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Elk responses to trail-based recreation on public forests

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ABSTRACT

Trail-based recreation is a popular use of public forests in the United States, and four types are common: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding. Effects on wildlife, however, are controversial and often a topic of land use debates. Accordingly, we studied trail-based recreation effects on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads. We hypothesized that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We evaluated elk responses using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. A given type of recreation was randomly selected and implemented twice daily along 32 km of designated recreation trails over a five-day period, followed by a nine-day control period of no human activity. Paired treatment and control replicates were repeated three times per year for each recreation type during spring-fall, 2003–2004. During treatments, locations of elk and recreationists were simultaneously collected with telemetry units. Elk locations also were collected during control periods. Elk avoided the trails during recreation treatments, shifting distribution farther out of view and to areas farthest from trails. Elk shifted distribution back toward trails during control periods of no human activity. Elk avoided recreationists in real time, with mean minimum separation distances from humans that varied from 558 to 879 m among the four treatments, 2–4 times farther than elk distances from trails during recreation. Separation distances maintained by elk from recreationists also were 3–5 times farther than mean distances at which elk could be viewed from trails. Distances between elk and recreationists were highest during ATV riding, lowest and similar during hiking and horseback riding, and intermediate during mountain biking. Our results support the hypothesis that elk avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. Forest managers can use results to help optimize trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests.

1. Introduction

Trail-based recreation is common on public forests in the United States, and four types are especially popular: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding (Cordell, 2012). ATV riding, in particular, has increased rapidly. The number of off-highway vehicle (OHV) riders reached 36 million in the early 2000s (Cordell, 2012), and is projected to increase ∼30–60% (to 62–75 million participants) by 2060 (Bowker et al., 2012). Increasing ATV use has prompted concerns about effects on wildlife (Proescholdt, 2007; Tarr et al., 2010; Webb and Wilshire, 2012), which include distribution shifts of populations away from trails; increased flight responses, movement rates and energetic costs; reduced foraging times; and reduced carrying capacity from cumulative effects (Havlick, 2002; Brillinger et al., 2004, 2011; Wisdom et al., 2004a; Preisler et al., 2006, 2013; Naylor et al., 2009; Ciuti et al., 2012).

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Mountain biking, hiking, and horseback riding also are popular uses of public lands in the United States (Cordell, 2012), and all three activities are among those projected to increase most in per capita participation by 2060 (Bowker et al., 2012). Mountain biking, in particular, is growing rapidly, with an increase in users of 22% from 2006 to 2015 (The Outdoor Foundation, 2016). In 2006, cycling (road and mountain biking) was the fourth-most popular recreational activity in the United States, behind fishing, camping, and running (Cordell, 2012); mountain biking had > 820 million user days in 2008 (Cordell, 2012).

In contrast to ATV riding, non-motorized forms of trail-based recreation often are considered benign by recreationists (Taylor and Knight, 2003a; Larson et al., 2016), but current knowledge indicates otherwise (Green and Higginbottom, 2000; Leung and Marion, 2000; Newsome and Moore, 2008; Naylor et al., 2009; Ciuti et al., 2012; Larson et al., 2016; Hennings and Soll, 2017). Effects on wildlife are similar to those of ATV riding (e.g., population displacement away from trails, Larson et al., 2016), but ATVs likely have more pronounced negative effects because of high levels of speed and noise and thus affect more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Naylor et al., 2009; Ciuti et al., 2012; Preisler et al., 2013). Motorized uses like ATV riding thus are more likely to have a greater impact than non-motorized recreation on wide-ranging mammals whose large home ranges put them in more frequent contact with the larger ranges and spatial influence of motorized riders (Wisdom et al., 2004a; Ciuti et al., 2012; Beyer et al., 2013).

Concerns about ATV use and the more general effects of motorized traffic on wildlife and other natural resources prompted the USDA Forest Service to revise its policy regarding motorized travel management on National Forests in 2005. A new regulation that year required that all roads, trails, and areas open to motorized use be formally designated to better manage vehicle traffic and prevent resource damage (USDA Forest Service, 2004; Federal Register, 2005; Adams and McCool, 2009). This change in policy acknowledged a variety of negative effects from unmanaged motorized uses, especially OHVs, whose numbers had been increasing steadily on National Forests (Cordell, 2005; Federal Register, 2005). Similar changes in policy have occurred on state-managed forests in response to negative effects of OHVs (Asah et al., 2012a, 2012b).

Despite the changes in public forest policy that occurred over a decade ago, current knowledge of both motorized and non-motorized recreation is not well-developed regarding the extent and intensity of effects at most spatial and temporal scales meaningful to wildlife populations (Gutzwiller et al., 2017). Wisdom et al. (2004a), Preisler et al. (2006, 2013), and Naylor et al. (2009) addressed some of these knowledge voids with their ungulate research in northeast Oregon, United States, and Ciuti et al. (2012) conducted a similar study in Alberta, Canada. Replication elsewhere and for many wildlife species, however, is lacking. Knowledge voids have likely contributed to ongoing public debate about recreational uses on public forests, particularly ATV riding (Asah et al., 2012a, 2012b). Public comments on National Forest travel management plans have been diverse and contentious (Yankoviak, 2005; Thompson, 2007), reflecting strong societal views in the face of limited knowledge and perceptions of overly restrictive federal policies (Adams and McCool, 2009).

In response to these issues, we studied effects of trail-based recreation on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads (e.g., Lyon, 1983; Cole et al., 1997, 2004; Rowland et al., 2000, 2004; Frair et al., 2008; Montgomery et al., 2012, 2013; Prokopenko et al., 2016). We hypothesized that populations of elk would avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests during non-hunting periods of late spring through early fall. We further hypothesized that avoidance would occur at distances that allow elk to stay out of view of recreationists, and that avoidance would be strongest in response to motorized recreation (ATV riding).

We tested our hypotheses by evaluating behavioral responses of elk to trail-based recreation using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. We had 2 objectives: (1) to document the degree of elk avoidance of trails during each recreation activity, compared to control periods of no activity; and (2) to evaluate direct, real-time responses of elk to recreationists during each type of recreation. We estimated distances between elk and the trails during recreation activities, and in real time between elk and recreationists based on simultaneous collection of telemetry locations of animals and humans. We provided context for interpreting results by estimating the distances at which elk could be viewed from the trails, per our hypothesis that avoidance occurs at distances that allow elk to hide from view. We also characterized differences in spatial distributions of elk during each type of recreation treatment versus paired control periods when no humans were present.

Research was conducted with approval and guidance by the Starkey Institutional Animal Care and Use Committee (IACUC 92-F-0004), as required by the United States Animal Welfare Act of 1985. We followed protocols established by the IACUC for conducting ungulate research at the Starkey Experimental Forest and Range (Wisdom et al., 1993).

2. Materials and methods

2.1. Study area

Research was conducted from April-October 2003–2004 at the USDA Forest Service Starkey Experimental Forest and Range (Starkey), 35 km southwest of La Grande in northeast Oregon, USA (Fig. 1A). In 1987, approximately 10,125 ha of elk summer range within Starkey were enclosed with a 2.4 m (8-foot) elk-proof fence for long-term ungulate research (Rowland et al., 1997; Wisdom, 2005). Our study was conducted in the 1453-ha Northeast Study Area (Fig. 1A), which is separated from Starkey's other study areas by elk-proof fence (Wisdom et al., 2005). The Northeast Study Area is further subdivided by elk-proof fence into 2 pastures, East (842 ha) and West (610 ha) (Stewart et al., 2005). Approximately 98 elk occupied the East Pasture (69 adult females, 16 calves, and 13 adult males) and 25 occupied the West Pasture (18 adult females, 2 calves, and 5 adult males). Elk were last hunted in the study area in 1996 as part of a rifle hunt of males to evaluate their responses to motorized versus non-motorized hunting access (Wisdom et al., 2004b). Our research did not include hunting and focused on the non-hunting periods of late spring through early fall.

Approximately 70% of the area was forested, arranged in a mosaic of patches interspersed with thin-soiled grasslands. Forested areas were composed of dry or mixed conifer types common to the interior western United States (Wisdom et al., 2005). Dominant tree species included Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*). Approximately 50% of the forest types underwent commercial timber harvest from 1992 to 1994 that included clearcutting, seed tree, and shelterwood prescriptions applied as small (1–22 ha) harvest units interspersed with untreated stands (Wisdom et al., 2004b). Regeneration cuts established a mosaic of open and closed forest structural conditions, interspersed with the less common open grasslands (Wisdom, 2004b). Rowland et al.,(1997), Stewart et al. (2005), Wisdom (2005), and Naylor et al. (2009) provide details about the study area and past research.

2.2. Data collection

2.2.1. Recreation treatments and locations of recreationists

We implemented ATV riding, mountain biking, hiking, and horseback riding as four separate types of recreation treatments to which elk responses were evaluated during spring-fall, 2003–2004. A given

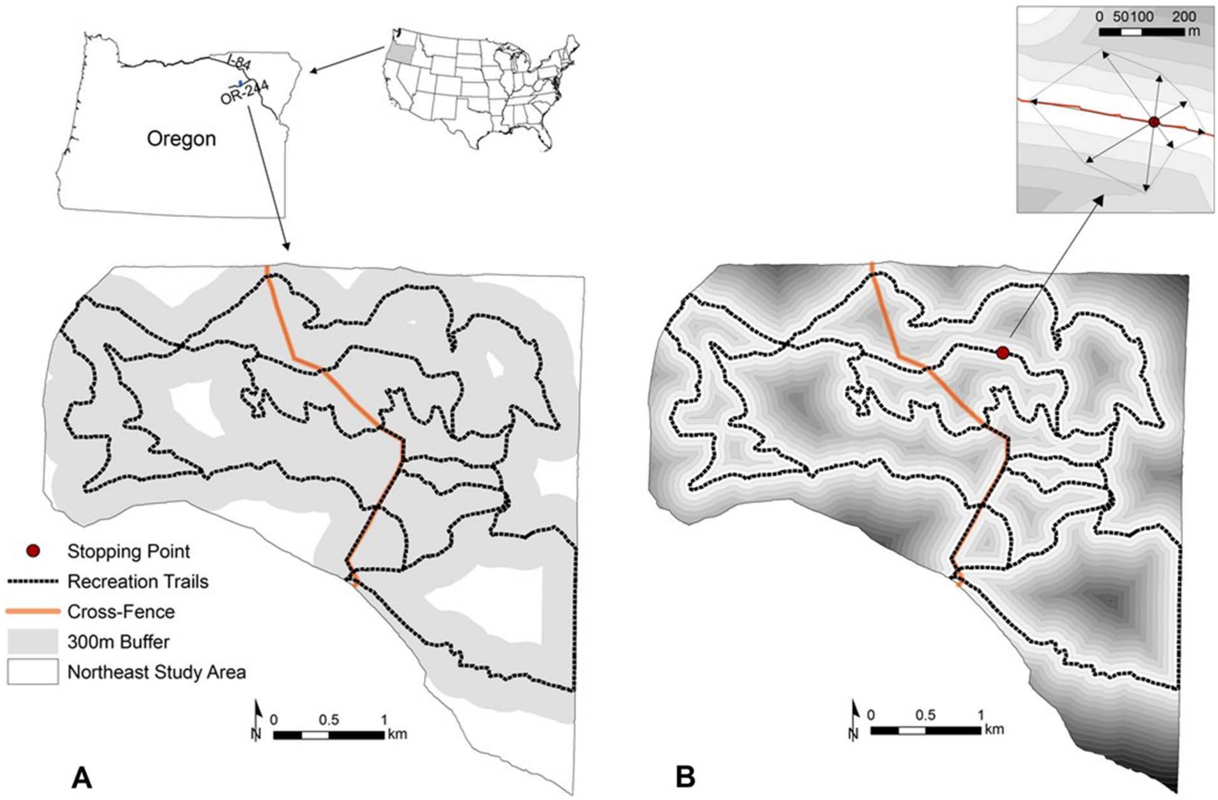

Fig. 1. Location of the 1453-ha Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA, with 32 km of recreation trails on which four recreation treatments were evaluated during 2003–2004 (A). Viewing distances were estimated in eight cardinal directions at sampling points every 0.2 km along trails (upper right, B), and 50-m distance intervals from the trails were mapped to estimate the percentage of study area in relation to viewing distances and elk locations (B).

treatment type was implemented over a five-day period, followed by nine days of control, during which no human activity occurred in the study area. Each pair of treatment and control replicates was applied three times/year for each of the four types of recreation (12 total treatment–control periods annually, 24 for the two years), with the order of treatment type randomly assigned. During each five-day period, the assigned treatment was implemented along 32 km of recreation trails that followed old road beds and trails typically used by recreationists on public forests (Fig. 1A) (Wisdom et al. 2004a). An initial two-week control period was implemented each year before treatments began.

Treatments were implemented by recreationists who traveled the trails once each morning (0800–1159 h local time) and afternoon (1200–1600 h local time) while carrying global positioning system (GPS) units to record their locations. Coverage of the 32 km of trails on a given morning or afternoon required one group of ATV riders or mountain bikers, two groups of hikers, and three groups of horseback riders because of differences in recreation speeds (Wisdom, unpublished data; see Section 4). Each of the two groups of hikers traversed one-half of the trails, and each of the three groups of horseback riders rode one-third. This design resulted in the same spatial coverage of recreationists on trails, and exposure of elk to recreationists, each morning and afternoon, but with different rates of speed (Naylor, 2006; see Section 4).

Each treatment followed a “tangential” experimental approach in which recreationists did not directly target or pursue elk, but remained along the pre-determined trails (Taylor and Knight, 2003b). Recreationists followed explicit instructions regarding these methods of implementing the treatments. See Naylor et al. (2009) for additional details about design and implementation of the treatments.

GPS units (Trimble 3C, Trimble, Inc.) worn by recreationists collected human locations continuously (every second). Mean spatial error of GPS locations was < 10 m, based on distances measured in ArcGIS (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA) between the plotted locations of recreationists and the geo-referenced location of the recreation trails (Wisdom, unpublished data).

2.2.2. *Telemetry locations of elk*

We used long-range aid to navigation (LORAN-C) and GPS telemetry (Johnson et al., 1998; Hansen and Riggs, 2008) to evaluate responses of 35 telemetered adult female elk to the four types of recreation. Telemetry locations were collected throughout each five-day treatment and paired nine-day control.

Telemetry collars were programmed to obtain one location/telemetered elk every 10 and 30 min under the LORAN-C and GPS systems, respectively, during recreation treatments. The higher relocation schedule of LORAN-C collars was designed to analyze the real-time responses of telemetered elk to the telemetered recreationists. Similar data were collected in 2002 and published earlier (Wisdom et al., 2004a), but with different response variables than considered here. All collars were programmed at 30-min relocation schedules during control periods. Limited battery life of GPS collars and sampling restrictions on the total number of LORAN-C locations that could be collected among all collars at Starkey study areas (Johnson et al., 1998) dictated the 30-min relocation schedule during control periods.

Spatial error of the elk telemetry locations was < 50 m and < 20 m for LORAN-C and GPS telemetry, respectively (Johnson et al., 1998; Hansen and Riggs, 2008). Fix success, defined as the percentage of programmed locations successfully obtained from collars, exceeded 98% for GPS data, indicating no need for bias correction (Frair et al., 2004; Nielson et al., 2009). Fix success for LORAN-C data averaged 65% and was largely associated with unbiased sources of random variation (Johnson et al., 1998). LORAN-C fix success varied slightly by location, however, and was corrected with a spatially-explicit algorithm developed for the study area (Johnson et al., 1998, 2000).

2.2.3. Viewing distances

At the conclusion of the study, we measured the distances at which we estimated an elk could be viewed from the recreation trails (Fig. 1B). Viewing distances provided context for interpreting the distances that elk maintained from the recreation trails and from recreationists during treatments, and for evaluating support for our hypothesis that elk would stay hidden from view of recreationists.

We sampled viewing distances approximately every 0.2 km along the trails, for a total of 231 sampling points. At each sampling point, we used a GPS unit (Trimble Unit TSCe, Trimble, Inc.) to spatially reference the point and used a laser rangefinder (Bushnell™ Yardage Pro 1000) to measure the distance at which we estimated an elk could be viewed. Because elk could be viewed at any possible angle from the trails, we measured distances in the eight cardinal compass directions, with 0 degrees set as straight ahead on the trail at a given sampling point (Fig. 1B).

Viewing distances can be interrupted by topography or vegetation, such that elk can be viewed at closer and farther distances but not in between. Consequently, for each of the eight angles, we measured the distance at which an elk could be viewed to the first point of visual obstruction, referred to as the "near" distance. We also measured the subsequent distance at which an elk could be viewed, beyond the first point of visual obstruction, referred to as the "far" distance. The far distance thus represented the distance at which elk could be viewed without consideration of the near distance obstruction. For a given viewing angle in which there were no obstructed areas between near and far distances, the near and far distances were identical and recorded as the same for both distances. By contrast, near and far distances could be substantially different where dense vegetation or topography obstructed views close to the trails, but open areas could be viewed farther from the trails. Rangefinder estimation errors generally were < 5% of the true distance (Wisdom, unpublished data), similar to published estimates of these technologies as tested in forest environments (Sicking, 1998).

2.3. Data analysis

2.3.1. Viewing distances from trails

We calculated the mean and 95% confidence interval (CI) of the near and the far viewing distances to which elk could be viewed from the recreation trails, considering all distances measured at the sampling points. We used each sampling point as a sample unit and the eight distance measurements/sampling point as subsamples. We averaged the values of the eight near viewing distances measured at each sampling point, and did the same for the eight far viewing distances, to estimate the mean values and 95% CIs.

We also calculated the percentage of near and far viewing distances by 50-m distance intervals away from the recreation trails (Fig. 1B), and the percentage of the study area within these distance categories. We did the same for the percentage of the study area from trails within the maximum viewing distance, estimated to be 300 m. Analyses provided insight about the percentage of the study area in which elk could be viewed from the recreation trails.

2.3.2. Avoidance of trails

We used analysis of variance (ANOVA) with random elk effects (i.e., each telemetered elk as a sample unit) to evaluate differences in mean distances (± 95% CIs) of elk from the nearest trail among the four recreation treatments and paired controls, and further summarized these distances in parallel boxplots with median notches (Chambers et al., 1983; Benjamini, 1988). Mean distances and boxplots of elk from the nearest trail were summarized for each telemetered elk/day/treatment type and control, pooled across like replicates, using observations that were averaged for each morning (0800–1159 h local time) and each afternoon (1200–1600 h local time). This analysis evaluated average responses to treatments across seasons and years, but accounting for diurnal effects (Wisdom et al., 2004a; Naylor et al., 2009). Prior analyses (Wisdom et al., 2004a; Wisdom, unpublished data) also indicated that elk in a given pasture responded to recreation treatments in both pastures, given the adjacency of trails and long distances of elk responses. Calculation of distances thus considered trails in both pastures. Results were further related to the mean near and far viewing distances (± 95% CIs) from trails.

We analyzed the spatial distribution of elk in relation to trails in two additional ways. First, we calculated the percentage of elk locations by 50-m distance intervals from the nearest trail during each treatment type and control, and percentage of near and far viewing distances by the 50-m intervals. Locations were pooled across animals. And second, we estimated and mapped kernel densities of elk locations during each treatment type and control. Kernel densities (Venables and Ripple, 1997) were based on the pooled locations among telemetered elk as an estimate of the stationary distribution of the population (Preisler et al., 2013) during each treatment type and control. We used a random subsample of locations from the recreation treatments equal to the number of locations during the corresponding control periods to estimate kernel densities and produce comparable maps.

Analyses of elk distances and distributions in relation to trails documented the degree of trail avoidance and whether the elk population shifted beyond viewing distances during the recreation treatments, and shifted back toward trails during control periods. If elk were farther from trails than they could be viewed during recreation, this would support our hypothesis that avoidance was related to elk staying hidden from view. Moreover, a shift in elk distributions closer to the trails during control periods, with more locations in view during these periods of no human activity, would further support this hypothesis as a potential cause-effect process.

2.3.3. Avoidance of recreationists

We analyzed the minimum separation distances that elk maintained from recreationists as a measure of how tolerant elk were to the proximity of humans. We first matched the locations of recreationists in time with the LORAN-C telemetry locations of elk (Preisler et al., 2006). LORAN-C elk locations were used because of the higher relocation frequency (every 10 min) compared to the GPS telemetry locations (every 30 min), thus providing a larger set of close matches in time. Each LORAN-C elk location was matched with the location of the nearest group of recreationists closest in time to the elk location, considering all locations of recreationists within a five-minute time window before each elk location. Time-matched locations of elk and recreationists were measured as the shortest Euclidean distance between each (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA).

To calculate the mean and 95% CI for the minimum separation distance/treatment type, we identified the distance of each LORAN-C elk to the nearest group of recreationists during each morning and each afternoon for each of the five days of a treatment replicate. This provided two observations of minimum distance/elk/day/treatment replicate, spanning the three seasons and two years. Minimum separation distances/elk for each morning and afternoon were used as subsamples, and a mean minimum distance of these values calculated for each animal among replicates of each treatment type. We then calculated the mean minimum distance and 95% CI among all LORAN-C telemetered elk (n = 19) across like replicates in the same manner as done for calculating mean distances from trails. We further analyzed the distribution of minimum separation distances of elk with boxplots and median notches by treatment type.

We considered minimum separation distance to be the most direct indicator of the spatial tolerance of elk to recreationists, particularly their tolerance to remain in view. Elk often seek edges close to cover or in cover, presumably for hiding from humans or predators, even during non-hunting periods of spring-fall (Witmer et al., 1985; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

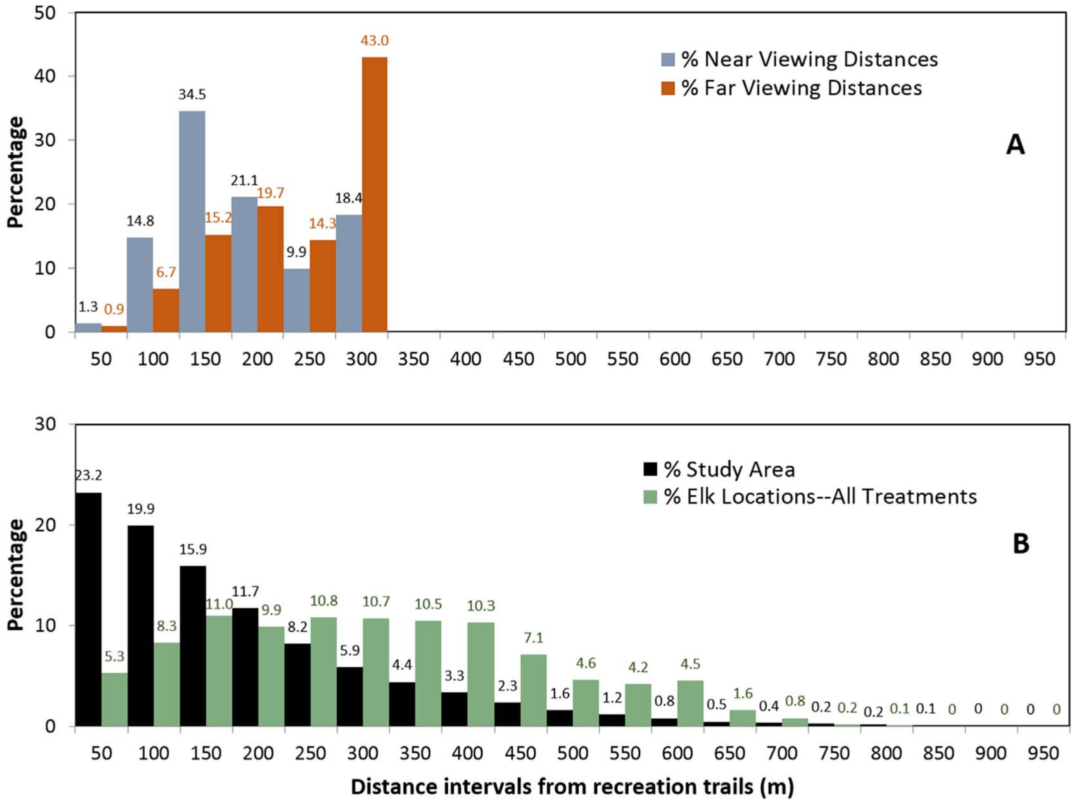

Fig. 2. Percentage of near and far viewing distance values by 50-m distance intervals from the recreation trails (A) in relation to the percentage of the study area and percentage of elk locations by intervals (B), Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Elk locations were from 35 telemetered elk monitored during all-terrain vehicle riding, mountain biking, hiking, and horseback riding, 2003–2004 combined.

Evaluation of separation distances in relation to viewing distances considered elk use of visual obstructions of cover and topography to hide from view as part of avoidance responses.

3. Results

3.1. Viewing distances from trails and area available for elk use

Mean near and far distances to which elk could be viewed from the recreation trails were 172 m and 222 m, respectively (Fig. 2A; Table 1). Over 50% of the study area was within the mean near viewing distance of 172 m, and > 70% was within the mean far viewing distance of 222 m, based on study area percentage by distance intervals from trails (Fig. 2A). Just 15% of the study area exceeded the maximum viewing distance of 300 m that was estimated for near and far viewing distances at 18% and 43% of the sampling points, respectively (Fig. 2A). The percentage of the study area available for elk use by 50-m distance intervals from trails (Fig. 1B, 2A) directly followed the patterns of study area percentage by viewing distance (Fig. 2A).

3.2. Elk avoidance of trails

We found significant differences in elk avoidance of trails among the four recreation treatments and paired controls (ANOVA, $P < .01$). Mean distances of elk from the recreation trails ranged from 239 to 310 m during the four recreation activities (Fig. 3; Table 1). Mean and median distances were significantly farther (non-overlapping 95% CIs and median notches) during ATV riding, mountain biking, and horseback riding than distances of these same telemetered elk during the paired control periods (Fig. 3; Table 1), indicating that elk moved away from the trails during recreation and back toward trails when no humans were present. During hiking, mean and median distances of elk from trails were similar to those during horseback riding, but elk movement back toward trails during the hiking control period was less distinct (Fig. 3), and CIs for the hiking treatment and control periods slightly overlapped (5-m overlap, Table 1).

Shifts of elk away from and back toward trails in the presence versus absence of recreationists were evident in the boxplot distributions (Fig. 3). Shifts also were evident spatially in the kernel densities of elk locations of paired treatment and control periods, shown in Fig. 4 for ATV and horseback riding. Similar spatial differences in kernel densities between treatment and control periods were found during mountain

Table 1
Mean (± 95% CI) near and far distances at which elk could be viewed from recreation trails, and mean distances (± 95% CIs) that elk maintained from nearest trail during all-terrain vehicle riding (ATV), mountain biking (BIKE), hiking (HIKE), and horseback riding (HORSE) treatments (T) and control periods (C), 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA.

Mean viewing distance (m) (N = 231)		Mean distance (m) of elk from nearest trail (N = 35)							
Near	Far	ATV		BIKE		HIKE		HORSE	
		T	C	T	C	T	C	T	C
172 (± 5)	222 (± 5)	311 (± 28)	237 (± 15)	286 (± 26)	197 (± 8)	276 (± 18)	248 (± 15)	240 (± 13)	172 (± 9)

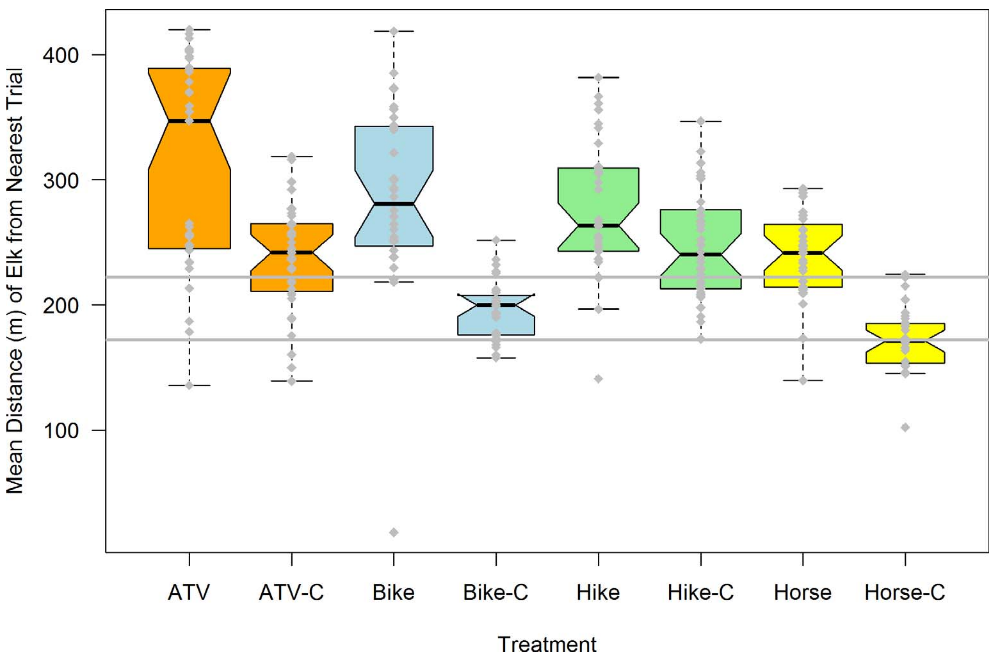

Fig. 3. Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in mean distances of telemetered elk (n = 35) from the nearest recreation trail during four types of recreation (all-terrain vehicle riding [ATV], mountain biking [Bike], hiking [Hike], horseback riding [Horse]) and corresponding control (C) periods, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Non-overlapping notches provide 'strong evidence' that the two medians differ (Chambers et al. 1983, p. 62; Benjamini, 1988). Silver dots show mean distances of individual elk. The two horizontal grey lines indicate the mean near (172 m) and mean far (222 m) viewing distances from trails.

biking. Shifts away from and back toward trails during the hiking treatment versus control periods were more subtle, as reflected in the small overlap of CIs of mean values (Table 1) and overlapping median notches (Fig. 3).

Mean and median distances of elk from the recreation trails were farther during ATV riding than during the three non-motorized types of recreation (non-overlapping CIs and notches); these distances were not different between mountain biking, hiking, and horseback riding (overlapping CIs and notches, Fig. 3; Table 1). Boxplot distributions, however, indicated an overall trend of strongest avoidance during ATV riding, followed by mountain biking, hiking, and horseback riding (Fig. 3). These trends were supported by the rank order of both mean and median values among the four treatments (Fig. 3; Table 1).

Variability in mean distances among individual elk, however, was highest (least precise) during ATV riding. Lower precision of elk response to ATV riding was evident in the longer boxplot below the median, and high number of individual mean distances farther below the median, compared to other types of recreation (Fig. 3), suggesting that ATV riding elicited either a hiding (stationary) or a flight (active) response (see Section 4). Higher precision was associated with elk responses to horseback riding and hiking, and during all control periods except hiking.

Mean distances of elk from the trails also were farther (non-overlapping CIs) during all four recreation activities than the mean near and far viewing distances (Table 1). The large majority of elk locations were well beyond the mean near and far viewing distances from trails, and 44% of all elk locations during the recreation treatments were beyond the maximum viewing distance of 300 m (Fig. 2B). This pattern was stronger during ATV riding and mountain biking, when 52% and 50% of all elk locations occurred > 300 m from the trails. The pattern was weaker during hiking and horseback riding, when 37% and 25% of elk locations were beyond the maximum viewing distance (Fig. 2B).

Almost one-half (44%) of elk locations occurred on just 15% of the study area farthest from trails and out of view (Fig. 2B). The large majority (85%) of the study area was within the maximum viewing distance of 300 m from the recreation trails, but only 56% of elk locations occurred in these distance intervals (Fig. 2B). These patterns were evident in the kernel densities of treatment versus control periods (Fig. 4).

3.3. Elk avoidance of recreationists

Mean minimum separation distances that elk maintained from recreationists were highest during ATV riding (879 m, ± 68 m), lowest and similar during hiking (547 m, ± 44 m) and horseback riding (558 m, ± 45 m), and intermediate during mountain biking (662 m, ± 53 m). Boxplot distributions and median notches followed this same pattern (Fig. 5): median distances were highest during ATV riding, followed by mountain biking, both of which had non-overlapping notches with each other and with the overlapping notches of hiking and horseback riding. The taller height of the boxplot above the median during ATV riding compared to other types of recreation (Fig. 5) further illustrated the stronger but less precise elk response to motorized recreation.

Separation distances from recreationists were significantly farther than elk distances from trails (non-overlapping CIs with those in Table 1), illustrating the difference in real-time responses of elk to recreationists (five-minute time windows each morning and afternoon) versus the more static responses to trails (8-h time window each day). Specifically, mean minimum distances of elk from recreationists (558–879 m) were 2–4 times farther than mean distances from trails (239–310 m, Table 1) during the same recreation periods. Differences in elk distances from recreationists also were more distinct and consistent (more precise) between the four treatments than those for distances from trails (boxplot variability across treatments in Fig. 3 versus 5), suggesting that the direct responses of elk to recreationists was more predictable than their indirect responses to trails.

Minimum separation distances also were 3–5 times farther than the mean near and far distances of 172 and 222 m at which elk could be viewed from the trails (non-overlapping CIs with those in Table 1), and 2–3 times farther than the maximum viewing distance of 300 m. Over 75% of the minimum distances between elk and recreationists exceeded the maximum viewing distance of 300 m (see boxplot portions above 300 m, Fig. 5), indicating a strong tendency of elk to be hidden from view of recreationists. This percentage of elk distances from recreationists beyond 300 m, estimated for a 5-min time window (Fig. 5), was higher than the estimate of 44% of elk locations beyond 300 m based on the more generic 8-h time window (Fig. 2B). The long "tails" of elk distances extremely far from recreationists (e.g., 1500–4000 m distances, per dotted lines in uppermost part of each boxplot, Fig. 5) were evident during all four recreation activities, indicating avoidance

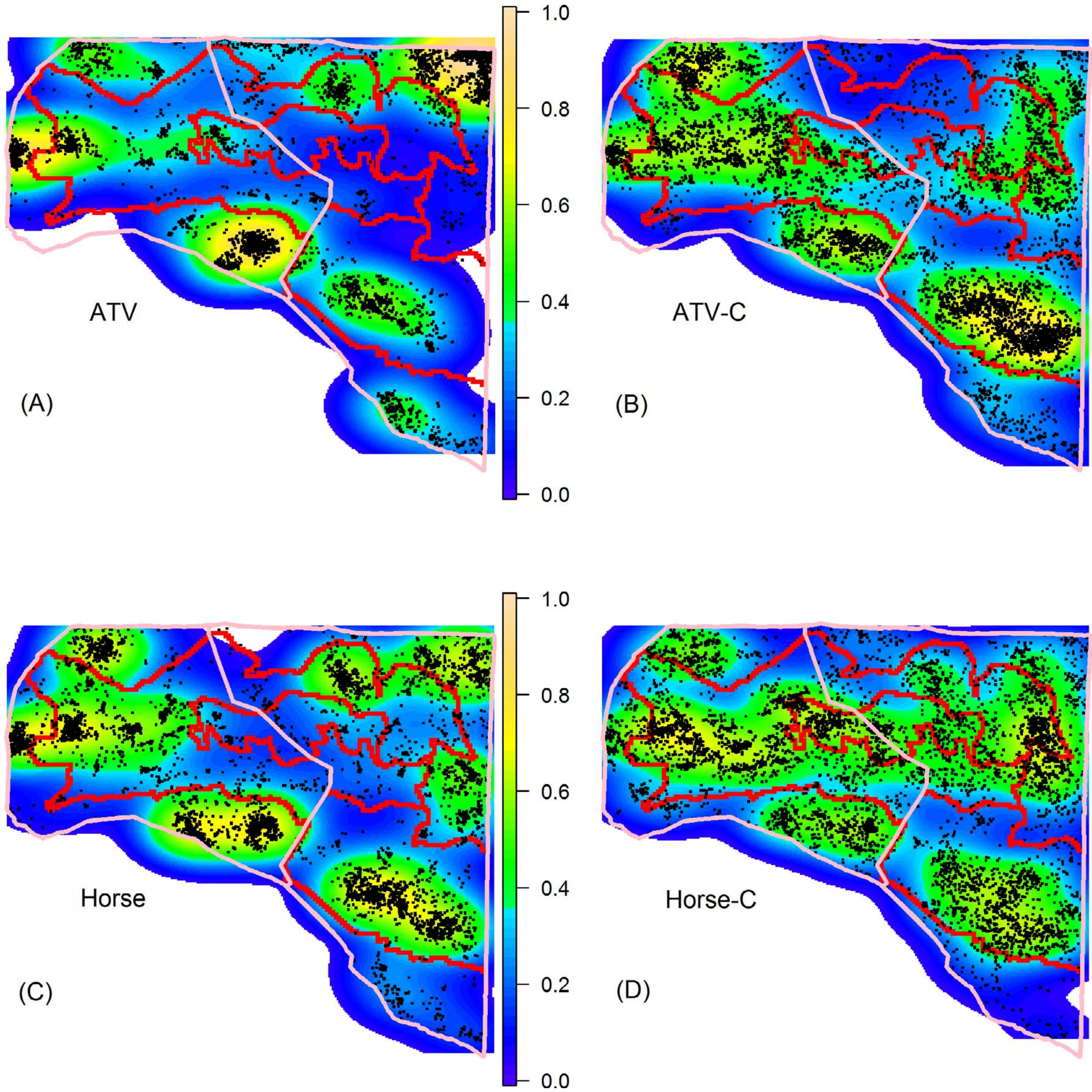

Fig. 4. Locations of 35 elk during ATV riding (ATV, A) and horseback riding (Horse, C) versus corresponding control periods (B and D), superimposed on estimates of the spatial probability distribution of elk locations, estimated as kernel densities, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Probability of use is scaled from 0 to 1, with higher use shown by warmer colors (yellow, then green) and lower use by cooler colors (light blue, then dark blue). Red lines are the recreation trails and pink lines fences. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses at distances as far as possible from recreationists.

4. Discussion

4.1. Elk avoidance of recreation trails and recreationists

Our results showed strong avoidance by elk to the recreation trails during each of the four types of recreation. Almost one-half of all elk telemetry locations during the recreation activities occurred on just 15% of the study area farthest from trails. Elk avoidance of recreation trails was strongest during ATV riding. Elk avoidance of trails during mountain biking, hiking and horseback riding was statistically similar but the distribution of elk locations during these three types of recreation indicated that elk shifted farther from trails during mountain biking.

Elk avoidance of trails was calculated as the mean distance of telemetered elk to trails, using data pooled for each animal across treatment and control replicates of each recreation type. Estimates thus represented the "average" distribution of elk in relation to trails during each recreation treatment, and did not account for finer temporal responses, such as potential population shifts away from and back toward trails as recreationists passed by a given area. By contrast, the minimum separation distances that elk maintained from recreationists in real time documented the direct effect of human movement on the species' behavior at five-minute time windows during each recreation treatment. Results showed that elk were quite sensitive to human presence, shifting distributions away from recreationists and farther out of view as the activities moved along the trails. The minimum daily distances maintained by elk from recreationists were notably large (averaging 558–879 m among treatments), indicating a strong spatial intolerance of elk to recreationists and well beyond areas visible from trails. Direct responses of elk to recreationists were stronger and more precise across treatments than their indirect responses to trails.

The pattern of long-distance avoidance by elk to recreationists was supported by real-time documentation of elk fleeing from approaching recreationists that was documented in earlier publications from data collected in our study area (Preisler et al., 2006, 2013). Flight responses of elk to the recreation activities in our study area showed substantially higher probabilities of flight than expected at distances of 500–1000 m (Wisdom et al., 2004a). Minimum separation distances in our study

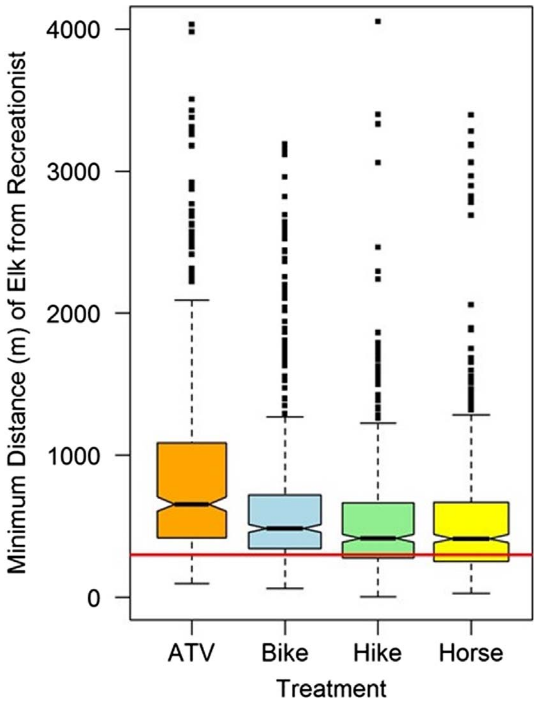

Fig. 5. Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in minimum separation distances of LORAN-C telemetered elk (n = 19) from recreationists during all-terrain vehicle riding (ATV), mountain biking (Bike), hiking (Hike), and horseback riding Horse, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Minimum distances were evaluated per elk/day, with two values per day (morning and afternoon) per elk. Horizontal red line shows the maximum viewing distance of 300 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

followed a similar pattern to these flight responses, with the latter modeled with 2002 elk telemetry data not used in our analysis (Wisdom et al., 2004a).

Separation distances maintained by elk from recreationists appear to represent a cause-effect process that we cannot attribute to other factors. We controlled for human access with our design of randomly selecting and implementing one type of recreation activity for a given five-day period, followed by a paired nine-day control period of no human activity. We further controlled for effects of season and year by replicating this design during spring, summer, and fall, and across years. Other factors influencing elk movements may have involved the two main predators of elk in our study area, cougars (*Puma concolor*) and black bears (*Ursus americanus*); however, these predators were constant background factors operating during both treatment and control periods (Wisdom et al., 2005). We know of no other factors beyond the recreation activities that would help explain our results.

4.2. Sensory cues used by elk to avoid recreationists

Long separation distances maintained by elk from recreationists beg the question: what types of sensory cues are elk using to react to humans? Large mammals and many other vertebrates have keen senses of smell, hearing, and sight that have evolved to detect predators (Hunter and Skinner, 1998; Lima and Dill, 1990; Bennett et al., 2009; Wikenros et al., 2015). Elk moved largely out of view during the recreation activities, suggesting visibility was a strong factor in avoidance of trails. However, viewing distances were based on human capacity to see elk, not vice versa. Moreover, ungulates such as elk can easily hear and smell humans at the distances that elk maintained from recreationists (see citations above), suggesting that any combination of sensory cues could have been used.

In addition, visual detection of humans can be impaired by obstructions of vegetation and topography, and auditory and olfactory cues to human presence are affected by wind speed and direction. Olfactory cues also were likely different for each recreation activity: ATVs emit a distinct gasoline odor and horses provide an additional olfactory cue beyond that of humans.

Each recreation activity also was associated with a different level of noise, which clearly affects wildlife (Barber et al., 2009). ATV riding is the loudest of the four recreation activities, with levels as high as 110 dB (Lovich and Bainbridge, 1999), and thus has high noise impact on wildlife (Bowles, 1995, Lovich and Bainbridge, 1999). It is unclear whether any of the other three recreation activities were louder than the others. We are not aware of any comparative research on noise associated with non-motorized forms of trail-based recreation.

Differences in speed of the recreation activities may also have provided additional cues for elk detection of recreationists. The speed of ATVs was > 2 times faster than mountain bikes, and > 4–5 times faster than hikers and horseback riders, respectively, during our study (Wisdom, unpublished data). Our treatment design ensured equal spatial coverage of the trail system by all four recreation treatments, but ATVs covered the trails at a faster rate each morning and afternoon. The higher speed of ATVs, combined with their substantially higher noise, may help explain the stronger avoidance response of elk to ATVs. The higher speed of ATVs might also have limited the reaction time of elk, as shown by some elk maintaining closer distances to trails and possibly hiding during this activity (see Wisdom et al. (2004a) for a related discussion of elk hiding versus flight responses to ATV riding). Given the wide variety of visual, auditory, and olfactory stimuli, different combinations of sensory cues were likely used by elk under varying conditions to detect and respond to recreationists.

4.3. Support for hypotheses on viewing, ATV effects, and forest roads

We identified three hypotheses for our analyses: (1) that elk avoidance would occur at distances that allow animals to stay out of view of recreationists; (2) that avoidance would be strongest in response to motorized recreation (ATV riding); and (3) that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We found support for all three hypotheses. Elk avoided trails and recreationists at distances largely beyond human view (hypothesis 1). This result agrees with past studies showing elk use of areas obstructed from view (e.g., Montgomery et al., 2012), sometimes referred to as “hiding cover” for elk (Thomas et al., 1979; Canfield et al., 1986; Lyon, 1987). Elk also use areas of steeper slopes, complex topography, or areas closer to cover-forage edges, presumably as a means of remaining hidden from humans or predators (e.g., Witmer et al., 1985; Thomas et al., 1988; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

Extensive timber harvest occurred on 35% of our study area during the 1990s, which uniformly increased openness of the landscape due to the even distribution of harvested vs. unharvested stand mosaics (Wisdom et al., 2004b). Viewing distances in our study increased in response to the extensive timber harvest and may have increased the distances that elk maintained from recreationists. The influence of silviculture and forest topography on viewing, and the subsequent recreation effects on wildlife sensitive to human presence, agrees with Lyon’s (1987) modeling of forest structure and topography to characterize hiding cover for elk.

Elk avoidance of ATVs also was stronger than to the three types of non-motorized recreation (hypothesis 2). Ciuti et al. (2012) found similar results in a comparative study of ATV riding, mountain biking, hiking, and horseback riding in Alberta, Canada. Other authors have inferred that ATV riding has a stronger effect on wildlife than non-motorized recreation because of higher noise and faster speeds, which influences more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Ciuti et al., 2012; Preisler et al., 2013). However, Larson et al.'s (2016) meta-analysis of recreation effects on wildlife suggested that non-motorized recreation had stronger effects than motorized (but differences were not statistically significant). Additional research is needed to address inconsistencies among studies and to investigate effects of trail-based recreation on fitness of different wildlife species and taxa.

Avoidance responses by elk to the recreation activities also were similar to those documented in relation to forest roads open to motorized traffic (hypothesis 3). Our review of the literature revealed displacement of elk from forest roads open to motorized traffic that often exceeded 0.5–1.5 km. Avoidance responses by elk distance to open roads, or to open road density, have been documented consistently and overwhelmingly by > 30 studies conducted during the past 5 decades in forested areas of western North America. Examples from each decade are Perry and Overly (1977), Lyon (1983), Cole et al. (1997), Rowland et al. (2000), and Prokopenko et al. (2016).

Distance responses by elk to recreationists during our study mirrored the general avoidance distances of 0.5–1.5 km or farther that were documented in many roads studies during non-hunting seasons. Elk sometimes move much longer distances (e.g., > 25 km) from public to private lands during hunting seasons when public forests are highly roaded and lack adequate security for elk to hide from hunters (Proffitt et al., 2013). We did not evaluate the effects of hunting, nor could we evaluate the potential for such longer-distance landscape responses by elk because of the study area enclosure.

Similarities between elk responses to trail-based recreation and forest roads also depend on the specific response variables evaluated and the spatial and temporal scales at which responses are measured. Different studies evaluated elk avoidance over different time periods (seasonal or multiple seasons in a year or multiple years) and spatial extents. Results will vary by sample size and the degree of "averaging" of avoidance effects by time of day, seasons, and years. This variation was obvious in our results. Analysis of elk distances to trails represented an average response over the eight-hour period of all days among all replicates of each treatment type. These avoidance distances were substantially less than the minimum separation distances maintained by elk from recreationists, as measured in five-minute time windows over the same eight-hour days and replicates. Minimum separation distances of elk from recreationists are a more direct measure of elk responses; we consider these results comparable to contemporary finer-scale distance responses of elk to open roads (e.g., Buchanan et al., 2014; Morris et al., 2016; Prokopenko et al., 2016; Ranglack et al., 2017).

4.4. Bias in visual observations of elk

Elk are widely distributed and occupy summer ranges on nearly every National Forest in the western United States (O'Gara and Dundas, 2002). Consequently, the species has been a topic of public comments as part of travel management planning on National Forests. Motorized recreationists often have commented that elk populations do not avoid OHVs because elk are observed while riding. We heard this comment numerous times during meetings we held with recreation stakeholders about our research. Of direct relevance to these public comments was the research by Naylor (2006), who summarized the distances at which elk were directly observed by recreationists during implementation of the recreation treatments in our study area. Elk were observed by recreationists at mean distances of 116–161 m among the four types of treatments (Naylor, 2006). These distances are shorter than or similar to the average near viewing distance of 172 m at which elk could be viewed without visual obstruction.

Telemetered elk, representing a random sample of female elk in our study area, maintained minimum separation distances that were 4–8 times farther from recreationists than the distances estimated by visual observation. Thus, a large percentage of telemetered elk were present beyond the distances at which visual observations were possible, and elk consistently maintained these longer distances during each type of recreation.

Recreationists in our study were able to observe a small portion of the elk population in view of trails, but unable to see the large majority of the elk population that remained hidden from view during recreation activities. Visual observations of elk during recreation thus could not detect the strong avoidance by elk that occurred out of view. This pattern explains the differences between motorized recreationists' comments about elk as part of travel management planning and the responses that we documented with telemetered elk in our study.

Stankowich (2008) summarized results from > 50 studies that reported results of flight distance of wild ungulate species in response to human activities. The majority of reported studies were based on visual observations, but no mention was given in Stankowich (2008) about the potential for bias with the use of visual observations in environments where viewing was substantially limited, or for ungulate species whose response to human presence is to remain out of view. Automated and remotely-sensed technologies are now available that document a variety of animal behaviors and responses to human activities without dependence on human observations (e.g., Cooke et al., 2004; Coulombe et al., 2006; Shepard et al., 2008; Naylor et al., 2009; Suraci et al., 2017).

4.5. Implications

Avoidance by elk to recreation trails and recreationists represents a form of "habitat compression," similar to that described for effects of forest roads open to traffic (Wisdom et al., 2000, Rowland et al., 2004, Buchanan et al., 2014, Prokopenko et al., 2016). Habitat compression in response to human activities is a form of habitat loss for species like elk (Rowland et al., 2004, Frair et al., 2008, Buchanan et al., 2014), considering the potentially large areas not used or used less in the presence of humans, and that otherwise might be selected by a species in the absence of humans. Habitat compression can ultimately lead to large-scale population shifts by elk from public forests to private lands, thus eliminating hunting and viewing opportunities on public lands (Proffitt et al., 2013).

To address these types of effects, forest managers could use our results to evaluate trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests. Although public forests are governed by laws and policies of multiple use, not all areas can be simultaneously co-managed for recreation and recreation-sensitive wildlife. Different land allocations can accommodate such competing uses, but often on different landscapes with clear objectives about which resources are featured. Optimizing land allocations through spatial analyses of trade-offs between competing forest uses (Wang et al., 2004), with the inclusion of human ecology mapping (McLain et al., 2013a, 2013b) and stakeholder engagement (Asah et al., 2012a, 2012b) is a forest planning approach that holds promise in helping address recreation and wildlife conflicts. We suggest that such an approach be considered in co-managing trail-based recreation and sensitive wildlife like elk on public forests.

Author contributions

BJ, LN, RA, and MW conceived, designed, and implemented the research; BJ, HP, LN, MR, and MW analyzed the data and wrote and edited the manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.01.032.

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