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Management and Conservation

Variation in Elk Response to Roads by Season, Sex, and Road Type

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ABSTRACT Despite the near universal recognition that roads negatively affect wildlife, the mechanisms that elicit animal responses to roads are often ambiguous or poorly understood. We conducted a multi-year, multi-season study to assess the relative influence of roads on elk (*Cervus elaphus*) in a human-dominated landscape in South Dakota. We evaluated the effects of habitat covariates including security cover, forage quality, distance to roads (primary, secondary, and tertiary), and visibility from roads at the home range scale. We radio-collared 28 elk (21 adult females and 7 adult males) and calculated seasonal (winter, spring, summer, and autumn) utilization distributions (UDs). We assigned habitat covariates to use percentiles within the UDs (1% increments; from 1 to 98 percentiles) and used spatially explicit mixed linear regression to model the relationship between use percentile and habitat covariates. For each season and sex, we evaluated 15 candidate models and used Akaike's Information Criterion weights (ω_i) to identify top-ranking models. We plotted influential coefficients from these models with 95% confidence intervals to examine the magnitude of effects. Our analysis revealed fundamental differences in response to roads, by road type, between sexes, and across seasons. Male elk established home ranges near roads devoid of vehicle traffic in winter, spring, and autumn. In summer, coinciding with peak vehicle traffic levels, male elk reduced their use of habitat that was both visible from and close to primary roads. Female elk subherds similarly responded to primary roads in spring and autumn, during times of year when they were calving and mating, respectively. In spring and summer, female elk subherds selected habitat near roads that were closed to vehicle traffic. Forage quality and security cover were influential in the periphery (>50th use percentile) of elk home ranges, whereas road covariates were more influential towards the core of elk home ranges. This analysis further demonstrates the utility of visibility from road metrics and suggests that the retention of vegetation structures that screen visibility potential from roads could be important components of elk management strategies. © 2012 The Wildlife Society.

KEY WORDS *Cervus elaphus*, elk, Euclidean distance, GIS, roads, utilization distribution, visibility.

Examining animal space use in relation to road networks has been a major focus of ecological research (Mace et al. 1996, Rowland et al. 2000, Speziale et al. 2008, Kerth and Melber 2009, Lambertucci et al. 2009). Roads have a variety of negative effects on wildlife (Forman and Alexander 1998) as they fragment habitat, present barriers to dispersal, and increase stress and direct mortality of wildlife (Swihart and Slade 1984, Spellerberg 1998, Millspaugh et al. 2001, Gibbs and Shriver 2002, Jaeger et al. 2005). These negative effects have ecological and evolutionary consequences for individual survivability, species viability, and biodiversity (Vos and Chardon 1998, Rondinini and Doncaster 2002, Fahrig 2003, Benítez-López et al. 2010). Road effects studies have documented that a vast array of species avoid habitat near roads (Mader 1984, Bowyer et al. 1999, Dyer et al. 2001, Whittington et al. 2004, McGregor et al. 2008). However, positive associations between animal space use and roads have also been reported (see review by Fahrig and Rytwinski 2009). Inconsistent patterns in response to roads have even been documented for the same species (e.g., caribou [*Rangifer tarandus*] see Dyer et al. 2001, Yost and Wright 2001). Thus, despite the overwhelmingly evidence of a negative influence of roads on wildlife, some ambiguity exists within road effects research.

Initial development of habitat models to describe elk (*Cervus elaphus*) habitat selection used road density or straight-line Euclidean distance as simple metrics for incorporating road effects (e.g., Thomas et al. 1979, Wisdom et al. 1986, Edge et al. 1987, Thomas et al. 1988, Rowland et al. 2000). These metrics, however, might be too simplistic as elk will select areas near roads if vegetation and topography screen animals from human view (Lyon 1979, Edge and

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Marcum 1991, Rowland et al. 2005). Other elk habitat models accounted for the spatial arrangement of road networks and line-of-sight distance from roads (Grover and Thompson 1986, Roloff 1998, Rowland et al. 2000, Roloff et al. 2001). Recent road effects research substantiates that visibility from roads and its interaction with Euclidean distance to roads better explain elk space use (Montgomery et al. 2012).

To fully understand the influence of forage quality, security cover, Euclidean distance to road, and visibility from roads on elk space use, we developed a multi-year, multi-season analysis using elk telemetry data in a human-dominated landscape. We assessed whether elk response to roads, at the home-range scale, varied by season, sex, and road type. We did so by fitting seasonal spatially explicit mixed linear regression models for male elk and female elk subherds by season.

STUDY AREA

Custer State Park encompasses 29,150 ha in the southern portion of the Black Hills region of South Dakota, USA (Fig. 1). The Black Hills (43°10′ to 44°50′ N latitude and 103°20′ to 104°50′ W longitude) are located on the Missouri Plateau of the Great Plains Province (Fenneman 1931). The climate is moister and subjected to less extreme temperatures than surrounding areas (Turner 1974). Coniferous forests dominated by ponderosa pine (*Pinus ponderosa*) constituted 42% of the unburned lands within Custer State Park at the time of data collection. Deciduous woodlands were common along drainage areas; flora included bur oak (*Quercus macrocarpa*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and green ash (*Fraxinus pennsylvanica*). Dominant grasses in Custer State Park included western wheatgrass (*Agropyron*

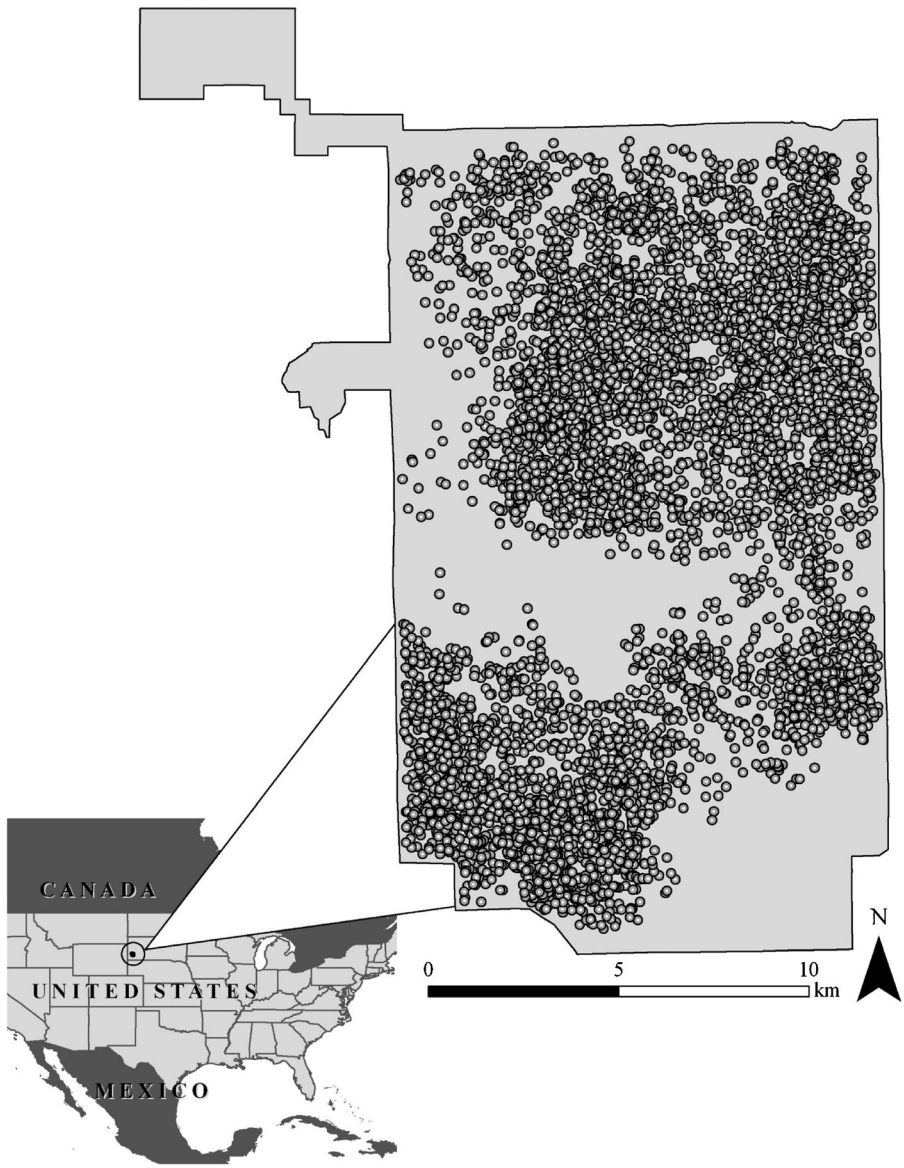

Figure 1. Elk telemetry locations from 28 different individuals collected in Custer State Park, South Dakota between 1993 and 1997.

smithii), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and buffalograss (*Buchloe dactyloides*). During our study, approximately 750–1,000 elk used Custer State Park (Millspaugh 1999). Human activities were pervasive with over 1.7 million visitors and 171 elk permits issued for annual sport and management hunts in 1997. The park maintained road and trail networks, which represented proxies for intensity of vehicle use (Perry and Overly 1977, Millspaugh et al. 2000). The area contained 103 km of primary roads, which were paved, maintained roads open to public vehicular traffic year round. Secondary roads covered in excess of 82 km and were seasonally maintained dirt roads open to vehicular traffic in summer and autumn. Tertiary roads were unmaintained dirt roads that were closed to vehicular traffic year round, apart from the hunting season when vehicles could be used to retrieve legally harvested elk. Tertiary roads were the most common with over 430 km of road in the park.

METHODS

Elk Telemetry

We collected telemetry locations from 28 elk (21 adult females and 7 adult males) from September 1993 to December 1997 (Fig. 1). Our techniques used to capture and radio-collar elk are described by Millspaugh et al. (1994, 1995). We systematically collected locations of radio-collared elk two to five times per week by triangulation or visual observation. For locations estimated by triangulation, we obtained compass azimuths using the loudest signal method (Springer 1979, Mech 1983). We conducted aerial tracking using dual, side-looking four-element Yagi antennas (Cushcraft, Keene, NH) or 2 H-antennas (Telonics, Mesa, AZ) with methodology described by Mech (1983). We used the computer program XYLOG (Dodge and Steiner 1986) to estimate elk locations using at least two azimuths (usually >2) from known locations (i.e., road intersections). We located elk at 28-hour intervals to ensure an equal representation of movements during different times of the day (Morgantini and Hudson 1979, Beyer and Haufler 1994). All persons involved in telemetry fieldwork participated in a telemetry accuracy assessment. We placed fixed transmitters in representative habitat types ($n = 133$) in which elk reside. Observers recorded azimuths at distances of 0.25–3.0 km from the transmitters. We used the deviation of the actual location from plotted location to estimate positional accuracy.

We assessed the relative influence of telemetry error on our analysis according to methods outlined by Montgomery et al. (2010, 2011). Montgomery et al. (2010, 2011) demonstrated that accuracy in habitat selection studies depends on mean telemetry error, covariate type (i.e., continuous or categorical), and patch size. For mean patch sizes typical of those in Custer State Park (i.e., $\leq$3 ha; Table 1), ignoring telemetry error or zonal majority sampling (identifying the category covering the majority of the error polygon; e.g., Mace et al. 1996, 1999) were found to perform best for categorical data (Montgomery et al. 2010). We examined the efficacy of both techniques for incorporating telemetry error into our analysis by comparing covariate values at all known elk locations to covariate values underlying a paired location with simulated positional error (Montgomery et al. 2010). We defined accuracy based on the percentage of covariate values from our known locations that equaled covariate values from our simulated locations.

Because elk space use is known to vary by sex (McCorquodale 2003), we developed separate models for male and female elk. We partitioned individual female elk telemetry locations into subherds ($n = 5$) using a social interaction analysis (Kernohan et al. 2001). This involved the creation of home ranges (95% fixed-kernel density estimates) and calculation of relative overlap in the ranges across spatial and temporal dimensions. We organized individual female elk into subherds when significant overlap in home ranges was documented (see Millspaugh et al. 2004 for a more detailed description of the methodology). We found adult male elk to maintain distinct home ranges and thus, we treated each adult male elk ($n = 7$) as an independent experimental unit. Furthermore, elk resource selection varies seasonally (Boyce 1991; Millspaugh 1995, 1999; Unsworth et al. 1998) and we portioned our modeling efforts between seasons corresponding to behavioral periods for elk. We used telemetry locations to develop utilization distributions (UD; Kernohan et al. 2001) by season. We developed separate UDs by season to model the effect of behavioral periods for elk and relative levels of vehicle use in Custer State Park. Thus, winter (16 Dec–15 Mar) corresponded to the winter survival period for elk and relatively low vehicle use, spring (16 Mar–15 Jun) corresponded to the spring calving period and moderate vehicle use, summer (16 Jun–15 Sep) corresponded to the summer forage and lactation period and peak vehicle use, and autumn (16 Sep–15 Dec) corresponded to the breeding and post-breeding periods and moderate vehicle use in Custer State Park. We estimated these UDs in R (R version 2.10.0, www.cran.r-project.org, accessed 1 Aug 2011) with a

Table 1. Patch size (ha) statistics of the categorical visibility rasters representing areas not visible and visible from primary, secondary, and tertiary roads in Custer State Park, South Dakota (1993–1997), by road type.

Road type	Visibility	Count	Min.	Max.	$\bar{x}$	SD
Primary	Not visible	14,713	0.01	15,912.00	1.4	131.87
	Visible	8,101	0.01	2,535.00	0.98	39.85
Secondary	Not visible	13,498	0.01	10,322.27	1.57	120.07
	Visible	7,557	0.01	2,088.51	0.98	32.77
Tertiary	Not visible	29,630	0.01	1,219.14	0.30	10.50
	Visible	7,699	0.01	19,186.61	2.56	218.67

bivariate plug-in matrix that calculated bandwidth along rotated axes for each male elk and female elk subherd (Kernohan et al. 2001, Gitzen and Millspaugh 2003, Gitzen et al. 2006). The R code produced evaluation grids of each UD at a resolution of 10 m. We imported these grids as rasters in ArcMap 9.2 (Environmental System Research Institute, Redlands, CA) and converted the UD values to percent volume contours at 1% intervals (with the 1st percentile corresponding to the highest use areas and the 98th percentile corresponding to the lowest use areas at the home range scale; Marzluff et al. 2004). These space use percentiles represented the response variable in our spatially explicit regression models.

Habitat Covariates

The habitat covariates in this analysis included forage quality (see Roloff et al. 2001), Euclidean distance to roads, visibility from roads, and distance to nearest security cover. We allowed for seasonal variation in forage quality scores because of changes in plant palatability, availability of forage types, and known phenological events (Roloff et al. 2001). Ranked (from high to low value) forage quality for elk included grasses (with variation between winter and non-winter seasons), forbs, shrubs, and deciduous trees (Gibbs 1993). We assumed that forage biomass was negatively associated with tree canopy cover (Riggs et al. 1996). The resultant rasters were forage quality scores (from no forage [0] to the highest quality forage [100]) for each season (winter, spring, summer, and autumn).

We estimated Euclidean distance to each road (primary, secondary, and tertiary) using the Spatial Analyst extension and the Euclidean distance tool in ArcMap 9.2 (Fig. 2A). Resultant rasters represented the distance from every 10×10 m cell of the study area to the nearest road (Fig. 2A).

We computed visibility by creating a vegetation-modified digital elevation model (VDEM). We derived the VDEM from a digital elevation model, road map layer, and vegetation raster (from 1997) attributed with tree density (trees/ha), canopy height (m), and understory shrub cover (%). We queried the vegetation raster for cells containing $\geq$150 trees/ha or understory cover $\geq$70% to identify vegetation patches dense enough to screen elk (Roloff et al. 2001). Patches generated via these criteria also served as our security cover layer. For raster cells that satisfied the screening criteria, we added vegetation height to the elevation in the digital elevation model. For those areas where the vegetation did not satisfy the visual screening criteria, we retained the original digital elevation value. Lastly, we assigned all road locations to their original elevations to model the effect of roads passing through screening vegetation.

Using the VDEM, we produced visibility rasters by road type (primary, secondary, and tertiary; Fig. 2B). We calculated line of sight distances using viewsheds at 10-m intervals along each road segment. Viewsheds integrated the screening effects of vegetation and topography in the form of the VDEM. Thus, in addition to areas screened by vegetation, areas screened by topographical barriers were also considered

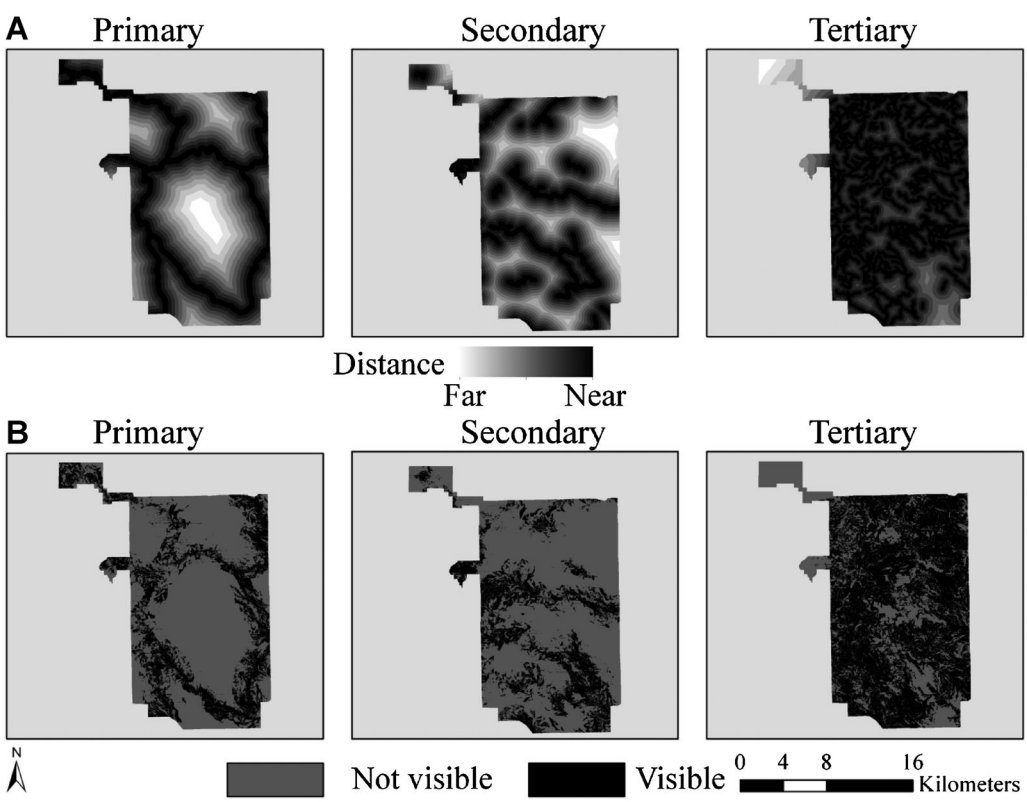

Figure 2. Covariates used in the spatially explicit regression models. (A) Euclidean distance to roads and (B) visibility from roads for primary, secondary, and tertiary road networks in Custer State Park, South Dakota (1993–1997).

not visible. We classified all areas that were not visible as 0 (invisible) and all remaining areas at a line of sight distance <1,600 m as 1 (visible). We selected this distance as the breakpoint because research finds that visibility effects on elk substantially diminish beyond 1,600 m (Witmer and deCalesta 1985, Hillis et al. 1991, Preisler et al. 2006). To create the distance to security cover raster, we identified habitat that was not visible from any road network based on the screening criteria outlined above. We then calculated the nearest distance from each 10 by 10-m cell of the study area and the nearest patch providing security cover.

Statistical Analysis

We standardized all covariates to a mean of 0 and evaluated the distribution for normality and homoscedasticity. We developed 15 a priori models to explain variation in elk space use. We analyzed models separately by season and sex (Appendices A–H available online at www.onlinelibrary.wiley.com). Most candidate models included distance to security cover and forage quality consistent with previous research that demonstrated the influence of these covariates on elk life history (Creel and Winnie 2005, Beck et al. 2006, Van Dyke and Darragh 2007, Hebblewhite et al. 2008, Christianson and Creel 2009). Most models also included at least one type of Euclidean distance to road as well as interactions with visibility from road, and interactions between seasonal forage and visibility from road.

We fit candidate models using a spatially explicit mixed linear regression model. As environmental features influence elk space use at various scales (Anderson et al. 2005*a*, *b*; Frair et al. 2005) and autocorrelation in space is inherent in all landscapes (Boyce 2006), our models accounted for spatial autocorrelation based on distances between elk telemetry locations. We coded these models using SAS PROC MIXED (version 9.2, SAS Institute, Inc., Cary, NC), which took the form:

$$Y_i = X\beta_i + Zu_i + e$$

where Y_i was the response variable (space use percentile) at each (ith) elk telemetry location, $X\beta_i$ represented vectors of the covariates at the ith elk telemetry location, Zu_i was the random effects term, and e was the spatially autocorrelated error term. We specified the subject factor at the individual level identifying that we expected a different correlative process for each male elk and female elk subherd. We used an information theoretic approach to model selection (Akaike's Information Criterion [AIC]) and ranked the performance of the models using AIC weights (ω_i; Burnham and Anderson 2002). All models with a $\omega_i \geq 1/8$th of the top-ranking model were averaged (Burnham and Anderson 2002, Bonnot et al. 2008). We graphed the mixed linear regression functions for all coefficients with a $P \leq 0.10$ in the top-ranking model(s).

RESULTS

We collected 9,770 elk telemetry locations (7,534 female and 2,236 male). We calculated UDs from 377 locations on average (min. = 132 and max. = 625) for female elk subherds and 89 locations on average (min. = 36 and max. = 170) for male elk. The assessment of mean telemetry error revealed a positional accuracy of 176.1 m (min. = 13.4, max. = 746.6, and SE = 12.4), with a mean error polygon of 9.27 ha. Our evaluation of techniques for incorporating telemetry error into the analysis indicated that the zonal majority technique was most accurate (Table 2). The zonal majority technique was 6–8% better than ignoring telemetry error and produced accuracies ≥86% for all categorical rasters examined (Table 2). None of the covariates in our study were correlated ($r > 0.50$) and after we log-transformed the response variable (space use percentile), the residuals approximated a normal and homoscedastic distribution.

We developed 15 a priori models by season ($n = 4$) and sex; therefore, we evaluated 120 models. We identified one top-ranking model for each season and sex combination apart from male elk in autumn where we averaged two top-ranking models (i.e., candidate models had a ω_i within one-eighth of the top-ranking model weight; Burnham and Anderson 2002, Bonnot et al. 2008; Table 3). Each of the top-ranking spatially explicit models had spatially autocorrelated variation that was dominant to uncorrelated variation. Thus, ≥99% of the residual variation in top-ranking models could be attributed to spatially autocorrelated errors. Among the top-ranking models, there were 12 coefficients with $P \leq 0.10$. We plotted these coefficients with 95% confidence intervals to examine the magnitude of effects (Figs. 3–6).

Winter

The top-ranking model describing male elk space included a significant effect of distance to tertiary roads ($P = 0.01$; Table 3). This model ($\omega_i = 0.49$) was over three times more likely to be the best approximating model when compared with the next ranked model ($\omega_i = 0.15$; Appendix A available online at www.onlinelibrary.wiley.com). In winter, male elk increased their space use, at the home-range scale, in areas closer to tertiary roads (Fig. 3A-1).

The top-ranking model describing female elk space use in winter included the interaction of Euclidean distance to secondary roads and visibility from secondary roads ($P = 0.08$; Table 3). This model ($\omega_i = 0.42$) was over twice as likely to be the best approximating model when compared with the next ranking model ($\omega_i = 0.19$; Appendix B available online at www.onlinelibrary.wiley.com). Female elk reduced their use of habitat that was close to secondary roads (Fig. 3B-1). However, as distance from secondary roads increased, female elk were more likely to use habitat that was not visible from secondary roads (Fig. 3B-1). Female elk

Table 2. Classification accuracy (proportion correct) by road visibility raster for ignore and zonal majority sampling techniques (see Montgomery et al. 2010). Results are based on elk telemetry data collected in Custer State Park, South Dakota (1993–1997).

Road visibility raster	Ignoring error	Zonal majority sampling
Primary	0.82	0.89
Secondary	0.85	0.91
Tertiary	0.78	0.86

Table 3. Most influential ($P \leq 0.10$) regression coefficients (SE) from the top-ranked models describing elk space use by season and sex in Custer State Park, South Dakota (1993–1997).

		Coefficients[a] (SE)							
Season	**Sex**	**DISTCOVER**	**EUCSEC**	**EUCTERT**	**EUCSEC × VISSEC = 0**	**EUCSEC × VISSEC = 1**	**FORAGE × VISSEC = 0**	**FORAGE × VISSEC = 1**	**EUCPRIM × VISPRIM = 0**	**EUCPRIM × VISPRIM = 1**
Winter	Males			0.082* (0.032)						
	Female subherds				−0.105* (0.054)	−0.001 (0.056)				
Spring	Males			0.063* (0.027)						
	Female subherds			0.063* (0.013)			−0.002 (0.020)	0.046* (0.019)	0.033 (0.060)	−0.157* (0.064)
Summer	Males	−0.050* (0.020)	−0.134* (0.104)						0.073 (0.134)	−0.318* (0.138)
	Female subherds			0.059* (0.012)						
Autumn	Males			0.065* (0.025)						
	Female subherds								0.077* (0.053)	−0.049 (0.055)

[a] FORAGE, forage quality score; DISTCOVER, distance to security cover; EUCPRIM, Euclidean distance to primary roads; EUCSEC, Euclidean distance to secondary roads; EUCTERT, Euclidean distance to tertiary roads; VISPRIM, visibility from primary roads; VISSEC, visibility from secondary roads.

* Predictor covariate significance at the 0.05 level.

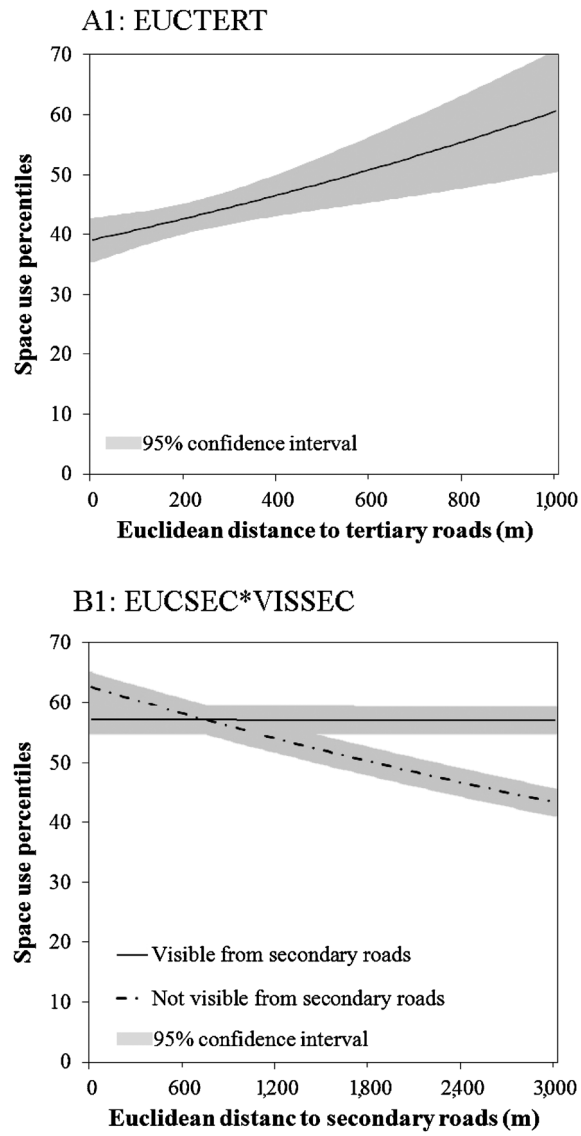

Figure 3. Spatial mixed linear regression functions of the most influential coefficients from the top-ranked model explaining (A) male and (B) female elk space use in winter, Custer State Park, South Dakota (1993–1997). EUCTERT = Euclidean distance to tertiary roads, EUCSEC = Euclidean distance to secondary roads, and VISSEC = visibility from secondary roads. The *y*-axis displays the response variable (space use percentiles) with the core areas of the home range near 1% and peripheral areas of the home range near 98%.

subherd space use within the home range changed very little in habitat visible from secondary roads (Fig. 3B-1).

Spring

The top-ranking model describing male elk space use in spring included the significant effect of distance to tertiary roads ($P = 0.02$; Table 3). This model ($\omega_i = 0.32$) was over twice as likely to be the best approximating model when compared with the next ranking model ($\omega_i = 0.14$; Appendix C available online at www.onlinelibrary.wiley.com). In spring, male elk increased their space use in areas close to tertiary roads (Fig. 4A-1).

The top-ranking model describing female elk subherd space use in spring was the most parameterized candidate

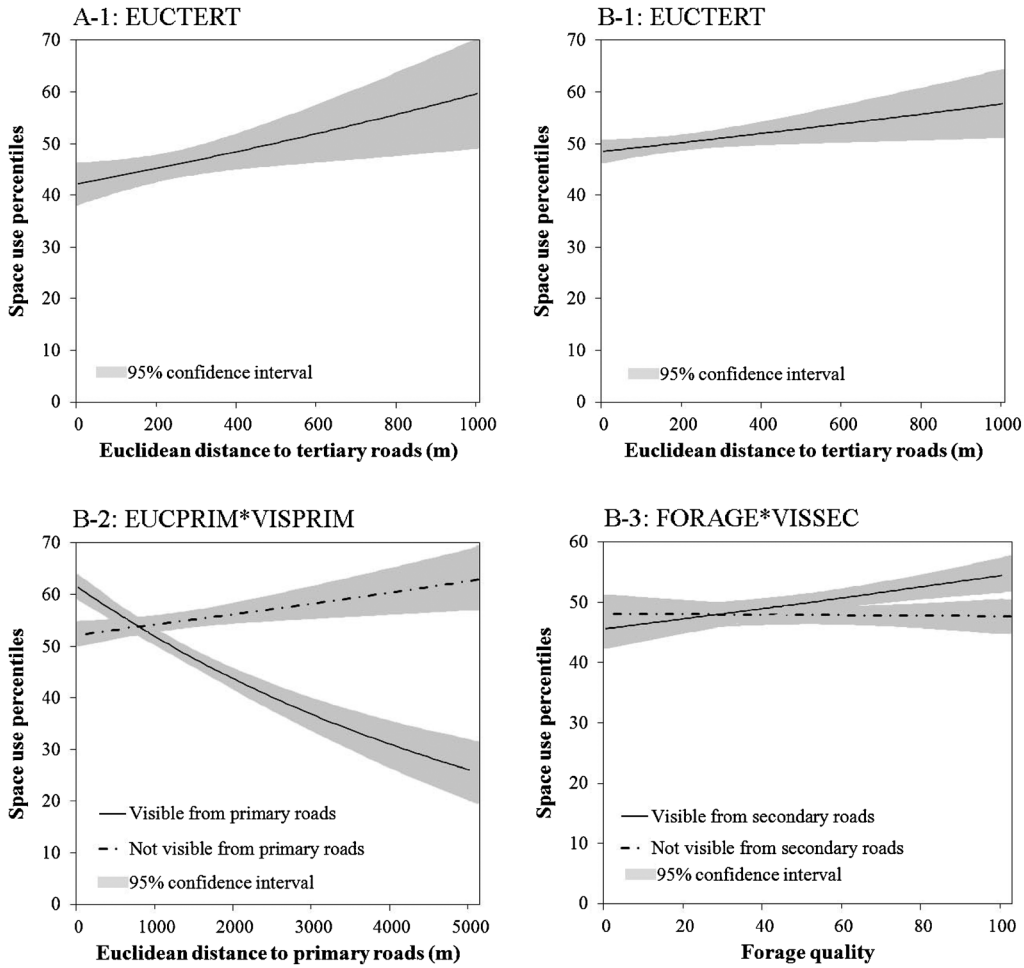

Figure 4. Regression functions of the most influential coefficients from the top-ranking model explaining (A) male and (B) female elk space use in spring, Custer State Park, South Dakota (1993–1997). EUCTERT = Euclidean distance to tertiary roads, EUCPRIM = Euclidean distance to primary roads, VISPRIM = visibility from primary roads, FORAGE = forage quality, and VISSEC = visibility from secondary roads. The *y*-axis displays the response variable (space use percentiles) with the core areas of the home range near 1% and peripheral areas of the home range near 98%.

model. This model ($\omega_i = 0.88$) received almost the full weight of evidence (Appendix D available online at www. onlinelibrary.wiley.com). It included the significant effects of Euclidean distance to tertiary roads ($P < 0.01$), the interaction between Euclidean distance to primary roads and visibility from primary roads ($P < 0.01$), and the interaction of forage quality and visibility from secondary roads ($P < 0.01$; Table 3). Female elk subherds increased their space use in areas close to tertiary roads (Fig. 4B-1). Female elk subherds reduced their use of habitat that was both visible from and close to primary roads (Fig. 4B-2). However, they were more likely to use habitat that was visible from primary roads as distance from primary roads increased (Fig. 4B-2). The trend was completely opposite in habitat that was not visible from primary roads (Fig. 4B-2). Finally, female elk exhibited greater use of higher quality forage areas if the areas were not visible from secondary roads (Fig. 4B-3).

Summer

The top-ranking model describing male elk space use in summer included the significant effects of distance to security cover ($P = 0.01$), Euclidean distance to secondary roads ($P = 0.02$), and the interaction of visibility and distance from primary roads ($P < 0.01$; Table 3). This model ($\omega_i = 0.38$) was 1.5 times more likely to be the best approximating model when compared with the next ranking model ($\omega_i = 0.26$; Appendix E available online at www. onlinelibrary.wiley.com). Male elk increased their use of habitat that was at a greater distance from security cover (Fig. 5A-1) and increased their use of habitat at a greater distance from secondary roads (Fig. 5A-2). Finally, male elk reduced their use of habitat that was both visible from and close to primary roads (Fig. 5A-3). However, male elk were more likely to use habitat that was visible from primary roads as distance from primary roads increased (Fig. 5A-3). The trend was completely opposite in habitat that was not visible from primary roads (Fig. 5A-3).

The top-ranking model ($\omega_i = 0.70$) describing female elk subherd space use in summer included the significant effect of distance to tertiary roads ($P < 0.01$; Table 3). This model was over six times more likely to be the best approximating model when compared with the next ranking model ($\omega_i = 0.11$; Appendix F available online at www. onlinelibrary.wiley.com). Female elk increased their space use in areas that were closer to tertiary roads (Fig. 5B-1).

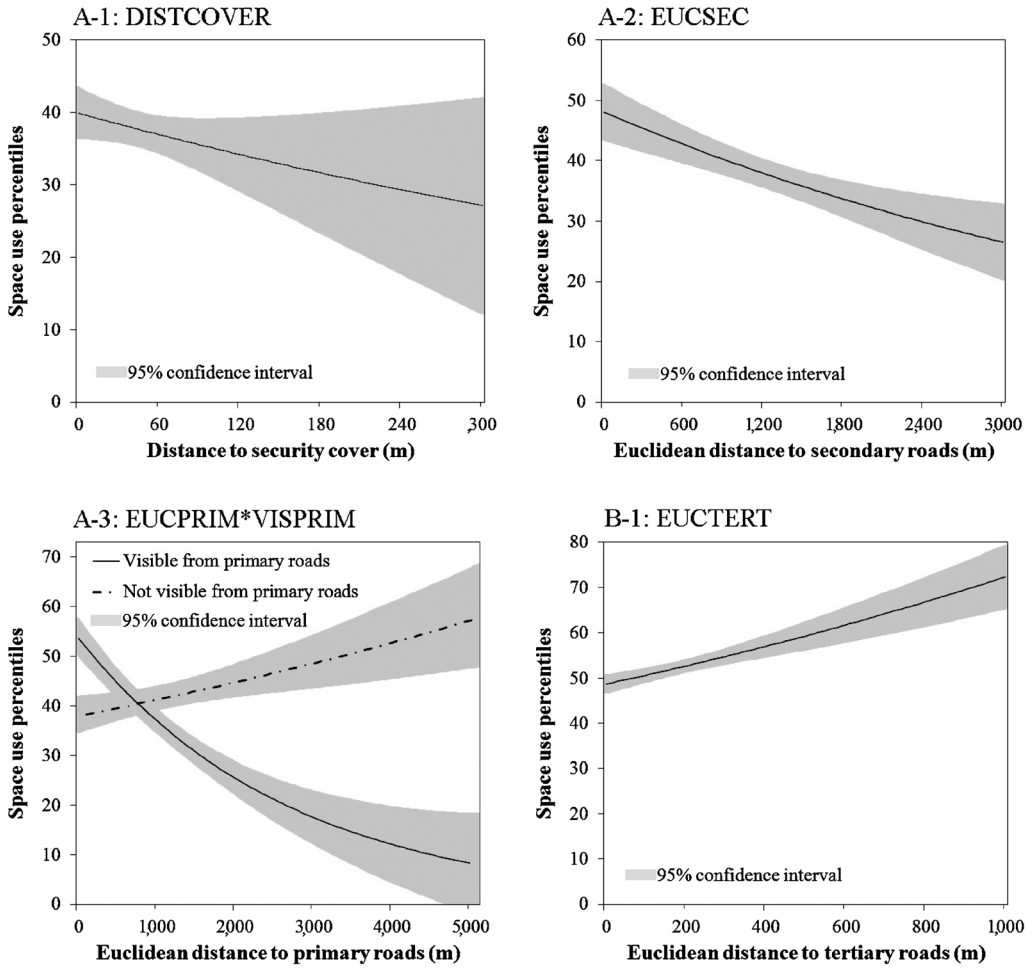

Figure 5. Regression functions of the most influential coefficients from the top-ranking model explaining (A) male and (B) female elk space use in summer, Custer State Park, South Dakota (1993–1997). DISTCOVER = distance to security cover, EUCSEC = Euclidean distance to secondary roads, EUCPRIM = Euclidean distance to primary roads, and VISPRIM = visibility from primary roads. The *y*-axis displays the response variable (space use percentiles) with the core areas of the home range near 1% and peripheral areas of the home range near 98%.

Autumn

We model averaged the two top-ranking models describing male elk space use in autumn as the second-ranking model was within one-eighth ω_i of the top model (Burnham and Anderson 2002, Bonnot et al. 2008; Appendix G available online at www.onlinelibrary.wiley.com). Model averaging revealed that distance to tertiary roads ($P < 0.01$; Table 3) significantly affected male elk space use in autumn. Male elk increased their use of habitat that was closer to tertiary roads (Fig. 6A-1).

The top-ranking model describing female elk subherd space use in autumn included the significant interaction of visibility from primary roads and distance to primary roads ($P = 0.02$; Table 3). This model ($\omega_i = 0.69$) was six times more likely to be the best approximating model when compared with the next ranking model ($\omega_i = 0.11$; Appendix H available online at www.onlinelibrary.wiley.com). Female elk subherds reduced their use of habitat that was both visible from and close to primary roads (Fig. 6B-1). However, they were more likely to use habitat that was visible from primary roads as distance from primary roads increased (Fig. 6B-1).

DISCUSSION

Our modeling process demonstrated the influence of different road types on elk space use across seasons and by sex. This influence was made clear by examining both Euclidean distance to roads as main effects and the interactions of Euclidean distance and visibility from roads. In general, elk established seasonal home ranges away from primary and secondary roads, those receiving the greatest traffic levels throughout the year, and near to tertiary roads, those closed to public vehicle traffic. The negative effect of primary and secondary roads on elk space use may conflict with existing research which suggests that elk can become habituated to roads with relatively consistent traffic levels (see Ward 1976, Wisdom et al. 2005, St. Clair and Forrest 2009). Avoidance of roads with greater traffic was particularly apparent for male elk in summer, when vehicle traffic peaks and remains relatively consistent throughout the season in Custer State Park. We documented similar avoidance of primary roads for female elk subherds in spring and autumn, corresponding to sensitive times of year when female elk are calving and mating.

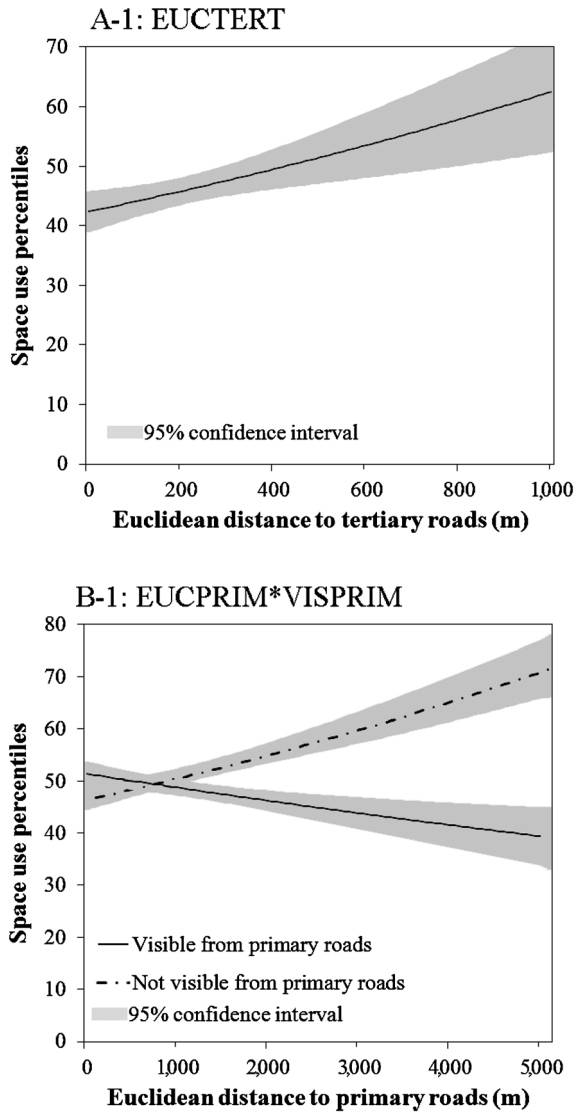

Figure 6. Regression functions of the most influential coefficients from the top-ranking model explaining (A) male and (B) female elk space use in autumn, Custer State Park, South Dakota (1993–1997). EUCTERT = Euclidean distance to tertiary roads, EUCPRIM = Euclidean distance to primary roads, and VISPRIM = visibility from primary roads. The *y*-axis displays the response variable (space use percentiles) with the core areas of the home range near 1% and peripheral areas of the home range near 98%.

Additionally, both male and female elk consistently organized their home ranges near tertiary roads. This result is at least partially a product of the ubiquitous distribution of tertiary roads in the landscape. Custer State Park has a high tertiary road density (e.g., averaging >67 m/ha) and no portion of the habitat within elk home ranges was >1 km from a tertiary road. A further 185 km of primary and secondary roads bisect Custer State Park and thus, the elk in our study could not avoid all roads simultaneously in their space use decisions. Therefore, understanding the influence of tertiary roads must be related to the other road networks in the landscape. Our study provides evidence that elk in this highly human-dominated landscape were more likely to use habitat in the vicinity of roads closed to vehicle traffic than roads associated with vehicle traffic, despite the relatively consistent and predictable nature of that traffic. However, although tertiary roads do not receive vehicle traffic, they do receive unpredictable human foot traffic (e.g., hikers, hunters; Millspaugh 1999). Thus, our study demonstrates that elk do not relate to all roads similarly and traffic levels on roads affect elk space use decisions (Rowland et al. 2000, Gagnon et al. 2007). These observations provide evidence that elk will use habitat near road networks if those roads are consistently closed to vehicle traffic and receive modest levels of use by humans on foot. More broadly, these results can be used to support road management activities in areas where elk inhabit road dense environments. Road management activities can be positively associated with elk survivability (Cole et al. 1997) and the re-colonization of open habitat by elk near to roads previously associated with vehicle traffic (Cole et al. 2004).

Primary roads influenced male elk space use in summer and female elk subherd space use in spring and autumn. In all cases, elk space use was negatively affected by proximity to and visibility from primary roads. Custer State Park hosts nearly 2 million visitors annually, the majority of which use primary roads (Millspaugh et al. 2001). Male elk clearly made summer space use decisions at the home range scale, considering the visibility from and distance to primary roads, corresponding to peak travel times in Custer State Park (Millspaugh 1999). This result is consistent with existing information, which identifies that male elk avoid areas with higher levels of anthropogenic disturbance, such as primary roads (Rost and Bailey 1979, Lyon and Ward 1982, Unsworth et al. 1993, McCorquodale 2003, Montgomery et al. 2012). Furthermore, these results correlate with observations of elk in the Rocky Mountain region, which document a heightened level of avoidance of roads used for industrial infrastructure (i.e., energy development) in summer (Powell 2003, Sawyer et al. 2007).

The space use decisions of female elk subherds in spring were most affected by primary roads. Powell (2003) similarly documented springtime elk avoidance of roads used for oil and gas development in Wyoming. Spring is a critical time for female elk when they are highly sensitive to disturbance because of their physiological condition associated with calving (Phillips and Alldredge 2000, Shively et al. 2005). Space use in spring is likely affected by the immediate need to successfully give birth, protect young, and access high-quality forage to support lactation (Vore and Schmidt 2001, Cook et al. 2004). Human disturbance of female elk in spring can influence survivability of dependent offspring (Phillips and Alldredge 2000) and as a result, female elk will avoid areas that present sources of disturbance (Unsworth et al. 1998). Our analysis supports these observations by illustrating that female elk subherds reduced their use of habitat within the home range that was both close to and visible from primary roads in spring. We observed the opposite relationship for habitat that was not visible from primary roads. Thus, although male elk and female elk subherds were negatively affected by primary roads in specific seasons, we found that

they controlled for increased traffic levels by using habitat that provided a visual barrier in areas near to primary roads.

Female elk space use in autumn was affected by distance to and visibility from primary roads, whereas male elk selected habitat near tertiary roads. Both male and female elk are influenced by disturbance associated with hunting in autumn (Hurley and Sargeant 1991, Millspaugh et al. 2000, Preisler et al. 2006, Proffitt et al. 2009). Hunting pressure is greater in areas with high road density and access (Unsworth et al. 1993, Hayes et al. 2002) and elk become increasingly sensitive to vehicular and non-vehicular traffic during autumn (Lyon et al. 1985, Hurley and Sargeant 1991, Burcham et al. 1999, Vieira et al. 2003, Proffitt et al. 2009). Elk space use decisions in autumn are also motivated by breeding. Male elk are actively trying to locate and herd receptive females in autumn when their space use patterns are broadly ranging and somewhat unpredictable (Geist 1982, Wolff and Van Horn 2003). Male and female elk space use patterns are likely correlated during the autumn breeding season and thus, we interpret male elk selection of habitat near tertiary roads as partially resulting from an avoidance of habitat in the vicinity of primary roads.

Security cover is known to be an integral component of elk ecology (Grover and Thompson 1986, Creel and Winnie 2005, Sawyer et al. 2007) and we expected that elk would use habitat closer to security cover. However, we detected an influence of security cover only for male elk and only in one season (summer). Furthermore, the regression trend indicated that male elk increased their use of habitat farther from security cover, which was an unexpected outcome. The absence of large predators such as wolves (*Canis lupus*) in Custer State Park may partially explain use of habitat away from security cover. Wolves regularly cause elk to select habitat in more closed areas that provide complex vegetation structure (Mao et al. 2005). Furthermore, given that human hunting was isolated to one season and poaching was uncommon, Custer State Park elk may not be particularly reliant on security cover.

Research indicates that elk will use habitat closer to roads at night when vehicle traffic is reduced (Millspaugh 1999). Our models did not explicitly consider time of day and we mention that this factor may have affected elk space use. For instance, forage quality influenced female elk subherd space use in spring, an effect that depended on road visibility. In spring, female elk tended to select high-quality forage in areas that were not visible from secondary roads, though the effect of visibility was relatively weak (i.e., small difference in the response given visibility; Fig. 4b). Elk often use productive grazing grounds in open areas because graminoids are a preferred forage during certain seasons (Creel and Winnie 2005; Christianson and Creel 2007, 2008), but human disturbance can cause elk to avoid open habitat during visible hours (Naylor et al. 2009). Thus, female elk in our study may have been using open areas visible from secondary roads in non-daylight hours (Millspaugh 1999). Accounting for time of day in which the elk telemetry location was recorded was beyond the scope of this analysis because our analysis focused on overall home range use, not time-specific resource selection patterns. We suggest that future analyses should consider high resolution global positioning system telemetry units where the sampling interval can include all time periods equally to account for temporal differences in resource selection (Beyer and Haufler 1994). With these data in mind, models could be subdivided not only by season but also by time of day to determine the impact of time of day on elk space use. Thereby, the effect of an interaction between forage quality and visibility from roads may be better understood through consideration of time of day.

The modeling design implemented in this analysis documented variation in elk response to roads by season, sex, and road type. Our results underscore the complexities associated with modeling elk space use and further demonstrate the utility of interaction effects between Euclidean distance to roads and visibility from roads across all seasons. These interaction terms illuminated key aspects of elk space use that were either speculative or poorly understood. Roads and visibility are important considerations for describing within-home range space use, but so is Euclidean distance to roads as main effects. Although our analysis supports integration of visibility into elk habitat modeling, we also acknowledge the continued and integral role that Euclidean distance to road plays in road effects research (e.g., Conner et al. 2003).

MANAGEMENT IMPLICATIONS

Researchers and managers should consider how distance and visibility interact when assessing road effects on elk. We suggest that visibility, as influenced by topography and vegetation, be managed to positively affect elk space use. Vegetation management (e.g., timber harvests, provision and maintenance of openings to provide elk forage) could be integrated with road visibility assessments to identify portions of the landscape protected from human view. Managers should consider retaining vegetation structures that screen elk from road networks, particularly for critical habitat areas and road systems that receive high vehicle use. Our analysis suggests that habitat in the vicinity of roads that are closed to public vehicle use might be used when road densities are high and roads receiving large volumes of vehicle traffic are in the system. Managers must consider the context of road effects because elk use of tertiary roads in landscapes without primary and secondary roads might differ from the patterns that we observed in our assessment. Thus, we recommend that researchers and managers conduct similar assessments in their study areas using the methods outlined in this manuscript to determine the effect of various road networks on elk behavior. We suggest that these assessments be framed across broad spatial and temporal dimensions to fully understand elk space use decisions.

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