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Abstract

Despite several studies that demonstrate general responses of elk (*Cervus elaphus*) to roads and people, land management agencies continue to struggle with management of off-highway vehicles, recreation, and roads. The Black Hills National Forest has a greater road density (3.2 km/km^2) than any other national forest. We used Global Positioning System (GPS) telemetry collars to quantify responses of elk to human activity by quantifying their movements during the 2000 and 2001 big game hunting seasons in the Black Hills, South Dakota. Three hunting seasons, 1 month each, occurred consecutively from 1 September to 30 November and included limited entry archery elk, limited entry firearm elk, and limited entry firearm deer (*Odocoileus* spp.). We used the number of licenses issued times the average days hunters were in the field to quantify human activity. Average distance/hr between successive locations increased during the 10-day interval that began on the opening date of the archery elk season ($P \leq 0.10$) compared to the previous 10 days in late August. Movements by elk following the opening of the firearm elk season were similar to those during the last 10 days of September, but greater ($P \leq 0.10$) than movements during the last 10 days of August. Elk movements during 10 days after the opening of the firearm deer season (1 November) were greater ($P \leq 0.05$) than both the last 10 days of August and the last 10 days of October. Movements increased on the opening weekends of hunting seasons and the day after Thanksgiving, which is a traditional day for hunting deer in the Black Hills. Individual animals selected habitats differently ($P < 0.01$) but also selected ($P < 0.10$) habitats different from those available within 500 m of locations for each 10-day interval only from 22 August through 31 October. Elk dispersion patterns relative to roads varied with the hunting season. During the archery season, elk were closer to primary and secondary roads than before the season. During the firearm elk and firearm deer seasons, elk moved away from primary and secondary roads. Based on foraging models, elk may require 0.5 hr of additional foraging time to accommodate greater movements resulting from human activity. In light of an increased demand for outdoor recreational opportunities, our study provided additional support for land management agencies to develop travel management policies that provide elk with areas of little human disturbance.

Key words: Black Hills, *Cervus elaphus*, elk, GPS telemetry, habitat selection, human activity, off-road vehicles, road density, South Dakota

Introduction

Others have documented a negative relation between roads and elk (e.g., Lyon 1979, Rowland et al. 2000) based on a premise that hunting quickly conditions elk to avoid people and roads (Christensen et al. 1991, Wertz et al. 1996). Greater hunter access and greater road densities increase the probability of elk mortality during hunting seasons (Unsworth et al. 1993). Even

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moderate disturbance to elk from limited-entry hunting seasons in Custer State Park, South Dakota, resulted in a redistribution of elk to areas that minimized contact with hunters (Millspaugh et al. 2000). However, in the absence of negative reinforcement, elk are not affected by people and may be attracted to areas where they are protected (Shultz and Bailey 1978, Thompson and Henderson 1998).

Behavioral response of elk to human activity is multi-faceted and likely specific to conditions of the area. For example, extent of security (Hillis et al. 1991) and topography can mitigate some negative responses to human disturbance (Edge and Marcum 1991). Elk respond differently to different recreational disturbances (Wisdom et al. 2004). Responses of elk to human activity include increased use of cover (Irwin and Peek 1983), increased movements (Cole et al. 1997), and avoidance of roads (Rowland et al. 2000). Ward and Cupal (1979) noted that humans on foot and the close-range discharge of a firearm resulted in increased heart-rates of elk. A single disturbance event/day can elicit a flight response by elk (Wisdom et al. 2004).

Although understanding the effects of human disturbance is important to manage elk populations, estimating elk response to disturbance, such as recreation, may be difficult because timing may constrain occurrence of human activity to weekends or hunting seasons. Before Global Positioning System (GPS) technology, episodes of monitoring elk distribution from radio telemetry also varied (e.g., Lyon and Canfield 1991) that potentially led to underestimating the effects of disturbance on elk; obtaining adequate sample sizes without disturbing elk and eliciting a response to the researcher also can be difficult. Development of GPS technology allows obtaining frequent locations of animals in a systematic manner without disturbing them. We studied the effects of human activity on the dispersion patterns and habitat selection by individual elk during three hunting seasons from 1 September to 30 November 2000 and 2001 in the Black Hills, South Dakota. We hypothesized that elk, in response to human disturbance, would increase movements, seek areas with relatively high cover, or avoid roads.

Study Area

We monitored instrumented elk in the Limestone Plateau area of the central Black Hills of western South Dakota (Fig. 1). Elevation ranged from approximately 1800 m in the southern part of the study area to 2040 m in the north. Annual precipitation averages 51-61 cm (Orr 1959). Ponderosa pine (*Pinus ponderosa*) is the dominant vegetation type, comprising 78 percent of the area. White spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*) occur on mesic sites and north-facing slopes and comprise 5 percent and 4 percent of the area, respectively. Aspen in this area is seral to both ponderosa pine and white spruce (Hoffman and Alexander 1987). Meadow and grassland vegetation types comprise 12 percent of the area and several uncommon vegetation types comprise the remainder of the study area.

The Black Hills National Forest has an average road density of 3.2 km/km^2 (T. Mills, GIS Specialist, Black Hills National Forest, personal communication); road density in our study area was 2.3 km/km^2. Forest travel policy allows motorized vehicle travel on and off roads throughout

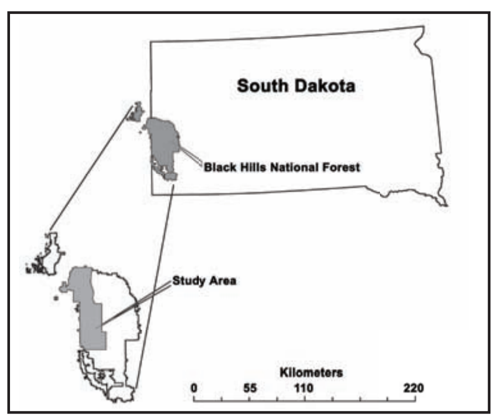

Figure 1. Map of South Dakota showing location of Black Hills National Forest and study area within the Black Hills National Forest boundary.

the forest except for special management areas (USDA Forest Service 1996). Our study area included 1133 km^2 (64%) of hunt unit 402 in the Black Hills of South Dakota.

Methods

Human Activity

We estimated human activity by multiplying the number of licenses times the average number of days spent hunting. We used statistics compiled by South Dakota Department of Game, Fish, and Parks (SDGFP) for the archery elk, firearm elk, and firearm deer seasons and from post-season mail surveys (Smith 2001). Permits for archery elk, firearm elk, and firearm anterless/spike deer licenses were specific to Hunt Unit 402. However, branch-antlered firearm deer licenses were issued for the entire Black Hills area. We estimated the number of deer licenses in Hunt Unit 402 by back calculating from hunter success rates and from estimates of harvest of branch-antlered deer in the unit to which we then added the antlerless/spike deer permits. During 2000, 73 archery elk licenses were issued and hunters averaged 10.8 days in the field; 344 firearm elk licenses were issued and hunters averaged 6.3 days in the field; and approximately 2848 deer licenses were attributed to this unit and hunters averaged 2.5 days in the field. During 2001, 80 archery elk licenses were issued and hunters averaged 12.4 days in the field; 410 firearm elk licenses were issued and hunters averaged 6.7 days in the field, and approximately 2480 deer licenses were associated with this unit and hunters averaged 2.8 days in the field.

GPS Telemetry

In February 2000, we used a net gun fired from a helicopter to capture four female elk from different herd groups. We equipped each elk with a GPS telemetry unit affixed to a vinyl collar and programmed to collect locations at 2-hr intervals from 22 August to 30 November. An electro-magnetic mechanism in each collar released the collar on 1 December 2001, collars were retrieved, and data were downloaded. During March to early April 2001, we captured 2 adult females and 2 yearling males using modified collapsible clover traps (McCullough 1975, Thompson et al. 1989). These collars released on 1 March 2002 at which time we retrieved the collars and downloaded the data.

More individuals with GPS collars would have been desirable. At the time of our study, GPS telemetry on animals was just emerging as a reliable technique to monitor animal distribution. Earlier in our study we had four collars and associated equipment from a different manufacturer costing > $25,000, all of which failed. We determined that strategy of obtaining multiple locations over short intervals from a few animals was better than standard radio telemetry on many more animals. Straight line distances between successive locations obtained by radio telemetry would have underestimated movements by elk in areas with very high road densities and repeated disturbance.

Mature male elk may differ from females in their response to roads (Marcum and Edge 1991). Yearling males were regularly observed with females and calves. As 2 year-olds, males segregated from cows and calves wandering movements were observed. Consequently, we believe these animals represent movements similar to those of females with GPS collars.

Analyses

Data from the GPS units in 2000 were differentially corrected using data from a base station about 16 km south of the study area. Selective availability of GPS satellites was discontinued and data from 2001 were not differentially corrected. We analyzed and present data obtained only during the daylight hours that coincided with the period of human activity. Euclidean distance between successive locations was calculated and standardized by calculating distance/hr between successful locations. We assigned locations to 10-day intervals from 22 August to 30 November; the interval 21 October to 31 October was 11 days, so the beginning of each hunting season was the first day of a 10-day interval. We displayed data for elk movements using box-and-whisker plots for 10-day intervals and for days within 10-day intervals. Because box-and-whisker plots display characteristics in the distribution of elk movements, they are useful for statistical tests for differing distributions. A control was not possible in this study, so we compared elk movements associated with increased human activity from hunters to elk movements before any hunting seasons (22-31 Aug) and the interval immediately before the firearm hunting seasons (21-30 Sep and 21-31 Oct, respectively). Because some movements might have been associated with seasonal activities of elk, we also compared movements for 10-day intervals before and after each hunting season opened. Consequently, we tested hypotheses that (1) elk movements during 10-day intervals of a hunting season did not differ from movements during 22–31 August, and (2) elk movements during 10-day intervals during the firearm seasons did not differ from the 10-day interval before the firearm seasons. Our data exhibited skewed distributions and we used multiple response permutation procedure (MRPP, Mielke and Berry 2001) to test for differences in distribution of elk movements among 10-day intervals. Multiple comparisons were made using the Peritz closure method (Petrondas and Gabriel 1983). These tests maintained experiment-wise error protection for determination of significant differences in the multiple range tests among 10-day intervals. Exact *P*-values are only available in the omnibus tests; we set significance of multiple range tests at predetermined α-levels. Consequently, we ran the procedure at $\alpha \leq 0.05$ and $\alpha \leq 0.10$ and reported the results accordingly.

We mapped and classified vegetation on private lands in the study area to vegetation structural stages described by Buttery and Gillam (1983) using 1:24,000 digital ortho-quad maps and 1:24000 aerial photographs. Ocular estimates of vegetation structural stage on private lands were referenced with vegetation structural stages of adjacent USDA Forest Service lands classified in the Resource Information System (RIS) for 4- to 32-ha land units. GIS coverage of the RIS data was then edited to include private lands. We used ArcInfo (Environmental Systems Research Institute 2001) to create 500 m buffers around each point, and intersected these with the GIS vegetation coverage. For analyses, we combined overstory canopy cover and diameter-at-breast height (DBH) categories of aspen and white spruce vegetation types because they comprised ≤ 5 percent of the area; ponderosa pine was combined across DBH categories into three overstory canopy cover categories (0-40%, 41-70%, and > 70%; Buttery and Gillam 1983). To evaluate whether elk selected for dense forest cover in response to human disturbance, we combined ponderosa pine > 70 percent overstory canopy cover and white spruce into a dense forest category. We then used a Design III model (Manly et al. 1993) to test the hypotheses that elk selected habitats randomly during each 10-day interval. Selection ratios resulting from these tests > 1 are indicative of preference while selection ratios < 1 are indicative of avoidance relative to availability in this study.

We adopted the road classification used by the Black Hills National Forest of primary (> 35 vehicles/week), secondary (7 - 35 vehicles/week), and primitive (< 7 vehicles/week) roads in the study area. We then generated 2290 random points with a uniform distribution across the study area using Animal Movements (Hooge et al. 1999) in ArcView 3.2 (Environmental Research Systems Institute 1998). Because elk were distributed farther from primary roads than secondary roads and farther from secondary roads than primitive roads (Benkobi et al. 2004), we assumed that the effects of roads on dispersion of elk were hierarchal. Therefore, we constructed buffer strips in ArcMap (Environmental Research Systems Institute 2001) around primary and secondary roads at distances that use and availability intersected (350 m for primary roads and 240 m for secondary roads, unpublished data, Rocky Mountain Research Station, Rapid City, SD). Before calculating the distance from random points to the nearest secondary road, we clipped the 350-m buffer around primary roads from the GIS coverage. Likewise, before calculating the distance from random points to the nearest primitive road, we clipped the buffers around primary and secondary roads from the coverage. We used Tukey's bi-weight method (Mosteller and Tukey 1977) to estimate average ± SE of distances to roads. We then constructed 95-percent confidence intervals around average distances from elk and random points to the various road categories. The distance of elk to roads during each 10-day interval was compared individually to the distance of random points to roads so as not to exceed the degrees of freedom for statistical tests.

Results

We obtained 2779 daytime GPS locations within our study area boundary. We censored 47 daytime GPS locations because they occurred outside the study area where we did not have GIS vegetation classification. GPS telemetry success rates, e.g., percent attempted locations that were successful, averaged 87 percent during our study and varied from 82 percent in late August to > 90 percent in November.

Human activity averaged 890 hunter-days during archery elk seasons, 2457 hunter-days during firearm elk seasons, and 7032 hunter-days during firearm deer seasons. Thus, each successive hunting season resulted in approximately a three-fold increase in human disturbance.

Elk movements

Archery Season.—Movements between successive daytime locations of elk differed ($P \leq 0.10$) between the 10-day interval from 22-31 August, before the archery season, and the 10-day interval from 1-10 September after the archery season opened (Table 1, Fig. 2). Before the archery season, elk were relatively sedentary in their behavior. From 1-10 September, movements of elk that exceeded the median increased substantially and were probably what the MRPP test was sensitive to. Box and whisker plots of hourly movements for days within 10-day intervals showed that elk rarely moved more than 500 m in an hour before the archery season. The median and average distance between elk locations before the archery

Table 1. Average distance per hour between elk locations from GPS telemetry in 10-day intervals from 22 August to 30 November.

Season / Dates	Distance (m) between locations: $\bar{x}$	±	SE	Median	Different from: 22-31 Aug[1]	Different from: last 10 days of previous season[2]
22 – 31 August	120	±	7.4	66	NA	
Archery Elk						
1 – 10 September	162	±	13.1	74	*	
11 – 20 September	119	±	9.3	57	NS	
21 – 30 September	153	±	11.9	73	*	
Firearm Elk						
1 – 10 October	176	±	13.4	90	*	NS
11 – 20 October	172	±	17.1	80	*	
21 – 31 October	126	±	10.9	58	NS	
Firearm Deer						
1 – 10 November	188	±	18.1	79	**	**
11 – 20 November	132	±	13.2	67	NS	
21 – 30 November	224	±	22.8	115	**	

[1] Results from MRPP test (Mielke and Berry 2001) using the Peritz closure method (Petrondas and Gabriel 1983) of movements by elk for 10-day intervals during hunting seasons with movements from 22 - 31 August. * = significance at $\alpha \leq 0.10$, ** = significance at $\alpha \leq 0.05$.

[2] Results from MRPP test (Mielke and Berry 2001) using Peritz closure method (Petrondas and Gabriel 1983) of movements by elk for the 10-day interval after the season opened with the previous 10-day interval. * = significance at $\alpha \leq 0.10$, ** = significance at $\alpha \leq 0.05$.

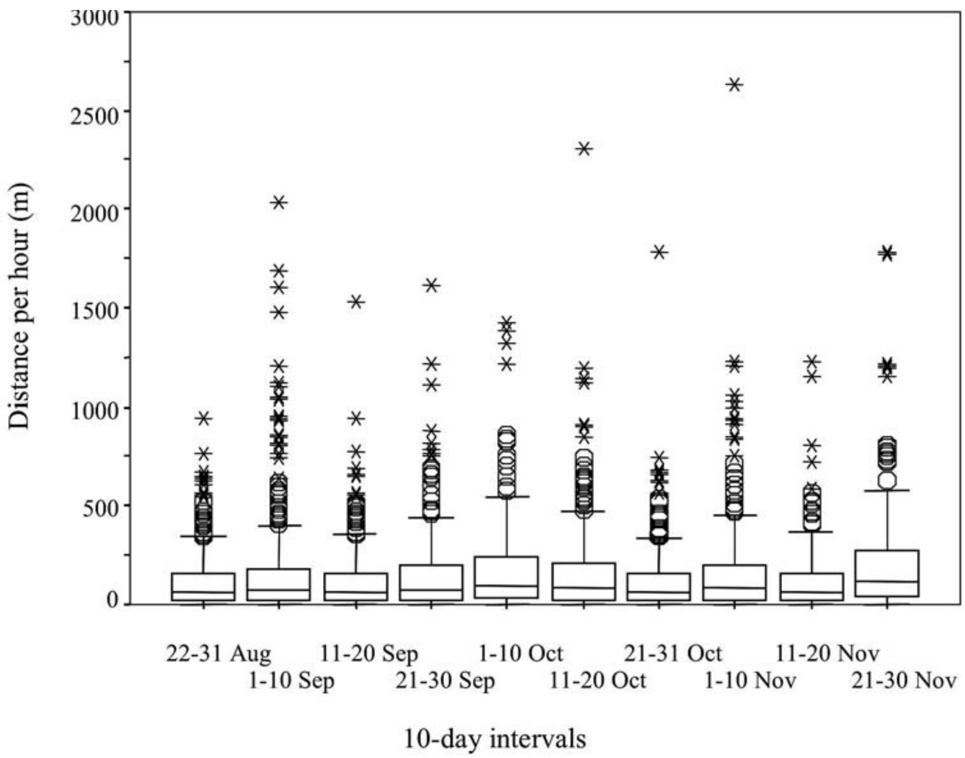

Figure 2. Box-and-whisker plots of distance per hour between GPS locations of elk for 10-day incremental periods from 22 August to 30 November of 2000 and 2001. Boxes represent the inner two quartiles above and below the median (indicated by a horizontal line) and whiskers are 1.5 times the inner quartile distance. Outliers are labeled with a circle and extreme values are labeled with an asterisk. To better show the differences between boxes the scale of distance per hour was limited to 1750/m hour. This resulted in elimination of 5 extreme data points.

season were 66 m and 120 m, respectively. Median distance between elk locations increased to 75 m and the average distance increased to 163 m the first 10 days of the archery season. The first weekend after the season opened was marked by increases in the spread of inner and outer quartile ranges above the median, but significant differences in these movements among days within the 10-day interval were not evident (Fig. 3). The 10-day interval from 11-20 September suggested a return to movement patterns observed before the archery season began ($P \geq 0.7$). Elk movements during the last 10 days of September exceeded ($P \leq 0.10$) those before the archery season began. The increased spread in the box-and-whisker plot the day before the firearm elk season was noteworthy. It occurred during the last weekend of the archery season.

Firearm Elk Season.—Movements (distance/hr) between successive elk locations during 1–10 October were similar ($P \geq 0.45$) to those during the last 10 days of the archery season (Table 1). Increased movements the last day of the archery elk season may have influenced this observed pattern. Elk movements from 1-10 October exceeded ($P \leq 0.10$) those from 22-31 August. Elk movements increased on the opening day of firearm elk season, and the first and second weekends of the season (Fig. 4). During the second 10-day interval of October, elk movements remained greater than 22-31 August ($P \leq 0.10$), but movements of elk the last 11 days of October were not different from late August ($P \geq 0.79$). Nonetheless, movements by elk increased during the last weekend of the season.

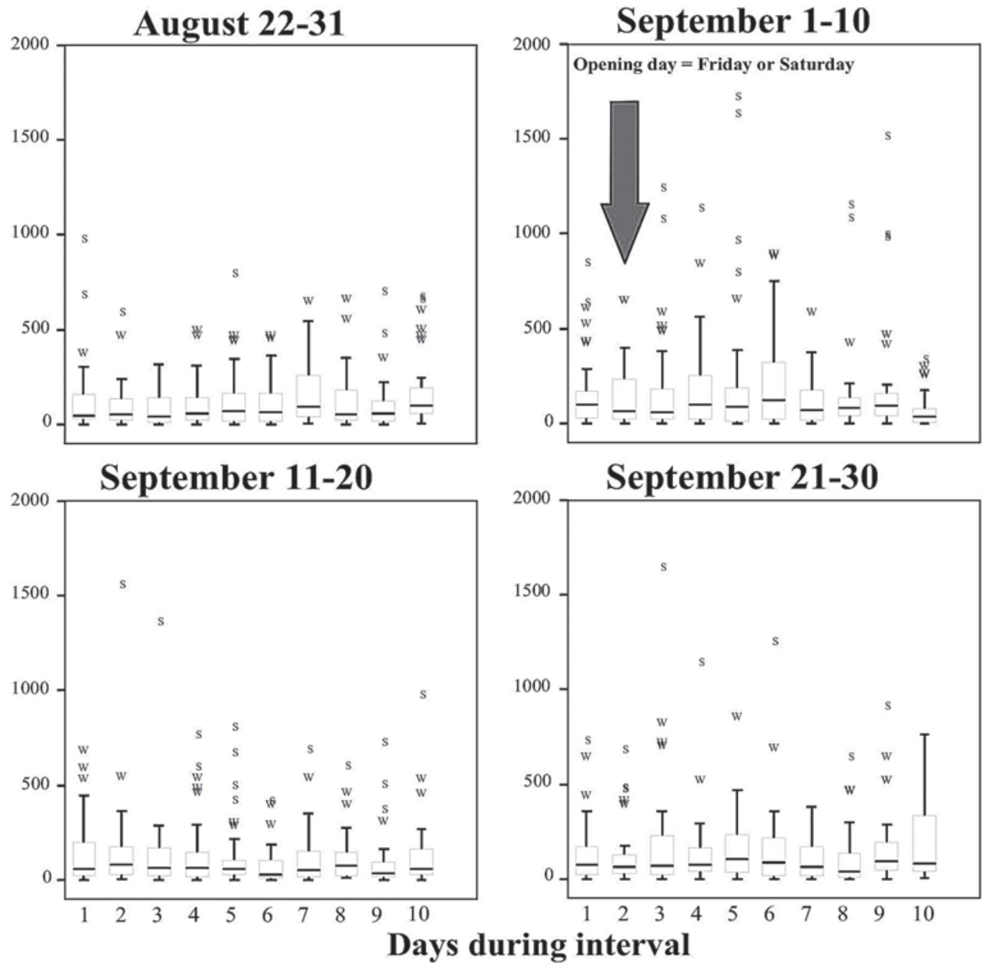

Figure 3. Box-and–whisker plots of distance per hour between successive GPS telemetry locations of elk from 22 August to 30 September of 2000 and 2001. Boxes represent the inner two quartiles above and below the median (indicated by a horizontal line) and whiskers are 1.5 times the inner quartile distance. Outliers are labeled with a w and extreme values are labeled with an s. Opening day of the archery elk season was a Friday or Saturday and the arrow indicates the first weekend.

Firearm Deer Season.—Elk movements after the opening of the firearm deer season on 1 November were greater ($P \leq 0.05$) than movements the last 10 days of the firearm elk season and greater ($P \leq 0.05$) than movements from 22-31 August (Table 1, Fig. 5). During the middle of the firearm deer season, elk movements were similar ($P \geq 0.97$) to those from 22-31 August. Movements by elk the last 10 days of the firearm deer season were greater ($P \leq 0.10$) than movements from 22-31 August. Average distance/hr between successive elk locations during this period exceeded that of any other 10-day interval during our study. We also observed a marked increase in dispersions of elk movements the day after Thanksgiving, a traditional day for deer hunting in the Black Hills.

Daytime elk movements the last 10 days of August averaged 1348 m/day. Daytime movements by elk increased 467 m/day for the first 10 days following the opening of archery elk on 1 September. After the opening of firearm elk season, daytime elk movements increased 566 m/day compared to the end of August. Daytime elk movements increased 544 m/day during the

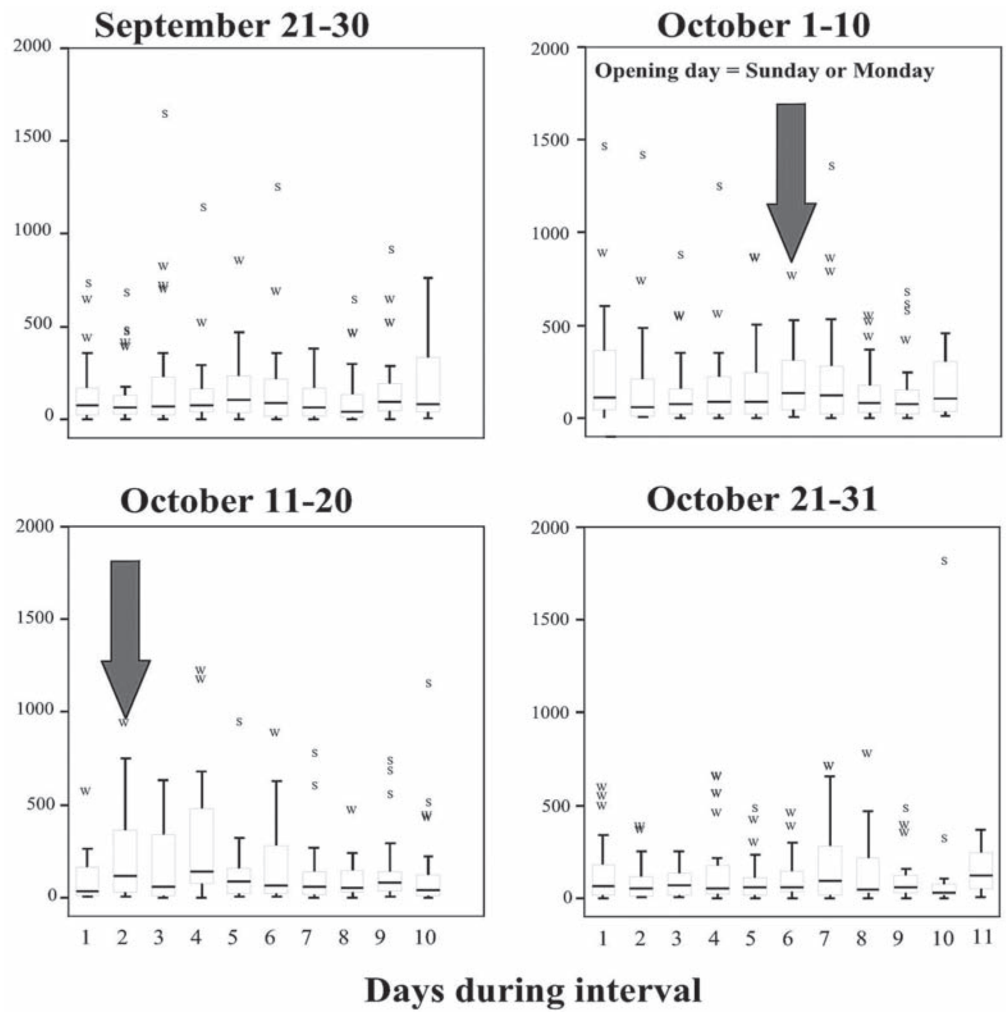

Figure 4. Box-and–whisker plots of distance per hour between successive GPS telemetry locations of elk from 21 September to 31 October of 2000 and 2001. See Figure 3 for explanation of box and whisker plots. Opening day of the firearm elk season was a Sunday or Monday and arrows indicate the first two weekends.

first 10 days of the firearm deer season when compared to the last 10 days of August, but increased 761 m/day during the last 10 days of November.

Dispersion of elk relative to habitat and roads

Elk selected habitats differently ($P < 0.10$) from habitats within 500 m of their locations during the 10-day intervals from 22 August thru 31 October. For the three 10-day intervals during November, patterns of habitat selection were not different from those available ≤ 500 m away ($P = 0.11$, 0.12, and 0.25, respectively). Habitat selection differed ($P < 0.01$) among animals during each 10-day interval. Although we can make few conclusive statements regarding the selection of habitats, a few patterns were evident: (1) the selection ratio for grasslands was positive prior to the opening of the archery elk season but was negative from 1 September through 30 November, and (2) we observed a clear pattern of declining selection ratios for grassland habitats associated with increasing human disturbance (Fig. 6). The selection ratio exhibited by elk during daylight

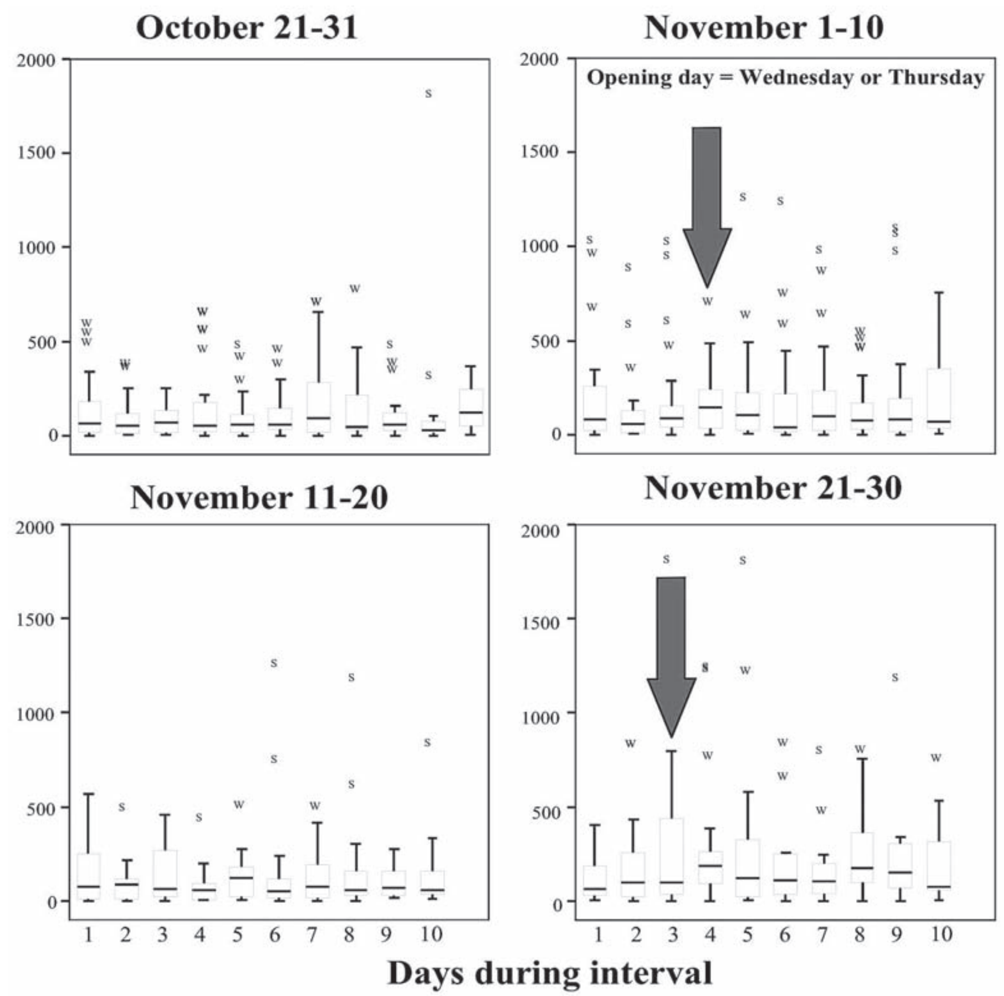

Figure 5. Box-and–whisker plots of distance per hour between successive GPS telemetry locations of elk from 21 October to 30 November of 2000 and 2001. See Figure 3 for explanation of box and whisker plots. Opening day of the firearm deer season was a Wednesday or Thursday and the arrows indicate the first weekend and the day after Thanksgiving.

periods was always positive for dense forest habitat (ponderosa pine or white spruce with > 70% overstory canopy cover).

After eliminating the effects of primary and secondary roads, elk were farther from primitive roads than random points within the study area for all 10-day intervals except 1-10 October (Table 2). Elk were farther from secondary roads through the period of 1-10 October after which elk dispersion patterns were indistinct relative to secondary roads. Elk locations relative to primary roads were similar to those for primitive roads in that elk were increasingly closer to primary roads during the 10-day intervals from 22 August to 10 October. After 11 October, the average distance of elk to primary roads increased through 30 November.

Discussion

Increased movement by elk coincided with increased human activity in the area followed by reduced movement similar to that before the hunting seasons. We believe that increased movement of elk following the opening of hunting seasons was a response to human activity and not to behavioral changes associated with fall

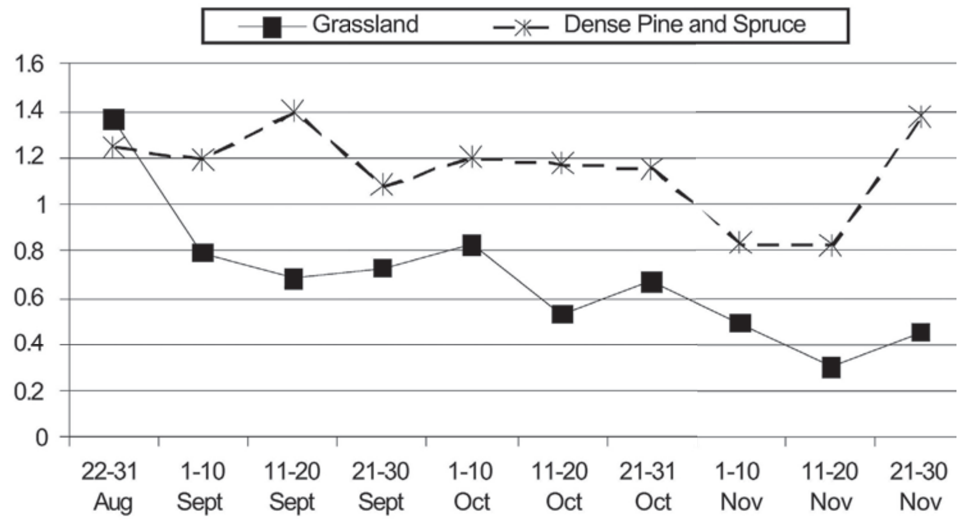

Figure 6. Selection ratios for grassland and dense forest (ponderosa pine > 70% overstory canopy cover and white spruce combined) for 10-day periods beginning in late August through 30 November.

rutting behavior.

Before 1 September, elk were relatively sedentary. In the days following the opening of the archery season, elk increased their movements, which might have been associated with recreation activities during Labor Day weekend. We believe that the increased movements by elk during the interval of 1-10 September did not result from human activities over Labor Day weekend because we detected significantly greater movements during the entire 10-day interval. Increased movements associated with the opening of the archery season were evident for ≥ 6 days. Conner et al. (2001) showed that elk behavior and movements were affected by archery hunters in Colorado. However, in Custer State Park, South Dakota, elk did not demonstrate significant behavioral responses to archery hunters in September (Millspaugh et al. 2000). The increased movements by elk during 21-30 September were likely influenced by scouting by firearm hunters and the end-of-season rush by archery hunters on 30 September.

The number of hunter-days that we recorded during the firearm elk season exceeded those during the archery season by about three times, and disturbance effects on elk movements lasted through the second weekend of the firearm season. In Custer State Park, South Dakota, elk avoided firearm hunters that was more notable in areas with less cover (Millspaugh et al. 2000). Increased movements by elk were also noted the day before the opening of the firearm elk season. Similar movement patterns by elk were noted before and after the firearm deer season. Opening of hunting seasons affected elk movements for about 6 days during the archery season, about 15 days during the firearm elk season, and about 10 days during the firearm deer season. Ward (1976), Hershey and Leege (1982), and Cassirer et al. (1992) noted effects of human activity and timber harvest on elk were often short term with elk returning to areas when the human activity ceased.

About 50 percent of our observations showed little or no movement between successive locations (lower quartile ranges) suggesting that elk remained nearly sedentary if undisturbed, perhaps in dense forest cover. We noted an increase in

Table 2. Average (± SE) distance (m) to the nearest primitive, secondary, or primary road of elk locations and random points for 10-day intervals between 22 August and 30 November of 2000 and 2001 in the Black Hills, South Dakota[1].

10-day interval	Classes of roads					
	Primitive roads[2]		Secondary roads		Primary roads	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
22 - 31 August	225.0	8.8A	2159.0	69.4A	1665.8	85.5
1 - 10 September	190.6	6.9A	2064.0	63.5A	1261.9	60.9B
11 - 20 September	198.9	7.8A	1898.7	64.8A	868.4	41.4B
21 - 30 September	185.2	7.3A	2233.5	77.5A	845.9	34.6B
1 - 10 October	166.2	7.7	2358.8	73.2A	708.0	36.4B
11 - 20 October	211.6	9.3A	1096.9	78.9B	918.2	52.6B
21 - 31 October	214.3	10.4A	1832.1	77.7A	1185.5	63.5B
1 - 10 November	210.2	9.4A	1314.1	80.5	1719.3	70.8
11 - 20 November	213.4	9.8A	1112.0	64.3B	2018.7	97.7
21 - 30 November	234.0	11.1A	1542.2	106.3	2456.0	109.5A
Random points	**145.0**	**3.1**	**1448.1**	**30.6**	**1854.2**	**34.9**

[1]Estimates of average distance in meters and SE were made using Tukey's bi-weight method (Mosteller and Tukey 1977).

[2]Average distance of elk locations for 10-day intervals within a column followed by letter A were significantly ($P \leq 0.05$) farther than random points from roads; averages followed by letter B were significantly ($P \leq 0.05$) closer than random points to roads.

the failure rate of GPS location attempts and the percent of locations that elk were bedded during October (unpubl. data, Rocky Mountain Research Station, Rapid City, SD). Percent of successful GPS locations was negatively correlated, ($r = -0.64$, $P = 0.05$) with the selection ratio for white spruce, suggesting that elk increasingly sought areas of dense forest, which would reduce success rates of GPS locations (Gamo et al. 2000). During periods of increased human disturbance, such as hunting seasons, elk seek areas that provide greater cover (Hurley and Sargent 1991, Lyon and Canfield 1991, Millspaugh et al. 2000). When dense forest comprised > 25 percent of the available habitat, the selection ratio exhibited by elk was > 1.0.

Increased movements by elk associated with human activity could contribute to weight loss by elk in the late fall or winter. An elk on a mixed forage diet weighing 259 kg (Parker et al. 1984) with estimated forage availability on our study area of 2283 kg/ha (unpubl. data, Rocky Mountain Research Station, Rapid City, SD) and forage digestibility of 45 percent (Hobbs et al. 1981) would require an extra 30-46 min/day of foraging during hunting seasons to compensate for energy expenditures associated with human disturbance. The increased foraging time would not be important except that the model (Parker et al. 1984) predicted that elk had to forage 17.75 hr/day to meet their basic needs of $70W_{kg}^{0.75}$. This foraging time requirement exceeded the theoretical foraging time limit of > 12-15 hr/day (Owen-Smith 1982, cited by Wickstrom et al. 1984).

Before the fall hunting seasons, elk selected open grassland habitats during daylight periods. Forage was more abundant in grasslands than other habitats (unpublished data, Rocky Mountain Research Station, Rapid City, SD). This pattern clearly changed once the hunting seasons began and elk avoided open grasslands during the day. Hourly movements by elk in the outer quartile ranges (upper whisker in Figs. 2-5) often were greater than the median projected for the entire day.

We believe that dispersion patterns of elk during hunting seasons relative to roads resulted from the types of equipment and methods used by hunters. Ward and Cupal

(1979) have shown that humans on foot and gunshots ≤ 300 m from elk elicit heart-rate and flight responses. Archery hunters are usually in the forest trying to get close to elk. Because of the limited opportunities for elk to avoid roads associated with the high density of roads, any disturbance on primary or secondary roads would probably push elk closer to a primitive road. In our study when the effects of primary and secondary roads were removed from the GIS, it was difficult to get > 150 m from a primitive road. By the second week of the firearm elk season, elk dispersion patterns relative to roads changed. "Road hunting" is common and types of habitat in which road categories occurred confounded any response by elk to disturbance on roads during firearm seasons. Primary roads were mostly in meadow drainages with low slope. Secondary roads occurred in narrower meadow drainages, valleys, and the forest, where visibility from these roads was less. Primitive roads were usually in forested areas. Although elk were closer to primary and secondary roads than random points, they remained > 700 m away and usually > 1 km from these roads. Effects of roads on elk dispersion patterns extend 400 m (Ward 1976) and likely farther (Hershey and Leege 1982, Rowland et al. 2000). Elk dispersion patterns relative to roads are not a simple matter of distance to the nearest road (Lyon 1983) and the response of elk to firearm hunters depends on the extent of cover (Lyon and Canfield 1991, Millspaugh et al. 2000). We attempted to separate road effects in a hierarchal manner from primary to primitive roads, but the repeated nature of disturbance, high road density, styles of hunting, and effective ranges of the harvest mechanisms used by hunters influenced elk dispersion patterns.

Management Implications

We could not use experimental controls to quantify the response of elk to human activity. If the response of elk to activity shown here resulted from normal behavioral changes in the fall, increased movements by elk associated with opening of hunting seasons would not have declined coincident with normal hunter participation. Human disturbance associated with hunting seasons probably cannot be eliminated because hunting is the primary method for controlling elk populations.

Nonetheless, as demand for outdoor recreation increases, we believe the response of elk to hunters provides a pattern of elk responses to human disturbance during other times of the year. Trends indicate that all-terrain vehicle and snowmobile use has increased dramatically in the past 10 years (Curtis 2000, International Snowmobile Manufacturers Association 2002, Federal Register 2003). In 2003, unrestricted off-highway recreation was recognized as one of four threats to the Nation's national forests (USDA Forest Service 2003). In national forests with high road densities and few restrictions on off-road vehicle recreation, there is little opportunity of elk to seek areas of low disturbance. In areas of low road density, elk select areas to avoid human disturbance (Lyon 1979, Rowland et al. 2000), often moving onto private lands (Vieira et al. 2003). In the Black Hills, elk responded to human disturbance most notably by increasing movements. Models of energy expenditures (Parker et al. 1984, Wickstrom et al. 1984) suggest that elk cannot compensate for the additional energy expended during fall and winter, but this subject needs additional research. Road closures may provide areas of reduced disturbance to elk.

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