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Research Article

Elk Resource Selection at Parturition Sites, Black Hills, South Dakota

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ABSTRACT We studied elk (*Cervus canadensis nelsoni*) parturition sites at coarse (314-km^2 and 7-km^2) and fine (0.2-ha) scales in the Black Hills, South Dakota, 2011–2013, following a period of population decline and poor calf recruitment. Our objective was to test whether female elk selected parturition sites across spatial scales in association with forage, terrain ruggedness, road density, or hiding and security cover. At coarse scales in forests and grasslands, female elk selected sites in areas with greater proportions of vegetation communities that provided forage (56–74% of area) and more rugged topography (194–248 m) than found at random. At coarse scales in grasslands, elk selected sites in areas with lower road densities ($\leq$1.24 km/plot). At the fine scale in forests and grasslands, female elk selected sites in areas with intermediate slope (19%), closer to water (355–610 m), and far from roads (541–791 m). Further, elk in forests and grasslands selected sites with intermediate security cover (50–88 m). We hypothesize elk selected for intermediate rugged terrain at larger scales for security from high road densities and human disturbance, but these areas may have placed elk in riskier environments for puma (*Puma concolor*) predation. Forest management that maintains open-canopied vegetation communities in less rugged areas and prevents ponderosa pine (*Pinus ponderosa*) encroachment of meadows to provide forage may be beneficial for elk. Further, elk parturition sites occurred close to roads, particularly on public lands, and agencies should consider road-use restrictions and vegetation buffers beside roads in areas with less rugged terrain, which may provide favorable calving habitat.

KEY WORDS Black Hills, calving habitat, elk, grasslands, parturition, ponderosa pine, resource selection.

In ungulates, parturition site selection varies among and within species, but needs to provide resources for the mother and young. Skovlin et al. (2002) noted that predator avoidance, forage quality, and hiding cover quantity are strong determinants of resources selected by elk (*Cervus canadensis nelsoni*). However, elk occur in a wide variety of vegetation types including grasslands, shrub steppe, and conifer forests during the parturition period (Skovlin et al. 2002). Consequently, variability in the resources at parturition sites can be expected. Further, spatial scale evaluated can affect results of resource selection analysis. In a conifer dominated landscape, parturient elk resource selection varied depending on scale (Rearden et al. 2011). In 1 sagebrush-dominated landscape, elk selected for greater hiding cover at parturition sites at all scales (Barbknecht et al. 2011).

Female elk are typically solitary immediately before parturition (Hudson et al. 2002), and selection of parturition resources such as hiding cover or foraging resources is based on localized movements of <1,500 m/day (Vore and Schmidt 2001, Brook 2010, Barbknecht et al. 2011). After birth, elk calves are initially "hiders" (Geist 1982) because they remain bedded for approximately the first 5 days of life. At this time, resources that provide cover for calves or conditions for the female to visually detect predators may be important (Thomas et al. 1979, Barbknecht et al. 2011, Rearden et al. 2011). Elk may prefer sites with high visibility where puma (*Puma concolor*) are the primary predators (Rearden et al. 2011).

Elk in the Black Hills, South Dakota, USA, occur in a wide variety of habitats. Our study population has been declining since 2006, which is of concern for game managers and hunters (South Dakota Department of Game, Fish, and

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Parks 2015). Some areas are heavily influenced by high road densities that average >2.1 km/km^2 (Rumble et al. 2005, Stubblefield et al. 2006, Montgomery et al. 2013) and human recreation that could negatively influence calving (Shively et al. 2005, Black Hills National Forest 2009). Predation, primarily from puma on elk calves, resulted in $\leq$27% annual survival of calves (Lehman 2015), so we hypothesized that predation was important in decisions of resource selection of parturition sites by female elk.

Our objectives were to evaluate resource selection characterizing elk parturition sites at coarse and fine spatial scales. Specifically, we assessed if resource selection at parturition is associated with forage, terrain ruggedness, road density, and potential hiding or security cover at coarse and fine spatial scales. In forests, we predicted elk would select for vegetation communities that provided greater forage at the larger scales; in grasslands, forage was abundant, and we predicted elk would select for hiding cover at all spatial scales. We predicted elk in both forests and grasslands would select for security cover at the fine scale, and we also predicted elk would avoid roads when selecting calving sites in both landscapes.

STUDY AREA

We conducted our work in Custer and Pennington counties in southwestern South Dakota in the southern Black Hills physiographic region (Flint 1955). Land ownership was mixed private and public land, including Custer State Park (CSP), which encompassed 286 km^2 in the central part of the study area (Fig. 1). Elk could move in and out of CSP as part of a larger Black Hills population except where CSP was bordered by Wind Cave National Park (WCNP), where elk rarely crossed the 1.8-m-tall fence along that border. Elevations ranged 1,108–2,208 m. The average road density in CSP was 2.1 km/km^2 (CSP, unpublished data) and the Black Hills National Forest averaged 3.2 km/km^2 (T. Mills, Black Hills National Forest, personal communication). The climate was semiarid and varied northwest to southeast, with average annual precipitation ranging 52–54 cm and average annual temperature ranging 6–9° C across the study area (National Climatic Data Center 2013). Vegetation varied considerably from northwest to southeast, where forests dominated the landscape at higher elevations and grasslands dominated the southeastern portion of the study area. The forested portions of our study area were dominated by ponderosa pine (*Pinus ponderosa*). Smaller patches of deciduous forest were characterized by aspen (*Populus tremuloides*), bur oak (*Quercus macrocarpa*), and paper birch (*Betula papyrifera*). Wildfire and mountain pine beetle (*Dendroctonus ponderosae*) infestations created natural openings throughout the study area. Western snowberry (*Symphoricarpos occidentalis*) and common juniper (*Juniperus communis*) were common shrubs in the understory of pine forests (Hoffman and Alexander 1987). The eastern third of the study area was primarily a prairie ecosystem with native mixed-grass prairie, agriculture fields, and prairie woodlands comprising green ash (*Fraxinus pennsylvanica*), cottonwood (*Populus deltoides*), and boxelder (*Acer negundo*). Common native grasses in the mixed-grass prairie included needle and thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Schizachyrium scoparium*), and prairie dropseed (*Sporobolus heterolepis*; Larson and Johnson 1999).

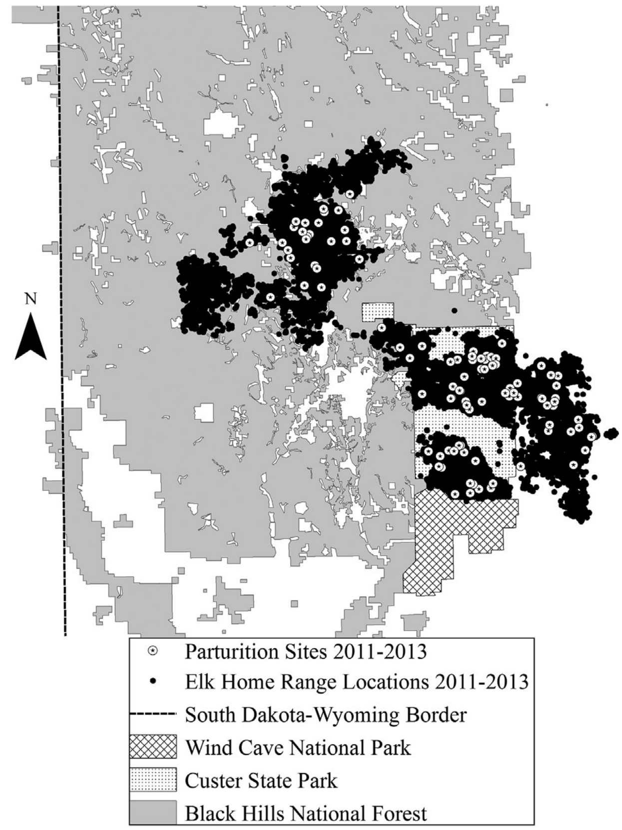

Figure 1. The Black Hills, South Dakota study area where we studied elk parturition sites during spring–summer, 2011–2013. Location data include elk satellite home range locations collected during spring and summer and parturition sites.

METHODS

Capture and Radio-Telemetry

We captured female elk by immobilizing them with darts fired from helicopters during February, 2011–2013. We sedated elk using butorphanol, azaperone, and medetomidine sedation protocol (Mich et al. 2008). After elk were sedated, we blindfolded them and fitted them with global positioning system (GPS) telemetry collars that included a very high frequency (VHF) transmitter (Telonics, Inc., Mesa, AZ; Advanced Telemetry Systems, Isanti, MN). We aged females as adults (>20 months) or yearlings (18–20 months of age) by extracting an upper canine tooth and evaluating cementum annuli (Matson's Lab, Milltown, MT; Hamlin et al. 2000). We assessed female elk for pregnancy using rectal palpation (Greer and Hawkins 1967, Vore and Schmidt 2001). We fit females suspected of being pregnant with a vaginal implant transmitter (VIT; Advanced Telemetry Systems; Barbknecht et al. 2009). We also collected a blood sample to verify pregnancy using serum assays for pregnancy-specific protein B (Noyes et al. 1997).

All handling, marking, and monitoring procedures were approved by the South Dakota State University Research Committee (Animal Care and Use Committee Approval Number 11-012A).

We located female elk using radio-transmitters daily from 1 April to 31 October of each year. Beginning 1 May, we monitored female elk behavior to determine if females were alone or relatively sedentary. These elk were then located twice daily, and we checked signals from the VIT each morning and evening. During the parturition period, we remained distant, and out of sight of elk, while checking VIT signals to minimize disturbance. We determined date of parturition and recorded expelled VIT locations using Universal Transverse Mercator coordinates with a handheld GPS unit. We considered a VIT location a probable calving site if we observed placenta material with blood or a cleared spot on the ground at the VIT site. Typically, we also observed a strong odor, moistened soil, and fresh fecal pellets at the VIT site. After the female and calf left the parturition site, we returned to measure habitat characteristics.

Habitat Descriptions

Coarse-scale.—We evaluated resources at used and potentially available parturition sites at 2 coarse scales to capture patterns of resource selection prior to parturition. Elk may move and make local resource selection decisions within a few days to a few hours before parturition (Vore and Schmidt 2001, Barbknecht et al. 2011); therefore, our methods considered elk movements immediately before parturition. For the 314-km^2 scale, we considered GPS satellite locations of elk movements 4 days previous to parturition. Given distinctive female movement patterns, this period has been hypothesized as an important time when females make decisions regarding calving sites (Vore and Schmidt 2001). The largest linear 4-day movement we observed previous to parturition was 10,478 m. Therefore, we created a 10,000-m-radius circular plot around each parturition site location that we considered as available to the female elk in a geographic information system (GIS) using ArcGIS 10.2 (ESRI, Redlands, CA). Within each 10,000-m-radius circular plot, we randomly selected 5 points and created a 1,000-m-radius circular plot around them and the parturition locations (Fig. 2); plots were allowed to overlap. We considered 1,000-m-radius plots given previous concerns of being able to disentangle resource relationships at smaller plot sizes (Rearden et al. 2011).

For the finer 7-km^2 scale, we evaluated daily elk movements during the 4-day pre-parturition period and determined daily movements averaged 1,535 m. Therefore, we generated a single 500-m-radius circular plot surrounding the parturition site and 4 additional 500-m-radius circular plots in the cardinal directions along a 1,500-m-radius perimeter (Fig. 2).

We intersected each 1,000-m-radius (314 ha herein) and 500-m-radius circular plot (79 ha herein) with the Black Hills National Forest (BHNF) Forest Service Vegetation (FSVEG) GIS coverage (BHNF, unpublished data) and the CSP Land Cover GIS coverage (CSP, unpublished data). We edited the GIS coverage to update polygons to reflect recent wildfires and mountain pine beetle (*D. ponderosae*) infested areas. We also added private land polygons using National Agricultural Imagery Program (NAIP) data (NAIP 2013).

Vegetation descriptions in the FSVEG coverage were described using a hierarchical classification based on vegetation types and structural stages (Buttery and Gillam 1983). Forested stands were usually classified as seedling or shrub (<2.54 cm diameter at breast height [DBH]), sapling or pole (2.54–22.9 cm DBH), or mature and saw timber (>22.9 cm DBH). The sapling or pole and mature or saw timber forest stands were further classified by overstory categories of 0–40%, 41–70%, and >70%.

We combined aspen and oak stands into a single deciduous category. Ponderosa pine sapling or pole stands averaged 19 cm DBH and mature or saw timber stands averaged 23 cm DBH, so we combined them but retained the overstory canopy cover classifications. We reclassified vegetation communities of grass and forb, and ponderosa pine and spruce ≤40% overstory canopy cover as forage, and ponderosa pine and spruce >40% overstory canopy cover as hiding cover (Bennett et al. 1987, Benkobi et al. 2004, Juntti and Rumble 2006, Rumble et al. 2007, Rumble and Gamo 2011). The resulting vegetation categories for our study included pine seedling or shrub, deciduous forest, forage, and hiding cover.

We calculated a terrain ruggedness index (Riley et al. 1999) using 30-m digital elevation model obtained from the BHNF, which provided an index of terrain heterogeneity (Riley et al. 1999). A high ruggedness index (498–958 m) indicated greater steepness of slopes and broken topography; moderate was defined as 240–497 m, intermediate at 162–239 m, slightly at 117–161 m, and a low ruggedness index (0–116 m) indicated gentle topography, or little slope (Riley et al. 1999). We calculated road density by intersecting the road coverages with the circular plots in ArcGIS. We expressed road density as length within each plot (km/plot). We only considered roads open to the public in our analysis.

Fine-scale.—We created a 100% minimum convex polygon of all female elk locations. Within this area, we used stratified random sampling (Cochran 1977) to select sites to quantify fine-scale characteristics available to female elk. Strata for the random sampling were the uncombined vegetation structural stages described above. Each year, we randomly selected 5–10 polygons for each stratum of the GIS vegetation coverage without replacement to ensure a broad distribution of random points and sufficient sampling of all the vegetation communities across the study area. We generated 1 random point in each of these polygons.

We quantified vegetative characteristics at use sites 3–5 days after the female and calf left the parturition site. We also measured and recorded vegetation characteristics at the random sites during the same period through 31 August each year.

We measured vegetative characteristics along 4, 25-m transects (0.20 ha) centered at parturition or random sites and oriented in the cardinal directions (Fig. 2). Fine-scale

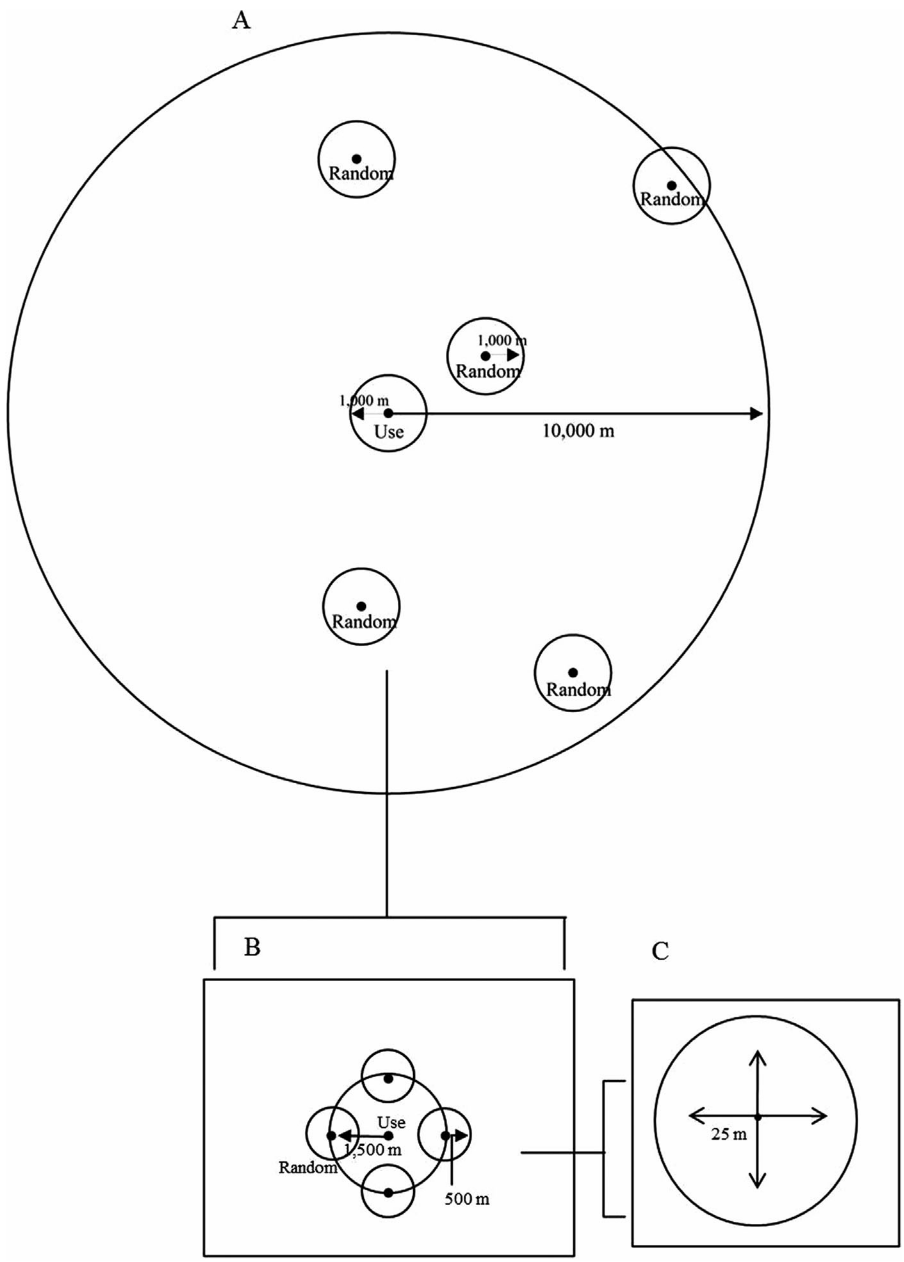

Figure 2. Sampling approach we used to assess use and availability of elk parturition sites in the Black Hills of South Dakota, 2011–2013 at the 314-km^2 coarse scale (A), the 7-km^2 coarse scale (B), and the 0.2-ha fine scale (C).

plot size was similar to previous investigations (Barbknecht et al. 2011, Rearden et al. 2011). We recorded overstory canopy cover at 1-m intervals along these transects ($n = 100$) using a densitometer (Stumpf 1993). We estimated percent canopy cover of total herbaceous cover, grass, forbs, and shrubs in a 0.1-m^2 quadrat (Daubenmire 1959) at 2-m intervals along the 4 transects ($n = 40$); we averaged data collected along transects for each site. We measured tree characteristics in a variable radius circular plot centered at the parturition or random site using a 10-factor prism (Sharpe et al. 1976) for all trees $\geq$15.24 cm DBH; we measured trees <15.24 cm DBH in a 5.03-m fixed radius plot. We recorded aspect using a compass for the prevailing downhill direction from the site; we estimated percent slope along this same gradient with a clinometer. We measured distance (m) to nearest water with NAIP imagery data from each year. We measured distance to nearest road using the road coverages. We interpolated downed woody debris (metric tons/ha) using a pictorial guide (Simmons 1982).

We estimated elk security cover (Thomas et al. 1979) for a standing and bedded elk at the parturition site using 2 vinyl cover cloths with 40 alternating black and white 15×15-cm^2. One cover cloth was centered at 110 cm above ground to represent a standing female elk and the other was centered at 35 cm above ground level to represent a bedded female elk. We tallied the number of squares that were not visible at 61 m and recorded the distance at which only 4 squares were visible (90% cover; Thomas et al. 1979) in 4 directions along lines projected from transects; we averaged data collected along transects for each site. Security cover was a surrogate covariate for predator avoidance and detection.

Resource Selection Analysis

Resource selection of elk parturition sites can vary from dense forests to open grasslands (Graf 1943, Picton 1960, Batchelor 1965, Barbknecht et al. 2011, Rearden et al. 2011). Therefore, we partitioned use and available but unused sites by forest and grasslands for all analyses. We removed random sites that fell within the boundary of WCNP from the analysis because we considered that area unavailable (Fig. 1). We developed an initial set of candidate models and discriminated among them using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We primarily developed models to evaluate whether forage or hiding cover components were being selected across spatial scales (Thomas et al. 1979, Barbknecht et al. 2011, Rearden et al. 2011). We considered additional models where we evaluated terrain characteristics related to predation and road avoidance, and road density associated with human disturbance across spatial scales (Edge and Marcum 1991, Koehler and Hornocker 1991, Millspaugh et al. 2001, Laundré and Hernández 2003, Montgomery et al. 2012).

Coarse-scale.—We modeled the probability an elk selected a parturition site from a set of potential parturition sites considered available with conditional logistic regression, which is equivalent to discrete choice models when there is 1 case/stratum (Cooper and Millspaugh 1999, Hosmer et al. 2013). We used conditional logistic regression because each parturition site was explicitly matched with 5 random sites at

Table 1. Mean covariate values and standard errors evaluated for elk parturition resource selection across 3 scales in the Black Hills, South Dakota, 2011–2013.

Covariate[a]	Scale	Parturition	SE	Random	SE
Forest models					
Forage (ha)	314 km^2	174.50	9.13	148.28	4.72
Hiding cover (ha)	314 km^2	95.02	8.38	118.94	5.08
Ruggedness (m)	314 km^2	241.63	4.52	228.18	2.88
Road density (km/plot)	314 km^2	4.41	0.48	4.99	0.25
Deciduous (ha)	314 km^2	27.98	3.39	14.13	0.87
Forage (ha)	7 km^2	46.20	2.94	42.53	1.41
Hiding cover (ha)	7 km^2	22.85	2.63	23.21	1.38
Ruggedness	7 km^2	243.94	5.42	238.49	2.85
Road density (km/plot)	7 km^2	1.03	0.15	1.02	0.08
Deciduous (ha)	7 km^2	6.69	1.06	7.01	0.50
Canopy (%)	0.20 ha	31.96	3.08	37.30	2.20
Slope (%)	0.20 ha	18.60	1.04	20.46	1.17
Woody debris (metric tons/ha)	0.20 ha	22.17	2.11	20.66	1.81
Tree density (trees/ha)	0.20 ha	257.34	35.76	238.64	21.14
Distance to water (m)	0.20 ha	544.69	42.45	950.16	68.76
Security cover (m)	0.20 ha	61.91	3.90	57.57	2.76
Distance to road (m)	0.20 ha	540.96	86.16	381.08	49.00
Forage cover (grass and forb cover [%])	0.20 ha	43.23	5.34	43.26	3.04
Shrubs (%)	0.20 ha	13.89	2.64	13.48	1.27
Grassland models					
Forage (ha)	314 km^2	231.78	6.55	206.56	4.57
Hiding cover (ha)	314 km^2	53.66	5.79	63.27	4.25
Ruggedness (m)	314 km^2	179.26	6.69	166.90	3.45
Road density (km/plot)	314 km^2	1.24	0.20	2.15	0.14
Deciduous (ha)	314 km^2	11.60	1.60	13.39	0.87
Forage (ha)	7 km^2	58.67	2.14	54.47	1.27
Hiding cover (ha)	7 km^2	13.31	1.92	12.79	1.08
Ruggedness	7 km^2	184.21	6.32	175.86	4.13
Road density (km/plot)	7 km^2	0.12	0.05	0.59	0.06
Deciduous (ha)	7 km^2	2.24	0.53	3.92	0.32
Canopy (%)	0.20 ha	29.62	3.31	23.98	3.26
Slope (%)	0.20 ha	17.08	1.17	20.06	2.09
Woody debris (metric tons/ha)	0.20 ha	14.60	1.83	9.60	1.41
Tree density (trees/ha)	0.20 ha	216.46	39.43	174.09	29.69
Distance to water (m)	0.20 ha	565.45	33.76	657.58	62.02
Security cover (m)	0.20 ha	59.05	3.47	112.85	14.89
Distance to road (m)	0.20 ha	791.07	73.69	609.11	59.67
Forage cover (grass and forb cover [%])	0.20 ha	50.06	3.95	47.87	4.36
Shrubs (%)	0.20 ha	7.89	1.73	7.82	1.57

[a] Covariates include forage = grassland and open pine and spruce ≤40% canopy cover (ha); hiding cover = ponderosa pine and spruce >40% canopy cover (ha); ruggedness = index computed using Riley et al. (1999); security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979); and forage cover = % understory grasses and forbs (grass and forb cover [%]). Covariates included in models may include non-linear forms such as quadratic transformation $= \beta_0 + \beta_1 x + \beta_2 x^2$, or natural log (pseudo-threshold) transformation $= \beta_0 + \beta_1 \log_e x$ (Franklin et al. 2000).

the 314-km^2 level and 4 random sites at the 7-km^2 level. The dataset included several instances where multiple parturition sites were selected by the same elk in sequential years, and we used robust sandwich variance estimators to account for dependence among these observations (White 1980, 1982). We implemented conditional logistic regression models with the clogit() function in the survival package, version 2.37-7, (Therneau and Grambsch 2000) in R version 3.1.2 (R Development Core Team 2014). We fit several models representing different sets of predictor variables thought to influence parturition site selection (Table 1). We first evaluated univariate models with untransformed, log-transformed, and quadratic-transformed variables (Franklin et al. 2000). We then used the transformation that resulted in the lowest quasi-likelihood under the independence model criterion (QIC; Pan 2001) when fitting multivariate models. We ranked models using QIC, and we report model-averaged coefficients and unconditional standard errors from all models within 2 ΔQIC units of the top model (Burnham and Anderson 2002).

Fine-scale.—We modeled used parturition sites and unused available parturition sites at the fine scale with case–control logistic regression (Hosmer et al. 2013). We used case–control logistic regression because sites considered available were not explicitly paired with parturition sites. Parturition events are rare and it is unlikely a female would have calved at any of the randomly available sites (i.e., we found no evidence of parturition sign at control sites and there is likely little or no contamination among controls). With little or no contamination in controls, slope parameters of the linear predictor in logistic regression are approximately unbiased (Keating and Cherry 2004), though high levels of contamination may lead to bias in slope parameters. We implemented case–control logistic regression with the glm() function in R version 3.1.2. We fit several models representing different sets of predictor variables thought to influence parturition site selection (Table 1). We first evaluated univariate models with untransformed, log-transformed, and quadratic-transformed variables (Franklin et al. 2000). We then used the transformation that resulted in the lowest AIC when fitting multivariate models. We ranked models using AIC (Burnham and Anderson 2002) and we report model-averaged coefficients and unconditional standard errors from all models within 2 ΔAIC units of the top model.

Assessing Model Fit

We evaluated the ability of our models to reasonably rank the suitability of parturition sites with cross-validation techniques described by Boyce et al. (2002). Briefly, we calculated Spearman's rank correlation between the area-adjusted frequency of predicted log odds ratios and the bin rank of ordered log odds ratios with leave-1-out cross validation. We first withheld observations from a single parturition site, fit models that were within 2 ΔQIC or ΔAIC, and predicted the log odds ratio of the withheld parturition site (using model-averaged predictions when necessary). We simultaneously predicted log odds ratios at available sites, which we categorized into 10 bins, ranked from low logs odds ratios to high ratios, of approximately equal sample size. We then calculated the area-adjusted frequency for the bin corresponding to the predicted log odds ratio of the parturition site as a value inversely proportional to the number of

Table 2. Model selection results comparing parturition sites for elk with random sites in forests at the 314-km^2, 7-km^2, and 0.20-ha scales in the Black Hills, South Dakota, 2011–2013. Only models with differences in quasi-likelihood under the independence model criterion (ΔQIC) or Akaike's Information Criterion (ΔAIC) <4 of the best model are presented. We also provide number of parameters (K) and model weights (w_i).

Forest models[a]	QIC/AIC	ΔQIC/ΔAIC	K	w_i
314-km^2 scale				
Forage + deciduous + ruggedness + ruggedness^2	120.94	0.00	4	0.65
Forage + hiding cover + deciduous + ruggedness + ruggedness^2 + road density	123.11	2.17	6	0.22
Hiding cover + deciduous + ruggedness + ruggedness^2	124.63	3.70	4	0.10
7-km^2 scale				
Forage	144.48	0.00	1	0.21
Forage + road density	145.64	1.16	2	0.12
Natural log ruggedness	145.99	1.50	1	0.10
Road density	146.07	1.59	1	0.10
Hiding cover	146.09	1.61	1	0.10
Forage + road density + natural log ruggedness	146.32	1.83	3	0.08
Natural log deciduous	146.47	1.99	1	0.08
Forage + natural log ruggedness + natural log deciduous	147.03	2.54	3	0.06
Natural log ruggedness + road density	147.05	2.57	2	0.06
Hiding cover + road density	147.36	2.87	2	0.05
Fine scale (0.20 ha)				
Slope + slope^2 + natural log distance to road + distance to water + distance to water^2 + security cover + security cover^2	168.68	0.00	8	0.72
Natural log distance to road + distance to water + distance to water^2+ security cover + security cover^2	171.38	2.70	6	0.19

[a] Covariates include forage = grassland and open pine and spruce (≤40% canopy cover; ha); deciduous = ha of deciduous forest; ruggedness = index computed using Riley et al. (1999); hiding cover = ponderosa pine and spruce >40% canopy cover (ha); road density = density of roads (km/plot); slope = % slope; distance to road = distance (m) to nearest open road; distance to water = distance (m) to nearest water source; and security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979). Covariates may include non-linear forms such as quadratic transformation = $\beta_0 + \beta_1 x + \beta_2 x^2$, or natural log (pseudo-threshold) transformation = $\beta_0 + \beta_1 \log_e x$ (Franklin et al. 2000).

available sites with log odds ratios that fell within the same bin. Finally, we summed area-adjusted frequencies for each bin over all iterations. We concluded models reasonably predicted parturition sites if Spearman's rank correlation (r_s) was positive, with a significant ($P \leq 0.10$) 1-sided test.

RESULTS

Capture and Parturition Sites

We used data from 58 female elk ($n = 56$ adults, $n = 2$ yearlings) in our analyses, resulting in 100 parturition sites. We removed random sites ($n = 11$ 314-ha plots and 5 79-ha plots) that were within the WCNP boundary. In forests, we used data from 28 adult female elk, and we evaluated 45 parturition sites with 224 random plots at the 314-km^2 scale, 180 random plots at the 7-km^2 scale, and 131 random sites at the fine scale. In grasslands, we used data from 30 female elk ($n = 28$ adults, $n = 2$ yearlings), and we evaluated 55 parturition sites with 265 random plots at the 314-km^2 scale, 215 random plots at the 7-km^2 scale, and 62 random sites at the fine scale. Median dates for parturition were 1 June 2011, 28 May 2012, and 3 June 2013. Ninety percent of births occurred by 15 June over the 3-year study.

Forests

The single top-ranked model of elk parturition site selection in forests at the 314-km^2 scale included the area of vegetation classified as forage and deciduous forest, and a quadratic ruggedness term as predictors, with no other models within 2 ΔQIC (Table 2 and Fig. 3). The Spearman rank correlation suggested that our top model reasonably predicted elk parturition sites ($r_s = 0.76$, $P < 0.01$). Parturition sites were most likely to occur in areas with high amounts of vegetation classified as both forage (log odds ratio = 0.82, SE = 0.24) and deciduous forest (log odds ratio = 0.93, SE = 0.18). Additionally, parturition sites were most likely to occur in areas of moderate ruggedness, with a peak at approximately 248 m (95% CI = 222–284).

The top-ranked models of elk parturition site selection in forests at the 7-km^2 scale included the area of vegetation classified as forage, hiding cover, deciduous forest, ruggedness index, and road density as variables, although there was considerable model selection uncertainty, and no variable had a strong influence on parturition site selection at this scale (i.e., model-averaged 95% CIs overlapped 0; Table 2). We did not conduct a Spearman correlation at this scale because of the lack of variable influence.

The single top-ranked model of elk parturition site selection in forests at the fine scale included natural log of distance to roads, and quadratic terms for percent slope, distance to water, and distance to 90% cover when bedded as variables, with no other models within 2 ΔAIC (Table 2 and Fig. 4). The Spearman rank correlation suggested that this model predicted elk parturition sites well ($r_s = 0.93$, $P < 0.01$). Parturition sites were most likely to occur in areas farther from roads (log odds ratio = 0.87, SE = 0.26). Additionally, peak selection occurred at approximately 19% slope (95% CI = 8–28), 355 m from water (95% CI = 0–2,466), and 88 m from 90% cover when bedded (95% CI = 0–247).

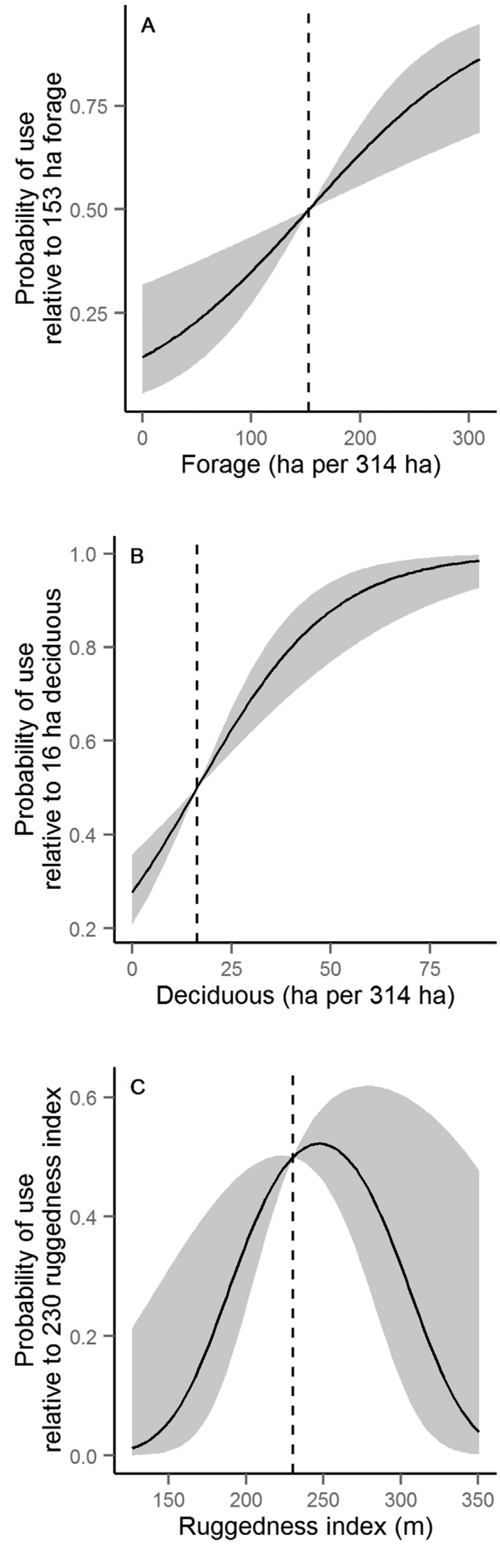

Figure 3. Relative probability of parturition resource selection for elk in forested habitats as a function of forage (A), deciduous forest (B), and ruggedness index (C) at the 314-km^2 coarse scale in the Black Hills, South Dakota, 2011–2013. We calculated probabilities relative to the mean value observed for that attribute (vertical dashed line). Each plot assumes an elk is faced with 2 choices of parturition sites and the values of all other attributes are equivalent among choices. Shaded areas represent 95% confidence intervals. The ruggedness index was quadratic transformed (Franklin et al. 2000).

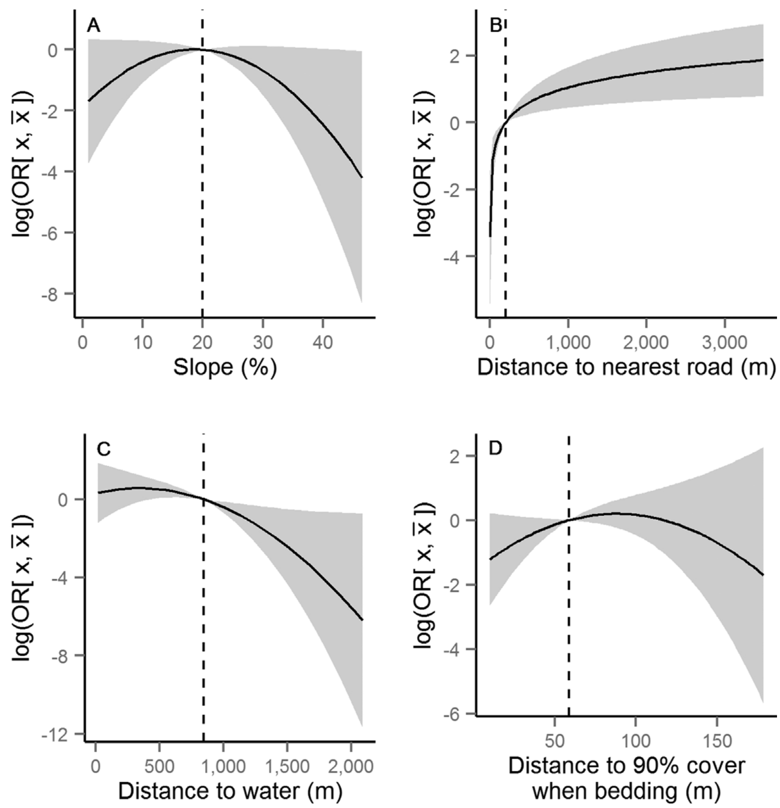

Figure 4. Log odds ratio (OR) of the probability of an elk in the in the Black Hills, South Dakota, 2011–2013, selecting a parturition site at the fine scale (0.20 ha). We calculated log odds relative to the mean value observed for that attribute (vertical dashed line). In forest habitats, percent slope (A), distance to nearest road (B), distance to water (C), and distance to 90% cover when bedding (D) were covariates in the best ranked model. Shaded areas represent 95% confidence intervals. Percent slope, distance to water, and distance to 90% cover were quadratic transformed, and distance to nearest road was natural log transformed (Franklin et al. 2000).

Grasslands

The single top-ranked model of elk parturition site selection in grasslands at the 314-km^2 scale included natural log for the area of vegetation classified as forage, linear term for road density, and a quadratic ruggedness term as variables, with no other models within 2 ΔQIC (Table 3 and Fig. 5). The Spearman rank correlation suggested that this model predicted elk parturition sites well ($r_s = 0.92$, $P < 0.01$). Parturition sites were most likely to occur in areas with high amounts of vegetation classified as forage (log odds ratio = 1.08, SE = 0.34), and low road density (log odds ratio = −0.39, SE = 0.18). Additionally, parturition sites were most likely to occur in areas of intermediate ruggedness with a peak of selection at approximately 226 m (95% CI = 193–289).

The single top-ranked model of elk parturition site selection in grasslands at the 7-km^2 scale included natural log terms for area of vegetation classified as forage, hiding cover, deciduous forest, and road density, and a quadratic ruggedness term as variables, with no other models within 2 ΔQIC (Table 3 and Fig. 6). The Spearman rank correlation suggested that the best model predicted elk parturition sites well ($r_s = 0.95$, $P < 0.01$). Predictions indicated that parturition sites were most likely to occur in areas with high amounts of vegetation classified as forage (log odds ratio = 0.63, SE = 0.18) and low road density (log odds ratio = −1.02, SE = 0.32). Additionally, peak selection occurred at approximately 194 m for ruggedness (95% CI = 170–220). Although the amount of vegetation classified as hiding cover and deciduous forest appeared in the top model, model predictions demonstrated no strong influence of these variables in parturition site selection (i.e., 95% CIs overlapped 0; Fig. 6).

The single top-ranked model of elk parturition site selection in grasslands at the fine scale included natural log of distance to roads, and quadratic terms for percent slope, distance to water, and distance to 90% cover when bedding as variables, with no other models within 2 ΔAIC (Table 3 and Fig. 7). The Spearman rank correlation suggested this model predicted elk parturition sites well ($r_s = 0.85$, $P < 0.01$). Parturition sites were most likely to occur in areas farther from roads (log odds ratio = 0.53, SE = 0.28). Additionally, peak selection occurred at approximately 19% slope (95% CI = 8–23), 610 m from water (95% CI = 0–1,375), and 50 m from 90% cover when bedded (95% CI = 0–380).

DISCUSSION

Female elk employed different resource selection strategies across spatial scales for selection of parturition sites. At the coarse scales, open-canopied vegetation communities that likely provided forage were more important than vegetation classified as hiding cover, lending support for foraging hypotheses offered by Hebblewhite et al. (2008) and Rearden

Table 3. Model selection results comparing parturition sites for elk with random sites in grasslands at the 314-km^2, 7-km^2, and 0.20-ha scales in the Black Hills, South Dakota, 2011–2013. Only models with differences in quasi-likelihood under the independence model criterion (ΔQIC) or Akaike's Information Criterion (ΔAIC) <4 of the best model are presented. We also provide number of parameters (K) and model weights (w_i).

Grassland models[a]	QIC/AIC	ΔQIC/ΔAIC	K	w_i
314-km^2 scale				
Natural log forage + road density + ruggedness + ruggedness^2	167.96	0.00	4	0.85
Natural log forage + hiding cover + hiding cover^2 + deciduous + ruggedness + ruggedness^2 + road density	171.83	3.88	7	0.12
7-km^2 scale				
Natural log forage + natural log hiding cover + natural log deciduous + natural log road density + ruggedness + ruggedness^2	134.03	0.00	6	0.75
Natural log forage + natural log road density + ruggedness + ruggedness^2	136.62	2.59	4	0.21
Fine scale (0.20 ha)				
Slope + slope^2 + natural log distance to road + distance to water + distance to water^2 + security cover + security cover^2	127.12	0.00	8	0.88

[a] Covariates include forage = grassland and open pine and spruce ($\leq$40% canopy cover; ha); deciduous = ha of deciduous forest; ruggedness = index computed using Riley et al. (1999); hiding cover = ponderosa pine and spruce >40% canopy cover (ha); road density = density of roads (km/plot); slope = % slope; distance to road = distance (m) to nearest open road; distance to water = distance (m) to nearest water source; and security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979). Covariates may include non-linear forms such as quadratic transformation = $\beta_0 + \beta_1 x + \beta_2 x^2$, or natural log (pseudo-threshold) transformation = $\beta_0 + \beta_1 \log_e x$ (Franklin et al. 2000).

et al. (2011). We were surprised that hiding cover was not found to affect site selection in grasslands because it was influential in non-forested sagebrush communities (Barbknecht et al. 2011). Elk diets primarily comprise grasses and forbs, and habitats with little or no overstory provide more forage (Wydeven and Dahlgren 1985). As pine basal area increases beyond about 18.5 m^2/ha, or approximately 40% overstory cover, understory production declines considerably in the Black Hills (Bennett et al. 1987, Uresk and Severson 1989). Additionally, predictions of the spatially explicit ArcHSI habitat model for elk in the Black Hills validated our categories and indicated the appropriate foraging and hiding cover opportunities exist for elk in these categories (Benkobi et al. 2004, Juntti and Rumble 2006, Rumble et al. 2007). Within the forested landscape, deciduous forests that were predominantly aspen were selected. Elk use aspen habitats primarily for foraging (Rumble et al. 2007, Kota and Bartos 2010, Rumble and Gamo 2011) and these communities in the Black Hills typically have extensive and diverse understories (Severson and Thilenius 1976, Larson and Johnson 1999).

Elk in our study exhibited use of areas with intermediate ruggedness away from roads in grasslands. In the Black Hills, primary and secondary roads typically occur in meadow drainages or in areas with gentle slope (Rumble et al. 2005), consistent with a low ruggedness index (Riley et al. 1999). Density of roads was very high across lands administered by the United States Forest Service and CSP, where all of the parturition sites in forests occurred. In forests at the larger scales, it would be difficult for elk to select areas of less road density because roads were ubiquitous (>2.1 km/km^2), and elk on public lands in the Black Hills have limited opportunities to avoid roads at such high road densities (Rumble et al. 2005). We hypothesize elk used topography to provide security from potential human disturbance in this heavily roaded system (Montgomery et al. 2012). Rugged topography can provide a buffer from roads and potential human disturbance in open habitats (Edge and Marcum 1991, Rowland et al. 2005). Distance to roads can be a powerful predictor of elk resource selection (Blan and West 1997, Millspaugh et al. 2001, Stubblefield et al. 2006, Sawyer et al. 2007, Montgomery et al. 2013). Higher levels of physiological indicators of stress, such as fecal glucocorticoids, have been observed in elk exposed to increased road density and traffic on roads during spring and summer in the Black Hills (Millspaugh et al. 2001). Elk in CSP and the Black Hills are exposed to moderate to high levels of vehicle disturbance during spring and summer (Montgomery et al. 2013). Providing screening cover from forest vegetation along roadways can help mitigate the negative effects of vehicle traffic disturbance (Hillis et al. 1991, Montgomery et al. 2013). Hillis et al. (1991) recommended forest vegetation as security cover for elk and it should provide cover out to a distance of at least 800 m from an open road. Mean distance of parturition sites from roads was <800 m in both forests and grasslands in our study.

We hypothesize that selection of intermediately rugged topography because of the increased potential of human disturbance in a heavily roaded system may have led to elk making space use decisions into riskier habitats where there is increased predation risk from puma. Roads and human disturbance can alter predator–prey relationships, exposing ungulates to higher predation risk (James and Stuart-Smith 2000, Dyer et al. 2001, Vors et al. 2007). Rugged or steep terrain, with dense vegetation would provide better habitat for successful puma predation (Ashman et al. 1983, Logan and Irwin 1985, Laing 1988, Koehler and Hornocker 1991, Laundré and Hernández 2003). Female elk during our study lived under precarious conditions during parturition because calves were exposed to high rates of predation by puma. Annual survival rates of calves were $\leq$27% for 3 years of the study and 26% of predation mortality occurred within 5 days of parturition (Lehman 2015), or during the hiding phase (Geist 1982). A substantial proportion (29%) of calf mortality from puma occurred within 400 m of the parturition site (South Dakota Game Fish and Parks, unpublished data).

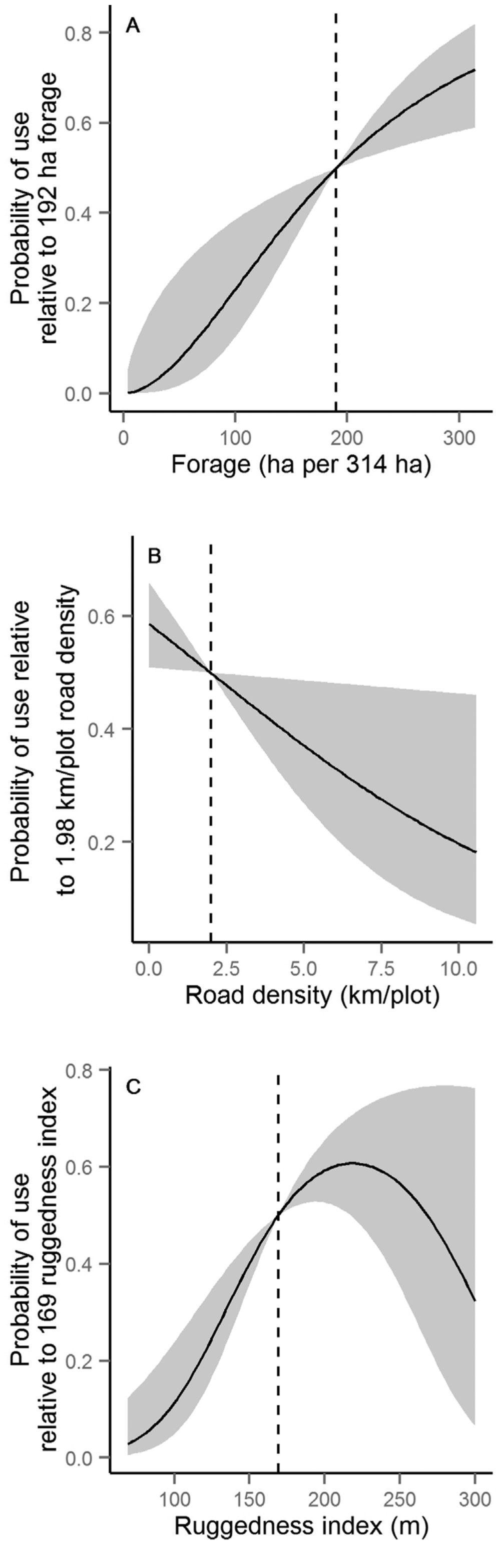

Figure 5. Relative probability of parturition resource selection for elk in grassland habitats as a function of forage (A), road density (B), and ruggedness index (C) at the 314-km^2 coarse scale, Black Hills, South Dakota, 2011–2013. We calculated probabilities relative to the mean value observed for that attribute (vertical dashed line). Each plot assumes an elk is faced with 2 choices of parturition sites and the values of all other attributes are equivalent among choices. Shaded areas represent 95% confidence intervals. Forage was natural log transformed and ruggedness index was quadratic transformed (Franklin et al. 2000).

At the fine scale, we hypothesize that high road densities and the potential for human disturbance and high levels of predation likely influenced parturition site selection. Elk may mitigate these risks by selecting for security cover. In grasslands, elk optimized security cover at approximately 50 m and in forests at approximately 90 m. In grasslands, those levels fall within what is considered optimal security cover (Thomas et al. 1979). In forests, elk selected for a slightly farther distance that could be related to increasing their ability to visually detect humans or puma in that habitat; elk in the dense forests of Oregon selected for greater visibility (>50 m), and it was hypothesized that elk were being vigilant for puma (Rearden et al. 2011).

In forests, security cover was provided by both vegetation and intermediate rugged terrain and slope. In grasslands, the security cover selected by female elk for parturition was provided by intermediate rugged terrain and slope rather than vegetation. In both vegetation communities, elk selected for intermediate levels of slope and were identical at approximately 19% at the fine scale. Selecting for intermediate levels of ruggedness in open habitat would provide for less detection of female elk by predators at greater distances, while still providing conditions necessary to detect predators if they approached in close proximity.

Intermediate levels of ruggedness in grasslands also provided screening cover from roads and human disturbance (Edge and Marcum 1991). Elk resource selection can be strongly influenced by the amount of security cover and proximity to roads (Nelson and Burnell 1975, Berry and Overly 1976, Perry and Overly 1977, Thomas et al. 1979, Lyon and Jensen 1980). In open foraging areas devoid of security cover, the flight response of elk tends to be higher in areas with roads (Lyon and Jensen 1980, Stankowich 2008).

Given the mobility of elk, it would seem the distances to water sources we observed may not be biologically relevant (Skovlin et al. 2002). Female elk in Washington used areas near springs during parturition and increased use near springs after the onset of lactation (McCorquodale et al. 1986). Water sources and associated riparian areas also provide abundant herbaceous forage (Witmer and deCalesta 1983, DelGiudice and Rodiek 1984). Resource selection near water sources is unclear and may suggest broader purposes than access to drinking water (Sargeant et al. 2014).

Our design of using maximum 4-day movements prior to parturition with 314-ha plots discerned patterns of resource selection better than our smaller 79-ha plot design; in forests, using average 4-day movements prior to parturition with 79-ha plots failed to detect any patterns of resource selection. Understanding the mechanisms driving selection of these principal resources could help resource managers develop strategies to ensure secure areas are available for female elk during the parturition period. Our results indicate elk will attempt to avoid roads when possible, but in our study area on public lands, this may not be possible because of high road density, and they used rugged terrain or forest vegetation to screen the calving site from potential human disturbance.

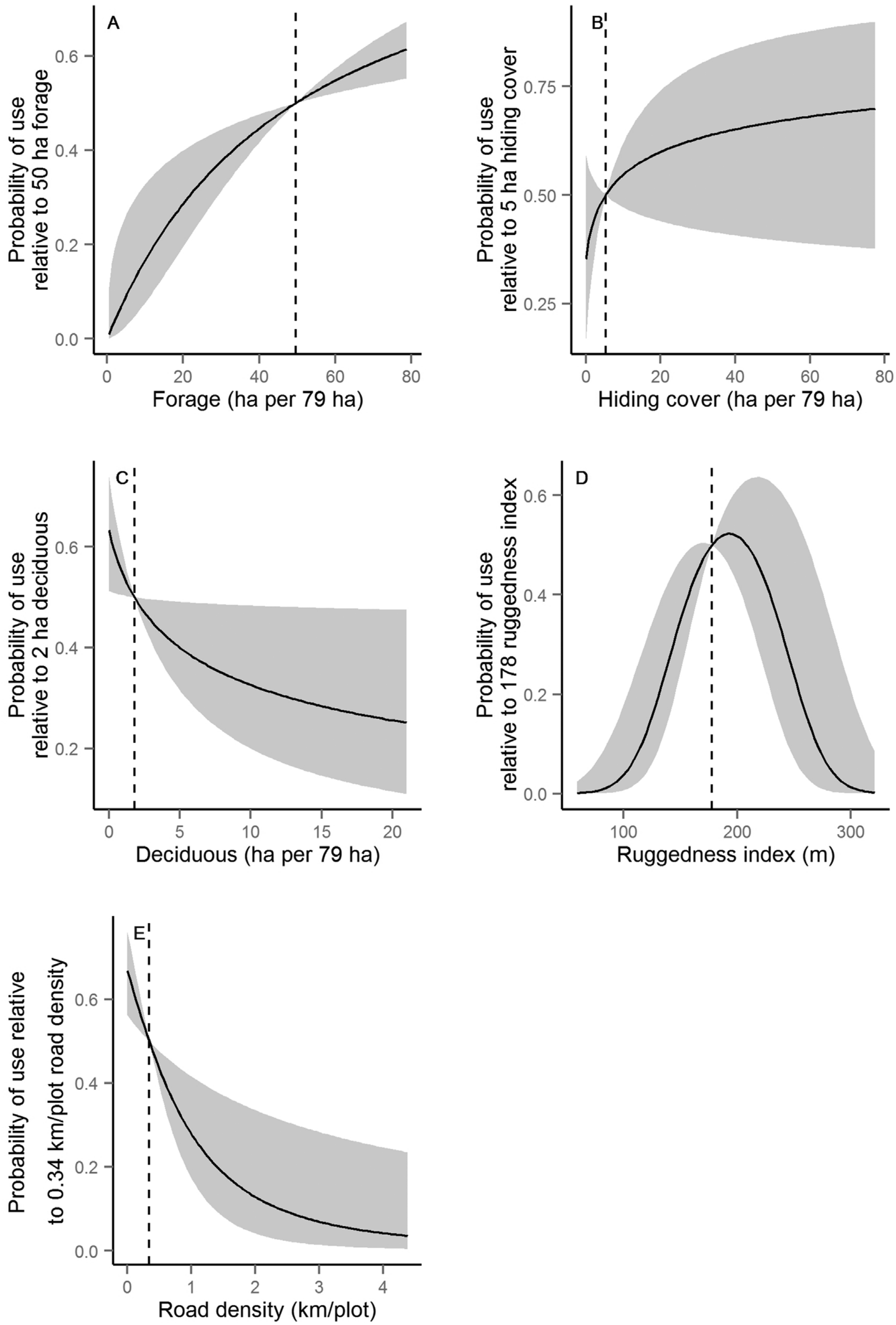

Figure 6. Relative probability of parturition resource selection for elk in grassland habitats as a function of forage (A), hiding cover (B), deciduous forest (C), ruggedness index (D), and road density (E) at the 7-km^2 coarse scale, Black Hills, South Dakota, 2011–2013. We calculated probabilities relative to the mean value observed for that attribute (vertical dashed line). Each plot assumes an elk is faced with 2 choices of parturition sites and the values of all other attributes are equivalent among choices. Shaded areas represent 95% confidence intervals. Ruggedness index was quadratic transformed and all other variables in the top ranked model were natural log transformed (Franklin et al. 2000).

MANAGEMENT IMPLICATIONS

Elk minimize human disturbance by moving away from roads and selecting parturition sites in intermediate rugged habitats, possibly putting them at risk from puma predation. If agencies want to enhance elk habitat, they should take into account the juxtaposition of rugged terrain, foraging habitat,

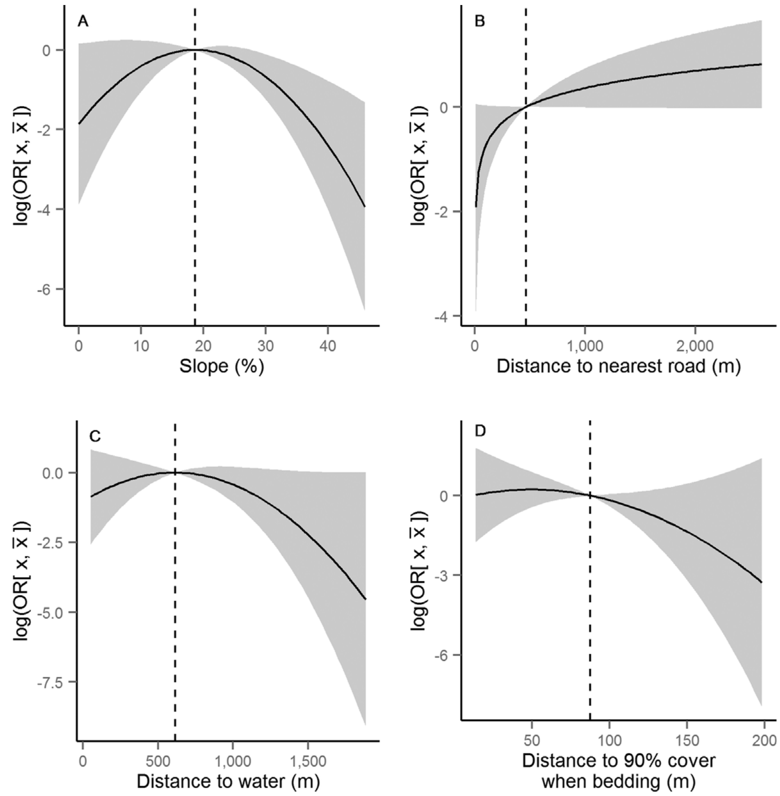

Figure 7. Log odds ratio (OR) of the probability of an elk in the in the Black Hills, South Dakota, 2011–2013 selecting a parturition site at the fine scale (0.20 ha). We calculated log odds relative to the mean value observed for that attribute (vertical dashed line). In grassland habitats, percent slope (A), distance to nearest road (B), distance to water (C), and distance to 90% cover when bedding (D) were covariates in the best ranked model. Shaded areas represent 95% confidence intervals. Percent slope, distance to water, and distance to 90% cover were quadratic transformed, and distance to nearest road was natural log transformed (Franklin et al. 2000).

and roads when devising road management plans. Most areas on public lands in the Black Hills have high road densities (>1.5 km/km^2; Rowland et al. 2000) that receive moderate-to-high vehicle traffic during spring and summer (Montgomery et al. 2013). Elk parturition sites occur close to roads, particularly on public lands, and if agencies want to minimize the influence of roads on elk parturition, they should consider road-use restrictions where open-canopied forest or meadows occur in less rugged terrain that may provide favorable calving habitat. Alternatively, providing forest vegetation as screening cover along roads may enhance security for female elk and their calves. On United States Forest Service lands, travel on many primitive public roads starts 15 May. Delaying the opening of roads to minimize human disturbance until at least 15 June may provide disturbance refugia for elk during parturition.

Past management of forested lands in the Black Hills maximized wood fiber production of ponderosa pine, resulting in tree basal area in the range of 12–19 m^2/ha, or approximately 40–70% overstory canopy cover. Recent forest management has been directed toward reducing the risk of mountain pine beetle infestation in forest stands and has resulted in stands with less basal area and a more open canopy. Forest management that maintains open canopied habitat and prevents pine encroachment of meadows is recommended. Further, we recommend targeting timber management, which promotes an open canopy in less rugged areas. Management practices that promote aspen, such as prescribed fire or mechanical thinning, would also benefit elk habitat for parturition sites.

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