A Different Time and Place Test of ArcHSI: A Spatially Explicit Habitat Model for Elk in the Black Hills

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Abstract

We tested predictions of the spatially explicit ArcHSI habitat model for elk. The distribution of elk relative to proximity of forage and cover differed from that predicted. Elk used areas near primary roads similar to that predicted by the model, but elk were farther from secondary roads. Elk used areas categorized as good (> 0.7), fair (> 0.42 to 0.7), and poor (≤ 0.42) HSI (habitat suitability index) from the model proportional to the distribution of the landscape during summer, but not winter. Evaluation of the cover component of the model showed elk used areas disproportional to the predicted value as cover. Foraging elk strongly selected areas predicted to have good forage and avoided areas predicted as fair or poor forage; selection for better forage was more pronounced during winter than summer. Forage and cover coefficients assigned to vegetation structural stages were tested and modified. Forage coefficients generally reflected the biomass of herbaceous vegetation available to elk.

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Acknowledgments

Executive Summary

Wildlife habitat models are important tools that help resource managers evaluate and disclose the probable effects of prospective land management actions on wildlife. We tested a spatially explicit habitat model for elk (ArcHSI) using telemetry data collected in the Black Hills, South Dakota. The distribution of elk estimated from telemetry, relative to proximity of forage and cover, differed from that predicted by ArcHSI. The distribution of elk relative to primary roads was similar to that predicted by the model, but elk were located farther from secondary roads than predicted by the model. After modifying the road effects component of ArcHSI, we tested the predicted habitat suitability index (HSI) from ArcHSI. Output from ArcHSI was categorized as good (> 0.7), fair (> 0.42 to 0.7), and poor (≤ 0.42), and elk selected areas in these categories proportional to the composition of the landscape during summer, but not during winter. The predicted value of forested stands for cover and forage for elk was also categorized as good, fair, or poor. Elk selected stands for cover different from the model predictions during summer and winter. In both summer and winter, foraging elk strongly selected areas predicted to have good forage HSI and avoided areas predicted as fair or poor forage. Selection for areas predicted as better forage was more pronounced during winter than summer. To test model coefficients for cover and forage assigned to vegetation structural stages, we compared bedded elk use with predicted use. Elk selected vegetation structural stages for cover different from composition of the area during both summer and winter. The correlation between values for cover assigned to vegetation structural stages and selection ratios from resource selection analyses was zero. Elk selected vegetation structural stages different from proportional availability for forage during summer and winter. The correlations between forage coefficients assigned to vegetation structural stages and selection ratios from analyses were significantly positive (r ≥ 0.70) during summer and winter. During summer, elk selected grasslands, aspen, and white spruce < 40 percent canopy closure for forage; all structural stages of ponderosa pine were selected less than their proportional area for forage by elk. During winter, elk preferentially selected grasslands and ponderosa pine < 40 percent canopy closure for foraging, but avoided ponderosa pine 40 to 70 percent canopy closure, and white spruce. Selection ratios for foraging from resource selection analyses were positively correlated (r = 0.61) with herbaceous biomass available in vegetation structural stages, suggesting that forage coefficients generally reflected the biomass of herbaceous vegetation available to elk.

We believe that the structure of this model has application for evaluating forest management prescriptions for elk habitat in other areas and in particular, ponderosa pine forests. However, forage and cover coefficients assigned to vegetation structural stages should be modified to reflect local conditions where the model is being applied.
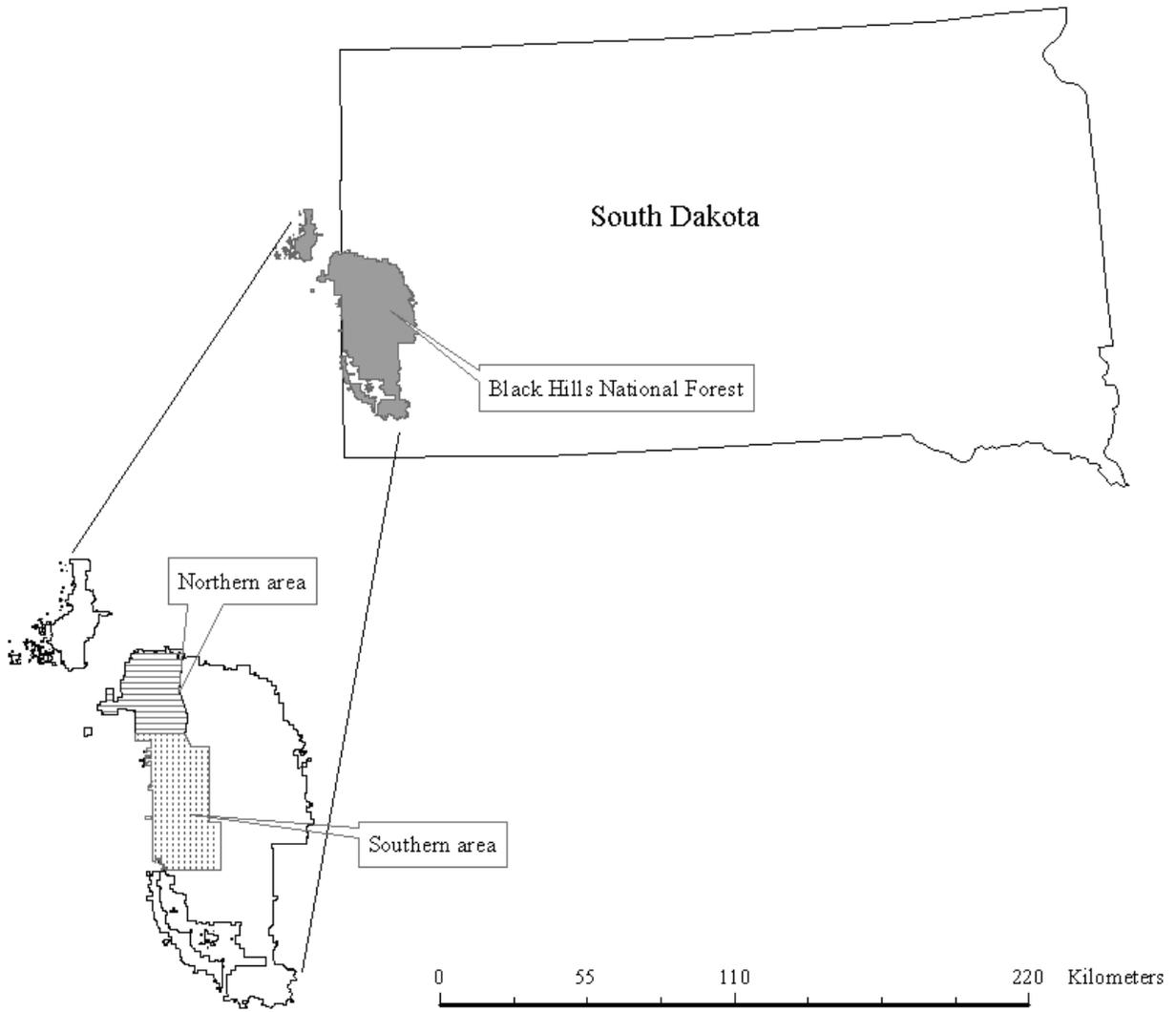
Figure 1. South Dakota and the Black Hills National Forest boundary with cutout of the north and south study areas.

Introduction

Habitat models have been used as tools for assessing effects of land management alterations on animals since the 1970s (Berry 1986). Pros and cons of various habitat models have been extensively debated. Application of untested models can be unreliable (Laymon and Barrett 1984), but wildlife models do not need to depict reality, rather they can simplify and provide useful results if the assumptions are understood and are correctly applied (Starfield 1997). The litmus test for a useful model should not be how well it predicts truth, but does it improve the decision process (Starfield 1997). Consequently, continuous testing and validation of wildlife habitat models should be encouraged.

Elk (*Cervus elaphus*) are particularly amenable to the use of habitat models for quantifying the effects of land alterations (Roloff and others 2001), perhaps because of the large research database that exists. Geographic information systems (GIS) have allowed results of habitat models to be visually displayed. Some models include spatially explicit components, such as roads or habitat juxtaposition, programmed in the GIS. Benkobi and others (2004) used elk locations from Custer State Park, South Dakota, to test predictions of a habitat effectiveness model (ArcHabcap, unpublished software, Black Hills National Forest, Custer, SD) patterned after models developed in Oregon and Washington (Thomas and others 1979; Thomas and others 1988; Wisdom and others 1986). Specifically, Benkobi and others (2004) tested the spatially explicit effects of roads and forage-cover proximity (habitat juxtaposition) and the mathematical calculations for combining model components of habitat effectiveness for elk. Juntti and Rumble (2006) wrote new code for this model (ArcHSI) that substantially reduced runtime and expanded the use of the model to personal computers with ArcGIS 8.1 (ESRI 2001) or newer software. Nonetheless, there remained a need to test and refine ArcHSI in environments where it is used by the Forest Service to evaluate alternatives for land management. Although expert opinion is a valid test of habitat models, validation research is a better approach for testing wildlife habitat models (Holthausen and others 1994). This paper reports the results of a validation test and subsequent modifications of a spatially explicit elk habitat suitability model in the Black Hills National Forest. This test represents a step toward the pragmatic modeling approach that builds from application of an initial imperfect model (Starfield 1997).

Methods

Study Area

Our study included two areas of the Black Hills in western South Dakota and eastern Wyoming (fig. 1). The southernmost area (hereafter referred to as the south area) was located on the Limestone Plateau. The northern study area (hereafter referred to as the north area) was located north of U.S. Highway 85 and included portions of the Limestone Plateau and steep canyons and drainages that occur as elevations drop to the surrounding mixed-grass prairies to the north. The north and south areas were originally separated. However, a few elk moved between these areas (Benkobi and others 2005) and we expanded the boundary of the south area to join the north area. Average annual precipitation of these areas is similar, but the north area receives 7 to 10 cm more precipitation from snow pack during winter than the south area (Orr 1959). Elevation declines rapidly near the northern boundary of the north area from approximately 2,040 to 1,280 m; in the south, elevation declines gradually from 2,040 to 1,800 m.

Ponderosa pine (*Pinus ponderosa*) is the dominant vegetation type, comprising 79 percent of the north area and 78 percent of the south area. White spruce (*Picea glauca*) comprises 2 percent of the north and < 1 percent of the south, while quaking aspen (*Populus tremuloides*) comprises 10 percent of the north area, but only 3 percent of the south area. White spruce and aspen occur on mesic sites and north-facing slopes in both areas (Hoffman and Alexander 1987). Aspen occurs as climax vegetation and as a seral community to ponderosa pine or white spruce in the Black Hills (Hoffman and Alexander 1987). Meadow and grassland vegetation comprised 7 percent of the north area and 12 percent of the south area. Remaining portions of the study areas were characterized by bur oak (*Quercus macrocarpa*), shrublands dominated by mountain mahogany (*Cercocarpus montanus*) and Rocky Mountain juniper (*Juniperus scopulorum*), and non-forested areas. Common understory shrubs in forested areas included snowberry (*Symphoricarpus occidentalis*), common juniper (*J. communis*), bur oak, bearberry (*Arctostaphylos uva-ursi*), *Ribes* spp., Oregon grape (*Mahonia repens*), and chokecherry (*Prunus virginiana*). Common graminoids in meadows and beneath forested stands include Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), timothy (*Phleum pratense*), green needlegrass (*Nasella viridula*), poverty oatgrass (*Danthonia spicata*), and fuzzyspike wild rye (*Elymus innovatus*).

Vegetation in the Black Hills National Forest is mapped and classified in a hierarchal system (Buttery and Gillam 1983). The hierarchal classification system is a surrogate seral stage model for forest vegetation based on vegetation type, structural stages, and overstory canopy cover (hereafter referred to as canopy closure to avoid confusion with use of habitats for cover by elk). Structural stages of vegetation types include grass/forb, shrub/seedling, sapling/pole forest (2.5 to 22.9 cm dbh), mature forest (> 22.9 cm dbh), and old growth forest (unpublished, RMRIS data dictionary, U.S. Forest Service, Rocky Mountain Region, Lakewood, Colorado). Within the sapling/pole and mature structural stages, canopy closure is categorized as 0 to 40 percent, 41 to 70 percent, and > 70 percent. This vegetation classification was applied to land units of approximately 4 to 32 ha delineated using topographic features such as ridges, valleys, and vegetation type.

We delineated and classified vegetation on private lands with the aid of 1:24,000 digital orthorphotograph maps and 1:24,000 color aerial photographs. Land units on private lands were identified and the boundaries were digitized using ArcEdit to be part of the GIS vegetation coverage. We used the adjacent classified Forest Service lands as references for the vegetation classification assignments.

Elk Capture and Telemetry

In August 1998, we captured and collared 22 female elk with VHF transmitters in the south area and 13 female elk in the north area using a net-gun fired from a helicopter. To ensure that these elk were a representative sample of the population, we divided the north and south areas into approximately equal quarters. Our capture protocol was to capture 20 percent of the elk in each of the quarters—20 percent could be captured as encountered and only two animals could be captured from a herd group. In late January and early February of 1999, we captured an additional 12 female elk in the north area and two female elk in the south area and placed VHF telemetry collars on them. VHF radio transmitters were equipped with mortality and activity sensors. In February 2000, four female elk were captured and geographic positioning system (GPS) telemetry collars were attached to them. Two of these elk were previously collared from earlier captures. In March and early April 2001, two female elk and two male yearling elk were captured using modified collapsible clover traps (McCullough 1975; Thompson and others 1989) and GPS collars were attached to them. Yearling male elk associate with herds of females with calves until they are approximately 2.5 years old, at which time they begin exploratory movements (Hurley and Sargeant 1991). Activity sensors in GPS collars

queried the position of the collar every second for 10 minutes immediately after a GPS location was recorded. If the collar was in a head down position > 10 percent of the time, but < 99 percent, we considered these locations foraging locations (Rumble and others 2001). GPS collars were programmed to drop off or quit collecting data on 1 December 2000 and 2001.

Elk with VHF telemetry collars were located from spring to fall during daylight hours at 1 to 2 week intervals from the ground with hand-held yagi antenna, from spring to fall or during winter from a fixed-wing aircraft or from the ground. We located elk from the time they were captured until 1 October 2001. When possible, we obtained visual confirmation of the locations. All visual locations were recorded with hand-held or aircraft GPS. The GPS telemetry collars recorded locations at 4-hr intervals during 2000 and 2-hr intervals during 2001.

Evaluation of the Model—Following tests of the ArcHabcap for elk, Benkobi and others (2004) recommended that (1) the distance that primary roads affect elk dispersion patterns be extended to 350 m; (2) the effects of primitive roads on elk should be eliminated; (3) habitat suitability within the area affected by roads should be reduced by 50 percent; and (4) the calculation of habitat effectiveness should combine model components using an arithmetic average that weighted forage values three times greater than cover or habitat juxtaposition. These recommendations were incorporated in the model we tested. New code that reduced run times for a large vegetation coverage was written in Arc Macro Language (ESRI 2001) and calculated habitat suitability (HSI) for elk (Juntti and Rumble 2006). Previous versions of this model estimated habitat effectiveness, which is the percent of area or time that is usable by elk excluding hunting season periods (Lyon and Christensen 1992). Habitat suitability is the ability of the habitat in its current condition to provide life requisites of a species (Ministry of Environment, Lands and Parks Resources Inventory 1999). Spatial components in the models included forage and cover juxtaposition and road effects (Juntti and Rumble 2006). The model used the PC version of ArcInfo 8.1 for a personal computer (ESRI 2001). The GIS vegetation coverage and road coverage were the inputs for the model. We ran the ArcHSI model for summer and winter for the north and south areas. We used k-means cluster analysis (SPSS 2001) to classify groups of HSI scores from the model into categories of > 70, > 0.42 to 0.70, and 0 to 0.42, which we assigned as good, fair, and poor, respectively.

Because distributions of elk are altered by disturbances during hunting seasons (Conner and others 2001; Millspaugh and others 2000; Rumble and others,

2005), we excluded elk locations from 1 September to 30 November from our tests of the model. We also excluded elk locations between 11 and 25 April because that was the period during which elk migrated to summer range (Benkobi and others 2005). To integrate daytime GPS locations with radio telemetry locations of elk, we randomly selected one GPS location between sunrise and sunset from each animal at 16-day intervals and included these with locations obtained from radio telemetry. The attributes of the GIS coverage output from ArcHSI were assigned to elk locations using a spatial join in ArcMap 8.1 (ESRI 2001).

We evaluated coefficients for forage and cover areas by creating 100-m intervals in both directions from forage-cover edges using proximity analysis in grid-cell modeling (ESRI 1999). Because these elk use open habitats more at night (Rumble and others 2001), we evaluated the elk distribution into openings from cover using the GPS nighttime locations. Mature ponderosa pine with 40 to 70 percent overstory closure was classified as both forage and cover in the model and a juxtaposition coefficient of 1.0 was assigned to this vegetation structural stage. Using the Design I resource selection analysis (Manly and others 2002), we evaluated the distribution of elk locations relative to forage-cover edges by comparing expected use by elk in 100-m intervals with observed use.

To test the effects of roads on the distribution of elk, we used proximity grid-cell analysis to create distance intervals from roads. For primary roads, the interval width was 50 m; for secondary roads, the interval width was 20 m; and for primitive roads, the interval width was 5 m. These interval widths were based on earlier test (Benkobi and others 2004) that we assumed would be sensitive to the response by elk. Predicted use by elk of each interval away from roads was tested using the Design I analysis (Manly and others 2002). We used linear regression (trend line) to estimate the distance from primary and secondary roads that elk use, intersected the expected use, and this was our estimate of the distance from roads that elk demonstrated avoidance (for example, Rowland and others 2000).

Following evaluation of roads and juxtaposition coefficients, we changed the distance values in ArcHSI regarding how roads influenced the distribution of elk and then applied the model to our study areas. Elk occurring in each of the study areas were distinct herds (Benkobi and others 2006), so independent tests of the ArcHSI model were made for the north and south study areas. We used the Design I analysis (Manly and others 2002) to test the hypothesis that elk selected areas of good, fair, and poor HSI categories proportional to their areal extent.

We used different data sets to test hypotheses of elk selection for predicted forage and cover HSI categories. We used daytime locations of bedded elk to test the hypothesis that elk selected HSI cover categories proportional to areal extent during summer and winter. To test the hypothesis that foraging elk selected HSI forage categories proportional to available, we used nighttime locations of elk equipped with GPS collars indicating elk foraging activity (Rumble and others 2001). For estimates of availability, the analysis of ArcHSI forage predictions necessitated the use of a subset of the GIS coverage of the study areas encompassing those GPS locations. These analyses were also made using the Design I analysis.

We then used the Design I analysis comparing elk selection of vegetation structural stages to evaluate the associated coefficients for forage or cover during summer and winter. We combined the diameter structural stage categories of quaking aspen and white spruce for these analyses to minimize the number of cells with fewer than five observations. We also combined ponderosa pine dbh categories for analyses comparing elk cover use. We used regression analysis to evaluate relations between selection ratios (1) resulting from resource selection analyses with forage and cover coefficients assigned to vegetation structural stages and (2) for forage and herbaceous biomass in vegetation structural stages.

Although we established hypotheses and tested them, our goal was not to modify the model to the point that elk selection of vegetation structural stages was proportional to the predicted HSI. This population of elk is managed below forage carrying capacity by the South Dakota Department of Game, Fish and Parks to reduce elk use of private lands and we expected elk to demonstrate differential selection for "better" habitats (for example, Fretwell and Lucas 1969). We assigned new forage coefficients to vegetation structural stages in the model based on relative herbaceous biomass and selection ratios; new cover coefficients were assigned to vegetation structural stages based primarily on the selection ratios from the Design I analyses (Manley and others 2002). In assigning new coefficients to vegetation structural stages, we assumed that a selection ratio of 1.0 (elk use equaled expected use) represented a coefficient of 0.5, selection ratios ≥ 1.0 were assigned coefficients 0.5 to 1.0, and selection ratios ≤ 1.0 were assigned coefficients 0 to 0.5. We placed an additional constraint on winter forage coefficients—they could not be larger than summer forage coefficients. We placed this constraint because during the summer, elk had full access to all structural stages so selection of forage habitat probably represented choices. During winter, however, elk were

concentrated and the selection ratios from analyses in some structural stages likely reflected the relatively higher elk densities.

Results

We obtained 1,235 locations of elk using VHF transmitters that we observed or were able to confidently place within a polygon from the GIS coverage. These were distributed as follows: north area summer—182, north area winter—222, south area summer—423, and south area winter—408. The GPS telemetry provided 2,676 night locations of foraging elk during summer and 881 night locations of foraging elk during winter. We obtained 465 locations of bedded elk from VHF collars that were used to assess elk selection of cover, 264 were during summer and 201 were during winter.

Habitat Juxtaposition

Summer and winter use by elk of juxtaposition band intervals into forage or cover areas from forage-cover edges were similar, so we combined the seasons for subsequent analyses. Interval bands of 100 m extended into forage areas from cover ≤ 300 m, while bands into cover extended ≤ 1000 m (fig. 2). In the north, elk use of band intervals from forage-cover edges was cover similar ($P = 0.63$) to expected use. However in the south area, elk avoided the first 100 m into cover from forage-cover edges ($P < 0.01$) and used the next interval out to 200 m proportional to availability. Elk selected intervals from 200 m to 400 m from cover ($P < 0.01$); the interval from 400 to 500 m was marginally selected ($P = 0.08$). Eliminating mature stands of ponderosa pine with 40 to 70 percent overstory closure did not affect the distribution patterns of elk relative to forage-cover edges.
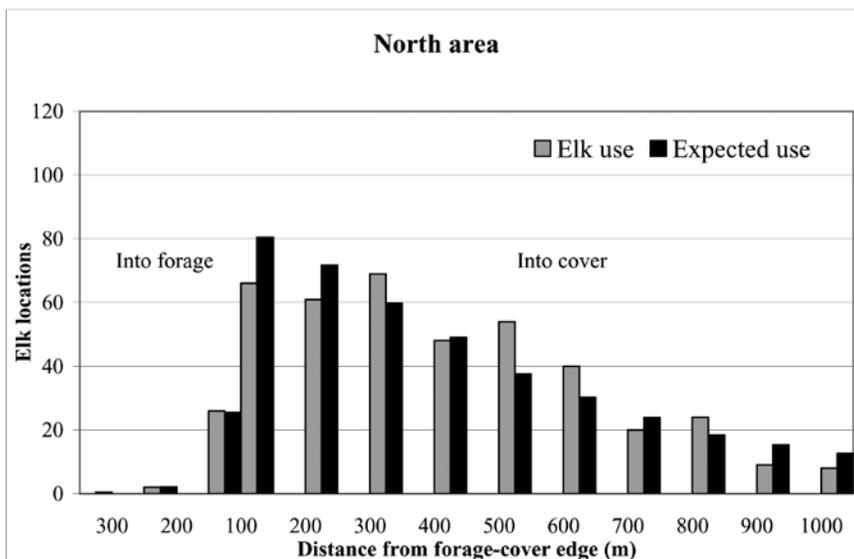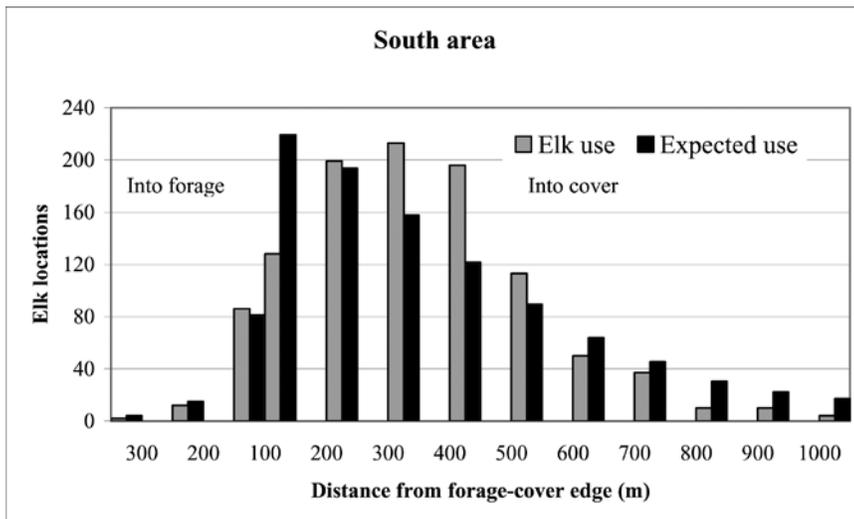

Figure 2. Radio telemetry locations (observed) of bedded elk (in cover); GPS telemetry locations of foraging elk (in forage); and expected elk locations in 100 m intervals from forage-cover edges.
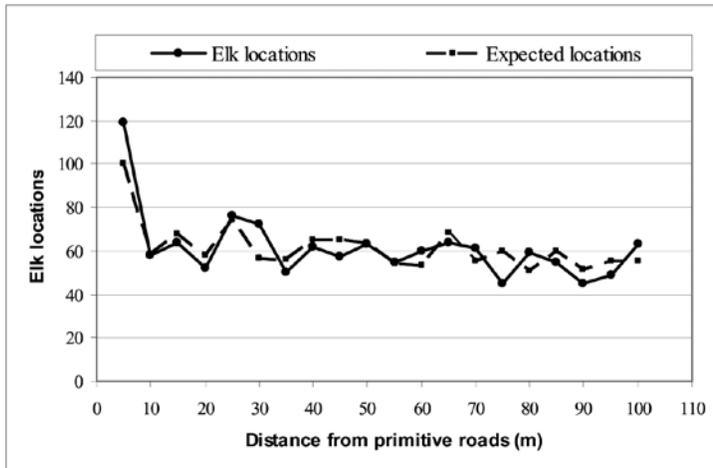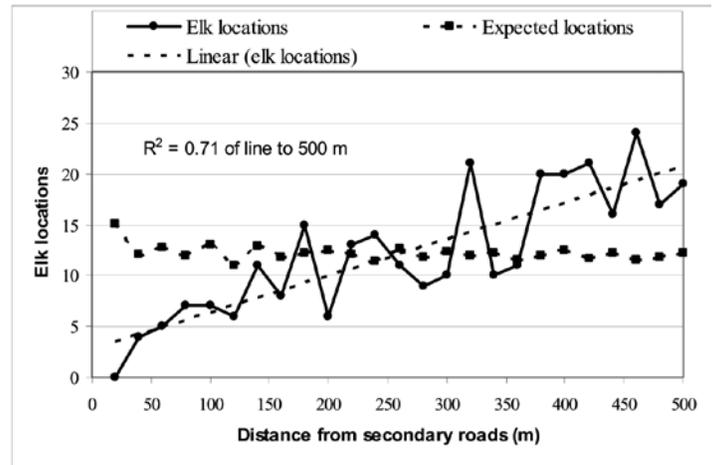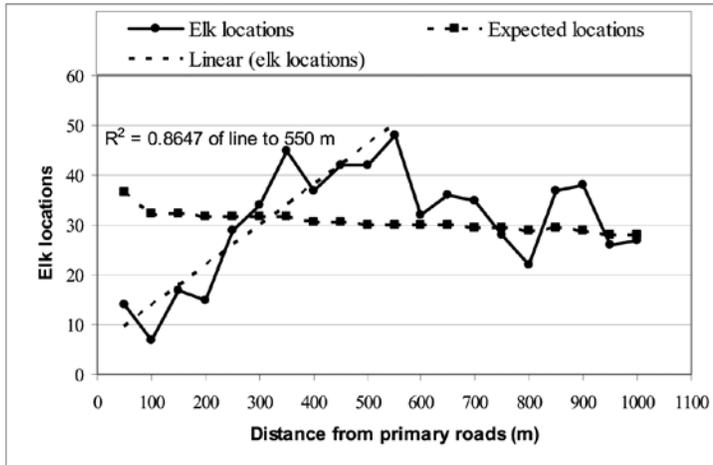
Figure 3. Elk locations from radio telemetry (observed) and expected elk locations of intervals from primary, secondary, and primitive roads. For the area of increasing selection by elk, a linear regression was plotted to estimate the distance that roads affected elk distribution.

Roads

Elk avoided areas near primary roads ($P < 0.01$). The estimate from linear regression of elk distribution relative to primary roads showed that avoidance of primary roads extended to approximately 350 m (fig. 3). Elk also avoided areas near secondary roads to a distance of approximately 260 m ($P < 0.01$). Elk demonstrated increased selection (positive slope to regression line) of both primary and secondary roads out to approximately 500 m. Elk did not show any patterns of avoidance or selection ($P = 0.43$) from expected of areas near primitive roads.

Habitat Suitability

VHF telemetry locations of elk differed from the categories predicted by ArcHSI. In the north area, elk selected areas predicted to have good HSI, and against areas predicted to have poor HSI during the summer ($X_2^2 = 7.5$, $P = 0.03$, fig. 4). During winter, the proportion of our study predicted as good HSI declined, and in the north, elk selected HSI categories similar to the proportional area ($X_2^2 = 0.38$, $P = 0.8$). In the south area, elk showed selectivity for areas predicted good HSI and

avoided areas predicted poor HSI during summer ($X_2^2 = 57.5$, $P < 0.01$, fig. 5). Winter elk distributions in the south differed from the proportional areas of HSI categories predicted by ArcHSI ($X_2^2 = 8.33$, $P = 0.02$). Specifically, elk selected habitats predicted to have poor HSI greater than expected ($P = 0.05$).

Cover—During the summer, bedded elk selected HSI cover categories different ($X_2^2 = 22.4$, $P < 0.01$) from model predictions (fig. 6). Elk selected areas predicted as good cover ($P = 0.10$), and avoided areas predicted as fair or poor cover ($P \leq 0.04$). During winter, bedded elk selected HSI cover categories different from those predicted by the model ($X_2^2 = 6.9$, $P = 0.03$). However, when multiple range tests were evaluated and no patterns of selection were evident among the categories ($P > 0.11$).

Elk avoided grasslands as cover ($P = 0.02$) during summer (table 1). Expected elk use was < 5 observations for several vegetation structural stages of aspen. Nonetheless, elk seemed to select for the shrub/seedling and > 70 percent overstory canopy closure stages of aspen for cover during summer ($P < 0.01$). For cover,
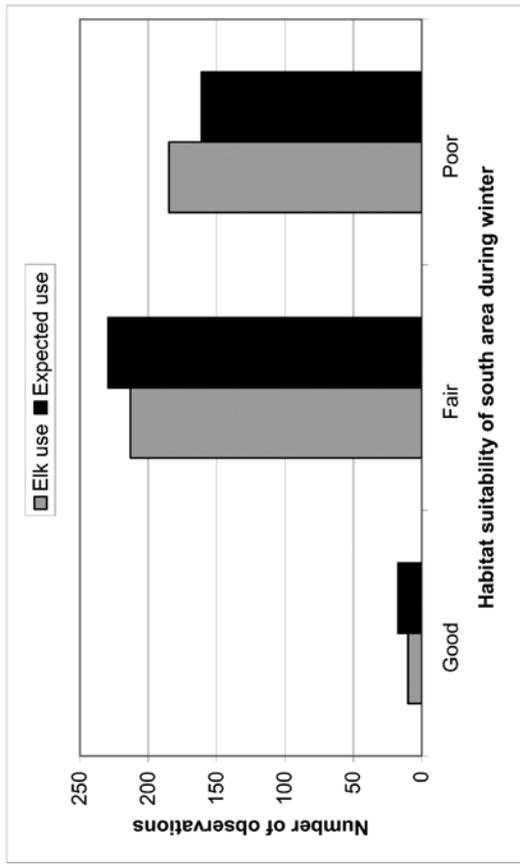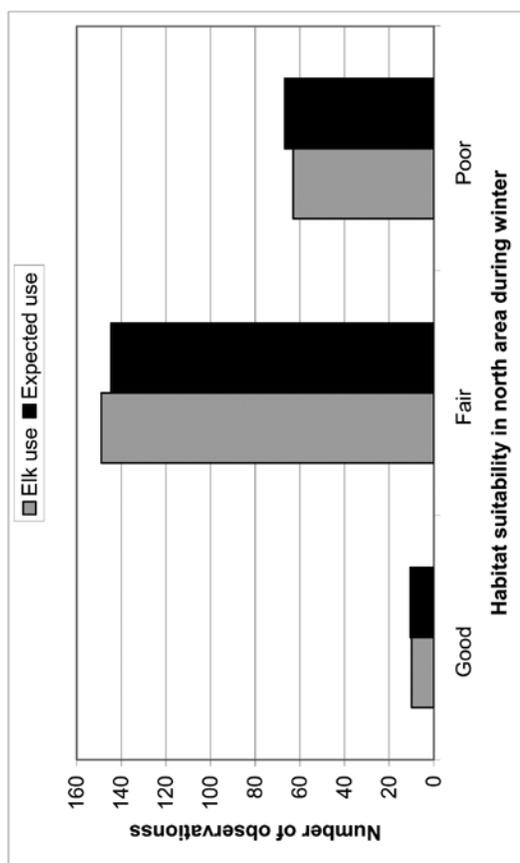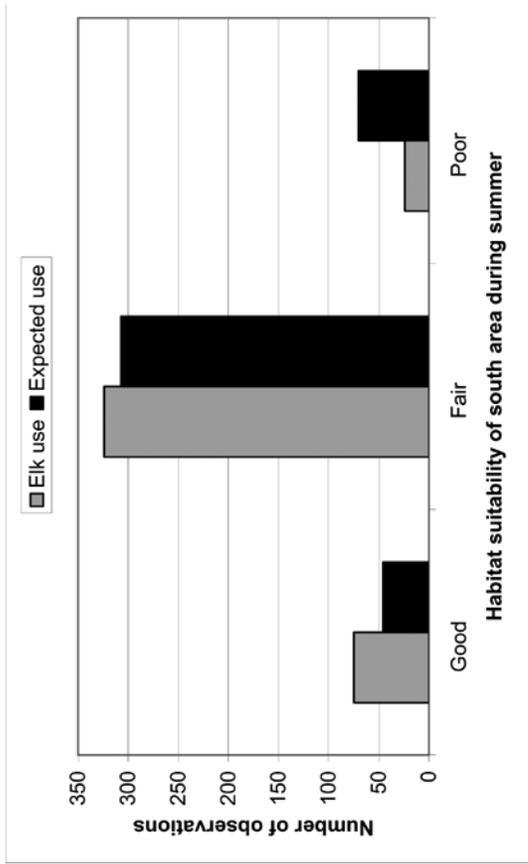
Figure 4. Daytime radio telemetry locations of elk (observed) and expected elk locations relative to habitat suitability predicted by the ArcHSI model during summer and winter for the north study area in the Black Hills, SD. Habitat suitability was calculated as of each polygon. Categories of HSI were poor: 0 to 0.42, fair: > 0.42 to 0.70, and good: > 0.7.
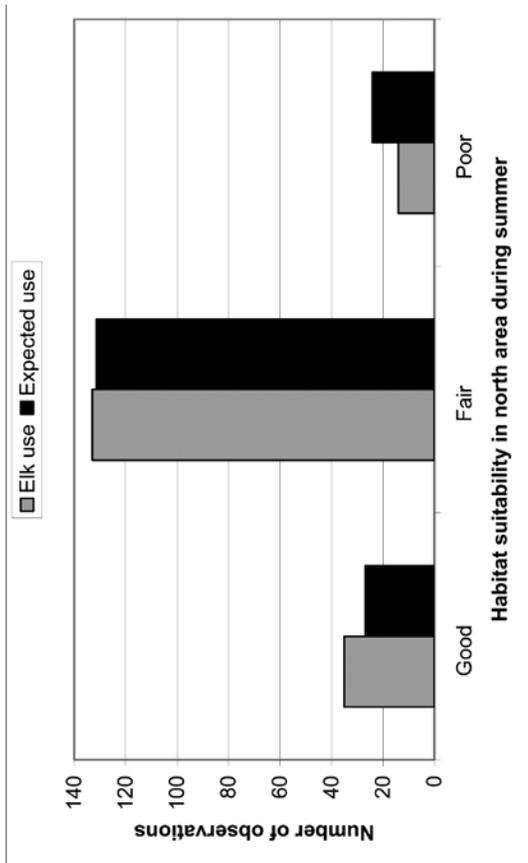
Figure 5. Daytime radio telemetry locations of elk (observed) and expected elk locations relative to habitat suitability predicted by the ArcHSI model during summer and winter for the south study area in the Black Hills, SD. See figure 4 for explanation of data.
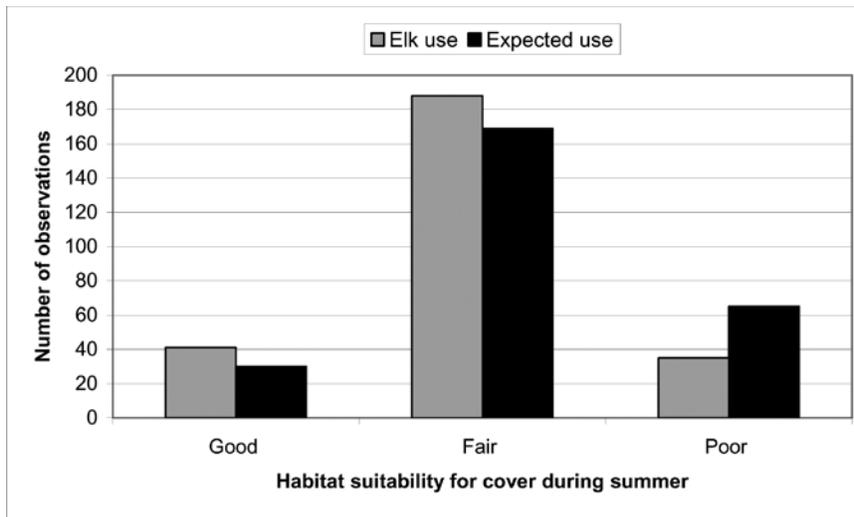
Figure 6. Daytime radio telemetry locations of bedded elk (observed) and expected elk locations relative to cover prediction by the ArcHSI model during summer and winter the Black Hills, SD. Habitat suitability cover values were reduced by 50 percent for areas ≤ 300 m from primary roads and ≤ 260 m from secondary roads.
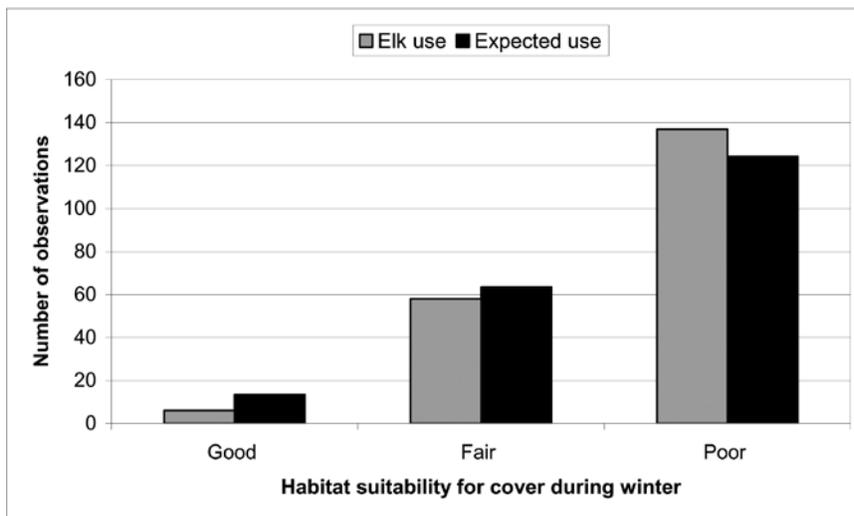
Table 1. Observed elk use (number of individuals) compared with expected use (number of individuals) of vegetation structural stages for cover during summer in the Black Hills, SD[1].

Vegetation structural stage	Cover coefficient in ArcHSI model	Observed elk use (# indiv.)	Expected elk use (# indiv.)	Selection ratio	Bonferroni adjusted *p*-value[2]
Grassland	0	13	30	0.4	0.02
Mountain shrub	0	4	2	1.7	
Aspen shrub/seedling	0.5	13	2	6.1	< 0.01
Aspen 0 to 40 percent overstory closure	0.5	11	5	2.1	
Aspen > 40 to 70 percent overstory closure	1.0	7	8	0.9	
Aspen > 70 percent overstory closure	1.0	7	2	3.2	0.02
Ponderosa pine shrub/seedling	0	3	3	1.1	
Ponderosa pine 0 to 40 percent overstory closure	0.5	84	87	1.0	
Ponderosa pine > 40 to 70 percent overstory closure	0.5	82	92	0.9	
Ponderosa pine > 70 percent overstory closure	1.0	5	22	0.2	< 0.01
White spruce shrub/seedling	0	1	0	2.7	
White spruce 0 to 40 percent overstory closure	0.5	17	4	4.6	< 0.01
White spruce > 40 to 70 percent overstory closure	0.5	14	4	3.6	< 0.01
White spruce > 70 percent overstory closure	1.0	2	1	1.5	

[1] Elk use determined from daytime VHF 3 telemetry locations of bedded elk and expected use determined from proportional area.
[2] Probability that the selection ratio was different from 1.0 or that selection differed from random use.

ponderosa pine ≤ 70 percent overstory canopy closure was used by elk similar to availability, but ponderosa pine > 70 percent canopy closure was avoided by bedded elk ($P < 0.01$). Expected use of white spruce ≤ 70 percent overstory canopy closure was low, but bedded elk selected this vegetation structural stage for cover during the summer ($P < 0.01$). During summer, selection ratios from resource selection analyses were not correlated (r < 0.01) with cover coefficients assigned to vegetation structural stages in the model.

During winter, bedded elk avoided grasslands ($P < 0.01$), but selected ponderosa pine < 40 percent canopy closure ($P < 0.01$, table 2). Coefficients for cover during winter were not correlated (r < 0.01) with selection ratios from the resource analysis of elk in vegetation structural stages. This was particularly evident in structural stages of ponderosa pine.

Forage—Elk showed strong selection for areas predicted as good forage HSI and avoided areas rated fair or poor forage HSI during summer and winter ($P < 0.01$, fig. 7). The selection ratio from analyses of predicted to be good HSI for forage during winter (5.86 ± 0.15) was stronger than during summer (2.17 ± 0.06).

During summer, night GPS locations of foraging elk showed clear selection for meadows, aspen with ≤ 70 percent overstory closure, white spruce shrub/seedling, and white spruce with ≤ 40 percent overstory closure ($P < 0.01$, table 3). All structural stages of ponderosa pine were used proportional to availability or avoided by foraging elk during summer ($P \geq 0.08$). Summer forage coefficients were correlated (r = 0.85) with selection ratios for vegetation structural stages. Selection ratios

were correlated (r = 0.61, fig. 8) with herbaceous biomass in vegetation structural stages. Theoretically, this regression should have a 0-intercept, but the intercept was influenced by high selection ratios for a few uncommon vegetation structural stages with less herbaceous biomass than meadows. During winter, meadows and mature ponderosa pine ≤ 40 percent overstory closure were selected by foraging elk ($P \leq 0.01$, table 4). During winter, foraging elk avoided mountain shrub, aspen > 70 percent overstory closure, all sapling/pole structural stages of ponderosa pine, mature ponderosa pine > 40 percent overstory canopy closure, and white spruce stands ($P \leq 0.07$). Winter forage coefficients for vegetation structural stages in the ArcHSI model were correlated (r = 0.70) with selection ratios exhibited by elk for vegetation structural stages. The correlation between selection ratios and herbaceous biomass was also positive (r = 0.60).

Discussion

Habitat Juxtaposition

Elk distribution in the Black Hills National Forest relative to forage-cover edges differed from patterns observed in western Oregon (Wisdom and others 1986), the Blue Mountains of eastern Oregon and Washington (Thomas and others 1988), and Custer State Park in the southeastern Black Hills (Benkobi and others 2004). Most noticeable was elk use similar to, or less than expected of areas ≤ 100 m into forage areas or greater than

Table 2. Observed elk use (number of individuals) compared with expected use (number of individuals) of vegetation structural stages for cover during winter in the Black Hills, SD[1].

Vegetation structural stage	Cover coefficient in ArcHSI model	Observed elk use (# indiv.)	Expected elk use (# indiv.)	Selection ratio	Bonferroni adjusted *p*-value[2]
Grassland	0	3	23	0.1	< 0.01
Mountain shrub	0	0	2	0.0	
Aspen shrub/seedling	0	4	2	2.4	
Aspen < 40 percent overstory closure	0	6	4	1.5	
Aspen > 40 to 70 percent overstory closure	0	5	6	0.8	
Aspen > 70 percent overstory closure	0	1	2	0.6	
Ponderosa pine shrub/seedling	0	4	2	1.9	
Ponderosa pine < 40 percent overstory closure	0.2	98	66	1.5	< 0.01
Ponderosa pine > 40 to 70 percent overstory closure	0.5	65	70	0.9	
Ponderosa pine > 70 percent overstory closure	1.0	9	17	0.5	
White spruce shrub/seedling	0	0	0	0.0	
White spruce < 40 percent overstory closure	0	0	3	0.0	
White spruce > 40 to 70 percent overstory closure	0	1	3	0.3	
White spruce > 70 percent overstory closure	0	0	1	0.0	

[1] Elk use determined from daytime VHF telemetry locations of bedded elk and expected use determined from proportional area.
[2] Probability that the selection ratio was different from 1.0 or that selection differed from random use.
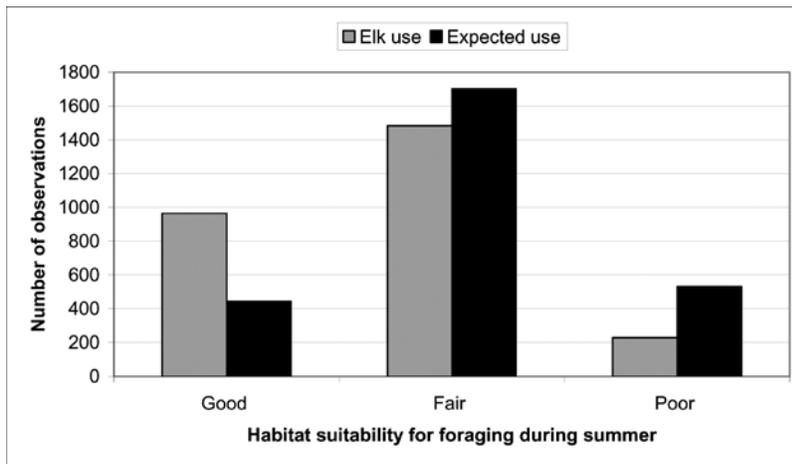
Figure 7. Nighttime GPS locations of foraging elk (observed) and expected elk locations relative to foraging habitat suitability predicted by the ArcHSI model during winter and summer in the Black Hills, SD. Habitat suitability foraging values were reduced by 50 percent for areas ≤ 300 m from primary roads and ≤ 260 m from secondary roads.
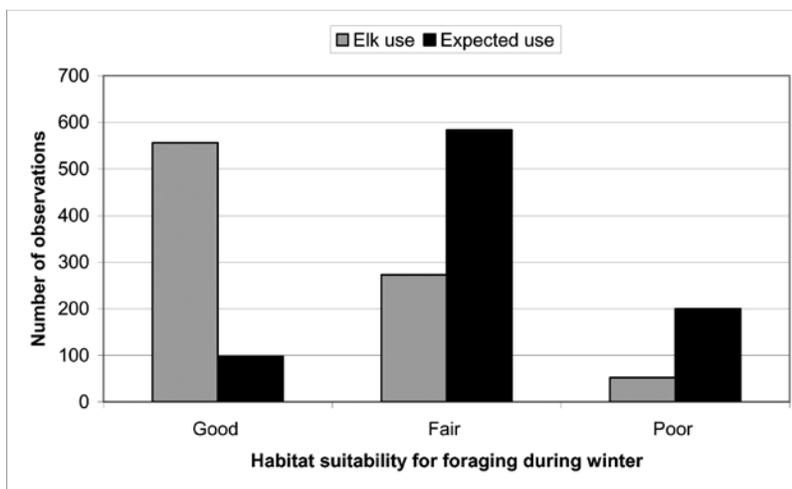
Table 3. Observed elk use (number of individuals)compared with expected use (number of individuals) of vegetation structural stages for foraging during summer in the Black Hills, SD[1].

Vegetation structural stage	Forage coefficient in ArcHSI model	Observed elk use (# indiv.)	Expected elk use (# indiv.)	Selection ratio	Bonferroni adjusted p-value[2]
Grassland	1.0	370	178	2.1	< 0.01
Mountain shrub	0.5	1	15	.1	< 0.01
Aspen shrub/seedling	1.0	35	12	3.0	< 0.01
Aspen 0 to 40 percent overstory closure	1.0	74	27	2.7	< 0.01
Aspen > 40 to 70 percent overstory closure	1.0	89	38	2.3	< 0.01
Aspen > 70 percent overstory closure	0.5	1	7	0.1	
Ponderosa pine shrub/seedling	1.0	18	15	1.2	
Ponderosa pine 2.5 to 23 cm dbh					
0 to 40 percent overstory closure	1.0	30	46	0.7	
> 40 to 70 percent overstory closure	0.5	32	85	0.4	< 0.01
> 70 percent overstory closure	0.2	1	22	0.0	< 0.01
Ponderosa pine > 23 cm dbh					
0 to 40 percent overstory closure	0.5	406	456	0.9	0.08
> 40 to 70 percent overstory closure	0.5	257	403	0.6	< 0.01
> 70 percent overstory closure	0.2	17	91	0.2	< 0.01
White spruce shrub/seedling	1.0	9	3	3.6	< 0.01
White spruce 0 to 40 percent overstory closure	1.0	91	25	3.6	< 0.01
White spruce > 40 to 70 percent overstory closure	0.5	26	27	1.0	
White spruce > 70 percent overstory closure	0.2	3	9	0.3	

[1] Elk use determined from nighttime GPS telemetry locations of foraging elk and expected use determined from proportional area.
[2] Probability that the selection ratio was different from 1.0 or that selection differed from random use.
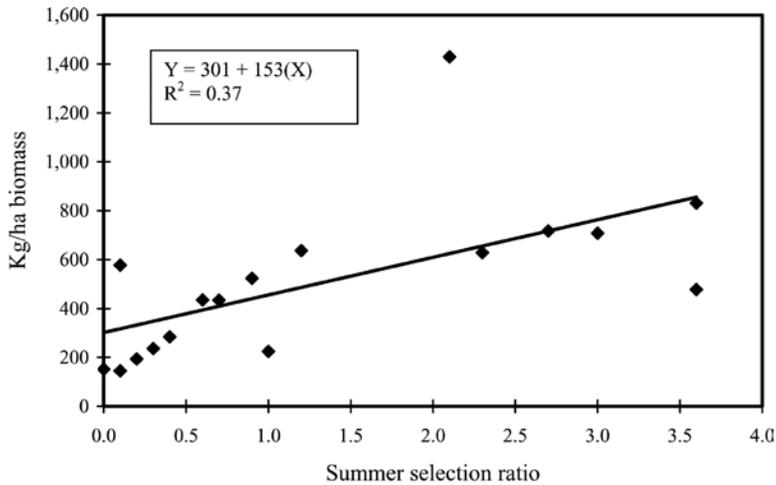
Figure 8. Linear regression of selection ratio from analysis of habitat selection by foraging elk with GPS collars in summer and winter on herbaceous biomass in vegetation structural stages of the Black Hills, SD.
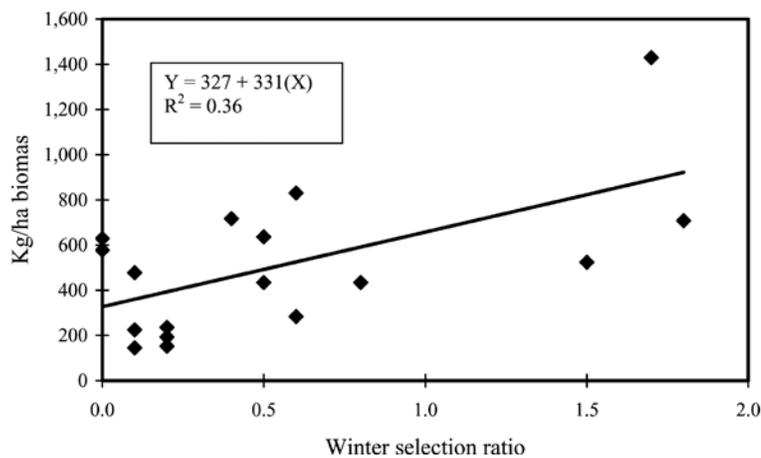
Table 4. Observed elk use (number of individuals) compared with expected use (number of individuals) of vegetation structural stages for foraging during winter in the Black Hills, SD[1].

Vegetation structural stage	Forage coefficient in ArcHSI model	Observed elk use (# indiv.)	Expected elk use (# indiv.)	Selection ratio	Bonferroni adjusted *p*-value[2]
Grassland	1.0	200	119	1.7	< 0.01
Mountain shrub	0.5	1	13	.1	0.02
Aspen shrub/seedling	1.0	10	6	1.8	
Aspen 0 to 40 percent overstory closure	0.5	4	11	0.4	
Aspen > 40 to 70 percent overstory closure	0.5	0	12	0.0	< 0.01
Aspen > 70 percent overstory canopy closure	0.2	0	1	0.0	
Ponderosa pine shrub/seedling	1.0	5	10	0.5	
Ponderosa pine 2.5 to 23 cm dbh					
0 to 40 percent overstory closure	1.0	19	36	0.5	0.07
> 40 to 70 percent overstory closure	0.5	43	74	0.6	< 0.01
> 70 percent overstory closure	0.2	3	16	0.2	< 0.02
Ponderosa pine > 23 cm dbh					
0 to 40 percent overstory closure	1.0	416	284	1.5	< 0.01
> 40 to 70 percent overstory closure	0.5	166	211	0.8	< 0.01
> 70 percent overstory closure	0.2	9	47	0.2	< 0.01
White spruce shrub/seedling	0.0	1	2	0.6	
White spruce 0 to 40 percent overstory closure	0.0	2	18	0.1	< 0.01
White spruce > 40 to 70 percent overstory closure	0.0	1	17	0.1	< 0.01
White spruce > 70 percent overstory closure	0.0	1	5	0.2	

[1] Elk use determined from nighttime GPS telemetry locations of foraging elk and expected use determined from proportional area.
[2] Probability that the selection ratio was different from 1.0 or that selection differed from random use.

expected in areas 200 to 600 m into cover. We believe these deviations from patterns observed elsewhere were influenced by avoidance of areas adjacent to primary roads and secondary roads (see next section). Most large meadows in our study area had a primary or secondary road resulting in greater use of areas by elk > 200 m from forest edges of meadows. We do not believe that the patterns observed warrant modifying coefficients for elk habitat suitability near forage—cover edges.

Roads

Negative effects of roads on elk are well documented (for example, Canfield and others 1999). Road densities that are < 1/2 of which occurred in our study reduce elk habitat by 40 percent (Lyon 1983). Primary and secondary roads in the Black Hills are forest roads with a gravel base. The elk distribution that we observed relative to primary roads was similar to that reported in Custer State Park. Because the trend line of elk locations intersected the expected locations curve at approximately 350 m, we recommend a 350 m buffer distance for primary road effects on elk in the Black Hills National Forest. Elk avoidance of areas adjacent to secondary roads in Custer State Park extended to 60 m (Benkobi and others 2004). However, in the central and northern Black Hills, secondary roads negatively affected elk up to 260 m from the road. We recommend that the coefficient for roads be applied to areas extending 260 m from secondary roads. Elk displacement from areas near primary and secondary roads resulted in selection for areas > 300 m from primary roads and > 260 m from secondary roads to approximately 550 m for both road classes. In the Blue Mountains of Oregon, elk showed increasing selection for areas corresponding to distances further from roads. This trend was evident up to 1.8 km from roads (Rowland and others 2000). Several studies have shown that elk are further from roads during day than at night (Ager and others 2003; Millspaugh 1999). We believe similar daytime movements by elk away from primary and secondary roads and into the forest for cover resulted in the increased selection for areas 260 to 550 m from these roads.

Primitive roads appeared to have little effect on the distribution of elk in this study and in Custer State Park (Benkobi and others 2004). The lack of a demonstrated effect of primitive roads on elk distribution is difficult to interpret. Other research has shown negative responses by elk to relatively low levels of disturbance by vehicles or humans (Cassirer and others 1992; Ward and Cupal 1979; Wisdom and others 2004). In Custer State Park, primitive roads were closed to public use explaining the lack of effect primitive roads had on elk distribution. However, we speculate that the distribution of elk relative to primitive roads in this study was a swamping effect from sporadic disturbance in an area with high density of primitive roads. We believe that elk response to roads was hierarchal, first avoiding primary roads, then secondary roads, and lastly primitive roads. When areas adjacent to primary and secondary roads were eliminated from the GIS, the average distance from primitive roads to random points was 145 m (Rumble and others 2005), leaving little opportunity for elk to avoid primitive roads during their daily travels of up to 3 km/day (Clutton-Brock and others 1982; Craighead 1973). It seems plausible that the conditioned response of elk to primitive roads at these densities would depend on the frequency of disturbance. During aerial telemetry flights, we occasionally observed elk on primitive roads. Unimproved access such as seismic or power lines, or gas rights-of-way, did not deter elk habitat selection in Canada (Jones and Hudson 2002). At this time, our data do not support inclusion of an effect for primitive roads on elk.

ArcHSI Predictions

The distribution of elk in areas predicted as good, fair, or poor overall HSI followed similar patterns to those reported by Benkobi and others (2004) for Custer State Park in the southern Black Hills. During summer, elk selected areas predicted by the model as good overall HSI and avoided areas predicted as poor overall HSI by the model. The overall HSI for both study areas decreased during winter, primarily because coefficients for aspen and white spruce were zero for both forage and cover. Elk winter ranges in the Black Hills occur at lower elevations than where white spruce and most of the aspen occur. The model did not perform as well during winter. In the north, elk did not prefer areas predicted to be good overall HIS. In the south, elk avoided areas predicted as good overall HSI. Thus, errors in some coefficients for model components were probable.

ArcHSI weighs forage habitat three times greater than cover or juxtaposition of habitats when computing the overall HSI. Nighttime GPS telemetry showed strong selection by elk for habitats with good forage HSI ratings. Selection for areas predicted to be good for forage habitats was even more pronounced during winter. Strong selection for forage habitats was supportive of the greater weight applied to forage coefficients in calculating HSI for an area. Forage digestibility declines during fall to winter and additional energy expenditures are incurred from travel and foraging in snow (Wickstrom and others 1984; Parker and others 1984). Increased selection by elk for areas predicted to have good forage HSI during winter was consistent with the ecology of elk.

Table 5. Proposed coefficients for forage and cover in vegetation structural stages for ArcHSI evaluated for elk use in the Limestone Plateau and northern Black Hills, SD.

Vegetation structural stage	Cover coefficient		Forage coefficient	
	Summer	Winter	Summer	Winter
Grassland	0.0	0.0	1.0	1.0
Mountain shrub	0.5	0.0	0.1	0.0
Aspen shrub/seedling	1.0	0.5	1.0	1.0
Aspen 0 to 40 percent overstory closure	1.0	0.5	1.0	0.2
Aspen > 40 to 70 percent overstory closure	1.0	0.5	1.0	0.2
Aspen > 70 percent overstory closure	1.0	0.0	0.2	0.1
Ponderosa pine shrub/seedling	0.5	0.5	0.5	0.2
Ponderosa pine 2.5 to 23 cm dbh				
0 to 40 percent overstory closure	0.5	0.7	0.3	0.2
> 40 to 70 percent overstory closure	0.5	0.5	0.2	0.2
> 70 percent overstory closure	0.7	0.3	0.1	0.1
Ponderosa pine > 23 cm dbh				
0 to 40 percent overstory closure	0.5	0.7	0.5	0.5
> 40 to 70 percent overstory closure	0.5	0.5	0.3	0.3
> 70 percent overstory closure	0.7	0.3	0.1	0.1
White spruce shrub/seedling	1.0	0.0	1.0	0.2
White spruce 0 to 40 percent overstory closure	1.0	0.0	1.0	0.0
White spruce > 40 to 70 percent overstory closure	1.0	0.0	0.5	0.0
White spruce > 70 percent overstory closure	1.0	0.0	0.2	0.0

Vegetation structural stages—Recommended coefficients for vegetation structural stages resulting from our analyses are in table 5. Coefficients for cover assigned to vegetation structural stages in ArcHSI were proportional to the percent of overstory closure, but elk use of vegetation structural stages was poorly predicted by the model. The initial coefficients for cover probably carried over from previous models when thermal cover was thought to be important for elk (see Cook and others 1998). Despite some use by bedded elk, the cover coefficient for grasslands should remain zero during summer. Although there were few observations of elk in the mountain shrub vegetation structural stage for cover during summer, our data indicates the value of this structural stage to elk as cover is greater than in previous models. For cover during summer, elk showed strong selection for all structural stages of aspen except the 40 to 70 percent overstory closure structural stage. Consequently, we believe the coefficients for cover in aspen during summer should be 1.0. Assuming that the criteria for elk hiding cover is obscuring 90 percent of a standing elk at 61 m (Thomas and others 1979), all structural stages of ponderosa pine in our study qualified as hiding cover. Open canopy stands of ponderosa pine had medium and tall shrubs, such as bur oak and common juniper, that contributed to the horizontal screening of elk and even more so for bedded elk. Ponderosa pine germinates readily in open stands in the Black Hills (Shepperd and Battaglia 2002) and saplings provided visual obstruction of elk. Vegetation structural stages of ponderosa pine ≤ 70 percent overstory closure averaged 300 to 400 kg/ha of herbaceous biomass (unpublished data, Rocky Mountain Research Station, Rapid City, South Dakota). We often observed groups of elk where some were bedded while others were foraging. Vegetation structural stages that provided a combination of forage and cover were sought by elk. Although elk avoided ponderosa pine with high overstory canopy cover for bedding during summer, we believe elk would have selected ponderosa pine > 70 percent overstory closure (for example, Millspaugh and others 1998) if aspen or white spruce had not been well distributed and available on elk summer ranges. Consequently, the coefficient for cover in ponderosa pine > 70 percent overstory cover should be < 1.0, but > 0.5. We assigned a cover coefficient of 0.7 to ponderosa pine > 70 percent overstory closure. Structural stages of ponderosa pine ≤ 70 percent overstory cover were used proportionally to available, and coefficients of 0.5 for the Black Hills are appropriate during summer.

Elk avoided bedding in grasslands and mountain shrub vegetation structural stages during winter so cover coefficients for these vegetation structural stages should be zero. Observations of elk in aspen during winter probably reflected occasions where undisturbed elk bedded near forage areas. Aspen was not common on elk winter range in our study, but it occasionally occurred along the edges of meadows on northeast slopes. Thus, despite some use by bedded elk, we suggest winter cover coefficients in aspen should not be greater than 0.5. We assigned a cover coefficient of 0.5 to shrub/seedling ponderosa pine because bedded elk demonstrated a selection for it.

Winter selection by elk for ponderosa pine with < 40 percent overstory closure suggests that this vegetation structural stage provided forage and cover. Selection by elk of vegetation structural stages providing both forage and cover are described by Wisdom and others (1986) as optimal cover. Consequently we recommend using a winter cover coefficient of 0.7 in ponderosa pine < 40 percent overstory closure. The value of open ponderosa pine as cover to elk during winter in other areas will depend on the understory vegetation. In more xeric sites than occurred in our study, a cover coefficient of 0.5 for open ponderosa pine would likely be appropriate. The selection against ponderosa pine with > 70 percent overstory closure is consistent with the hypotheses (1) elk do not require thermal cover during winter (Cook and others 1998), or (2) forage is of greater importance to elk than cover. Given a choice, elk in our study selected open canopy pine forest over dense canopy forest during winter and the winter cover coefficient for ponderosa pine > 70 percent overstory closure should be < 0.5. These alterations to the cover coefficients are likely study area specific and changes elsewhere should be supported by quantitative measurement of elk hiding cover described by (Thomas and others 1979).

Foraging elk strongly selected structural stages with greater herbaceous vegetation, used vegetation structural stages with moderate amounts of herbaceous vegetation in random patterns, and avoided those stages with the least herbaceous vegetation. Correlation between selection ratios and standing biomass confirmed that elk selected forage habitats approximately proportional to the amount of available forage. Although grasslands had the greatest herbaceous biomass, they did not have the greatest selection ratio. Nonetheless, grasslands typically have the greatest herbaceous biomass and we assigned them a forage coefficient of 1.0 because elk in the Black Hills are primarily grazers (Wydeven and Dahlgren 1983). Standing biomass in the mountain shrub vegetation structural stage averaged only 145 ± 40 ($\overline{x}$ ± SE) kg/ha. Consequently, the summer forage coefficient for mountain shrub should be 0.1. All structural stages of aspen had strong selection by foraging elk and should be assigned forage coefficients of 1.0 during summer. During summer, foraging elk avoided all tree stages of ponderosa pine > 40 percent overstory closure, suggesting that coefficients in ArcHSI were overestimated. We recommend forage coefficients of 0.3 to 0.1 for increasing canopy closure in sapling pole ponderosa pine and 0.5 to 0.1 for the mature structural stages of ponderosa pine. Herbaceous biomass in sapling/pole ponderosa pine < 40 percent overstory canopy closure averaged approximately 20 percent less than mature

ponderosa pine < 40 percent overstory closure. The forage coefficient of 0.3 reflects lower available herbaceous vegetation. The selection of white spruce for forage was not expected despite high coefficients for summer forage in some structural stages of white spruce. Examination of the foraging locations in white spruce showed that 25 percent were along the interface between meadow and spruce stands or resulted from mapping errors in the delineation of the stand boundaries that included portions of adjacent meadows. Consequently, we did not modify the forage coefficients in ArcHSI for white spruce.

During winter, foraging elk selected vegetation structural stages approximately proportional to estimates of herbaceous biomass. Variability in the relation between herbaceous biomass and winter selection ratios exhibited by foraging elk likely reflected greater density of animals on a constricted winter range (Benkobi and others 2005). Some vegetation structural stages were rare or absent on winter ranges. Meadows received the greatest use during winter by foraging elk. During the winter of 2001, we observed extensive browsing by elk of shrub/seedling stages of aspen following a wildfire that burned approximately 65 percent of the winter range (Benkobi and others 2005). Coefficients in shrub/seedling aspen should remain 1.0. Elk avoided foraging in the tree structural stages of aspen during winter. We recommend winter forage coefficients for tree stages of aspen be 0.2 for stages ≤ 70 percent overstory closure and 0.1 for stages > 70 percent overstory closure. Avoidance of winter foraging in sapling/pole structural stages of ponderosa pine > 40 percent overstory cover suggests that forage coefficients should be 0.2, 0.2, and 0.1 for the canopy closure categories of ≤ 40 percent, > 40 to 70 percent, and > 70 percent of sapling pole ponderosa pine, respectively. Mature ponderosa pine ≤ 40 percent overstory closure was given a forage coefficient of 0.5, which was limited by the summer forage coefficient. High density of elk on winter range would result in use of marginal habitats by elk (Fretwell and Lucas 1969). Winter forage coefficients in structural stages of ponderosa pine > 40 percent overstory closure reflected the reduced herbaceous biomass and selection ratios by foraging elk.

Figure 9 shows the outcome of modifications to ArcHSI forage and cover coefficients. While there is circularity in using the same data to retest ArcHSI, we believe some post hoc review of the model output after modifying forage and cover coefficients was warranted. The overall HSI for our study area declined from the previous version of the model. Winter applications showed decreased overall HIS, which was expected because aspen and white spruce occur at higher
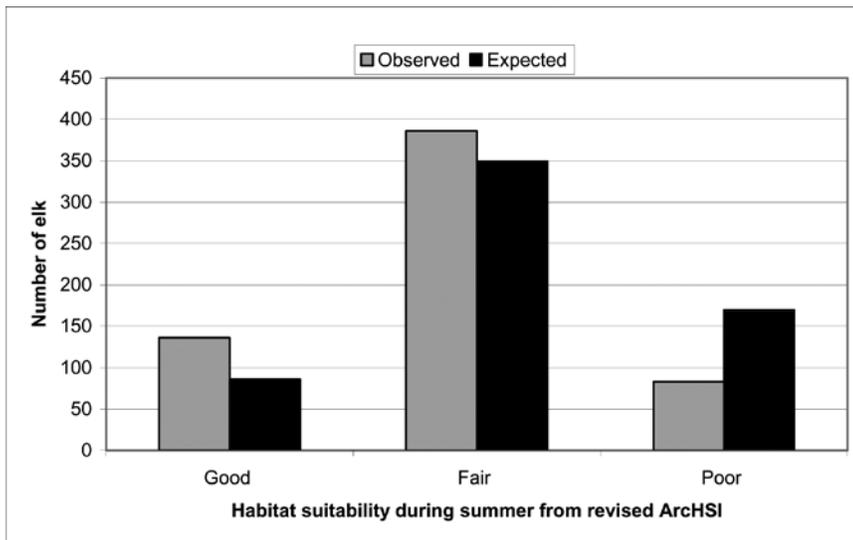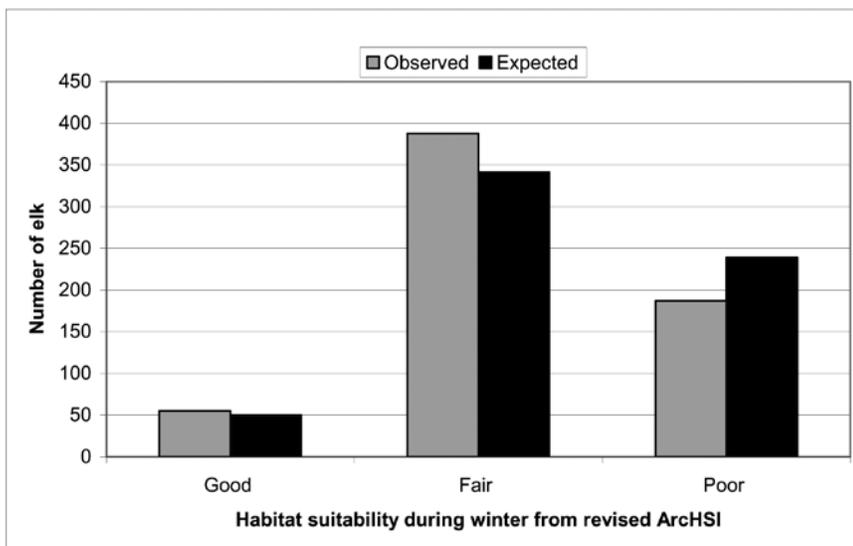
Figure 9. Daytime radio telemetry elk locations (observed) and expected elk locations relative to habitat suitability predicted by the ArcHSI model during summer and winter after modifying forage and cover coefficients to reflect habitat selection by elk in the Black Hills, SD.

elevations than the elk winter ranges in the Black Hills and had little value for elk during winter. Finally, modifications to coefficients eliminated the selection for habitats predicted as poor HSI.

Conclusion

Habitat models provide repeatable quantitative evaluations and tend to simplify the complicated habitat requirements of animals (Starfield 1997). Our test confirmed the need for validation of ArcHSI before widespread use and commitment of resources (Laymon and Barret 1984; O'Neil and others 1988; Shamberger and O'Neil 1986). This study represented the second test of a spatially explicit elk model in the Black Hills. In the Black Hills National Forest, both primary roads and secondary roads pushed herds farther back than reported

by Benkobi and others (2004). Primitive roads did not appear to affect elk distributions, which is contrary to studies in other areas. Coefficients for the distance that primitive roads affect elk habitat could be derived from studies in areas with lower densities of roads than occur in the Black Hills. Patterns of elk distribution associated with juxtaposition of forage-cover edges were influenced by primary and secondary roads that traversed most of the large meadows (foraging areas). When we incorporated road effects from this study into the model recommendations of Benkobi and others (2004), results during winter suggested that modification to the coefficients for forage and cover were necessary. Vegetative conditions that meet the cover requirements for elk are likely specific to local physical and environmental conditions. In our study, forage and cover were available in some structural stages of ponderosa pine. Elk did not select for high overstory closure for cover during winter.

This study and others (Jones and Hudson 2002) demonstrated that biomass of herbaceous vegetation largely determines foraging habitats of elk. Consequently, HSI coefficients for elk foraging habitats can be estimated by comparing relative herbaceous standing crop among vegetation structural stages. We believe that the structure of this model has application for evaluating forest management prescriptions for elk habitat in other areas and in particular, ponderosa pine forests. However, forage and cover coefficients assigned to vegetation structural stages should be modified to reflect local conditions where the model is being applied.

Literature Cited

Ager, A.A.; Johnson, B.K.; Kern, J.W.; Kie, J.G. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076-1088.

Benkobi, L.; Rumble, M.A.; Brundige, G.C.; Millspaugh, J.J. 2004. Refinement of the Arc-Habcap model to predict habitat effectiveness for elk. Research Paper RMRS-RP-51. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 18 p.

Benkobi, L.; Rumble, M.A.; Stubblefield, C.H.; Gamo, R.S.; Millspaugh, J.J. 2005. Seasonal migration by female elk in the Black Hills of South Dakota and Wyoming. Prairie Naturalist 37:151-165.

Berry, K.H. 1986. Introduction: Development, testing, and application of wildlife-habitat models. In: Verner, J.; Morrison, M.L.; Ralph, C.J., editors. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Madison, WI: University of Wisconsin Press: 3-4.

Buttery, R.F.; Gillam, B.C. 1983. Forested ecosystems. In: Hoover, R.L.; Wills, D.L., editors. Managing forested lands for wildlife. Denver, CO: Colorado Division of Wildlife in cooperation with U.S. Department of Agriculture, Forest Service, Rocky Mountain Region: 43-71.

Canfield, J.E.; Lyon, L.J.; Hillis, J.M.; Thompson, M.J. 1999. Ungulates. In: Joslin, G.; Youmans, H., coordinators. Montana Chapter of The Wildlife Society: Effect of recreation on Rocky Mountain wildlife: A review for Montana, Committee on Effects of Recreation on Wildlife, http://www.montanatws.org. 6.1-6.25.

Cassirer, E.F., Freddy, D.J.; Ables, E.D. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375-381.

Clutton-Brock, T.H.; Guinness, F.E.; Albon, S.D. 1982. Red Deer: Behavior and ecology of two sexes. Chicago IL: University of Chicago Press.

Conner, M.M.; White, G.C.; Freddy, D.J. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926-940.

Cook, J.G.; Irwin, L.L.; Bryant, L.D.; Riggs, R.A.; Thomas, J.W. 1998. Relations of forest cover and condition of elk: A test of the thermal cover hypothesis in summer and winter. Wildlife Monographs No. 141.

Craighead, J.J.; Craighead, F.C.; Ruff, R.L.; O'Gara, B.W. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by bio-telemetry. Wildlife Monographs No. 33.

ESRI. 1999. ARC/INFO. Redlands, CA: Environmental Systems Research Institute, Inc.

ESRI. 2001. ArcMap 8.1. Redlands, CA: Environmental Systems Research Institute, Inc.

Fretwell, S.D.; Lucas, H.L., Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds: Theoretical development. Acta Biometrica 19:16-36.

Hoffman, G.R.; Alexander, R.R. 1987. Forest vegetation types of the Black Hills National Forest of South Dakota and Wyoming: A habitat type classification. Research Paper RM-276. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Holthausen, R.S.; Wisdom, M.J.; Pierce, J.; Edwards, D.K.; and Rowland, M.M. 1994. Using expert opinion to evaluate a habitat effectiveness model for elk in western Oregon and Washington. Research Paper PNW-RP-479. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Hurley, M.A.; Sargeant, G.A. 1991. Effects of hunting and land management on elk habitat use, movement patterns, and mortality in western Montana. In: Christensen, A.G.; Lyon, L.J.; Lonner, T.N., compilers. Bozeman, MT: Proceedings of elk vulnerability symposium. Montana State University.

Jones, P.F.; Hudson, R.J. 2002. Winter habitat selection at three spatial scales by American elk, *Cervus elaphus*, in west-central Alberta. Canadian Field Naturalist 116:183-191.

Juntti, T.M.; Rumble, M.A. 2006. Arc habitat suitability index computer software. General Technical Report RMRS-GTR-180WWW. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 31 p.

Laymon, S.A.; Barrett, R.H. 1984. Developing and testing habitat-capability models: Pitfalls and recommendations. In: Verner, J.; Morrison, M.L.; Ralph, C.J., editors. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Madison WI: University of Wisconsin Press: 87-91.

Lyon, L.J. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 81:592-595.

Lyon, L.J.; Christensen, A.G. 1992. A partial glossary of elk management terms. General Technical Report INT-288. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Manly, B.F.J.; McDonald, L.L.; Thomas, D.L.; McDonald, T.L.; Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies. Dordrecht, Netherlands: Kluwer Academic Publishers.

McCullough, D.R. 1975. Modifications of the clover deer trap. California Fish and Game 61:242-244.

Millspaugh, J.J.; Raedeke, K.J.; Brundige, G.C.; Willmott, C.C. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills, SD: consideration for thermal cover management. American Midland Naturalist 139:133-140.

Millspaugh, J.J.; Brundige, G.C.; Gitzen, R.A.; Raedeke, K.J. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994-1003.

Ministry of Environment, Lands and Parks Resources Inventory. 1999. British Columbia Wildlife Habitat

Rating Standards. British Columbia, Canada: Terrestrial Ecosystems Task Force Resources Inventory Committee, http://srmwww.gov.bc.ca/risc/pubs/teecolo/whrs/.

O'Neil, L.; Roberts, T.H.; Wakeley, J.S.; Teaford, J.W. 1988. A procedure to modify habitat suitability index models. Wildlife Society Bulletin: 16:33-36.

Orr, H.K. 1959. Precipitation and streamflow in the Black Hills. Station Paper No. 44. Fort Collins, CO. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Parker, K.L.; Robbins, C.T.; Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

Roloff, G.J.; Millspaugh, J.J.; Gitzen, R.A.; Brundige, G.C. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain Elk. Journal of Wildlife Management 65:899-914.

Rowland, M.M; Wisdom, M.J.; Johnson, B.K.; Kie, J.G.. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672-684.

Rumble, MA.; Benkobi, L.; Lindzey, F.; Gamo, R.S. 2001. Evaluating elk habitat interactions with GPS collars. In: Sibbald, A.M.; Gordon, I.J., editors. Aberdeen, Scotland, UK: Tracking animals with GPS. Macaulay Land Use Research Institute: 11-17.

Rumble, M.A.; Benkobi, L.; Gamo, R.S. 2005. Elk responses to humans in a densely roaded area. Intermountain Journal of Science (1-2):10-24.

Shamberger, M.L.; O'Neil, L.J. 1986. Concepts and Constraints of Habitat-model testing. In: Verner, J.; Morrison, M.L.; Ralph, C.J., editors. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Madison, WI: University of Wisconsin Press: 5-10.

Shepperd, W.D.; Battaglia, M.A. 2002. Ecology, silviculture and management of Black Hills, ponderosa pine. General Technical Report RMRS-GTR-97. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 112 p.

SPSS. 2001. SPSS 11.3. Chicago, IL: SPSS, Inc.

Starfield, A.M. 1997. A pragmatic approach to modeling wildlife management. Journal of Wildlife Management 61:261-270.

Thomas, J.W.; Black, H., Jr.; Scherzinger, R.J.; Pedersen, R.J. 1979. Chapter 8: Deer and elk. In: Thomas, J.W., ed. Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. Washington, DC: U.S. Department of Agriculture, Forest Service.

Thomas, J.W.; Leckenby, D.A.; Henjum, M.; Pederson, R.J.; Bryant, L.D. 1988. Habitat effectiveness index for elk on Blue Mountain winter ranges. General Technical Report PNW-218. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Thompson, M.J.; Henderson, R.E.; Lemke, T.H.; Sterling, B.A. 1989. Evaluation of a collapsible clover trap for elk. Wildlife Society Bulletin 17:287-290.

Ward, A.L.; Cupal, J.J. 1979. Telemetered heart rate of three elk as affected by activity and human disturbance. In: Shaw, J., ed. Symposium on dispersed recreation and natural resource management. Logan, UT: Utah State University, College of Natural Resources: 47-56.

Wickstrom, M.L.; Robbins, C.T.; Hanley, T.A.; Spalinger, D.E.; Parish, S.M. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285-1301.

Wisdom, M.J.; Bright, L.R.; Carey, C.G.; Hines, W.W.; Peterson, R.J.; Smithey, D.A.; Thomas, J.W.; Witmer, G.W. 1986. A model to evaluate elk habitat in western Oregon. Publication No. R6-F&WL216-1986. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

Wisdom, M.J., Preisler, H.K.; Cimon, N.J.; Johnson, B.K. 2004. Effects of off-road recreation on mule deer and elk. Transactions of the North American Wildlife and Natural Resources Conference 69:531-550.

Wydeven, A.P; Dahlgren, R.B. 1983. Food habits of elk in the northern Great Plains. Journal of Wildlife Management 47:916-923.

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