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Habitat use by elk (*cervus elaphus*) within structural stages of a managed forest of the northcentral United States

Mark A. Rumble*, R. Scott Gamo[1]

Forest and Grassland Research Laboratory, U.S. Forest Service, Rocky Mountain Research Station, 8221 South Highway 16, Rapid City, SD 57702, USA

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ABSTRACT

Timber management is the most prominent land management activity in the Black Hills National Forest in the northcentral United States. Management units are stands 4–32 ha in size and are described using a hierarchal vegetative description including vegetation type, size class (age), and overstory canopy cover. For the most part, these stands are relatively homogeneous resulting from decades of even-aged management. Because elk (*Cervus elaphus*) select habitats at different scales from home ranges to microsites, it is important for managers to know how elk utilize vegetative conditions within these stands. We compared vegetative conditions at microsites selected by elk to the vegetative conditions of similarly classified stands to enable managers to better understand how timber management affects elk habitat. Within these relatively homogeneous forest stands under even-age management of the Black Hills, elk demonstrated selection for particular forest attributes. Vegetative conditions that provide cover for elk were selected for in open stands (both aspen and pine), but while in dense stands, elk selected for more open conditions. The elk hiding cover model should be adjusted for this forest.

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1. Introduction

North American elk (*Cervus elaphus*) are a highly desirable species for both consumptive and non-consumptive uses in the Black Hills and elsewhere (Bunnel et al., 2002). Through the 1990s, elk populations in the Black Hills increased and conflicts with private lands, livestock, timber resources, off-highway vehicles and other recreational demands were common (A. Carter, unpubl. rep., South Dakota Department of Game Fish and Parks, Pierre, SD, 2002). The Black Hills National Forest (BHNF) provides habitat to approximately 4000 elk. Timber management is the most prominent resource management in the BHNF. The BHNF harvests >50% of the timber in the U.S. Forest Service, Rocky Mountain Region, and in 2007, more timber was harvested from the BHNF than any other National Forest (pers. commun., Blaine Cook, Silviculturist, BHNF, Custer, SD).

Management of the timber resource of the BHNF occurs in land units (stands) approximately 4–32 ha in size. Stands are classified in a hierarchal manner based on vegetation type, diameter-at-breast height (DBH), and overstory canopy cover called vegetation structural stages (Buttery and Gillam, 1983). Within these stands, the size and density of trees were traditionally managed under an even-aged silvicultural prescription using a two-step shelterwood harvest strategy (Boldt and Van Duesen, 1974) for about 50 years. Currently, stands are managed to achieve desired condition objectives that are ascribed to vegetation structural stages (Land and Resource Management Plan, BHNF, Custer SD, 1996) and alternative management scenarios have been suggested that include individual- and group-tree selection to increase within stand diversity.

Habitat selection by ungulates, including those in forested ecosystems, involves a series of decisions that are made over a variety of scales (Johnson et al., 2001; Anderson et al., 2005). These “decisions” or selections may be viewed hierarchally as animals select ranges, home ranges, stands, and sites for foraging, bedding or parturition (Johnson, 1980). The scale that selection occurs and selection of resources by ungulates vary depending on vegetation types, forage abundance, forage quality, how animals perceive risk, or behavior (Millspaugh et al., 1998; Johnson et al., 2001; Anderson et al., 2005; Bowyer and Kie, 2006; Long et al., 2009). Habitats that are organized in broad vegetative categories such as conifer, hardwoods, or grasslands are not descriptive of vegetative changes associated with forests managed using shelterwood silvicultural prescriptions. There is evidence for selection of resources by elk at the stand level in the Black Hills (Benkobi et al., 2004; Rumble et al., 2007). However, analysis of resource selection that considered sites and stands simultaneously regardless of vegetation structural stage suggested site characteristics were more important drivers of elk resource selection than stand characteristics (Rumble and Gamo, 2011). As the main driver of vegetation change on the BHNF, timber

* Corresponding author. Tel.: +1 605 716 2174; fax: +1 605 3946627.
E-mail address: mrumble@fs.fed.us (M.A. Rumble).
[1] Present address: Wyoming Game and Fish, Cheyenne, WY 82006, USA.

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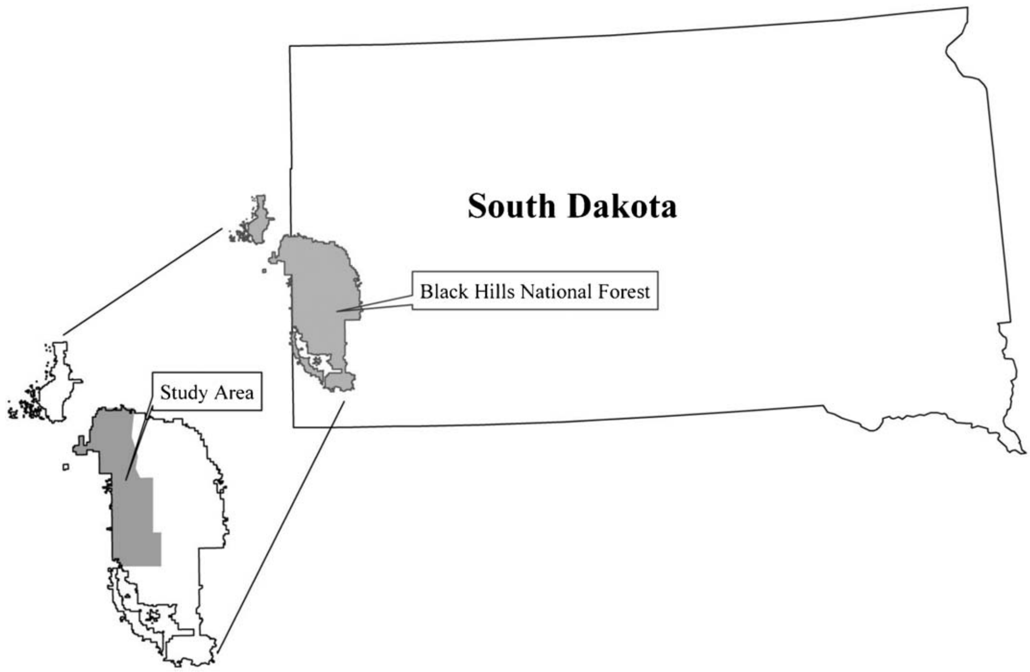

Figure 1. Study area for evaluating elk habitat in the west central and northern Black Hills of South Dakota, 1998–2001.

management practices can affect habitats chosen by elk and other wildlife and thus, in that context, it is important to understand how elk use managed stands. Our objective was to evaluate whether elk selected resources within relatively homogeneous vegetation structural stages ascribed to stands. We hypothesized that the vegetation classification captured the variation in forest conditions, so elk would not exhibit selection of specific vegetative conditions within vegetation structural stages assigned to stands. In this paper we examine patterns of selection by elk across spectrum of structural stages available to elk, and typical of forests in the Black Hills of South Dakota.

2. Study area

The Black Hills are an island of forest surrounded by prairies in western South Dakota and eastern Wyoming. They extend approximately 198 km north to south and 99 km east to west. Elevations range from 915 m in the eastern foothills to 2207 m in a central granitic core and on the western uplifted Limestone Plateau. The climate is continental; winter temperatures vary with elevations and average from 5 °C to 7 °C. January is the coldest month (−11° to 2 °C) while July and August are the warmest months (15–29 °C). Annual precipitation also varies with elevation and ranges from 46 cm to 66 cm (Orr, 1959) with June as the wettest month. Winter precipitation is greater in the northern and western portions. The precipitation patterns coupled with the Stovho Soil Complex make the Limestone Plateau highly productive in terms of herbaceous growth (Bennett et al., 1987).

Our research area included the west portions of the central and northern Black Hills (Fig. 1). Elevation declines from approximately 2100 m to 1200 m along the northern boundary of the BHNF where the forest meets the prairie (Thilenius, 1972) and steep canyons and drainages are characteristic of this area. The southern 2/3 of the study area included the Limestone Plateau with elevations ranging from approximately 2100 m and declining gradually to approximately 1800 m near the south boundary of our study area. Precipitation and snow depths decrease with the loss of elevation from approximately 56 cm to <50 cm (Orr, 1959).

The dominant vegetation type is ponderosa pine (*Pinus ponderosa*) which occupied 78% of our study area. White spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*) occur in mesic sites and at high elevations on slopes with northerly aspects (Hoffman and Alexander, 1987) and comprise about 7% and 4% of the study area respectively: grasslands or meadows comprised about 10% of the area. Road density in the northern area varied from 2.51 km/km^2 in southern portions of the study area to 2.13 km/km^2 in the northern portions.

Manitoban elk (*C. e. manitobensis*) that historically existed in the Black Hills were extirpated in the late 1800s (Bryant and Maser, 1982). Rocky Mountain elk were introduced into the Black Hills from the Yellowstone region of Wyoming between 1912 and 1914 (Turner, 1974). Our study area included 2 elk hunt units. Populations in the northern unit (∼northern 1/3 of study area) were increasing about 20% per year with an average ratio of 30 calves per 100 females in the winter during our study (1998–2001); elk populations in the southern unit (southern 2/3 of study area) were increasing about 30% per year with an average of 45 calves for 100 female elk during our study (unpubl. reps., Elk Management in South Dakota, South Dakota Dept. Game Fish and Parks, Pierre, SD, 1995 and 2001). During our study, elk were dispersed over both areas in small herds. There was some movement of animals between these units, but it was not substantial (Benkobi et al., 2005).

3. Methods

3.1. Capture and telemetry

Seasonal migratory patterns of this elk population were unknown when we initiated the study and we wanted to capture elk across a large area on summer range to sample different subherds. Thus, we divided the study area into north and south units and further divided each of these into 4 subunits. Our protocol allowed for capturing and radio-collaring 5 females in each subunit; and 5 females at random across the study area. Males were captured opportunistically in the south subunit. No more than 2 elk were captured from a single subherd. To maximize animal safety during this summertime capture, we (1) limited the capture period from sunrise to 1200 h; (2) discontinued daily capture if air temperature exceeded 29 °C; (3) limited direct pursuit of elk to 5 min; (4) hobbled and blindfolded elk immediately after capture; and (5) monitored rectal temperature and other signs of stress for elk (unpubl., Aviation operation plan for helicopter net-gunning, Rocky Mtn. Res. Stn., Rapid City, SD). Our goal was to mark 45 female and 20 male elk with radio collars. In August 1998, using a helicopter and netgun, we captured 21 females and 14 males in the south unit and 13 females from the north unit. In January 1999, we captured and radio-collared 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 and radio-collared 2 females and 2 yearling males using clover traps (McCullough, 1975; Thompson et al., 1989) in the south unit. VHF radio collars weighed approximately 600 g and were placed on elk using vinyl neck collars. Each transmitter was equipped with a head-position activity sensor and mortality sensor that changed the pulse of the radio signal. Eight of the elk were equipped with global positioning system (GPS) collars weighing approximately 1600 g that also had VHF transmitters and for this paper, we utilized locations of these animals obtained using the VHF transmitters.

We used VHF radio-telemetry, both ground based and from aircraft, to determine elk sites in this study. Between August 1998 and October 2001, we located each radio-collared elk two to three times each month. During snow-free periods, we approached radio-collared elk on foot with a hand-held two-element yagi antenna and we obtained visual confirmation of the foraging or bedding sites. During winter, we located elk from a fixed-wing 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 locations as the aircraft passed over the observed animal(s). We recorded the Universal Transverse Mercator (UTM) coordinates (North American Datum 1927, Zone 13) obtained from a hand-held GPS receiver for each location. Occurrence of multiple radio-collared individuals in a herd was recorded as a single site. Associated with each location, we recorded whether the radio-collared animal was bedded or foraging by direct observation or as facilitated by the pulse rate of the transmitter from the head-position activity sensor. The behavior of the radio-collared animal determined the assignment of the site as foraging or bedding.

3.2. Vegetation measurements

We returned to the sites where elk were observed within a week to measure vegetation at that site. At both bed and forage sites we established 2, 60-m transects perpendicular to each other and centered over the location of the observed animal. The directional orientation of the first transect was selected randomly. We estimated forest characteristics at the intersection of these transects using a variable radius plot determined from a 10-factor prism (Sharpe et al., 1976) for trees ≥15.2 cm DBH; trees <15.2 cm DBH were measured in a 5.03 m fixed-radius plot. We recorded species and DBH of all live trees and calculated trees per ha, basal area per ha and average DBH from these data. Downed woody debris at each site was interpolated from photo guides developed in the Black Hills (Photo series for quantifying forest residues in the Black Hills, U.S. For. Serv., Rocky Mtn. Reg., AFM 831, 1982). We estimated overstory (angular) canopy cover using a convex spherical densiometer (Griffing, 1985; Nuttle, 1997) at the intersection of transects and 30 m away on each transect ($n = 5$). Along each transect, we estimated percent vegetative cover in 0.1 m^2 quadrats (Daubenmire, 1959) at 2-m intervals ($n = 60$) for total cover; and categories of grasses, forbs and shrubs; and shrub species. For understory categories that had senesced, we estimated cover to the best of our ability that would have been present in the growing season. We did this so all sites would be comparable to account for the leaflessness during winter. We tabulated all stems <2.54 cm DBH and <2 m tall in 2, 1 m × 30 m belt plots along transects. At the intersection of the transects at 70 cm aboveground, we placed a 1-(tall) × 2-(wide) m vinyl cover cloth with 40 alternating black and white 25 cm × 25 cm squares. 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. These estimates quantified security cover defined as percent of a standing elk obscured at 61 m (e.g., Thomas et al., 1979). During the second year of our study, we added a second cover cloth measurement at ground level (representing a bedded elk) for which we recorded the number of squares visible at 61 m and the distance at which only 4 squares were visible.

We collected similar measurements from sites selected from a stratified random sampling of each study area from July to September of 1999, 2000 and 2001. Strata for the random measurements were vegetation types and structural stages that were drawn with replacement from a geographic information system (GIS) coverage of forest vegetation (Land and Resource Management Plan, BHNF, Custer, SD, 1996). Vegetation types included grasslands, aspen, ponderosa pine and white spruce. Structural stages were visualized as the stages forest vegetation progresses through following a disturbance such as fire or timber management (Buttery and Gillam, 1983). Depending on the extent of and disturbance type, vegetation structural stages included grass/forb, seedling/shrub, sapling pole (2.5–22.8 cm DBH), mature (>22.8–41 cm DBH) and old-growth (>41 cm); sapling pole and mature trees stages were divided into 3 overstory canopy cover categories of 0–40%, >40–70% and >70%. Selected polygons were divided into a 50-m grid, of which we randomly selected 1 point in each polygon and recorded the coordinates in a GPS. We repeated this procedure each year and drew new random points to measure. Private lands within the study area boundary were measured as a separate stratum at the outset, but were later assigned to the vegetation classification based on interpretation of 1:24,000 air photographs and digital orthoquads. We located the random sites in the field aided with a hand-held GPS unit. We sampled 5–10 polygons in each stratum each year. However, to avoid re-sampling the same polygons for strata that comprised a small percentage of the study areas, we measured fewer sites in those strata.

3.3. Analyses

We calculated an average for each variable at each site and used the sites as our experimental unit. Most ponderosa pine stands were >25 cm DBH, whereas most aspen stands were <25 cm DBH. Thus, we combined the tree size categories of vegetation types and analyzed data using vegetation type and overstory canopy cover categories. We eliminated variables that did not occur on <10% of the sites and then used principal components analysis to identify important variables that captured the vegetation structure. We compared vegetation characteristics at sites selected by elk with random sites within vegetation structural stages using multiple response permutation procedure (MRPP) which is an iterative randomization test of distribution that is not predicated on assumptions about the data (Mielke and Berry, 2001). We report results of the MRPP test for variables that were directly relevant to the description of the vegetation structural stage and other significant variables. We did not have enough observations to evaluate bedded and feeding elk within vegetation structural stages separately, so we reported the number of observations of radio marked individuals that were foraging or bedded but we regularly observed other elk foraging and bedded simultaneously within the same herd. We conducted analyses of vegetation characteristics at sites selected by elk within vegetation type/overstory categories using multiple response permutation procedure (Mielke and Berry, 2001).

4. Results

We characterized vegetation at 615 sites where radio-collared elk were observed and 509 random sites. Three hundred twenty-one elk locations were identified as bed sites and 294 were forage sites; 497 observations were of females and 118 observations were males (Table 1). In general, elk were spread across the study area in relatively small herds. Slightly larger groups occurred in the northern portion of the study area (5.3 ± 0.3, [$\bar{x} \pm$ SE]) than in the southern portions (4.4 ± 0.3). We examined our data for vegetative patterns that differences between sexes and seasons, and found no meaningful results. We attributed this to the overall homogeneity of vegetation patterns on the Limestone Plateau of the Black Hills.

Most of the elk in aspen occurred in stands with ≤70% overstory canopy cover; only 6 observations occurred in aspen with >70% overstory canopy cover (Table 1). Elk used structural stages of aspen with ≤70% overstory equally for both foraging and bedding ($n = 27$ of 54 observations). Although sample sizes were small most observations of elk in aspen with >70% overstory were bedded. When in aspen, elk seemed to select for sites with lower density of trees. Elk also selected for lower ($P \leq 0.01$) basal area while in aspen with 0–40% canopy cover than occurred at random sites; but in aspen with 41–70% canopy cover, selection for lower basal area was not evident, despite selection for lower tree density. Elk selected for sites with less ($P \leq 0.01$) western snowberry and about 6% cover of common juniper in aspen stands. Ponderosa pine was typically present in aspen stands selected by elk and occasionally ponderosa pine was the dominant tree in terms of basal area over aspen or birch.

While in grasslands, 98% of elk observations were recorded as foraging. Grassland sites selected by elk had more ($P < 0.01$) grass cover and less ($P = 0.02$) forb cover than random grassland sites. While in grasslands, elk were typically located near cover edges, thus sites contained a few trees but did not differ from the tree component in random grassland sites.

Elk used ponderosa pine with 0–40% overstory cover for bedding and foraging similarly (49% and 51% of observations, respectively). Within these open canopy pine stands, elk sites had slightly greater pine basal area ($P = 0.07$) and overstory cover ($P = 0.01$), less standing visual obstruction ($P < 0.01$), less understory vegetation ($P = 0.05$), but more grass cover, less shrub cover ($P < 0.01$), less western snowberry ($P < 0.01$), and less forb cover ($P < 0.01$) than random estimate within this vegetation structural stage.

Of the elk observations in ponderosa pine with 41–70% overstory cover, 60% were bedded and 40% were foraging. While in these stands, elk sites had less pine and aspen basal area ($P = 0.05$), less standing visual obstruction ($P < 0.01$), less forb cover ($P < 0.01$), less shrub cover ($P = 0.07$), less western snowberry cover ($P < 0.01$), and less common juniper cover ($P = 0.06$) than random estimates in these stands.

In dense ponderosa pine (>70% overstory cover), 65% of elk observations were identified as bedded and 35% were forage sites. Within these stands, elk sites had less pine basal area ($P = 0.08$), more understory cover ($P = 0.07$), more grass cover ($P = 0.04$), less forb cover ($P = 0.05$), more shrub cover ($P = 0.05$), but less western snow berry cover ($P < 0.01$), and more common juniper cover ($P = 0.04$) than random sites.

5. Discussion

The decisions elk make in selecting habitats vary among scales (Anderson et al., 2005). Forest stands in the Black Hills, particularly ponderosa pine, have been managed extensively under even-aged management for at least the past 50 years and third-order selection (e.g., Johnson, 1980) by elk is evident (Rumble et al., 2007). Consequently, we expected a high degree of homogeneity within stands of similar vegetation structural stage that were selected by elk. Nonetheless, we discovered patterns of selection within stands that differed from the average conditions in stands with the same vegetative structural stage classification. Heterogeneity in forest conditions within stands was greater than we expected. Basal area from silviculture prescriptions for small research plots when subdivided varies ±18–20% within the plot (Schmid et al., 2007).

Aspen regenerates following disturbances such as fire or clear cutting by sprouting often resulting in even-aged stands as well. Nonetheless, elk selected sites within stands of similar vegetative characteristics that differed from characteristics ascribed to a particular vegetation structural stage. In all structural stages of aspen, elk selected sites with fewer stems and less basal area than typical of stand descriptions. Aspen in the Black Hills typically has extensive and diverse understory vegetation (Severson and Thilenius, 1976) in which both western snowberry and white coralberry (*S. albus*) occur (Larson and Johnson, 1999). However, snowberry was a minor component in the aspen stands in our study and elk selected sites with even less snowberry than was usually found in the aspen stands. We often observed elk bedded in or near common juniper in both aspen and pine stands. Selection of sites in open aspen stands with common juniper corresponded with sites that also had some ponderosa pine; 13 of 19 sites with >5% cover by common juniper also had ponderosa pine at the site. In the next decade, forest management direction will be to increase the extent of aspen from 4% to about 8% of the Black Hills (Phase II, Amend. 6, Black Hills Land and Resource Management Plan, BHNF, Custer, SD, 2005). Management of aspen usually entails removal of conifer trees to slow seral progression to a conifer vegetation type and cutting to promote sprouting (e.g., Fitzgerald and Bailey, 1984; Jones and Schier, 1985; Mueggler, 1985).

Elk used grasslands in the Black Hills more extensively at night for foraging than during the day (Rumble et al., 2007). Diurnal use of grasslands by elk was nearly always (98%) for foraging. This selection was manifested by selection for greater grass cover at elk sites. Graminoids, and in particular Kentucky bluegrass (*Poa pratensis*), were prominent food items of elk in the southern Black Hills (Wydeven and Dahlgren, 1983). Elk sought out grass-dominated areas (predominantly meadows) as well in our study. If trees were present near elk sites in grasslands, they comprised only a minor component of the vegetation. We suspect trees probably provided increased security as these sites would typically have been near the forest meadow edge.

Ponderosa pine comprised >80% of this study area and is managed intensively for timber production in the Black Hills predominantly using even-aged management. Interestingly, we found that elk used open canopy ponderosa pine (≤40% overstory canopy cover) equally for foraging and bedding. Within open pine stands, elk selected sites that represented slightly more dense stands than occurred on average. This was evident by the increased pine basal area, overstory canopy cover, and standing visual obstruction. During the daytime, we believe elk selected these sites within open pine stands that provided a higher degree of security cover. These areas also provided shade with subsequent lower daytime air temperatures for elk (Millspaugh et al., 1998). The percentage of bedded observations increased when elk selected ponderosa pine stands with greater overstory canopy cover. Within the ponderosa pine with 40–70% overstory cover elk sought out similar conditions as

Table 1
Key forest characteristics at elk and random sites in grasslands, aspen, and ponderosa pine vegetation structural stages of the central and northern Black Hills, SD.[a,b]

Vegetation structural stage (vegetation characteristic)	Elk sites $\bar{x} \pm$ SE	Random sites $\bar{x} \pm$ SE	P-value[c]
Aspen 0–40% overstory canopy cover	n = 25	n = 44	
Aspen basal area (m^2/ha)	5.1 ± 1.1	10.5 ± 1.5	0.01
Aspen density (trees/ha)	348.2 ± 75.9	1458.9 ± 279.2	<0.01
Ponderosa pine basal area (m^2/ha)	8.1 ± 2.1	5.1 ± 1.3	0.11
Percent overstory canopy cover	51.9 ± 4.2	47.3 ± 2.6	0.46
Percent total understory cover (n = 19)[d]	66.7 ± 4.5	80.7 ± 2.2	<0.01
Percent grass cover (n = 19)	29.2 ± 4.9	35.5 ± 3.3	0.12
Percent forb cover (n = 19)	20.3 ± 3.8	36.7 ± 2.6	<0.01
Percent shrub cover (n = 19)	25.5 ± 2.7	31.0 ± 2.4	0.10
Percent common juniper cover	6.5 ± 1.1	3.6 ± 0.6	0.01
Percent western snowberry cover	1.5 ± 0.4	3.8 ± 0.5	<0.01
Aspen 41–70% overstory canopy cover	n = 29	n = 41	
Aspen basal area	9.3 ± 2.2	11.1 ± 1.6	0.33
Aspen density (trees/ha)	614.5 ± 133.6	1212.5 ± 165.9	<0.01
Ponderosa pine basal area (m^2/ha)	6.2 ± 1.6	6.4 ± 1.6	0.82
Percent overstory canopy cover	60.6 ± 4.1	52.2 ± 3.1	0.16
Percent total understory cover (n = 13)	73.7 ± 3.5	78.2 ± 2.6	0.26
Percent grass cover (n = 13)	31.3 ± 4.4	31.3 ± 3.6	1.00
Percent forb cover (n = 13)	25.5 ± 5.0	33.2 ± 2.8	0.05
Percent shrub cover (n = 13)	28.1 ± 2.6	31.3 ± 2.1	0.40
Percent common juniper cover	5.8 ± 1.3	3.9 ± 0.9	0.14
Percent western snowberry cover	0.8 ± 0.3	3.8 ± 0.4	<0.01
Aspen >70% overstory canopy cover	n = 6	n = 50	
Aspen basal area	4.7 ± 2.8	16.2 ± 1.8	0.03
Aspen density (trees/ha)	332.9 ± 168.4	1513.7 ± 195.2	0.02
Ponderosa pine basal area (m^2/ha)	12.6 ± 6.2	4.6 ± 1.0	0.25
Percent overstory canopy cover	62.3 ± 7.8	64.8 ± 2.8	0.90
Percent total understory cover	73.0 ± 13.7	79.1 ± 7.1	1.00
Percent grass cover	34.6 ± 10.9	28.3 ± 3.1	0.89
Percent forb cover	17.6 ± 5.8	33.8 ± 2.4	0.07
Percent shrub cover	27.6 ± 7.0	33.1 ± 2.1	0.70
Percent common juniper cover	2.0 ± 1.2	2.1 ± 0.6	0.81
Percent western snowberry cover	0.4 ± 0.4	3.0 ± 0.4	<0.01
Grasslands	n = 25	n = 44	
Aspen basal area	3.6 ± 1.1	2.8 ± 1.0	0.40
Ponderosa pine basal area	2.6 ± 1.0	1.8 ± 0.8	0.41
Percent overstory canopy cover	15.6 ± 4.6	11.8 ± 0.8	0.74
Percent total understory cover (n = 16)	85.1 ± 2.5	85.1 ± 1.5	1.00
Percent grass cover (n = 16)	64.0 ± 6.2	59.6 ± 3.6	<0.01
Percent forb cover (n = 16)	30.1 ± 6.1	32.8 ± 2.0	0.02
Percent shrub cover (n = 16)	12.0 ± 3.0	10.9 ± 1.9	0.81
Percent western snowberry cover	1.2 ± 0.6	3.3 ± 0.7	0.09
Ponderosa pine 0–40% overstory canopy cover	n = 232	n = 75	
Aspen basal area	1.2 ± 0.2	1.6 ± 0.6	0.78
Ponderosa pine basal area	14.6 ± 0.7	13.4 ± 1.4	0.07
Percent overstory canopy cover	46.7 ± 1.2	40.3 ± 2.3	0.01
Standing visual obstruction (n = 214)[e]	59.3 ± 1.8	74.5 ± 2.8	<0.01
Percent total understory cover (n = 145)	62.5 ± 1.7	68.8 ± 1.9	0.05
Percent grass cover (n = 145)	33.1 ± 1.6	28.7 ± 2.1	0.10
Percent forb cover (n = 145)	14.1 ± 1.1	19.3 ± 1.6	<0.01
Percent shrub cover (n = 145)	24.5 ± 1.1	30.9 ± 1.8	<0.01
Percent common juniper	4.3 ± 0.39	3.9 ± 0.67	0.48
Percent western snowberry	0.8 ± .02	4.1 ± 0.3	<0.01
Ponderosa pine 41–70% overstory canopy cover	n = 180	n = 64	
Aspen basal area	0.9 ± 0.2	2.3 ± 0.7	0.06
Ponderosa pine basal area	18.3 ± 1.0	21.5 ± 1.6	0.06
Percent overstory canopy cover	50.6 ± 1.4	52.7 ± 2.1	0.50
Standing visual obstruction (n = 162)	66.5 ± 1.8	80.0 ± 2.8	<0.01
Percent total understory cover (n = 126)	58.7 ± 1.9	63.9 ± 2.8	0.16
Percent grass cover (n = 126)	28.5 ± 1.8	24.3 ± 2.3	0.22
Percent forb cover (n = 126)	11.1 ± 1.2	18.6 ± 2.0	<0.01
Percent shrub cover (n = 126)	26.2 ± 1.2	30.8 ± 2.1	0.07
Percent common juniper	5.1 ± 0.60	7.5 ± 1.25	0.06
Percent western snowberry	0.6 ± 0.1	2.8 ± 0.4	<0.01
Ponderosa pine >70% overstory canopy cover	n = 20	n = 55	
Aspen basal area	2.6 ± 1.2	1.6 ± 0.7	0.36
Ponderosa pine basal area	21.5 ± 3.9	27.8 ± 1.7	0.08
Percent overstory canopy cover	71.4 ± 3.9	68.9 ± 2.0	0.31
Standing visual obstruction (n = 19)	81.5 ± 5.8	88.3 ± 2.3	0.41
Percent total understory cover (n = 14)	53.5 ± 4.2	46.0 ± 3.4	0.07
Percent grass cover (n = 14)	18.4 ± 3.9	11.0 ± 1.4	0.04

Table 1 (*Continued*)

Vegetation structural stage (vegetation characteristic)	Elk sites x̄ ± SE	Random sites x̄ ± SE	P-value[c]
Percent forb cover ($n = 14$)	5.9 ± 1.7	12.4 ± 1.7	0.05
Percent shrub cover ($n = 14$)	31.6 ± 2.5	25.9 ± 1.9	0.05
Percent common juniper	9.0 ± 2.1	4.9 ± 1.0	0.04
Percent western snowberry	0.5 ± 0.2	2.2 ± 0.3	<0.01

[a] Key characteristics were identified through data reduction and principal components. Vegetation characteristics directly relevant to the description of the vegetation structural stages and other significant characteristics are reported.
[b] Vegetation structural stages are hierarchal classification of forest vegetation of 10–32 ha stands from vegetation type, diameter-at-breast height, and overstory canopy cover (Buttery and Gillam, 1983) and are used by the basis of management, planning and inventory by the Black Hills Nation Forest.
[c] Multiple response permutation test (Mielke and Berry, 2001) of equal distributions.
[d] Sample sizes in parentheses apply to analyses of understory characteristics of elk that had <10% snow cover or standing visual obstruction was not measured at some early elk locations.
[e] Standing visual obstruction was tallied as counts of squares visible and converted to percent obstruction for interpretation in table.

in the open pine. For example, even though most elk in pine stands with 40–70% overstory cover were bedded, basal area of ponderosa pine at elk sites was similar ($P = 0.62$, MRPP test) to that in the ponderosa pine <40% overstory canopy cover. Within the pine stands with >70% overstory canopy cover, there was a tendency for elk to select sites with less tree basal area. Although most elk in these stands were bedded, there were very few observations in dense pine stands. Thus, in ponderosa pine stands elk appeared to select moderately open stands.

As pine basal area increases beyond about 18.5 m^2/ha (approximately 40% overstory cover [Bennett et al., 1987]) understory production declines dramatically (Uresk and Severson, 1989). Our study occurred on very productive soils in the Black Hills (Bennett et al., 1987). The precipitation patterns in the Black Hills differ from other western landscapes and 85% of the precipitation occurs during the spring and summer growing season. After >50 years of even-aged management we found there is enough within stand diversity to enable elk to select sites that provided both security and forage.

We were surprised that sites selected by elk had less hiding cover than random sites. Even though the Black Hills have extremely high road densities (~3.2 km/km^2, 1996 Land and Resource Management Plan, BHNF, Custer, SD), most observations of radio-collared elk in ponderosa pine occurred in sites that provided only 50–60% obstruction of a standing elk at 61 m, which was less cover than was available at random sites in ponderosa pine stands with $\leq$70% overstory cover. During our study, we only observed 1 natural mortality event (of 80 total radio-collared individuals): a female elk was killed from an attempted, but failed, mountain lion (*Puma concolor*) attack. Hence, we do not believe the observed patterns of selection were driven exclusively by avoidance of predation (e.g., Laundre, 2010) or human activity associated with road densities (Lyon, 1983; Unsworth et al., 1993; Lyon and Christensen, 2002). Consequently, we believe the definition of hiding cover for elk should be revised for this forest area. The range of ponderosa pine basal area selected by most elk varied from about 15 to 18 m^2/ha. Despite the reduced security cover at sites selected by elk in this study, the surrounding forest in these stands could have been denser and provided additional security. Elk selection of forest sites under even-age management of ponderosa pine may vary throughout the west.

6. Implications for forest management

Most of the BHNF is managed for the 41–70% canopy cover category. Despite >50 years of intensive even-aged management in ponderosa pine stands of the BHNF, there currently is enough heterogeneity inherent in even-aged prescriptions that this elk population can meet or exceed its habitat resource needs. Current trends toward managing stands of ponderosa pine for less tree basal area and overstory cover should consider maintaining patches of higher canopy cover within stands of $\leq$40% canopy cover, as elk selected denser forest conditions while in these stands. In addition, elk hiding cover modeling efforts for the BHNF should be revised from Thomas et al. (1979) and subsequent models to more accurately reflect the use patterns exhibited by elk in this forest.

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