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Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00248

Wildlife Biology 2017: wlb.00248
doi: 10.2981/wlb.00248

Subject Editor: Henrik Andrén. Editor-in-Chief: Ilse Storch. Accepted 1 September 2016

Characteristics of successful puma kill sites of elk in the Black Hills, South Dakota

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Elk *Cervus canadensis nelsoni* in the Black Hills, South Dakota, have been declining since 2006 and there is concern by resource managers and hunters that puma *Puma concolor* predation may be contributing to declining herds. We evaluated characteristics at sites where puma successfully killed elk in the Black Hills of South Dakota. We evaluated characteristics at coarse (79-ha plots) and fine (0.2-ha plot) scales across the landscape. Our primary objective was to obtain a better understanding of vegetation and terrain characteristics that may have facilitated greater susceptibility of elk to predation by puma. We evaluated effects of road density, terrain heterogeneity, probability of elk use, and vegetation variables at 62 puma kill sites of elk and 186 random sites to identify key landscape attributes where elk were killed by puma. Elk were killed by puma in high use areas. Elk were also killed in areas that had greater amounts of edge and intermediate ruggedness at the coarse scale. Further, elk were killed in areas with greater small tree density and woody debris at the fine scale. High germination rates of ponderosa pine trees are unique to the Black Hills and provide dense patches of cover for puma. We hypothesize that cover from small trees and woody debris provided conditions where puma could stalk elk in areas with optimal security cover for elk. We suggest managers implement vegetation management practices that reduce small tree density and woody debris in areas with greater density of meadow–forest edge if they are interested in potentially diminishing hiding cover for puma in elk high use areas.

Predator and prey decisions may change during the hunting process, and spatial scale of landscape attributes may influence how carnivores approach and kill their prey and hence the resulting probability of predation (Hebblewhite et al. 2005, Hilborn et al. 2012). Early in the hunting process large carnivores may search for prey across a large home range, whereas the final stages of greatest predation risk such as attacking, killing and consuming prey may occur over smaller areas, spanning just a few meters (Lima 1998, Gorini et al. 2012).

Foraging ungulates make tradeoffs in the use of space where the most energetically valuable habitats may also place them vulnerable to predation (Lima 1998, Hebblewhite and Merrill 2009). Most research on antipredator behavior related to elk *Cervus canadensis nelsoni* has focused on elk–wolf *Canis lupus* relationships where elk changed their resource selection from open meadows to conifers in an attempt to offset predation and interactions occurred over several km and potentially for several days (Creel et al. 2005, Winnie and Creel 2007, Liley and Creel 2007, Creel et al. 2008). Elk may weigh predation risk and alter their foraging behaviors or vigilance levels in response to predation pressure from wolves (Laundré et al. 2001).

Foraging habitats for elk are often in areas with less overstory canopy of trees which produces greater forage quantity in the understory, but these foraging areas are often near the edges of more dense hiding cover (Lagueux 2002, Skovlin et al. 2002, Rumble and Gamo 2011). Puma *Puma concolor* need to be close to prey to successfully kill, often within several meters (Laundré and Hernández 2003), and puma may use the resource selection of patterns of ungulates to their advantage. Transition zones from hiding cover to foraging areas have been hypothesized as providing areas where puma may have greater success of killing prey (Laundré and Hernández 2003).

Rearden et al. (2011) and Lehman et al. (2016) hypothesized that elk selected birthing sites with more visibility and less concealment cover at the fine scale as a strategy to try and reduce risk of puma predation (Rearden et al. 2011, Lehman et al. 2016). Elk are an important prey species for puma and in some areas can be the primary prey of puma (Hornocker 1970, Husseman et al. 2003, Clark et al. 2014). A better understanding of vegetation and terrain structure that facilitate predation by puma and factors contributing to prey vulnerability are needed (Hornocker and Negri 2010). Kill sites have been described as sites where puma successfully

stalk and kill prey (Koehler and Hornocker 1991, Laundré and Hernández 2003); however, much of the previous literature did not differentiate cache sites from kill sites. Resources used at puma kill sites versus cache sites can be quite different as puma may drag prey to cache sites as far away as 200 m from kill sites (Laundré and Hernández 2003). Pumas cache their prey under vegetation or may cover it with available debris to hide the killed prey from scavengers or competitors (Shaw 1989, Sunquist and Sunquist 1989).

Stalking felids are thought to need greater topography at the coarse scale for close approach before attacking (Ashman et al. 1983, Logan and Irwin 1985, Koehler and Hornocker 1991, Ockenfels 1994). Another important coarse scale variable of influence is the quantity of edge habitats, or the amount of meadow and forest ecotone. Puma killed mule deer during winter on the edge of open meadow and forest habitats, and it was hypothesized that such areas provided the necessary conditions for seeing and successfully stalking deer (Altendorf et al. 2001, Laundré and Hernández 2003, Holmes and Laundré 2006). Puma killed elk near forest and meadow edges in Oregon (Rearden et al. 2011).

Stalking felids are thought to need vegetation at the fine scale for close approach before attacking (Elliott et al. 1977, Van Orsdol 1984, Logan and Irwin 1985, Koehler and Hornocker 1991, Laundré and Hernández 2003); however puma are known to successfully kill prey in areas unrelated to dense vegetation (Katnik 2002, Pierce et al. 2004). In Oregon, puma predation sites of elk had less concealment by vegetation at the fine scale (Rearden et al. 2011). In open vegetation communities with few trees it appears sufficient understory plants can provide concealment for puma to kill prey (Dickson et al. 2005).

We initiated this study because elk in our study area had been declining since 2006 and there was a concern by wildlife managers and hunters that puma predation were contributing to the declining herds in the Black Hills (South Dakota Department of Game, Fish and Parks 2015, Lehman 2015). Our primary objective was to identify vegetation and terrain characteristics at coarse and fine scales associated with successful kill sites of elk by puma while controlling for differential use within a home range. We directly test the competing hypothesis of scale characteristics by evaluating coarse and fine scale in the same modeling framework. We hypothesized successful puma kill sites of elk would be in areas of moderate to high rugged terrain (Riley et al. 1999) and higher amounts of meadow and forest edge when compared to random sites for influential coarse scale variables. We hypothesized understory grassland vegetation provided greater concealment cover than found at random as an influential fine scale variable. We conclude with identifying some specific resource characteristics that may benefit resource managers and provide information for future research.

Material and methods

Study area

The study was in Custer and Pennington counties in southwestern South Dakota in the southern part of the Black Hills physiographic region (Flint 1955). Land ownership included private and public land, including the Black Hills National Forest (BHNF) and Custer State Park (CSP), which encompasses 286 km^2 in the central part of the study area (Fig. 1). Elevations ranged from 1108 m to 2208 m. Average road density within CSP was 2.1 km km^{-2} (CSP unpubl.) and the BHNF was 3.2 km km^{-2} (T. Mills, Black Hills National Forest, pers. comm.). The climate was semi-arid with average annual precipitation ranging from 52–54 cm and average annual temperature ranging from 6–9°C across the study area (National Climatic Data Center 2013). Vegetation varies from northwest to southeast. Coniferous forests dominate the landscape at higher elevations in the northwest portion of the study area and mixed-grass prairie dominated lower elevations of the southeastern portion. The forested portions of the study area were dominated by ponderosa pine *Pinus ponderosa* forest. 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 mixed-grass prairie included native grasses such as needle and thread *Stipa comata*, western wheatgrass *Pascopyrum smithii*, blue grama *Bouteloua gracilis*, little bluestem *Schizachyrium scoparium* and prairie dropseed *Sporobolus heterolepis*. The prairie woodlands were primarily green ash *Fraxinus pennsylvanica*, cottonwood *Populus deltoides* and boxelder *Acer negundo* (Larson and Johnson 1999). Agriculture was primarily alfalfa (*Medicago sativa*) with some small grains such as oats *Avena* spp. and wheat *Triticum* spp. plantings.

Elk capture and radio-marking

We captured female elk using tranquilizer dart guns from helicopters during February 2011–2013. Elk were sedated using butorphanol, azaperone, and medetomidine sedation protocol (Mich et al. 2008). After elk were sedated, we blindfolded and fitted them with GPS telemetry unit that included a very high frequency (VHF) transmitter (Telonics Inc. or Advanced Telemetry Systems Inc.). Transmitters had a sensor that changed to mortality pulse after four hours of inactivity. Female elk were inspected for pregnancy using rectal palpation (Greer and Hawkins 1967, Vore and Schmidt 2001). Females suspected of being pregnant were fitted with a vaginal implant transmitter (VIT) (Barbknecht et al. 2009) (Advanced Telemetry Systems). We located female elk daily from 1 April–31 October of each year. Beginning 1 May, we monitored female elk twice daily to determine if females were located alone or started to localize activity in one area before parturition. Once VITs were expelled due to parturition we attempted to find calves (Barbknecht et al. 2011). Once found, the calf was fitted with an expandable VHF radio-collar also with mortality sensor (Advanced Telemetry Systems). We monitored calf survival daily through 30 September of each year, and 5 days per week the rest of the year.

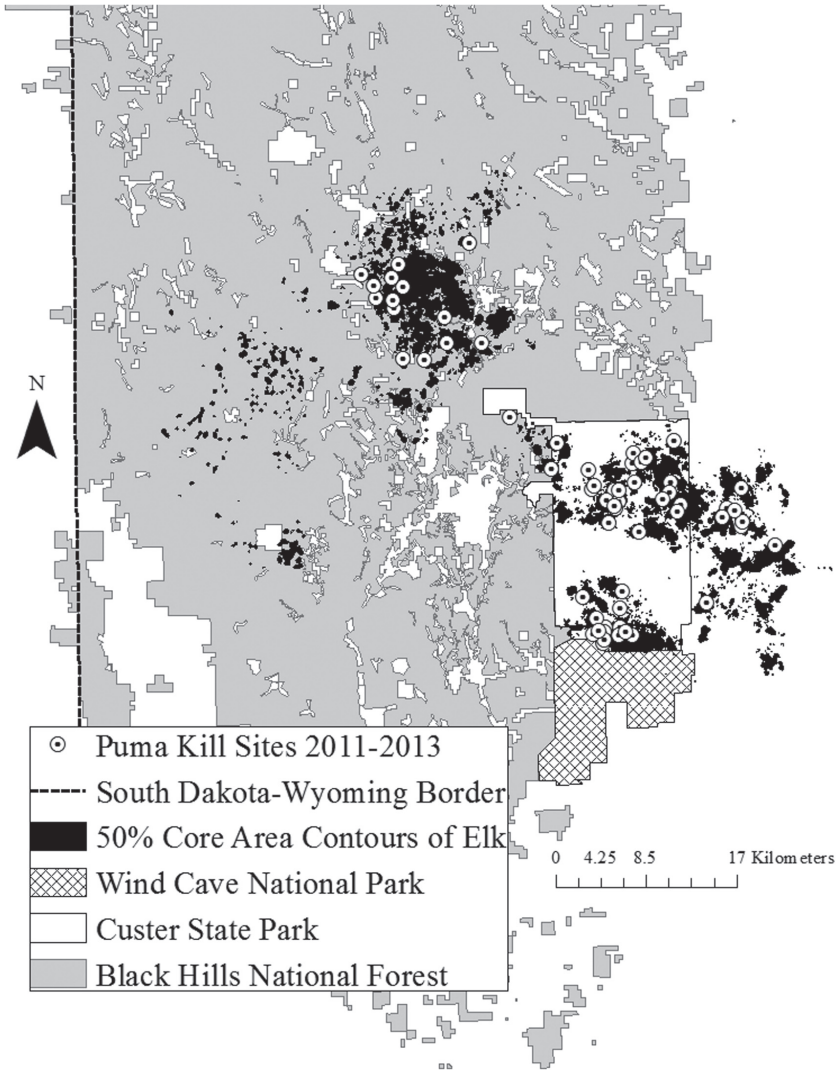

Figure 1. The Black Hills, South Dakota study area where we studied susceptibility of elk to puma predation, 2011–2013. We reference puma kill sites of elk relative to 50% Brownian bridge movement model core area contours during summer–fall (parturition through 31 October) and winter (November 1 thru parturition of the subsequent year).

Determination of puma kill sites

Elk were checked for mortalities at least once daily, so when the signal from a transmitter indicated mortality, we investigated the site in ≤ 24 h. If we found a carcass, we photographed and necropsied the carcass immediately for signs of hemorrhaging and bite marks, and bite marks were measured to the nearest mm with calipers. We classified cause of mortality as predation when evidence at the mortality site indicated that the elk had been alive when attacked (e.g. hemorrhaging). We also investigated the area for cache sign, drag marks, scat, and searched shrubs, downed woody debris, and other vegetation at the site for hairs of predators (O'Gara 1978). From the carcass or cache site we were able to follow tracks, drag marks, blood and hair to the kill site location where pumas attacked elk. Typically tracks and disturbed debris such as rolled rocks, disturbed pine needles and woody debris indicated a linear track of 5–25 m where the kill occurred (Laundré and Hernández 2003). Areas of the carcass that had bite marks were swabbed for saliva. Saliva, predator hairs and scat were sent to the Laboratory for Ecological, Evolutionary and Conservation Genetics at the Univ. of Idaho for mitochondrial deoxyribonucleic acid (DNA) analysis to determine the predator species presence at the site (Onorato et al. 2006). The species of origin for each sample was determined using mitochondrial DNA fragment analysis (De Barba et al. 2014). For purposes of this study we only evaluated kill sites that were confirmed to be from puma. Using a Geographic Positioning System we marked each kill site and returned to the site to measure topographical and vegetative characteristics once the elk was completely consumed or was abandoned.

Kill site covariates

We modeled elk predation risk with data collected at known predation sites and at randomly available sites within an elk's home range (99% contours). We first estimated elk home ranges with Brownian bridge movement models (BBMMs), assuming a 50 m grid size (Horne et al. 2007, implemented

with the 'BBMM' package (Nielson et al. 2014) in program R ver. 3.1.0, 2014, <www.r-project.org>) with GPS transmitters that were set to collect satellite waypoints every 1.5–2 h daily. We estimated two home ranges annually: one during summer–fall (parturition thru 31 October) and the other during winter (November 1 thru parturition of the subsequent year). For females that were barren or aborted calves, we used the median parturition date for each year as the start time for the summer–fall season. In addition to 99% contours we also generated 50% contours (core areas) for both time periods. We obtained the estimated probability an elk would use the grid cell within which used and available points were located from the BBMM that corresponded to the season when an elk was killed, which we used to account for differential use within a home range when modeling characteristics of kill sites.

We selected randomly available sites within an elk's home range using stratified sampling (Cochran 1977) after we intersected home range polygons with the BHNF Forest Service Vegetation (FSVEG) geographic information system (GIS) coverages (BHNF unpubl.) and the CSP Land Cover GIS coverages (CSP unpubl.). We randomly selected, without replacement, 20–30 polygons from each of the three vegetation community categories described below, and within each of these polygons we selected one random point. Each GIS coverage assigned polygons with the following vegetation community categories (Buttery and Gillam 1983): 1) open-canopied vegetation, which combined open-canopied forest (0–40% overstory canopy cover) and meadows; 2) moderate-canopied forest vegetation (41–70% overstory canopy cover); and 3) dense forest vegetation which combined forests with $>70\%$ overstory canopy cover and seedling or shrub. Annually, we edited the GIS coverage to update polygons to the appropriate structural stage affected by recent wildfires and mountain pine beetle *Dendroctonus ponderosae* infested areas. We also added structural stage assignments to private lands by comparing 1-m ground sample distance resolution satellite imagery (National Agricultural Imagery Program, NAIP; <http://datagateway.nrcs.usda.gov/>, accessed 1 October 2013) to adjacent inventory data from CSP and BHNF.

Coarse-scale variables

Resource evaluation at 500 m has also been considered in previous investigations (Atwood et al. 2007, Rearden et al. 2011). At the coarse scale, we summarized area of vegetation community categories within a 500-m radius (79 ha hereafter) circle centered at kill and randomly available sites. We modeled kill sites as a function of vegetation community, terrain ruggedness index, road density, and edge density.

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/79 ha plot). We only included roads open to the public in our analysis. Edge of forest and grasslands was determined by digitizing NAIP imagery data where forest and meadow ecotones occurred and edge was calculated by intersecting the ecotone layer with circular plots in ArcGIS and was expressed as length within each plot (km/79 ha plot).

Fine-scale evaluation

At the fine scale we summarized vegetation characteristics from four 25-m transects (0.20 ha), centered around kill or random sites and oriented in the cardinal directions. Fine-scale plot size was similar to previous investigations (Laundré and Hernández 2003, Rearden et al. 2011). At the fine scale, we modeled puma kill sites as a function of percent cover of grasses; large tree (≥ 15.24 cm DBH) density; small tree (<15.24 cm DBH) density, percent slope; distance to nearest road; downed woody debris; and elk security cover. We measured percent cover of total herbaceous cover, grasses, forbs and shrubs within a 0.1-m^2 quadrat (Daubenmire 1959) at 2-m intervals along the four transects ($n = 40$ measurements per site) and averaged over all measurements at each site. We measured DBH of all trees ≥ 15.24 cm DBH in a variable radius circular plot centered at the kill or random site using a 10-factor prism (Sharpe et al. 1976) and measured trees <15.24 cm DBH within in a 5.03-m fixed radius plot centered at the kill or random site, from which we calculated average DBH, and density at each site. We measured percent slope of the prevailing downhill direction with a clinometer. We measured distance (m) to nearest road using the road coverages (BHNF unpubl., CSP unpubl.) within ArcGIS. Downed woody debris (metric tons ha^{-1}) was interpolated using a pictorial guide (Simmons 1982).

We estimated elk security cover (Thomas et al. 1979) for a standing and bedded elk at sites using two vinyl cover cloths with 40 alternating black and white 15×15 cm squares. 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 four 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 (Thomas et al. 1979).

Resource selection analysis

We modeled puma kill sites and random sites at both scales using case-control logistic regression (Hosmer et al. 2013). We used case-control logistic regression because puma kill events are rare and it is unlikely a puma would have killed an elk at any of the randomly available sites (i.e. we found no evidence of puma kill sign at random 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

Table 1. Mean covariate values and standard errors evaluated for puma kill sites of elk across 2 scales in the Black Hills, South Dakota, 2011–2013.

Covariate[a]	Scale	Kill Site	SE	Random	SE
Open-canopied vegetation (ha)	79 ha	51.03	2.36	36.80	1.70
Moderate-canopied forest vegetation (ha)	79 ha	16.83	1.68	22.89	1.24
Dense forest vegetation (ha)	79 ha	9.78	1.57	16.71	1.33
Edge (km plot^{-1})	79 ha	5.08	0.50	2.08	0.21
Ruggedness index (m)	79 ha	214.17	6.39	229.72	4.63
Road density (km plot^{-1})	79 ha	1.55	0.16	1.66	0.10
Large tree density (trees ha^{-1})	0.20 ha	172.93	36.34	212.88	17.22
Small tree density (trees ha^{-1})	0.20 ha	1199.93	219.13	680.09	103.60
Slope (%)	0.20 ha	21.23	1.47	20.42	1.06
Woody debris (metric tons ha^{-1})	0.20 ha	7.90	1.07	7.71	0.58
Distance to road (m)	0.20 ha	825.89	80.10	467.33	40.21
Security cover (m)	0.20 ha	58.53	6.44	75.31	5.63
Grass cover (%)	0.20 ha	47.64	3.37	35.28	2.11

[a]Covariates include open-canopied vegetation = grassland and forest ≤ 40% canopy cover (ha), moderate-canopied forest vegetation = forest 41–70% canopy cover (ha), dense forest vegetation = forest > 70% canopy cover (ha), edge = km of meadow and forest edge (km/79 ha plot), ruggedness index (m) computed using Riley et al. 1999, road density = density of roads (km/79 ha plot), large tree density = trees/ha for trees ≥ 15.24 cm diameter at breast height, small tree density = trees/ha for trees < 15.24 cm diameter at breast height, slope = % slope, woody debris = metric tons/ha of woody debris on the ground, distance to road = distance (m) to nearest open road, security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979), and grass cover = % understory grasses.

unbiased (Keating and Cherry 2004), though high levels of contamination may lead to bias in slope parameters. We fit several models representing different sets of predictor variables thought to influence kill sites (Table 1). We first evaluated univariate models with untransformed, log-transformed and quadratic-transformed variables (Franklin et al. 2000). We then used whichever univariate transformation resulted in the lowest AIC when fitting multivariate models. For multivariate models we considered models with and without the continuous variable of 'elk use' which was extracted from 99% BBMM home range contours (Table 2). We ranked models using Akaike's information criterion (Burnham and Anderson 2002) and present all models < 6 ΔAIC units of the top model. We implemented logistic regression with the 'glm()' function in R ver. 3.2.1 (<www.r-project.org>).

Further, we compared puma kill sites that occurred within 50% contour BBMM elk core areas versus kill sites that occurred outside core areas at both scales with logistic regression univariate tests. We calculated unit odds ratios and provide 95% confidence intervals for all univariate comparisons (Hosmer et al. 2013).

Table 2. Description of competing candidate models developed to describe resources used by puma to successfully kill elk; both coarse scale (79-ha plots) and fine scale (0.20-ha plots) models were evaluated in the Black Hills, South Dakota 2011–2013.

Model	Covariates (units)[a]	Model	Covariates (units)[a]
Coarse		Fine	
1	Open-canopied vegetation (ha)	20	Large tree density (trees ha^{-1})
2	Moderate-canopied forest vegetation (ha)	21	Small tree density (trees ha^{-1})
3	Dense forest vegetation (ha)	22	Slope (%)
4	Edge (km plot^{-1})	23	Woody debris (metric tons ha^{-1})
5	Ruggedness index (m; Riley et al. 1999)	24	Distance to road (m)
6	Road density (km plot^{-1})	25	Security cover (m)
7	Edge + Ruggedness + Road density	26	Grass cover (%)
8	Open-canopied vegetation + Edge	27	Small tree density + Distance to road
9	Open-canopied vegetation + Ruggedness	28	Small tree density + Distance to road + Security cover
10	Open-canopied vegetation + Road density	29	Small tree density + Distance to road + Security cover + Grass cover
11	Open-canopied vegetation + Edge + Ruggedness + Road density	30	Distance to road + Security cover
12	Moderate-canopied forest vegetation + Edge	31	Distance to road + Grass cover
13	Moderate-canopied forest vegetation + Ruggedness	32	Woody debris + Security cover + Grass cover
14	Moderate-canopied forest vegetation + Road density	33	Global
15	Moderate-canopied forest vegetation + Edge+ Ruggedness+ Road density		
16	Dense forest vegetation + Edge		
17	Dense forest vegetation + Ruggedness		
18	Dense forest vegetation + Road density		
19	Dense forest vegetation + Edge+ Ruggedness+ Road density		

[a]We considered linear, natural log (pseudo-threshold) transformed, and quadratic transformed forms of covariate values (Franklin et al. 2000). We also considered multivariate models with and without the continuous covariate "elk use" which was the probability of elk use extracted from 99% Brownian Bridge Movement Models.

Assessing model fit

We evaluated the ability of our models to correctly predict kill sites with cross-validation techniques described by Boyce et al. (2002). 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 kill site, fit models that were within 2 ΔAIC of the top-ranked model, and predicted the log odds ratio of the withheld kill site. We simultaneously predicted log odds ratios at random 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 kill site as a value inversely proportional to the number of random 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 kill sites if Spearman's rank correlation (r_s) was positive, with a significant ($p \leq 0.10$) 1-sided test.

Results

Puma kill sites

Over the three-year study period, 58 female elk (n = 56 adults, n = 2 yearlings) and 125 calves were radio-marked and available for kill by puma in our study area. We measured 62 successful puma kill sites and 186 random sites. Of the successful kills 5 were adult female elk that ranged in age from 4 to 14 years, and 57 were calves that ranged in age from 1 to 258 days (mean age in days = 49.70, 95% CI = 33.03–66.40). Further, 52 kills occurred in forest, or with tree canopy cover, and 10 occurred in areas with no canopy from trees, or in open grasslands. Kills occurred primarily in 50% elk core areas (n = 39, 63%) with fewer outside core areas (n = 23, 27%).

Covariates related to puma kill sites of elk

Covariates did not differ ($p > 0.05$ for univariate t-tests) between adult and calf elk and therefore characteristics at kill sites were pooled for resource analysis. The top-ranked model describing puma kill sites of elk was the global model including all covariates of potential influence with no other models within 2 ΔAIC (Table 3). Our top model reasonably predicted puma kill sites ($r_s = 0.74$, $p < 0.01$). We therefore report results obtained from the global model. Successful puma kill sites of elk were most likely to occur in areas with greater amounts of woody debris (log odds-ratio = 1.21, SE = 0.36) and greater small tree density (log odds-ratio = 1.62, SE = 0.59 for first-order term) (Fig. 2). Additionally, peak occurrence of kills was at approximately 9 km of edge per plot (95% CI = 7–16), 163 m of ruggedness (95% CI = 0–1091), and 0.0007 for probability of elk use (95% CI = 0.0005–0.001) (Fig. 2). The mean value was 0.00006 and range was 8.78×10^{-10} – 0.00116 for estimated probability of elk use. For small tree density it should be noted that the second-order term, although important in single-variable models, had 95% confidence intervals that overlapped 0 in the global model. The other covariates in the global model had log odds-ratios with 95% CIs that overlapped 0.

Puma kills and elk core area evaluation

Several characteristics differed outside 50% elk core areas when compared with inside core areas (Table 4). At the coarse scale puma kill sites had greater amounts of dense forest outside 50% elk core areas than inside core areas (log odds-ratio = 0.61, SE = 0.31). At the fine scale puma kill sites had greater small tree density (log odds-ratio = 0.99, SE = 0.36), were closer to roads (log odds-ratio = –0.62, SE = 0.30), less distance to 90% security cover when bedding (log odds-ratio = –0.61, SE = 0.31), and had less grass cover (log odds-ratio = –0.69, SE = 0.30) outside 50% elk core areas than inside core areas; Table 4).

Discussion

Elk were primarily killed by puma within the core of their home range in high use areas. After accounting for differential use within their home range, we found both coarse and fine scale variables were important predictors of puma kill

Table 3. Model selection results comparing successful puma kill sites of elk against random sites in the Black Hills, South Dakota 2011–2013. Only models with ΔAIC < 6 of the best model are presented.

Models[a]	AIC	ΔAIC	K	w_i
$logit(\hat{Y}_i)$ = Global model: Open (Q) + Moderate + Dense + Edge (Q) + Ruggedness (Q) + Road density + Large tree density (Q)+ Small tree density (Q) + Slope (Q) + Woody debris (NL) + Distance to road (NL) + Security cover (NL) + Grass cover (NL) + Elk use (Q)	159.56	0.00	22	0.74
$logit(\hat{Y}_i)$ = Moderate + Edge (Q) + Ruggedness (Q) + Road density + Elk use (Q)	164.80	5.24	9	0.05
$logit(\hat{Y}_i)$ = Moderate + Edge (Q) + Elk use (Q)	164.88	5.32	6	0.05
$logit(\hat{Y}_i)$ = Edge (Q) + Elk use (Q)	165.25	5.69	5	0.04

[a]Covariates include: Open = open canopied vegetation of grassland and forest ≤ 40% canopy cover (ha), Moderate = moderate-canopied forest vegetation with 41–70% canopy cover (ha), Dense = forest vegetation > 70% canopy cover (ha), Edge = km of meadow and forest edge (km/79 ha plot), Ruggedness = ruggedness index computed using Riley et al. 1999, Road density = density of roads (km/79 ha plot), Large tree density = trees/ha for trees ≥ 15.24 cm diameter at breast height, Small tree density = trees/ha for trees < 15.24 cm diameter at breast height, Slope = % slope, Woody debris = metric tons ha^{-1} of woody debris on ground, Distance to road = distance (m) to nearest open road, Security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979), Grass cover = % understory grasses, and Elk use = probability of elk use extracted from 99% Brownian bridge movement models. Covariates may include non-linear forms such as quadratic transform = $\beta_0 + \beta_1 x + \beta_2 x^2$ (Q), or natural log (pseudo-threshold) transformation = $\beta_0 + \beta_1 \log_e x$ (NL) (Franklin et al. 2000).

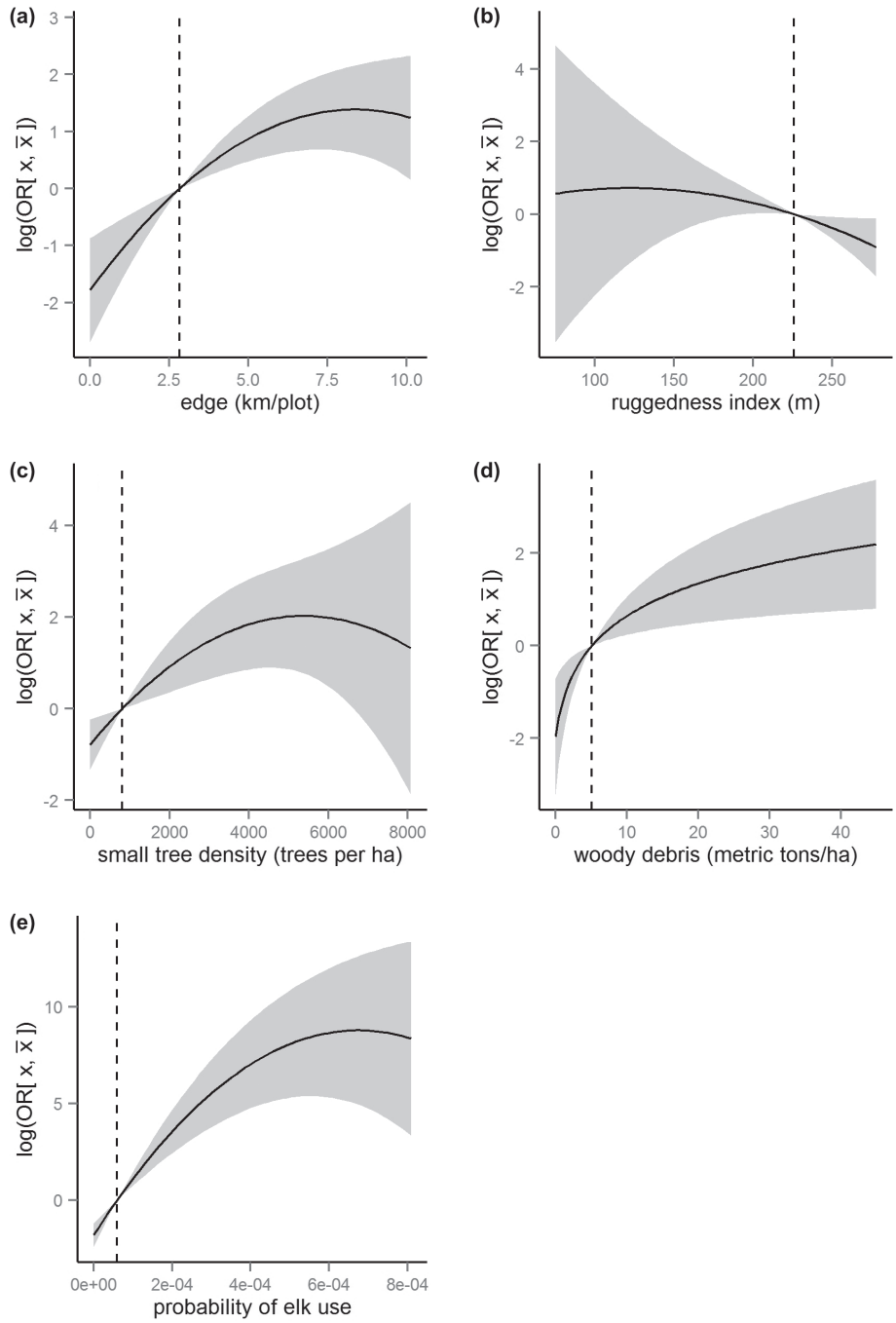

Figure 2. Log odds ratios (OR) for variables in the best ranked model where puma killed elk in the Black Hills, South Dakota, 2011–2013. Coarse scale (79 ha) variables included amount of edge (a) and ruggedness index (b); fine scale (0.20 ha) variables included density of small trees (< 15.24 cm diameter at breast height) (c), woody debris (d), and probability of elk use (e) We calculated log odds relative to the mean value observed for that attribute (vertical dashed line). Edge, ruggedness index, small tree density and elk use were quadratic transformed; woody debris was natural log transformed (Franklin et al. 2000).

sites. Our hypothesis that puma kill sites would be along meadow and forest ecotones similar to other ungulate studies (Altendorf et al. 2001, Laundré and Hernández 2003, Holmes and Laundré 2006, Rearden et al. 2011) was supported. We further hypothesized that puma would be more likely to kill elk in more rugged terrain based on previous investigations. However, our observations differed from previous investigations suggesting stalking felids need greater topography at the coarse scale (Ashman et al. 1983, Logan and Irwin 1985, Koehler and Hornocker 1991, Ockenfels 1994). Our results indicate that steep topography is not necessary and terrain ruggedness at kill sites was less than observed at random sites. Puma predations did occur in areas with some topography, or in areas classified as intermediate ruggedness (Riley et al. 1999). However, ruggedness was less than where elk selected parturition sites in forests, and similar to ruggedness values where elk selected parturition sites in grasslands in the Black Hills (Lehman et al. 2016).

Table 4. Means, standard errors (SE), coefficients and standard errors (Coeff [SE]), odds ratios (OR) and odds ratio 95% confidence intervals (95% CI) from univariate logistic regressions comparing successful puma kill sites within elk 50% core areas versus kill sites outside elk 50% core areas. Coarse scale (79-ha plots) and fine scale (0.20-ha plots) results from the Black Hills, South Dakota 2011–2013.

	Inside 50% core area		Outside 50% core area				
Covariates[a]	Mean	SE	Mean	SE	Coeff (SE)	OR	95% CI
Coarse scale							
Open-canopied vegetation (ha)	53.14	2.86	47.45	4.08	–0.31 (0.27)	0.73	0.432–1.25
Moderate-canopied forest vegetation (ha)	17.56	2.20	15.59	2.63	–0.15 (0.27)	0.86	0.507–1.461
Dense forest vegetation (ha)	7.19	1.43	14.17	3.32	0.61 (0.31)	1.84	1.002–3.379
Edge (km plot^{-1})	5.12	0.64	5.01	0.82	–0.03 (0.27)	0.97	0.572–1.647
Ruggedness index (m; Riley et al. 1999)	212.67	8.49	216.71	9.69	0.08 (0.27)	1.08	0.638–1.839
Road density (km plot^{-1})	1.41	0.19	1.78	0.28	0.29 (0.27)	1.34	0.787–2.269
Fine scale							
Large tree density (trees ha^{-1})	171.67	51.79	175.06	44.92	0.01 (0.26)	1.01	0.607–1.681
Small tree density (trees ha^{-1})	659.82	154.64	2115.78	477.77	0.99 (0.36)	2.69	1.329–5.450
Slope (%)	22.14	1.81	19.70	2.53	–0.22 (0.27)	0.80	0.473–1.362
Woody debris (metric tons ha^{-1})	7.40	1.38	8.76	1.71	0.16 (0.26)	1.17	0.705–1.953
Distance to road (m)	926.64	103.03	655.04	121.50	–0.62 (0.30)	0.54	0.299–0.969
Security cover (m)	64.55	8.52	48.32	9.50	–0.61 (0.31)	0.54	0.296–0.998
Grass cover (%)	52.82	3.84	38.85	6.03	–0.69 (0.30)	0.50	0.279–0.903

[a]Covariates include open-canopied vegetation = grassland and forest ≤ 40% canopy cover (ha), moderate-canopied forest vegetation = forest 41–70% canopy cover (ha), dense forest vegetation = forest > 70% canopy cover (ha), edge = km of meadow and forest edge (km/79 ha plot), ruggedness index (m) computed using Riley et al. 1999, road density = density of roads (km/79 ha plot), large tree density = trees/ha for trees ≥ 15.24 cm diameter at breast height, small tree density = trees/ha for trees < 15.24 cm diameter at breast height, slope = % slope, woody debris = metric tons/ha of woody debris on the ground, distance to road = distance (m) to nearest open road, security cover = distance (m) a bedded elk would be 90% obscured (Thomas et al. 1979), and grass cover = % understory grasses.

It has been hypothesized that the fine scale (< 100 m) is where decisions are made by ambush predators such as puma to attack and kill prey (Lima 1998, Caro et al. 2004, Miller et al. 2015). Meadow and forest edges are often sites of dense patches of seedlings and saplings because of increased sunlight and reduced competition from larger trees at the fine scale. A pattern of kill site characteristics emerged at the fine scale where greater density of small trees may have led to increased susceptibility of elk. Puma were using more than 1.5 times greater small tree density at kill sites than found at random and they may have used dense patches of pine seedlings or saplings to successfully stalk elk. Germination and growth rates of young trees of ponderosa pine are unique to the Black Hills as germination rates of seedlings are robust due to timing of optimal temperature and precipitation during the growing season leading to unique productivity and tree regeneration success (Shepperd and Battaglia 2002, Battaglia et al. 2008). In Idaho, Husseman et al. (2003) noted that dense spruce trees provided concealment cover and were utilized by puma to predate elk. We also surmise that puma may have utilized concealment cover from greater woody debris on the forest floor and not understory grassland vegetation as we hypothesized. Future investigations could further our understanding of these relationships by evaluating radio-marked puma and elk interactions across the landscape.

Several variables related to density of trees, security cover, grass cover and road density differed for successful puma kill sites when compared between within 50% elk core areas versus outside core areas. We suspect the patterns observed were more related to elk resource selection patterns versus puma kill site characteristics. Elk in our study area have already been documented to select for open-canopied habitats, optimal security cover, and avoidance of roads (Lehman et al. 2016).

In elk populations, managers should consider puma as a potential mechanism causing variable or low recruitment (Raithel et al. 2007, Clark et al. 2014). Annual calf elk survival in our study area was ≤ 27% (Lehman 2015). Understanding what resources contribute to elk vulnerability by puma are needed as elk can be the primary prey of puma and potentially a factor influencing their demographics (Hornocker and Negri 2010, Raithel et al. 2007, Clark et al. 2014). Understanding the relationship tree density plays in providing edge for both predation by puma and security cover by elk needs further evaluation. For puma and elk interactions, elk antipredator strategies may include selecting areas to better visually detect puma (Rearden et al. 2011, Lehman et al. 2016), whereas puma are selecting for dense vegetation hiding cover (Dickson et al. 2005) which could potentially influence locations where puma successfully capture elk (i.e. accessibility) (Trainor and Schmitz 2014, Miller et al. 2015). Elk security cover at puma kill sites was roughly 60 m, or a distance considered as ideal security cover for elk (Thomas et al. 1979). Elk are clearly accessible to puma under ideal security cover situations, and future investigations could evaluate this puma–elk interaction, and build upon the resource relationships presented in this study.

We suggest managers take into account the following considerations if interested in reducing habitat features which provide hiding cover for puma in elk areas. Vegetation management reducing small tree density may decrease puma hiding cover, and small tree reductions should be focused in areas with greater density of meadow–forest edge. If both mature and small trees are removed, understory grass development may be attractive for elk for foraging but residual woody debris left on the ground from logging operations may provide hiding cover for puma. Removal of residual

woody debris may reduce puma hiding cover. When developing vegetation management plans or timber sales, agencies should consider noncommercial thinning of small trees in areas with greater amounts of meadow and forest edge, and whole tree removal versus lop-and-scatter methods will help reduce woody debris.

Acknowledgments –Field support was provided by S. R. Lindsey, J. J. Kragel, A. N. Coleman, K. D. Kaskie, N. D. Markl, D. T. Fogarty, T. M. Gingery, M. N. Lenny, G. S. Lenny, G. C. Brundige, L. L. Flack and K. W. Knudsen. Additional field assistance and technical support was provided by The U.S. Forest Service Rocky Mountain Research Station, the University of Missouri and West Virginia University.
Funding – Funding for this research was provided by the Rocky Mountain Elk Foundation and the South Dakota Department of Game, Fish and Parks, Federal Aid to Wildlife Restoration Fund (Project W-75-R-53, No. 7544). B. D. Jansen, B. N. Kertson, and M. L. Elbroch reviewed earlier drafts of this manuscript.
Permits – 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).

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