	Sapling/pole	>70%	27
Ponderosa pine	Mature	0–40%	46
Ponderosa pine	Mature	41–70%	40
Ponderosa pine	Mature	>70%	28
Ponderosa pine	Old-growth	NA	9
White spruce	Grass/forb	NA	5
White spruce	Seedling/shrub	NA	3
White spruce	Tree	0–40%	17
White spruce	Tree	41–70%	23
White spruce	Tree	>71%	16

¹Vegetation classification described by Buttery and Gillam (1983).

We used classification and regression trees (Breiman et al. 1984, SPSS Answer Tree 3.0 2002) to identify important variables from this reduced data set for classifying sites as elk feeding or bed sites, or random sites. Classification and regression trees are ideal for modeling species response to variables (e.g., Grubb and King 1991, Grubb et al. 2002, O'Conner and Wagner 2004) when there is cross-scale correlation because at each node (where the classification tree branches) variables are evaluated independent of previous nodes (Battin and Lawler 2006). There are obvious cross-scale correlations in vegetation of stands and microhabitat characteristics (e.g., Uresk and Severson 1989). To avoid overfitting the model, we manually pruned the branches if leaves (the resulting classification of sites) in the newly created branches were predominantly the same classification as the leaf they were drawn from. For instance, if both leaves (classification results from the node) in the created branch were mostly comprised of random sites and random sites were the predominant category in the previous leaf, we pruned that branch. We also used Random Forests (RF, [Liaw and Wiener 2002, R 2.10.1, R Foundation for Statistical Computing, 2009]), which fits many classification trees to a data set and combines the results to develop variable importance plots and for out-of-bag bootstrap estimates of the error rate (Breiman 2001, Cutler et al. 2007). Random Forests is less susceptible to overfitting models than a single classification and regression tree (Evans and Cushman 2009). We considered stand level and microhabitat conditions simultaneously in the classification and regression trees.

RESULTS

In August 1998, we captured 21 female and 14 male elk in the south unit and 13 female elk from the north unit. In January 1999, we captured 2 females and 5 males in the south and 12 females in the north and in February 2000, we captured 4 females and 5 males in the south unit. In March–April 2001 we trapped 2 females and 2 yearling males in clover traps in the south unit.

We measured 412 vegetation sites where radiocollared elk were observed; 225 of which were elk bed sites and 187 were feeding sites of elk. We also quantified stand and microhabitat characteristics at 509 random sites. The reduced variable set after cluster analysis and principle component analyses that captured the variation in vegetative characteristics in our study area is displayed in Table 2. Extensive exploratory analyses showed no meaningful differences ($P \leq 0.10$) in vegetation characteristics between sites used by male and female elk or elk sites among seasons. Thus, we combined vegetation sites for male and female elk for further analyses.

Total road length in the 250 m buffer distinguished elk sites from most random sites (Fig. 2). Some random sites (24%) with ≤ 11.4 m of roads within 250 m buffer around the sites were included in the leaf containing all elk sites.

The branch with the leaf comprised of only random sites was a terminal leaf (not further portioned). Percent cover of western snowberry partitioned the leaf containing elk sites (and 24% of random sites) into a leaf comprised of mostly elk feeding sites and another comprised of mostly elk bed sites. Because this threshold for snowberry was low (0.02%), it essentially represented presence or absence of snowberry at the site. The leaf comprised of mostly elk bed sites was terminal. Grasslands or open forest vegetation structural stages were identified with elk feeding sites at the next node and random sites were identified with shrub/seedling, sapling/pole $>40\%$ overstory canopy cover, and mature ($>70\%$) overstory canopy cover structural stages.

Despite being the second variable entered into the classification and regression tree, variable importance plots (see Cutler et al. 2007:2784 for explanation) showed western snowberry was the most important variable for classifying feeding or bedded elk from random sites, followed by total roads and stand structural stage (Fig. 3). Kinnikinnick (*Arctostaphylos uva ursi*), primitive roads, and slope at the site were surrogate variables for variables immediately above them (Fig. 3). Out-of-bag error estimates from 300 iterations of RF indicated good predictive capability of this 3-variable model as approximately 85% of sites were correctly classified. Including additional branches and leaves (up to 6) reduced the error rate 2–3% (Fig. 4).

DISCUSSION

Elk avoidance of roads is perhaps the most universal feature negatively affecting elk distributions (Lyon 1984, Rowland et al. 2000). Total road length was the first classifier separating all elk sites from random sites in our study and the threshold of ≤ 11.4 m within 250 m was low; elk avoided sites adjacent to roads. No other variable was as definitive in separating random sites from elk sites. Because we use random (and not unused) sites, we expected some misclassification of random sites with elk sites. High road densities have been associated with larger elk home ranges (Jones and Hudson 2002, Benkobi et al. 2005, Anderson et al. 2005). Despite the inverse relation between roads at large spatial scales, elk may not avoid roads at smaller spatial scales (e.g., Jones and Hudson 2002, Anderson et al. 2005). Studies with lower road densities than occurred in the Black Hills would be less likely to demonstrate strong negative effects of roads in resource selection functions at small spatial scales because of the inverse relation between availability of resources and the strength of selection exhibited by elk through analyses (Boyce et al. 2003). Our findings suggest that avoidance of roads by elk occurred in their selection of microhabitats. Preliminary analyses of a larger data set for which only stand level information was available did not identify roads as important (unpublished data, Rocky Mountain Research

Station, Rapid City, South Dakota, USA) perhaps because of the pervasive extent of roads throughout our study area (Rumble et al. 2005). Previously, we demonstrated avoidance of improved roads (gravel) to distance of ≥ 260 m

by elk (Rumble et al. 2007) and the threshold of 11.4 m of roads within the 250 m radius around these elk sites is consistent with those findings.

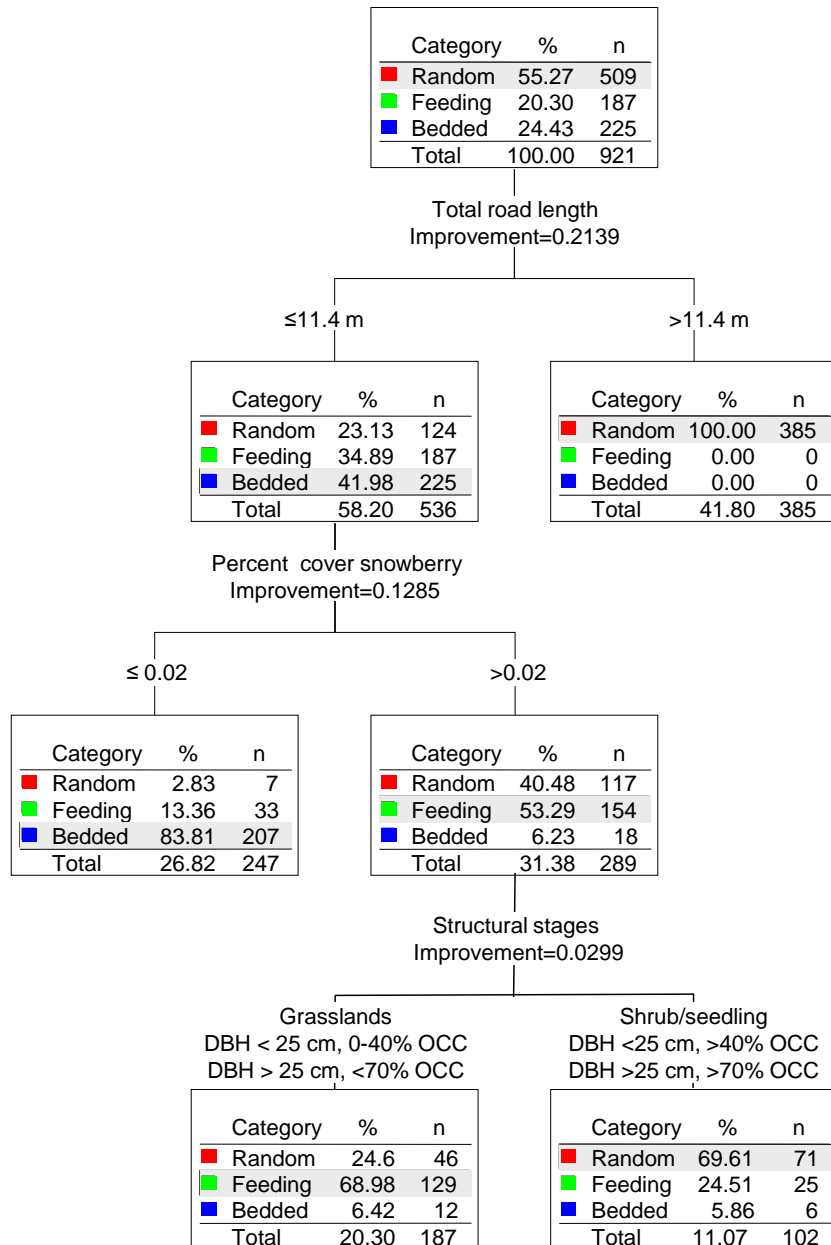


Figure 2. Classification tree of vegetation characteristics at elk sites at multiple scales in the Black Hills, South Dakota, 1998–2001. Shaded portions of classification tree indicate the dominant class assignment for each node.

Table 2. Important variables after hierarchal cluster analysis and principal component analysis included in classification and regression tree analysis to identify elk resource selection at two scales in the Black Hills, South Dakota, 1998–2001.

Variable Name
Site characteristics
Percent slope
Aspect
Downed woody debris (metric tons/acre)
Percent overstory canopy cover
Percent visual obstruction of standing elk
Density of tall shrubs
Basal area of ponderosa pine
Basal area of white spruce
Basal area of aspen (<i>Populus tremuloides</i>)/paper birch (<i>Betula papyrifera</i>)
Percent total understory vegetative cover
Percent canopy cover grasses
Percent canopy cover forbs
Percent canopy cover shrubs
Percent canopy cover common juniper (<i>Juniperus communis</i>),
Percent canopy cover kinnikinnick (<i>Arctostaphylos uva ursi</i>),
Percent canopy cover chokecherry (<i>Prunus virginiana</i>),
Percent canopy cover western snowberry (<i>Symphoricarpos occidentalis</i>)
Stand level variables
Area of vegetation types ¹
Area of vegetation type overstory canopy cover categories ¹
Area of each vegetation type, structural stage, overstory canopy cover categories ¹
Structural stage of stand site occurred ²
Average percent slope of stand
Aspect of stand
Length of primary roads
Length of secondary roads
Length of primitive roads
Total length of roads

¹ Vegetation classification from Buttery and Gillam (1983); ² Combined vegetation type, structural stage, and overstory canopy cover categories from Buttery and Gillam (1983).

The second nodes of the classification tree partitioned sites selected by elk as those characterized by vegetation typical of open canopy forest/meadows or closed canopy forests. The low threshold for snowberry and its surrogate kinnikinnick associated with feed sites essentially

represented presence or absence of these plants associated with open canopy forests (Larson and Johnson 1999) at elk feeding sites. The final node represented stands where elk were observed and attempted to classify stands used for feeding versus stands used for bedding. Because of the

inverse relation between forage availability and tree canopy cover, open stands would have less forage than meadows, but more than stands with moderate to dense canopies (Uresk and Severson 1989). Frair et al. (2005) noted that elk selected foraging sites in areas of intermediate herbaceous vegetation to minimize risk of predation. Bed sites were characterized only by stand level characteristics at the third node and, not surprisingly, elk selected bed sites within stands with a more closed forest canopy. We expected elk to select dense stands for bedding for either

hiding cover or perhaps thermal cover during summer (Millspaugh et al. 1998). However, only 19% of our elk observations occurred at temperatures where selection of cover for thermal regulation was expected (e.g., Parker and Robbins 1984). Therefore, we hypothesize that bed sites were selected for hiding cover. Open to moderate canopy forest provide intermediate forage for elk and have low movement costs allowing elk to feed and bed in the same vegetation stand (Frair et al. 2005).

Variables

- Percent canopy cover western snowberry
- Percent canopy cover kinnikinnick
- Total roads within 250 m
- Primitive roads within 250 m
- Structural stage of stand
- Slope of site
- Slope of stand
- Overstory canopy cover of stand
- Vegetation type of stand
- Percent canopy cover forbs
- Percent canopy cover grasses
- Total basal area aspen at site
- Percent total understory cover
- Grasslands within 250 m
- Ponderosa pine <40% overstory cover within 250 m
- Aspen within 250 m
- Basal area of ponderosa pine at site
- Shrublands within 250 m
- Percent canopy cover shrubs
- Secondary roads within 250 m
- Ponderosa pine > 70% overstory cover within 250 m
- Area of white spruce within 250 m
- Percent canopy cover common juniper
- Percent canopy cover chokecherry
- Basal area of white spruce
- Aspect of the stand
- Primary roads
- Pine forest 40-70% overstory cover within 250 m
- Woody debris
- Aspect of site

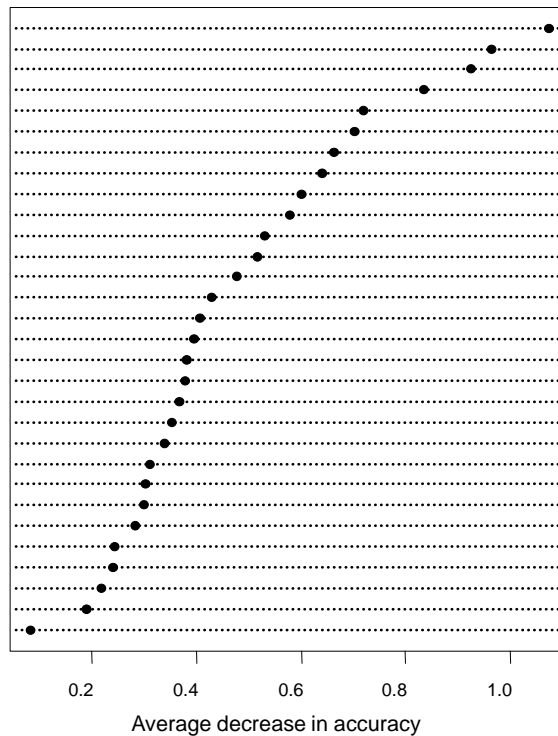


Figure 3. Variable importance plots of stand and microsite vegetative characteristics measured at elk and random sites. Decrease in accuracy shows relative importance of variables to classification accuracy through iterative removal of variables in 300 random forest classification and regression tree analyses.

MANAGEMENT IMPLICATIONS

Our findings suggest that microsite selection by elk was more important than selection of stands. Multiple scale resource selection in the Black Hills by elk may be a bottom up compilation of resources selected at microsites and resource selection at broader scales may be a compilation of decisions made in the selection of microsites. The projected future condition of the Black Hills National Forest will be

more open forest that will provide increased forage for elk. However, any benefits to elk from the management for open to moderate canopy forest could be negated by disturbance from people on roads. To address correlations inherent in vegetative patterns across multiple scales, future research evaluating whether resource selection across multiple scales is a compilation of microsites or a hierarchical series of decisions from landscape to microsites is warranted.

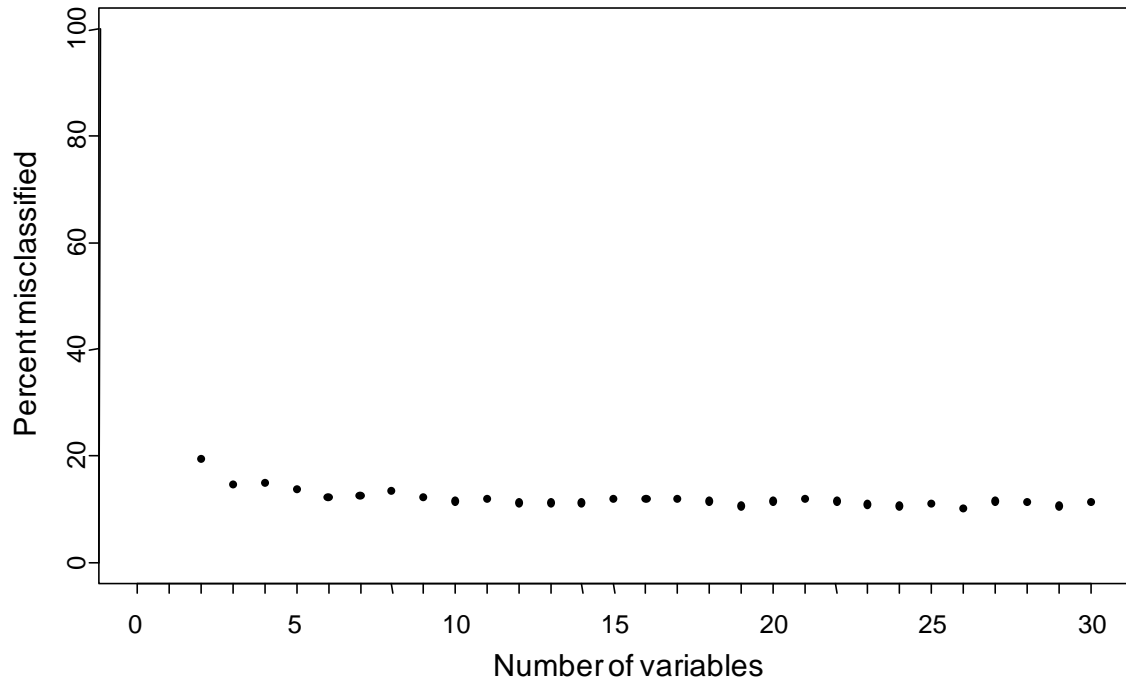


Figure 4. Out-of-bag error estimate of classification and regression trees as a function of the number of variables included from 300 iterations of random forest classification and regression tree analyses. Including more than 3 variables in the classification and regression tree does not substantially reduce the misclassification rate.

ACKNOWLEDGMENTS

This research was supported by U.S. Forest Service Rocky Mountain Research Station (Study Plan No. 933), Black Hills National Forest (ISA-203-01-004), South Dakota Department of Game, Fish and Parks (RMRS-98113-CC), U.S. Fish and Wildlife Service, Federal Aid Project (W-75-R-121), and the Rocky Mountain Elk Foundation (SD00268). L. Conroy, L. Flack, C. Holte, and M. Tarby assisted with collection of field data. We thank J. Kie and S. Rupp for providing comments on earlier drafts of our manuscript.

LITERATURE CITED

- Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Sowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management* 69:298–310.
- Battin, J., and J. J. Lawler. 2006. Cross-correlations and the design and analysis of avian habitat selection studies. *The Condor* 108:59–70.
- Benkobi, L., M. A. Rumble, C. H. Stubblefield, R. S. Gamo, and J. J. Millsbaugh. 2005. Seasonal migration and home ranges of female elk in the Black Hills of South Dakota and Wyoming. *The Prairie Naturalist* 37:151–165.
- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone Park. *Ecoscience* 10:421–431.
- Breiman, L. 2001. Random forests. *Machine Learning* 45: 5–32.
- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks/Cole, Monterey, California, USA.
- Buttery, R. F., and B. C. Gillam. 1983. Ecosystem descriptions. Pages 42–71 in R. L. Hoover and D. L. Willis, coordinators. *Managing forested lands for wildlife*. Colorado Division of Wildlife in cooperation with the USDA, Forest Service Rocky Mountain Region, Denver, USA.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red Deer: behavior and ecology of two sexes*. University of Chicago Press, Chicago, Illinois, USA.
- Cutler, D. R., T. C. Edwards, Jr., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. L. Lawler. 2007. Random forest classification in ecology. *Ecology* 88:2783–2792.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43–64.

- Evans, J. S., and S. A. Cushman. 2009. Gradient modeling of conifer species using random forests. *Landscape Ecology* 24:673–683.
- Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.
- Griffing, J. P. 1985. The spherical densiometer revisited. Southwest Habiter 6. U.S. Forest Service, Region 3, Albuquerque, New Mexico, USA.
- Grubb, T. G., and R. M. King. 1991. Assessing human disturbance of breeding bald eagles with classification tree models. *Journal of Wildlife Management* 55:500–511.
- Grubb, T. G., W. L. Robinson, and W. W. Bowerman. 2002. Effects of watercraft on bald eagles nesting in Voyageurs National Park. *Wildlife Society Bulletin* 30:156–161.
- Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation types of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. Research Paper RM-276, U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Jacques, C. N., J. A. Jenks, C. S. Deperno, J. D. Sievers, T. W. Grovenburg, T. J. Brinkman, C. C. Swanson, and B. A. Stillings. 2009. Evaluating ungulate mortality associated with helicopter net-gun captures in the Northern Great Plains. *Journal of Wildlife Management* 73:1282–1291.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Jones, P. F., and R. J. Hudson. 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. *Canadian Field-Naturalist* 116:183–191.
- Larson, G. E., and J. R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota Agricultural Experiment Station B732. South Dakota State University, Brookings, USA.
- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R News* 2:18–22.
- Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry* 81:592–595, 613.
- Lyon, L. J. 1984. Field tests of elk/timber coordination guidelines. U.S. Forest Service, Intermountain Forest and Range Experiment Station Research Paper INT-325, Ogden, Utah, USA.
- McCullough, D. R. 1975. Modifications of the clover deer trap. *California Fish and Game* 61:242–244.
- Millsbaugh, J. J., K. J. Raedeke, G. C. Brundige, and C. C. Willmott. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills, South Dakota: considerations for thermal cover management. *American Midland Naturalist* 139:133–140.
- Nuttall, T. 1997. Densiometer bias: are we measuring the forest or the trees? *Wildlife Society Bulletin* 25:610–611.
- O’Conner, R. J., and T. L. Wagner. 2004. A test of regression tree-tree model of species distribution. *Auk* 121:604–609.
- Orr, H. K. 1959. Precipitation and streamflow in the Black Hills. Station Paper RM-44. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Parker, K. L., and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. *Canadian Journal of Zoology* 62:1409–1422.
- R Development Core Team. 2009. R: A language and environment for statistical computing. R Statistical Computing, Vienna, Austria.
- 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.
- Rumble, M. A., L. Benkobi, and R. S. Gamo. 2005. Elk responses to humans in a densely roaded area. *Intermountain Journal of Sciences* 11:10–24.
- Rumble, M. A., L. Benkobi, and R. S. Gamo. 2007. A different time and place test of a spatially explicit habitat model for elk in the Black Hills. Research Paper RM-RP-64. U.S. Forest Service, Rocky Mountain Research Station. Fort Collins, Colorado, USA.
- Sharpe, G. W., C. W. Hendee and S. W. Allen. 1976. Introduction to Forestry. McGraw-Hill Book Co., New York, New York, USA.
- SPSS. 2001. Base 11.0 user’s guide. SPSS Inc., Chicago, Illinois, USA.
- SPSS Answer Tree 3.0. 2002. AnswerTree 3.0 user’s guide. SPSS Inc., Chicago, Illinois, USA.
- Stubblefield, C. H., K. T. Vierling, and M. A. Rumble. 2006. Landscape-scale attributes of elk centers of activity in the central Black Hills of South Dakota. *Journal of Wildlife Management* 70:1060–1069.
- 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 Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322–330.
- Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and elk. Pages 104–127 in J. W. Thomas, editor. *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. U.S. Forest Service, Agriculture

- Handbook No. 553. U.S. Government Printing Office, Washington, D.C., USA.
- Thompson, M. J., R. E. Henderson, T. H. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. *Wildlife Society Bulletin* 17:287–290.
- Uresk, D. W., and K. E. Severson. 1989. Understory-overstory relationships in ponderosa pine forests, Black Hills, South Dakota. *Journal of Range Management* 42:203–208.
- Visscher, D. R., and E. H. Merrill. 2009. Temporal dynamics of forage succession for elk at two scales: implications of forest management. *Forest Ecology and Management* 257:96–106.
- Webb, S. L., J. S. Lewis, D. G. Hewitt, M. W. Hellickson, and F. C. Bryant. 2008. Assessing the helicopter and net gun as a capture technique for white-tailed deer. *Journal of Wildlife Management* 72:310–314.

*Submitted 14 April 2010. Accepted 31 December 2010.
Associate Editor was Christopher N. Jacques.*