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Authors: Montgomery, Robert A., Roloff, Gary J., and Millspaugh, Joshua J.

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Original article

Importance of visibility when evaluating animal response to roads

Robert A. Montgomery, Gary J. Roloff & Joshua J. Millspaugh

Roads increase risk to animals via direct and indirect mechanisms yet, both positive and negative effects of animal space use in relation to roads have been reported. These contrasting reports may not actually represent animal ecology, but could be a product of the primary variable used to test the relationship between animals and roads. Animal-road associations are often evaluated using Euclidean distance. Euclidean, or straight-line, distance fails to account for the screening effects of vegetation and topography and may document spurious relationships. We evaluated the influence of Euclidean distance, visibility from road and forage quality on summer space use for male elk *Cervus elaphus* and female elk subherds in Custer State Park, South Dakota, USA. Models that included interactions with visibility from road metrics outperformed models that included only Euclidean distance to road as main effects. Elk response to roads varied by sex and road type, which functioned as an index for vehicle use. Male elk selected habitat away from roads with the greatest vehicle use, an effect that was greater if habitat was visible from those roads. Female elk tended to select habitat with high forage quality in areas visible from roads closed to vehicle use. Interestingly, both male and female elk selected habitat away from roads with secondary vehicle use and near to roads devoid of traffic, regardless of visibility. Our analysis highlights the importance of including both Euclidean distance and visibility from road metrics. Road effects research may be incomplete without consideration of visibility from roads, particularly for large mammals in landscapes with intense road use.

Key words: Cervus elaphus, elk, Euclidean distance, forage quality, roads, utilization distribution, visibility

Robert A. Montgomery, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources Building, Columbia, Missouri 65211, USA, and Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824, USA - e-mail: montg164@msu.edu
Gary J. Roloff, Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824, USA - e-mail: roloff@msu.edu
Joshua J. Millspaugh, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources Building, Columbia, Missouri 65211, USA - e-mail: millspaughj@missouri.edu

Corresponding author: Robert A. Montgomery

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Roads tend to negatively impact animal populations (Trombulak & Frissell 2000). Habitat directly adjacent to roads is more fragmented, is of lower quality and has higher wildlife mortality rates, resulting from vehicle-animal collisions, than corresponding habitat devoid of roads (Forman et al. 2003, Keller & Largiadér 2003, Kramer-Schadt et al. 2004, Litvaitis & Tash 2008). Roads can act as barriers to organism movement and dispersal, and thus, habitat intersected with roads can have lower biodiversity (Vos & Chardon 1998, Rondinini & Doncaster 2002, Benítez-López et al. 2010). Furthermore, roads correspond to an increase in anthropogenic disturbance, which elevates animal stress response (Wasser et al. 1997, Millspaugh et al. 2001). Given these negative effects, it is reasonable to assume that animals would avoid habitat in the vicinity of roads.

Studies designed to test the association between animal space use and roads have reported both positive and negative relationships. In many cases, animals are road averse and select habitat farther away from roads (Bowyer et al. 1999, Dyer et al. 2001). Other studies have demonstrated that animals are undeterred by roads and, depending on road type, traffic volume and timing of road use, will select habitat in the vicinity of roads (e.g. Yost & Wright

2001, see Fahrig & Rytwinski 2009 for review). The polarity of these findings may not actually be a product of animal ecology, but could result from the variables used to examine animal space use in relation to roads (Rowland et al. 2000, Jaeger et al. 2005). Historically, the primary variable used to test animal-road associations has been Euclidean distance (Clark et al. 1993, Boal & Mannan 1998, Forys et al. 2002, Conner et al. 2003, Menzel et al. 2005). Euclidean distance provides the minimum straight-line distance between two points (e.g. an animal location and a road segment; Kang 2008). Euclidean distance is undoubtedly useful in road effects research, but this metric ignores the screening potential of vegetation and topography as a means to reduce human disturbances that often accompany roads.

Roads also facilitate human disturbance of animals through wildlife viewing. Ecological tourism and wildlife viewing are rapidly expanding pursuits worldwide (Giannecchini 1993), and more people in wild areas and national parks exacerbate the negative effects of roads on wildlife (Newsome et al. 2002, Ament et al. 2008). Animals often respond more negatively to humans than to vehicles (Papouchis et al. 2001, Whittington et al. 2004, 2005) because animals sometimes become habituated to moving traffic (Falk et al. 1978, MacArthur et al. 1982, Whittington et al. 2004). When animals are visible from roads, traffic is likely to stop and potentially disrupt animal behaviour. Therefore, the visibility of habitat from a road influences animal space use patterns (Lyon 1979, Edge & Marcum 1991, Dyer et al. 2001, Dickson et al. 2005, Preisler et al. 2006, Hayward & Hayward 2009). Animals may vary their use of habitat adjacent to a road depending on visibility from road, particularly if desirable resources (like high quality forage) are available. In this case, Euclidean distance could report a spurious relationship between animal space use and roads.

We examined the response of elk *Cervus elaphus* to roads in Custer State Park, South Dakota (SD), USA. We hypothesized that models developed to describe elk space use in relation to roads would be improved by incorporating visibility. We also anticipated that elk space use would vary by road type, which indexes vehicle use. We tested these hypotheses using a spatially-explicit approach to regress summer elk space use on various combinations of Euclidean distance, visibility from road and forage quality metrics. We developed separate models for male elk and female elk subherds given known variation in space use patterns by sex (McCorquodale 2003).

Material and methods

Study area

We analyzed elk space use in Custer State Park, SD, USA, from 1993 to 1997 (Fig. 1). During our study, estimates of elk abundance in the park were between 750 and 1,000 animals (Millspaugh 1999). At this time, about 42% of Custer State Park was dominated by ponderosa pine *Pinus ponderosa* forest. The remaining area was comprised of open, grassland

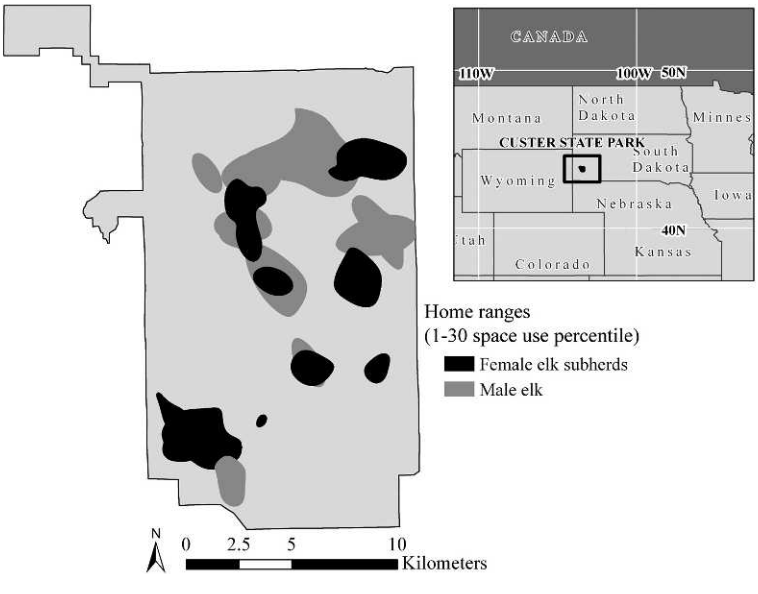


Figure 1. Female elk subherd and male elk utilization distributions (UDs) in Custer State Park, South Dakota, USA. The figure displays the 1st third (1-30 space use percentiles) of the UDs for the five female elk subherds and six male elk in our study. They were derived from telemetry locations recorded in summer during 1993-1997.

communities with deciduous woodlands commonly occurring along drainage systems. The extensive road and trail network included approximately 103 km of primary roads (maintained and paved), 82 km of secondary roads (maintained and dirt) and 434 km of tertiary roads (unmaintained and primitive). These different roads represent indices for relative anthropogenic use (Perry & Overly 1977, Millspaugh et al. 2000). More than 1.7 million tourists visit the park annually and most of this activity occurs during the summer months (June 15 - September 15) on primary roads (Millspaugh 1999), which have posted speed limits of between 15 and 35 miles per hour (mph). Secondary roads are maintained dirt roads open to the public in summer with speed limits of 15-20 mph. Tertiary roads are unmaintained dirt roads that are closed to public vehicle use. During the study period, Custer State Park received an average of 5,242 user groups/week on each segment of primary roads, 422 user groups on each segment of secondary roads, and seven user groups on each segment of tertiary roads (see Millspaugh 1999: Table 20 on page 147).

Response variable

We collected telemetry locations from 18 female and six male elk during the summer months (June 15 - September 15) to coincide with peak anthropogenic road use. We relocated collared elk by triangulation of the signal and visual observation between two and five times/week. We conducted an assessment of telemetry error by relocating fixed transmitters in representative habitat types within the study area. We determined accuracy by calculating the deviation from the true location to the location estimated via azimuths taken between 0.25 and 3.0 km from the transmitter (see Millspaugh et al. 2004). The female elk in our sample were distributed in five spatially disjoint subherds (Millspaugh et al. 2004) whereas male elk maintained distinct spatial patterns. Thus, we created utilization distributions (UDs) for each individual male elk and female elk subherd. We created the UDs in R (R version 2.10.0; available at: http://www.cran.r-project.org, and last accessed on 1 July 2011) using a bivariate plug-in matrix (Kernohan et al. 2001, Gitzen & Millspaugh 2003, Gitzen et al. 2006). This matrix allowed for parameter smoothing along rotated axes for each female elk subherd and male elk home range. The UDs resulting from our process were 10 m resolution, corresponding to the minimum grain of our analysis (see Fig. 1). We converted the height of the UDs (i.e. the probability density estimates within each grid) to percent volume contours at 1% intervals representing space use percentiles in ArcMap 9.2 (Environmental System Research Institute, Redlands, California, USA; Marzluff et al. 2004). The final data set contained 1-98% space use percentiles which functioned as the response variable in our spatial regression models with 1% corresponding to core-use areas and 98% corresponding to the periphery of the UD.

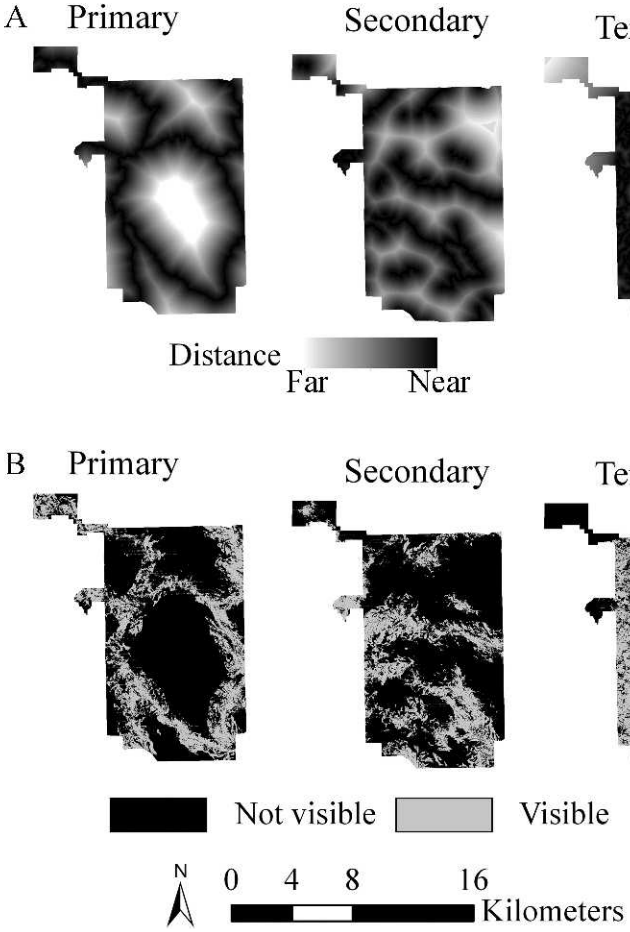
Predictor covariates

We developed predictor covariates for spatial regression modeling representing Euclidean distance rasters (to primary, secondary and tertiary roads), visibility from road rasters (from primary, secondary and tertiary roads) and summer forage. We calculated the Euclidean distance to road and visibility from road rasters by road type because intensity of vehicle use varied between primary, secondary and tertiary roads (Millspaugh et al. 2000). We calculated Euclidean distance rasters, representing distance from each cell (at a 10-m resolution) in the study area to the nearest road using the Spatial Analyst extension and the Euclidean distance tool in ArcMap 9.2. The predictor covariates developed from this process were Euclidean distance to primary (eucprim), secondary (eucsec) and tertiary roads (euctert; Fig. 2A).

To map the areas visible from roads, we derived a vegetation-modified digital elevation model (VDEM; 10 m resolution) from a digital elevation model (USGS) and a vegetation type raster (1:12,500 aerial photography of Custer State Park) attributed with tree density (trees/ha), canopy height (m) and understory shrub cover (in %). To identify vegetation patches that would serve as a visual barrier, we queried the vegetation raster for cells containing ≥ 150 trees/ha or understory cover $\geq 70\%$ (Roloff et al. 2001). For cells that satisfied one or both of these criteria, we added the height of the vegetation to the elevation values in the digital elevation model. When the vegetation did not satisfy the visual screening criteria, we retained the original digital elevation values. All roads retained their original elevations so that we accurately modeled roads passing through screening vegetation within the VDEM.

To document visibility of habitat from roads, we generated viewsheds representing the area visible to the human eye from locations (at 10-m intervals) along every road segment. We assumed that the height of the observer was 2 m above the road. With the VDEM, we identified cells that were not visible from roads. These cells were coded as 0 (not visible)

Figure 2. Euclidean distance to road and visibility from road metrics for different road networks in Custer State Park, South Dakota, USA, during 1993-1997. A) displays the Euclidean distance to road rasters and B) shows the visibility from road rasters. Primary roads are paved and annually maintained, secondary roads are seasonally maintained and tertiary roads are primitive, unmaintained and closed to public vehicle use.



while all other cells were initially coded as 1 (visible). Maximum viewing distance (i.e. the distance at which observer presence influences elk habitat selection) has been documented to asymptote at 1,600 m (Witmer & deCalesta 1985, Preisler et al. 2006). Therefore, we calculated line of sight distances using the Arc/Info VISIBILITY algorithm (Environmental Systems Research Institute, Redlands, California, USA). We coded all visible cells $>$ 1,600 m from a road as 0, implying that visibility effects on elk space use were non-existent at this distance. The end result of this approach was rasters (at 10-m resolution) that defined each grid cell throughout the park as visible or not visible (visprim, vissec and vistert; see Fig. 2B).

We derived summer forage quality (forage) by collating data from forage production tables and vegetation inventories for ecological land units (i.e. combination of soil and vegetation cover type; Roloff et al. 2001). We based relative scores on quantity and quality of available forage and modified the scores according to tree canopy cover, forage species composition, plant phenology and palatability ratings consistent with the summer period in Custer State Park (Roloff et al. 2001). We assumed that soils producing the greatest forage biomass were optimal and that biomass decreased as tree canopy cover increased (reviewed by Riggs et al. 1996). Available forage in decreasing order of importance was grasses (with differentiation between cool and warm season species), forbs, shrubs and deciduous woody tree species (Gibbs 1993). A more detailed description of seasonal forage quality derivation is provided in Roloff et al. (2001).

Telemetry error

Assignment of the predictor covariates and response variable (i.e. elk space use percentiles) to each elk telemetry location can be complicated by large telemetry errors (Montgomery et al. 2010, 2011). Montgomery et al. (2010, 2011) described a process for identifying the best approach for incorporating telemetry error into point-based analyses. This process is sensitive to mean telemetry error, data layer resolution and mean patch size for categorical covariates (Montgomery et al. 2010, 2011). Montgomery et al. (2010) determined that with small mean patch sizes (1 ha), categorical covariates and mean telemetry error consistent with our study (176.1 m), two techniques performed best. These included ignoring the telemetry error or selecting the covariate category representing the majority of the mean error polygon. We created a paired-error location for every observed elk location in our data set. Relative accuracy was determined by comparing the covariate values associated with the error locations generated from the ignore and majority techniques to the observed locations (Montgomery et al. 2010). We ignored the telemetry error to assign covariate values to elk telemetry locations for our continuous covariates, consistent with the findings from Montgomery et al. (2010: Table 2) for these data.

Spatial regression models

We developed 18 *a priori* models representing different effects of Euclidean distance, visibility and forage quality on elk space use (Table 1). These models were devised to test specific hypotheses representing the potential mechanisms influencing elk space use while attempting to determine which road types were most influential in relation to space use by male elk and female elk subherds. We hypothesized that elk response to roads could be best explained by five categories of models including: 1) Euclidean distance to roads as main effects for each road type considered separately (Rowland et al. 2000; models 1-3 in Table 1), 2) visibility from roads as main effects for each road type considered separately (Edge & Marcum 1991; models 4-6 in Table 1), 3) interactions between Euclidean distance to roads and visibility from roads for each road type considered separately (based on contentio by Lyon 1979; models 7-9 in Table 1), 4) Euclidean distance as main effects and interactions between Euclidean distance to roads and visibility from roads while varying road type (models 7-9 in Table 1), and 5) forage quality, Euclidean distance to roads as main effects and interactions between forage quality and visibility from roads while varying road type (models 10-12 in Table 1). We considered interactions between forage quality and visibility from road metrics because forage quality has been shown to be an important determinant of elk reproductive performance and space use (Cook et al. 1996, Beck et al. 2006, Hebblewhite et al. 2008), and we hypothesized that elk may adjust their use of these resources depending on visibility from roads.

Due to spatial autocorrelation in elk space use patterns, we fit separate models describing female elk subherd and male elk space use with a spatial mixed

Table 1. The 18 *a priori* models developed to explain male elk and female elk subherd space use patterns in Custer State Park, South Dakota, USA, during 1993-1997.

Model	Covariate composition	Hypothesis
1	eucprim	Euclidean distance to primary roads, secondary roads and tertiary roads considered separately
2	eucsec	
3	euctert	
4	visprim	Visibility from primary roads, secondary roads and tertiary roads considered separately
5	vissec	
6	vistert	
7	eucprim*visprim	Interactions between Euclidean distance to roads and visibility from roads while varying road type
8	eucsec*vissec	
9	euctert*vistert	
10	eucprim*visprim eucsec euctert	Euclidean distance to roads as main effects and interactions between Euclidean distance to roads and visibility from roads while varying road type
11	eucprim eucsec*vissec euctert	
12	eucprim eucsec euctert*vistert	
13	forage eucprim eucsec forage*visprim	Forage, Euclidean distance to roads as main effects, and interactions between forage and visibility from roads while varying road type
14	forage eucprim eucsec forage*vissec	
15	forage eucprim euctert forage*visprim	
16	forage eucprim euctert forage*vistert	
17	forage eucsec euctert forage*vissec	
18	forage eucsec euctert forage*vistert	

Table 2. Patch size statistics (in ha) for the road visibility rasters describing areas within Custer State Park, South Dakato, USA, during 1993-1997 that were not visible and visible from road networks (primary, secondary and tertiary).

Road type	Raster	Count	Minimum	Maximum	$\bar{x}$	SD
Primary	Not visible	14713	0.01	15912.00	1.40	131.87
	Visible	8101	0.01	2535.00	0.98	39.85
Secondary	Not visible	13498	0.01	10322.27	1.57	120.07
	Visible	7557	0.01	2088.51	0.98	32.77
Tertiary	Not visible	29630	0.01	1219.14	0.30	10.50
	Visible	7699	0.01	19186.61	2.56	218.67

linear regression. These models were fit as:

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

where Y_i is the log-transformed response variable (space use percentile within the UD) at each (ith) elk telemetry location, $X\beta_i$ represents the vectors of the predictor covariates at the ith elk telemetry location, Zu_i is the random effects term and e is the error term which is spatially autocorrelated based on distances between elk telemetry locations. We specified the interaction of individual elk with the month in which the telemetry location was recorded as a random effect in the model (i.e. random slope). We nested these effects within individual elk (with females grouped within subherds) as we expected telemetry locations within the UD to be correlated among individual elk. We selected a spherical covariance structure and fit these models in SAS PROC MIXED (version 9.2, Cary, North Carolina, USA). We evaluated model parameters using maximum likelihood estimation and ranked model performance based on Akaike Information Criteria (AIC) and AIC weights (w_i; Burnham & Anderson 2002). We model-averaged the models with a w_i within 1/8th of the top-ranking model (Burnham & Anderson 2002, Bonnot et al. 2008). We then plotted influential coefficients featured in the top-ranking models and fit 95% confidence intervals to examine the magnitude of the effects.

Table 3. Mean accuracy of the ignore and majority techniques from our simulation of the telemetry error inherent to our elk locations in Custer State Park, South Dakota, USA, during 1993-1997.

Road visibility raster	Ignore technique	Majority technique
Primary	0.82	0.88
Secondary	0.85	0.92
Tertiary	0.79	0.86

Results

Radio-telemetry accuracy from 133 known transmitter locations was 176.1 m (SE = 12.4, range: 13.4-746.6). Average categorical raster patch size for the visible from road rasters was < 3 ha, though variable (Table 2). The best technique for incorporating telemetry error into assignment of categorical covariate values was the majority technique (Table 3). Mean accuracies for the majority technique were $\geq 6\%$ better than the ignore technique for visibility rasters associated with primary, secondary and tertiary roads (see Table 3). Accuracies were $> 85\%$ for each road visibility raster (see Table 3). None of the covariates exhibited collinearity and the residuals of the log-transformed elk space use percentiles were approximately normal and homoscedastic.

Our telemetry-relocation efforts resulted in 2,482 elk locations (N = 566 locations for male elk and N = 1,916 locations for female elk subherds; see Fig. 1). Summer female elk subherds (N = 5) and male elk (N = 6) UDs were based on averages of 383 (range: 161-602) and 94 (range: 36-170) telemetry locations, respectively. Elk responded to road networks differently. Of the elk locations, 76% were in areas that were not visible to primary roads, 83% to secondary roads and 10% to tertiary roads (see Fig. 2B). Furthermore, most of the elk locations (87%) were in areas that provided elk forage (i.e. forage quality > 0).

The top-ranking model describing female elk subherd space use included forage quality, Euclidean distance to secondary and tertiary roads as main effects, and an interaction between forage quality and visibility from tertiary roads (Table 4). No other model considered was within 1/8th w_i of this model. The top-ranking model was roughly twice as likely to be the best approximating model when compared to the next-ranking model (AIC $w_i = 0.16$; Appendix I).

Table 4. Best approximating model predicting female elk subherd space use and the best approximating models predicting male elk space use in Custer State Park, South Dakota, USA, during 1993-1997. Regression coefficients with their corresponding standard errors (in parentheses) are presented.

		Regression coefficients[1]							
	Model #	forage	eucprim	eucsec	euctert	visprim	vistert	forage*vistert	eucprim*visprim
Female	18	0.0003 (0.0003)	-	-0.065 (0.032)	0.049 (0.010)	-	-0.097 (0.040)	0.002 (0.001)	-
Male	10	-	-0.142 (0.106)	-0.112 (0.051)	0.048 (0.022)	0.029 (0.079)	-	-	0.128 (0.104)
	3	-	-	-	0.053 (0.022)	-	-	-	-
	2	-	-	-0.116 (0.052)	-	-	-	-	-
Model-average			-0.142 (0.106)	-0.114 (0.051)	0.051 (0.037)	0.029 (0.079)			0.128 (0.104)

[1] forage = forage quality score, eucprim = Euclidean distance to primary roads, eucsec = Euclidean distance to secondary roads, euctert = Euclidean distance to tertiary roads, visprim = visibility from primary roads, vistert = visibility from tertiary roads.

We model-averaged the three top-ranking models describing male elk space use as both the second and third-ranking models were within 1/8th w_i of the top model (Appendix II). Model-averaging included Euclidean distance to secondary and tertiary roads as main effects and an interaction between Euclidean distance to primary roads and visibility from primary roads (see Table 4).

Female elk subherds used areas farther from secondary roads and closer to tertiary roads regardless of whether the habitat was visible (see Table 4; Fig. 3A and B). However, the effect of forage quality was modulated by visibility from tertiary roads (see Fig. 3C). While female elk subherds changed their space use very little according to the quality of forage, they tended to use areas more if they were visible from tertiary roads (see Fig. 3C).

Male elk space use was affected by interactions between Euclidean distance to primary roads and visibility from primary roads as well as Euclidean distance to secondary roads and tertiary roads as main effects (see Table 4; Fig. 4). Male elk were more likely to use habitat not visible from primary roads at closer distances to those roads (see Fig. 4A). However, male elk used habitat visible from primary roads as distance from primary roads increased. Male elk similarly selected habitat away from secondary roads, though this effect was not modulated by visibility (see Fig. 4B). Finally, male elk exhibited greater use of habitat that was closer to tertiary roads irrespective of visibility (see Fig. 4C).

Discussion

Models including visibility from road metrics outperformed models that included only Euclidean distance to road as main effects. The inclusion of interactions between road visibility and Euclidean distance improved our understanding of male elk space use while interactions between road visibility and forage quality improved our understanding of female elk subherd space use as influenced by roads. However, our analysis also demonstrated the continued importance of measuring animal response to road based on Euclidean distance as main effects. Euclidean distance to secondary roads and Euclidean distance to tertiary roads were featured in the best approximating models describing male and female elk subherd space use. Thus, our study provides evidence that models including both Euclidean distance to road as main effects and interaction effects with visibility from road metrics could present the most parsimonious way to describe animal space use in relation to roads, at least for large mammals inhabiting areas with intense road use.

Male elk and female elk subherd space use were importantly similar with respect to secondary and tertiary roads. In both instances, male and female elk avoided habitat near to secondary roads and selected habitat near to tertiary roads. Of the elk locations in our study, > 80% were recorded in areas that were not visible from secondary roads. Just 10% of these locations were in areas not visible from tertiary roads. Custer State Park has extensive road networks

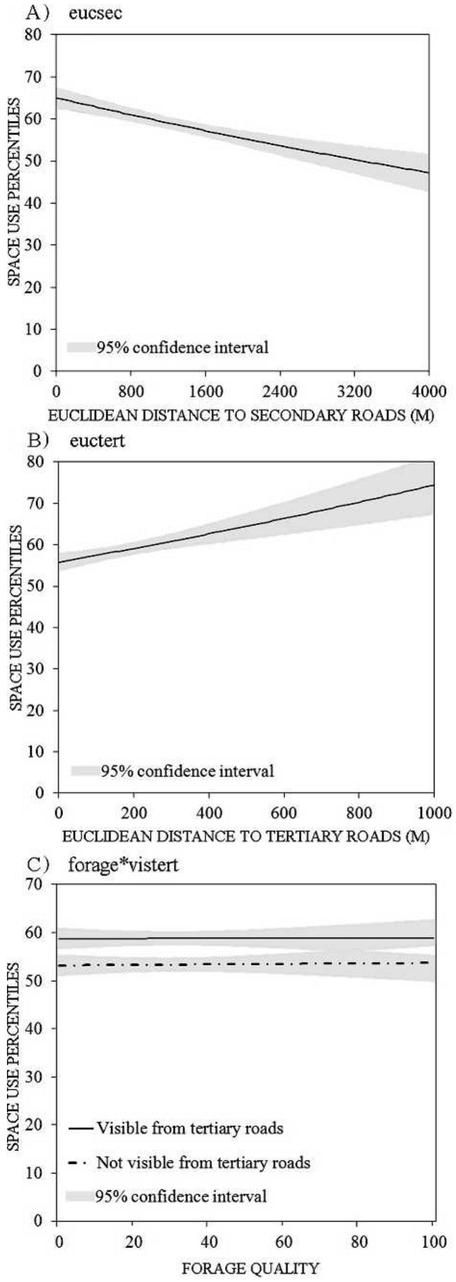


Figure 3. Spatial regression functions of the covariates from the best approximating model for the female elk subherd model, Custer State Park, South Dakota, USA, during 1993-1997. A) represents Euclidean distance to secondary roads, B) is Euclidean distance to tertiary roads and C) the interaction of forage quality and visibility from tertiary roads. The 95% confidence intervals of the regression functions are also presented. The y-axis represents the response variable (space use percentiles) with 1% corresponding to core-use areas and 98% corresponding to the periphery of the UD.

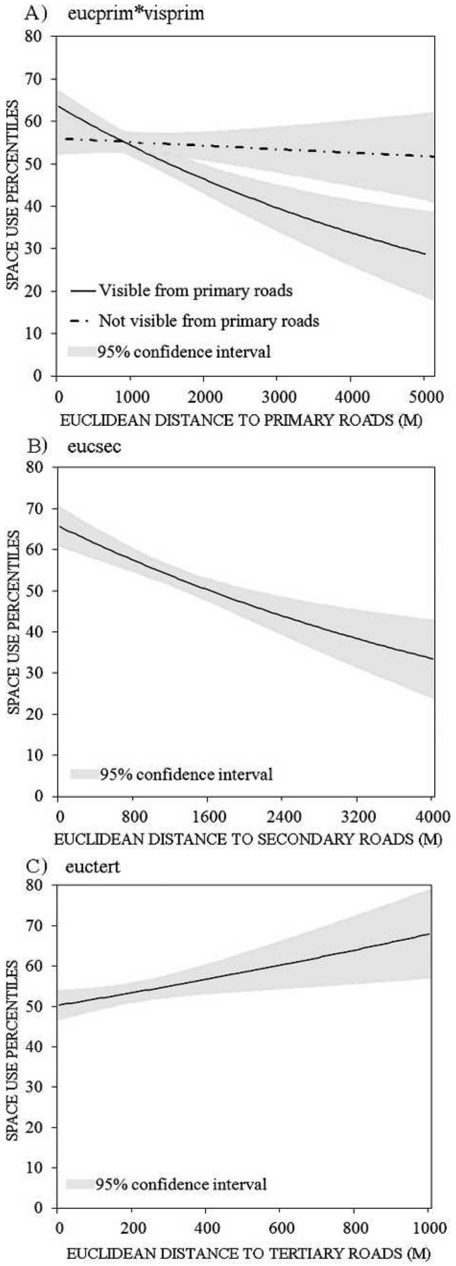


Figure 4. Spatial regression functions of the covariates from the best approximating model(s) for the male elk model, Custer State Park, South Dakota, USA, during 1993-1997. A) displays the interaction of Euclidean distance to primary roads and visibility from primary roads, B) the Euclidean distance to secondary roads and C) the Euclidean distance to tertiary roads. The 95% confidence intervals of the regression functions are also presented. The y-axis represents the response variable (space use percentiles) with 1% corresponding to core-use areas and 98% corresponding to the periphery of the UD.

with tertiary roads being the most common. These roads are primitive unmaintained dirt tracks that are closed to vehicle use in summer. In comparison, secondary roads are open to public vehicle use and receive roughly 60 times as many user groups/week/road segment when compared to tertiary roads. The road-dense environment of Custer State Park determined that elk could not avoid all roads in their space use decisions. Our results suggest that elk were more likely to select habitat near to tertiary roads which are closed to vehicle use and have relatively low levels of anthropogenic disturbance.

We also documented variation in elk response to roads by sex. Male elk tended to select habitat away from primary roads, an effect that was modulated by visibility from primary roads, whereas female elk subherds did not respond to primary roads. Furthermore, female elk subherds altered their use of habitat providing forage quality according to visibility from tertiary roads. These results further substantiate that elk and a variety of other species perceive road types and vehicle use differently (Clark et al. 2001, Dickson & Beier 2002, Ager et al. 2003, Gagnon et al. 2007, Reynolds-Hogland & Mitchell 2007) and that these relationships vary by sex (McCorquodale 2003). Male elk in our study were risk averse, selecting habitat a great distance from primary roads which are associated with intense vehicle use in summer averaging over 5,000 user groups/week/road segment. Our observation of the risk-averse tendencies of male elk is consistent with previous research which demonstrates that male elk select habitat with consistently lower human activity than female elk (Unsworth et al. 1993, McCorquodale 2003).

Forage availability and quality are important determinants of elk space use (Cook et al. 1996, Beck et al. 2006, Van Dyke & Darragh 2007, Hebblewhite et al. 2008). We did not, however, detect the importance of forage quality in any of our top-ranking models describing male elk space use. Forage is only one part of life history trade-offs (Lima 2002, Hebblewhite & Merrill 2009) and it is clear that avoiding risk associated with roads was of considerable importance for male elk. The predictive power of covariates changes depending on scale of use within the home range, a pattern consistent with theories of hierarchical habitat selection (Searle et al. 2008) and results from other studies (McLoughlin et al. 2002, Mårell & Edenius 2006, Mayor et al. 2009), with foraging often more important at smaller scales and risk assessments at larger scales (Fortin et al. 2005, Boyce 2006). Male elk space use patterns were most influenced by risk assessments associated with roads with the highest vehicle traffic.

Female elk tended to use habitat that provided forage potential and was visible from tertiary roads. We suggest that forage potential could be improved in areas visible from tertiary roads. Norwegian red deer *Cervus elaphus*, for instance, regularly forage in productive open fields in the vicinity of road networks (Godvik et al. 2009). We also expect that female elk used open habitat because it enabled them to be vigilant to disturbance associated with tertiary roads in summer (e.g. hiking and horseback riding). Elk have been found to utilize disturbed landscapes adjacent to certain roads if the roads are not associated with high predation risk (Stubblefield et al. 2006, Hebblewhite et al. 2009). Elk risk of mortality from predation and hunting is often positively associated with road networks (Unsworth 1993, Gratson & Whitman 2000a,b, Frair et al. 2007, 2008, Hebblewhite et al. 2009). Tertiary roads in Custer State Park likely have low mortality risk because these roads are closed to vehicular traffic, there are few large predators (with the exception of mountain lions *Puma concolor*) in the park and hunting is prohibited in summer.

Our analysis highlights the importance of considering the effects of screening vegetation and topography in studies examining animal space use as influenced by roads. This facet of elk ecology has been suggested though not quantitatively assessed. Lyon (1979) purported that elk were largely road averse, but would use habitat near roads if vegetation provided adequate security cover (see also Dyer et al. 2001 for caribou *Rangifer tarandus*). Our analysis not only supports Lyon's (1979) theory, but also presents a framework by which researchers can investigate the influence of visibility from roads to determine the relevance of these metrics in their study area. We have demonstrated that including interactions between Euclidean distance to road and visibility from road can improve our understanding of animal space use patterns in relation to roads. Covariates of this type have the power to reveal how the space use decisions of animals relate to screening vegetation or topography and distance to roads and may help to clarify some of the ambiguity that exists with respect to animal response to roads.

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Appendices

Appendix 1. Rank of the 18 *a priori* models developed to explain female elk subherd space use in Custer State Park, South Dakota, USA, during 1993-1997. Corresponding ΔAIC scores and AIC weights (w_i) are also presented.

Rank	Candidate model	k	ΔAIC	w_i
1	forage eucsec euctert forage*vistert	9	0.00	0.34
2	forage eucprim euctert forage*visprim	9	1.30	0.18
3	forage eucsec euctert forage*vissec	9	2.50	0.10
4	eucprim*visprim eucsec euctert	9	2.60	0.09
5	forage eucprim euctert forage*vistert	9	2.80	0.08
6	eucprim eucsec*vissec euctert	9	3.00	0.08
7	eucprim eucsec euctert*vistert	9	3.30	0.06
8	Euctert	5	3.80	0.05
9	euctert*vistert	7	5.30	0.02
10	forage eucprim eucsec forage*visprim	9	14.60	0.00
11	Visprim	5	17.20	0.00
12	eucprim*visprim	7	17.20	0.00
13	Eucsec	5	17.90	0.00
14	Vissec	5	19.60	0.00
15	Eucprim	5	19.70	0.00
16	eucsec*vissec	7	19.80	0.00
17	forage eucprim eucsec forage*vissec	9	21.30	0.00
18	Vistert	5	21.70	0.00

Appendix II. Rank of the 18 *a priori* models developed to explain male elk space use in Custer State Park, South Dakota, USA, during 1993-1997. Corresponding ΔAIC scores and AIC weights (w_i) are also presented.

Rank	Candidate model	k	ΔAIC	w_i
1	eucprim*visprim eucsec euctert	10	0.00	0.24
2	Euctert	6	0.60	0.18
3	Eucsec	6	1.40	0.12
4	eucprim eucsec*vissec euctert	10	1.50	0.11
5	eucprim eucsec euctert*vistert	10	3.00	0.05
6	forage eucsec euctert forage*vissec	10	3.20	0.05
7	forage eucsec euctert forage*vistert	10	3.40	0.04
8	eucsec*vissec	8	3.70	0.04
9	Visprim	6	3.90	0.03
10	euctert*vistert	8	4.50	0.03
11	Vissec	6	4.90	0.02
12	Vistert	6	5.50	0.02
13	forage eucprim eucsec forage*visprim	10	5.50	0.02
14	forage eucprim euctert forage*visprim	10	5.60	0.01
15	eucprim*visprim	8	5.70	0.01
16	Eucprim	6	6.00	0.01
17	forage eucprim eucsec forage*vissec	10	7.30	0.01
18	forage eucprim euctert forage*vistert	10	7.50	0.01