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Research Article

Resource Selection by Cougars: Influence of Behavioral State and Season

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ABSTRACT An understanding of how a predator uses the landscape can assist in developing management plans. We modeled resource selection by cougars (*Puma concolor*) during 2 behavioral states (moving and killing) and 2 seasons (summer and winter) with respect to landscape characteristics using locations from global positioning system (GPS)-collared cougars in the Pryor Mountains, Montana and Wyoming, USA. Furthermore, we examined predation-specific resource selection at 2 scales (fine and coarse). When possible, we backtracked from cache sites to kill sites and used a fine-scale analysis to examine landscape characteristics of confirmed kills. At this fine scale, kill sites had less horizontal visibility, were more likely to be in juniper (*Juniperus* spp.)-mountain mahogany (*Cercocarpus ledifolius*), and were less likely to be in grassland vegetation. For the coarse-scale analysis of predation risk, we used the entire dataset of kills by buffering each cache site by 94.9 m, which was the 95% upper cut-off point of the known distances dragged from kill sites to cache sites, thereby creating buffered cache sites that had a high probability of containing the kill site. We modeled seasonal cougar predation site selection by constructing resource selection functions for these buffered cache sites. The top model for summer predation risk consisted of vegetation class, distance to water, and slope. The top model for winter predation risk included vegetation class and elevation. These predation risk models were similar to but simpler than the resource selection models developed from the moving locations. Essentially, the behavioral state (i.e., killing vs. moving) of the cougar had little influence on resource selection, indicating that cougars are generally in hunting mode while moving through their landscape. To potentially reduce cougar predation on mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) in our study area, managers can intersect the cougar predation-risk resource selection functions with deer and sheep habitat to guide habitat modification efforts aimed at increasing horizontal visibility in risky vegetation classes. © 2016 The Wildlife Society.

KEY WORDS bighorn sheep, cougar, movement, *Ovis canadensis*, predation, *Puma concolor*, resource selection.

Interactions between predators and their prey have been of interest to ecologists and managers because conservation and management planning often benefit from an understanding of predator–prey relationships (Ballard et al. 2001). How a predator uses its surrounding landscape, particularly during different behavioral states (Wilmers et al. 2013, Zeller et al. 2014), can provide insights into predator behavior and potential interactions with their prey. Through predation, cougars (*Puma concolor*) can exert strong pressures on their prey populations (Bleich and Taylor 1998, Hayes et al. 2000, Robinson et al. 2002, Cooley et al. 2008). A population of cougars in Nevada nearly caused a local extinction of porcupines (*Erethizon dorsatum*; Schweitzer et al. 1997), and in British Columbia, Wittmer et al. (2005) reported cougar predation to be limiting caribou (*Rangifer tarandus caribou*) survival. In Nevada and California, cougar populations have influenced small populations of bighorn sheep (*Ovis canadensis*) toward extirpation (Wehausen 1996).

Cougars are an elusive ambush predator whose habitat selection and predation patterns intertwine (Husseman et al. 2003, Laundré and Hernandez 2003, Holmes and Laundré 2006). As an ambush predator evolved for short bursts of speed, cougars must approach their prey undetected to within relatively close distances to make a successful kill (Hornocker 1970). Cougars are unlikely to complete a kill if they initiate an ambush attempt >25 m from their potential prey (Young and Goldman 1946, Holmes and Laundré 2006). Previous research has reported cougars select for certain landscape features (e.g., thick vegetation, rock outcroppings), presumably because these features provide cover and facilitate the successful stalking and killing of prey (Holmes and Laundré 2006, Atwood et al. 2009, Kunkel et al. 2013). Atwood et al. (2009) reported cougars used areas with more structural complexity, whereas Kunkel et al. (2013) reported cougars selected for more rugged terrain. In southern California,

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Dickson and Beier (2002) reported cougars selected for riparian habitats, against grasslands, and against human-dominated habitats. Husseman et al. (2003) reported that sites with cougar kills had lower horizontal visibility than random sites.

With some exceptions, many studies examining cougar kill site characteristics have had to rely, at least in part, upon the characteristics of cache sites because of the difficulty of detecting actual kill sites (Logan and Irwin 1985, Laundré and Hernandez 2003, Woodruff 2006). Although general cougar habitat use and cache site characteristics can give some insight into the interplay of cougar predation patterns and habitat characteristics, kill site characteristics are critical to understanding spatial predation risk (Gervasi et al. 2013). In northwestern Utah and southern Idaho, Laundré and Hernandez (2003) reported distinctions between cache and kill site characteristics by backtracking to kill sites from cache sites. They reported differences in tree characteristics (i.e., density and diameters at breast height) between kill and cache sites and selection for specific habitat characteristics at mule deer (*Odocoileus hemionus*) kill sites, specifically juniper (*Juniperus* spp.)–pinyon (*Pinus edulis*) vegetation and proximity to forest edges.

Cougar predation upon bighorn sheep and feral horses has been documented in the Pryor Mountains of Montana and Wyoming (Schoenecker 2004, Bureau of Land Management 2009). Area land managers have an interest in increasing the bighorn sheep herd, while reducing feral horse numbers. Understanding the factors influencing cougar predation is fundamental toward making sound management decisions. Although cougar predation and habitat use has been described in other areas of western North America (Ruth and Murphy 2010, Wilmers et al. 2013, Knopff et al. 2014, Zeller et al. 2014), little is known with regards to cougar space use in the Pryor Mountains, particularly concerning how resource selection changes with behavioral state and season. If cougar predation is influenced by landscape characteristics, managers may have an opportunity to manipulate predation by changing these habitat features. For example, if cover provided by Utah juniper (*Juniperus osteosperma*) is linked to an increased likelihood of cougar predation, then juniper removal may present an opportunity to lessen predation risk. This may provide for non-lethal approaches to management in areas where it is undesirable to remove cougars.

Our first objective was to examine and compare the characteristics of cougar kill sites to randomly generated sites at a fine scale (i.e., within 25 m of the kill site, the distance in which a cougar would likely have been to initiate a successful ambush). For this analysis, we examined slope, aspect, elevation, vegetation class, and horizontal visibility. Our second objective was to analyze kill site selection at a coarse-scale by examining buffered cache sites that had a high likelihood of containing actual kill sites. For this analysis, we were able to work with the complete set of kills to enhance our analysis and level of inference. This larger dataset enabled us to model predation risk separately by season, a distinction important to cougar habitat use (Koehler and Hornocker 1991). We included the same landscape characteristics we measured for our fine-scale analysis (excluding horizontal visibility) with the addition of distance to low-use roads, distance to high-use roads, distance to water, and ruggedness. For our final objective, we further elucidated factors influencing cougar landscape use by comparing seasonal resource selection of cougars while they moved across the landscape to the predation resource selection models. In effect, we compared how seasonal resource selection may change when cougars move through the landscape versus when they kill prey, thereby examining how the behavioral state (Wilmers et al. 2013, Zeller et al. 2014) of the animal influences resource selection.

We anticipated that selection for habitat characteristics that confer hunting advantages would be more pronounced at kill sites than when cougars traveled through the landscape. We predicted cougars would select for kill sites in areas with thick (i.e., obscuring) vegetation and high values of ruggedness year-round, and open habitats while traveling. We also predicted they would select for southerly aspects and lower elevations in the winter, and northerly aspects and higher elevations in the summer (Logan and Irwin 1985, Pierce et al. 1999). We anticipated our fine-scale analysis would document that kill sites had lower-than-average measures of horizontal visibility (Husseman et al. 2003).

STUDY AREA

We conducted this study in the southern portion of the Pryor Mountains of northcentral Wyoming and southcentral Montana, USA. The 2,553-km^2 study area included the Bighorn Canyon National Recreation Area (BCNRA), the Pryor Mountain Wild Horse Range (PMWHR), a portion of the Crow Reservation, the Custer National Forest, Bureau of Land Management (BLM) property, and private properties (Fig. 1). The habitat and topography of the Pryor Mountains was extremely variable. One notable feature was Bighorn Canyon itself with cliffs up to 300 m high. Several waterways flowed through the study area: Bighorn River, Crooked Creek, Dryhead Creek, and Sage Creek. Additional water sources included several seasonal creeks, natural springs, and anthropogenic water sources. The southern portion of the study area consisted of desert badlands, expanses of sagebrush (*Artemisia* spp.), and desert shrublands. The northern portion was characterized by steep timbered slopes, high alpine meadows, and sagebrush steppes. Rugged, incised canyons were prevalent throughout the study area. Using the vegetation community classifications developed for the BCNRA (Knight et al. 1987) and the nearby Bighorn Mountains (Logan and Irwin 1985), we classified vegetation as sagebrush, coniferous forest, juniper-mountain mahogany (*Cercocarpus ledifolius*) woodland, desert shrubland, grassland, deciduous shrubland, riparian, or developed.

Elevations ranged from 950 m to 2,700 m. The climate was characterized by hot summers with temperatures exceeding 32°C and cold winters with temperatures below −15°C. There was a north-south precipitation gradient with an

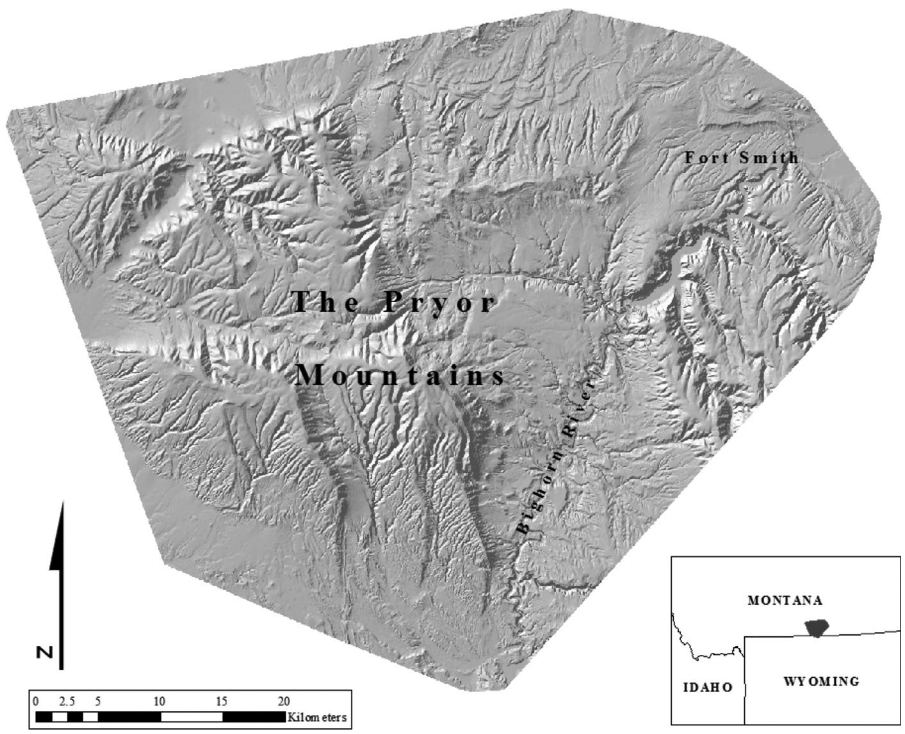

Fig. 1. The 2,553-km^2 study area in the southern Pryor Mountains of Wyoming and Montana, USA. The study area was formed by creating a minimum convex polygon of all recorded cougar locations obtained in 2011–2012.

average annual precipitation of 16.9 cm in the south and 45.8 cm in the north, with most precipitation falling as rain during May and June (Western Regional Climate Center, www.wrcc.dri.edu/climate-summaries, accessed 21 Jun 2013). Because the study site exhibited strong seasonality, we defined 2 seasons: summer (16 Apr–15 Oct) and winter (16 Oct–15 Apr).

Cougars and American black bears (*Ursus americanus*) were the apex predators of the area. Other mammals in the study area included coyote (*Canis latrans*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), beaver (*Castor canadensis*), and porcupine. The main ungulate species were mule deer, feral horses, and domestic cattle. Additional ungulates included a small population of Rocky Mountain bighorn sheep and a few white-tailed deer (*Odocoileus virginianus*). The bighorn sheep population was estimated to be 107 females and lambs (95% CI: 75–172) in 2012 (Kissell 2013) and the feral horse population was approximately 170 individuals (J. M. Bybee, Bureau of Land Management, personal communication), exceeding the management objective of 90–120 horses (Bureau of Land Management 2009).

METHODS

We captured resident adult cougars using hounds (Hornocker 1970) or box traps (Shuler 1992) between January 2011 and March 2012. We immobilized cougars with ketamine hydrochloride and xylazine hydrochloride, and fitted them with Telonics GEN3 global positioning system (GPS) collars (Telonics, Mesa, AZ, USA). We programmed the collars to record 8 locations/diel period with locations recorded at 2-hour intervals during nocturnal periods and 6-hour intervals during diurnal periods. We retrieved collars following automatic drop-off. Animal capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees of the National Wildlife Research Center (QA-1811) and Utah State University (no.1516).

Fine-Scale Kill Site Analyses

The first stage of our analysis was a fine-scale ($\leq$25 m of confirmed kill locations) comparison of characteristics of kill sites to random sites. We visited clusters of GPS locations to identify cougar kills (Anderson and Lindzey 2003, Blake and Gese 2016). Once prey carcasses were located, field personnel attempted to backtrack to the location where the cougar first made physical contact with the prey item. We called this location of the kill site, although in some cases it would be more accurately termed the ambush site (i.e., if the prey animal traveled farther before succumbing to the attack). When we located a possible kill site, we assigned it a confidence level: 1 denoting extreme confidence and 3 indicating only moderate confidence. Determinations of confidence levels were based upon the presence of characteristics including signs of impact or struggle, blood, clumps of hair, or drag marks. After censoring the potential kill sites with the lowest confidence level, we retained only high-confidence kill sites for the fine-scale analysis.

We generated 218 random sites in a geographic information system (GIS) across the study area and visited them to compare to the known kill sites. We measured slope and aspect on a fine-grain scale ($\leq$5 m of the kill site). During our analysis, we treated aspect as a categorical variable, binning it based on degrees: north (0–44.99, 315–360), east (45–134.99), south (135–224.99), and west (225–314.99). We recorded the dominant vegetation class ≤25 m of the kill site. We followed Logan and Irwin (1985) and Knight et al. (1987) in classifying vegetation types of the study area. We assigned vegetation classes to kill sites by identifying the vegetation class as described by Knight et al. (1987), with the greatest percent cover. We obtained horizontal visibility measures at 14 m and 25 m using the staff-ball method (Collins and Becker 2001, Greene 2010). In addition to comparing horizontal visibility between kill sites and random sites, we examined differences in horizontal visibility specifically in the juniper-mountain mahogany vegetation class. The juniper-mountain mahogany class was the only vegetation class that contained a useful sample size of kill sites and Bighorn Canyon National Recreation Area staff has been focusing their habitat modification efforts in this vegetation class. We obtained elevations by intersecting the kill sites with a 30-m digital elevation model (DEM; United States Geological Survey 2011). We compared means of continuous variables with Welch's 2-sample t-tests. We used 1-sided t-tests to test whether horizontal visibility was lower at kill than at random sites, and 2-sided t-tests to test for differences in the means of other continuous variables. We analyzed the categorical variables, aspect and vegetation class, with 2-sample proportion tests. We used a significance level of $P \leq 0.10$.

Resource Selection Functions: Moving and Buffered Cache Sites

In our second analysis, we constructed resource selection functions (RSFs; Manly et al. 2002) to analyze kill site selection by cougars at a coarse-scale (≤94.9 m of the cache site, which was the upper cut-off point of the known distances carcasses were dragged, thereby creating buffered cache sites that each had a 95% chance of containing a kill site). We again examined selection by comparing buffered cache sites to randomly generated (i.e., available) sites (see below) with respect to several landscape covariates. We developed a summer and a winter predation risk RSF with a fixed-effect logistic regression model. For comparison to our predation RSFs, we built seasonal RSFs using the locations of the cougars as they moved through the landscape (i.e., movement RSFs, detailed below) using a fixed-effect logistic regression model, thereby allowing comparison of seasonal resource selection by cougars during 2 different behavioral states (i.e., moving vs. killing prey).

Landscape covariates.—We used ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA, USA) to analyze all spatial data. We used 30-m resolution DEMs from the United States Geological Survey (2011) National Elevation Dataset to derive elevation, slope, and aspect layers. We derived a ruggedness layer from these 30-m DEMs following the procedure described by Sappington et al. (2007). We used road layers from the 2012 TIGER/Line Shapefiles (U.S. Census Bureau 2012). We subdivided roads into high- and low-use classes based on the MAF/TIGER (Master Address File/Topologically Integrated Geographic Encoding and Referencing) Feature Classification Codes. We adjusted the road class assignments based on our personal knowledge. We obtained stream data from the United States Geological Survey (2007) National Hydrography Dataset and used the Feature-Code classification system to retain only perennial water sources. We calculated distance to roads and distance to water layers using the Euclidean Distance tool in ArcMap. We developed a vegetation class layer by downloading and joining data tiles from the Northwest GAP Analysis Program (NWGAP 2007). We collapsed the NWGAP vegetation types into 8 classes: sagebrush, coniferous forest, juniper-mountain mahogany woodland, desert shrubland, grassland, deciduous shrubland, riparian, and developed; we excluded unknown or rare vegetation types from our analyses. All layers were projected into NAD83 Zone 12N. We resampled all layers to ensure they were orthogonal and then clipped them to the study area.

Used and available buffered cache sites.—Buffered cache sites enabled us to examine the habitat characteristics in an area that was highly likely to have contained the kill site allowing us to use the full dataset of cache sites (as opposed to our fine-scale kill site analysis where we were limited to a smaller sample of confirmed kill sites) to build seasonal RSFs modeling the risk of cougar predation. We examined selection at the third-order scale (Johnson 1980) using each cougar's home range to define the potential kill sites available to that animal. We developed 95% kernel density estimate (KDE) home ranges and generated 3 available buffered cache sites for every used buffered cache site. We intersected used and available buffered cache sites with each landscape covariate layer in Geospatial Modeling Environment (Geospatial Modeling Environment Version 0.7.2.0, www.spatialecology.com, accessed 5 Apr 2013) using the Isectpolyrst tool. For continuous variables (i.e., elevation, slope, ruggedness, distance to low-use roads, distance to high-use roads, distance to water), we calculated means of raster cells within the buffered cache site and for categorical variables (i.e., aspect, vegetation class), we calculated the proportions of categorical variables (e.g., 0.60 south, 0.40 east) within each buffered cache site. We assigned aspect and vegetation classes based on the proportionally dominant class. In the case of no differentiation between 2 aspects, we randomly assigned one. In the case of no differentiation between 2 vegetation classes, we examined aerial imagery and site notes to make a decision. We tested for collinearity between the landscape covariates of each RSF by conducting variance inflation factor (VIF) tests for each pair of covariates. We tested for collinearity between pairs of covariates containing ≥1 categorical covariate with generalized variance inflation factor (GVIF) tests. All scores were between 1 and 2, indicating that there were no issues with collinearity (Neter et al. 1996). We exported this dataset to conduct analysis in R (R Version 2.13.2, www.r-project.org, accessed 30 Sep 2011).

Used and available moving locations.—To build our movement RSFs, we first removed locations from our dataset that were associated with capture (i.e., locations within 48 hr of capture), denning, known injuries, and confirmed kill site clusters. We also removed all clusters at which we did not confirm a kill with the view that kills may have been made but not detected at these clusters, or the cougar was probably resting. We followed the procedures described above, generating 3 available locations for each used location in each cougar's home range and intersecting locations with landscape covariate layers. Results of VIF and GVIF tests again produced scores between 1 and 2, indicating that there were no issues with collinearity (Neter et al. 1996).

Fitting and selecting the RSF models.—Based on knowledge of cougar ecology and the results of the exploratory univariate analyses, plausible lists of candidate models were developed a priori for the summer and winter buffered cache sites and for summer and winter cougar movements. To fit and select the predation and movement models, we used the following exponential fixed-effects RSF (Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n) \quad (1)$$

where relative probability of use, $w(x)$, is described by landscape covariate, x_n, and beta-coeffecient, β_n. We dropped the intercept, β_O, from the equation because it was meaningless in our use-availability study design (Manly et al. 2002) and unnecessary without the inclusion of a random intercept.

We ranked models with Akaike's Information Criterion with a correction for small sample sizes (AIC_c; Burnham and Anderson 2002). We interpreted the ΔAIC_c values following the guidelines provided by Burnham and Anderson (2002): ΔAIC_c 0–2: substantial empirical support of the model, ΔAIC_c 4–7: considerably less empirical support of the model, ΔAIC_c >10: essentially no empirical support of the model. When several competing models had ΔAIC_c 0–2, we retained the most parsimonious model to avoid the inclusion of uninformative parameters (Arnold 2010).

Model validation and projection.—We evaluated our top performing models with the k-fold cross validation technique (Boyce et al. 2002, Fernández et al. 2003). This process entailed randomly splitting the datasets into k partitions (folds) and using $n - 1$ folds (the training set) to fit the model and then testing the model by its ability to predict the remaining fold (the testing set). We used 5 folds and this process was repeated 5 times so that each fold served as the training fold a single time. We averaged the results from these cross-validations to produce a single cross-validation estimate of accuracy. Because the estimates can be variable (Maindonald 2007), we iterated this process 100 times to calculate the mean cross-validation estimate of accuracy (between 0 and 1) for the top-performing summer and winter predation risk and movement models.

Table 1. Fine-scale analysis of landscape covariates at kill and random sites of cougars in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012. We tested differences in means with Welch's 2-sample t-tests for continuous variables and with 2-sample proportion tests for categorical variables. Empty cells indicate instances where it was not possible to generate a P-value because of low expected values. Significant covariates are indicated with an asterisk.

Landscape covariates	Kill sites	Random sites	P
Continuous covariates			
Slope (degrees)	16.90	14.03	0.231
Horizontal visibility at 14 m (%)*	56.37	68.50	0.022
Horizontal visibility at 25 m (%)*	37.85	53.32	0.008
JM[a] horizontal visibility at 14 m (%)	49.51	50.12	0.465
JM horizontal visibility at 25 m (%)	27.90	33.90	0.191
Elevation (m)*	1,581.05	1,742.99	0.020
Aspect (%)			
Flat	0.00	1.38	
North	10.35	14.68	
East	41.38	29.36	0.188
South	27.59	27.52	0.994
West	20.69	27.06	0.464
Vegetation (%)			
Coniferous forest	16.67	24.77	0.328
Deciduous shrubland	0.00	0.92	
Desert shrubland	3.33	2.29	
Grassland*	6.67	22.48	0.045
Juniper-mountain mahogany*	56.67	27.06	<0.001
Riparian	0.00	1.84	
Sagebrush	16.67	20.64	0.611

[a] JM = juniper-mountain mahogany.

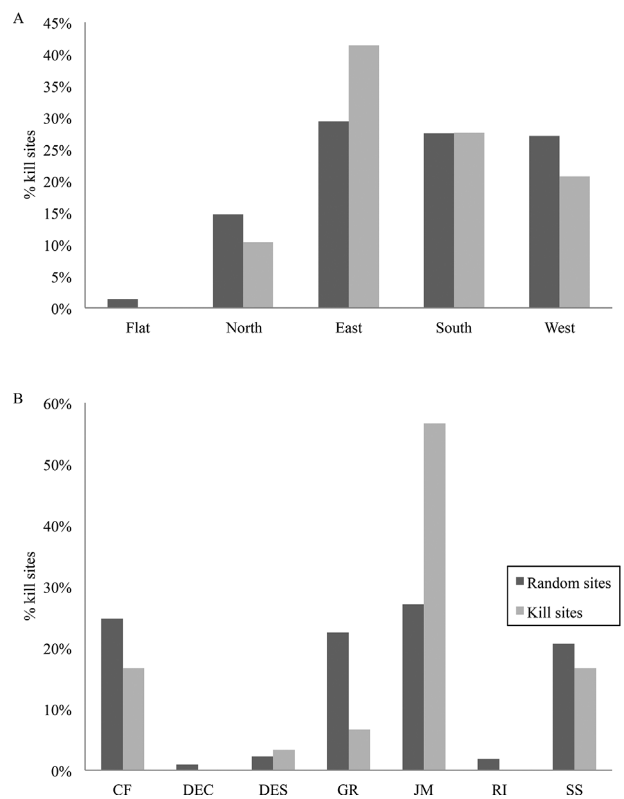

Fig. 2. Percentages of random and kill sites in different A) aspect categories, and B) vegetation classes, for cougars in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012. CF = coniferous forest, DEC = deciduous shrubland, DES = desert shrubland, GR = grassland, JM = juniper–mountain mahogany, RI = riparian, SS = sagebrush.

Using the Raster Calculator in ArcMap, we projected the top summer and winter models across the study site for the predation risk and movement RSFs. We entered the β-coefficients from the top model of each RSF along with the landscape covariate layers into Equation (1) to project the relative probabilities of a pixel being a kill site or a moving location, $w(x)$, spatially across the landscape. To scale the resulting raster pixel values between 0 and 1, we divided these raster layers by the maximum pixel value of each RSF. Pixels with unknown or extremely rare classifications (e.g., open water) were excluded from this analysis.

RESULTS

We captured, fitted with GPS collars, and monitored 5 cougars between 168 and 417 days (i.e., 1,432 cougar-days). Our GPS fix success rate was 81%.

Fine-Scale Kill Site Analysis

We visited 388 clusters and located 194 cache sites with prey remains. Prey items consisted of mule deer (72.2%), bighorn sheep (8.2%), a deer of unknown species (0.5%), an unidentifiable ungulate (0.5%), an elk (*Cervus canadensis*; 0.5%), and a variety of non-ungulate prey (18.0%) including beavers, raccoons, porcupines, coyotes, and single instances of a striped skunk (*Mephitis mephitis*), American marten (*Martes americana*), mallard (*Anas platyrhynchos*), red fox, and a cougar; no feral horses were killed by cougars (Blake and Gese 2016). Of the 194 cache sites, we were able to successfully backtrack to 35 kill sites associated with these cache sites. We censured the lowest confidence level kill sites and retained 30 sites in which we were able to confidently identify a kill site. We visited 218 random sites for comparison (Table 1). At 14 m, the mean percent horizontal

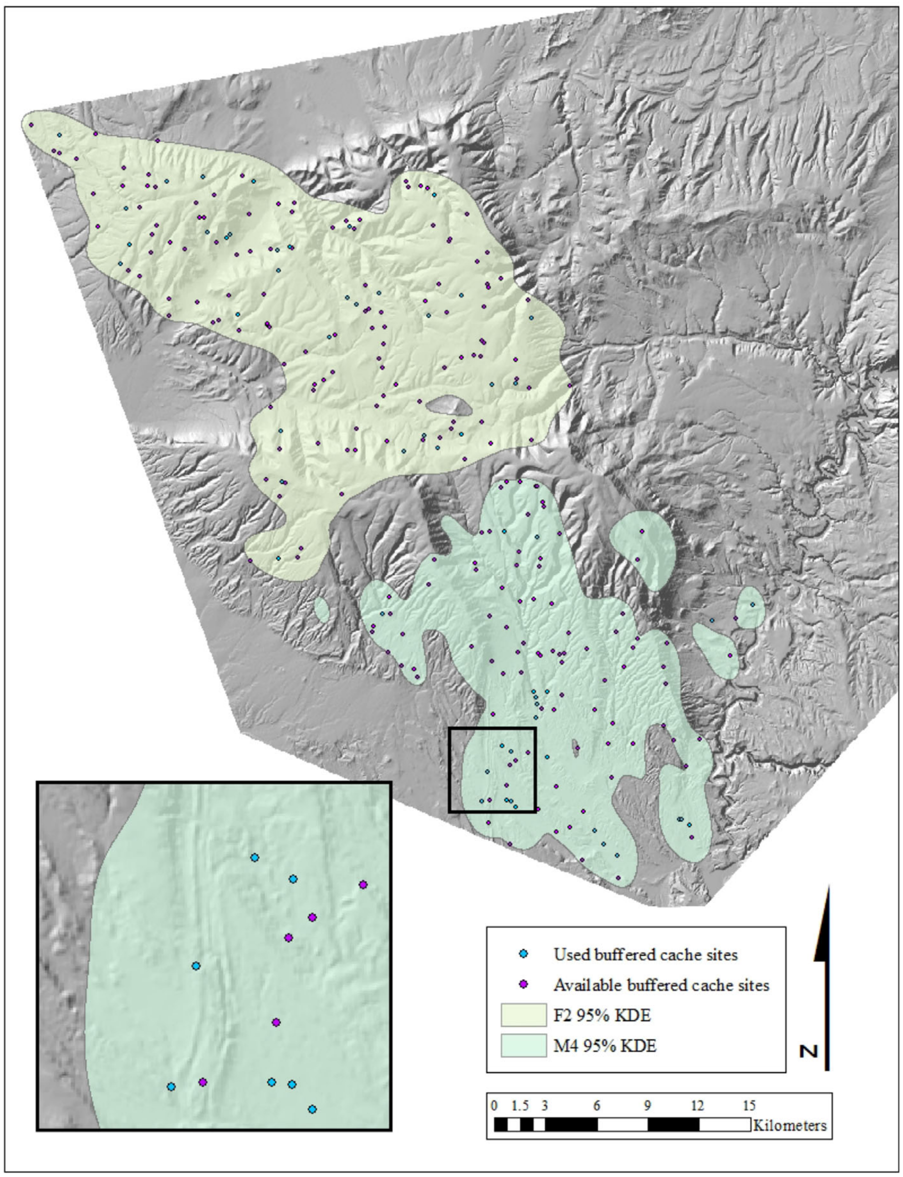

Fig. 3. Two cougar home ranges (95% kernel density estimates [KDE]) showing used and available buffered cache sites, Pryor Mountains of Wyoming and Montana, USA, 2011–2012.

Table 2. Top 10 candidate models for cougar predation risk determined from buffered cache sites and random sites during summer in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012; top model is indicated with an asterisk.

Model description	K^a	Log likelihood	AIC_c^b	ΔAIC_c
Water + slope^2 + aspect + veg	12	−192.43	409.71	0.00
Water + slope^2 + veg*	9	−195.66	409.82	0.10
Low-use roads + water + slope^2 + veg	10	−194.80	410.19	0.48
Water + elev + rugged + slope^2 + aspect + veg	14	−190.54	410.23	0.52
Water + rugged + slope^2 + aspect + veg	13	−191.69	410.38	0.67
Full[c] + slope^2	16	−188.50	410.51	0.80
Water + elev + slope^2 + veg	10	−195.23	411.07	1.35
Full + rugged^2 + slope^2	17	−188.50	412.70	2.99
Full − roads + slope^2 − rugged + elev^2	14	−191.80	412.75	3.04
Full − high-use roads + elev^2 + slope^2	16	−189.77	413.05	3.34

[a] K = number of parameters.
[b] AIC_c = Akaike's Information Criterion with a correction for small sample sizes.
[c] Full model = distance to high-use roads + distance to low-use roads + distance to water (water) + elevation (elev) + ruggedness (rugged) + slope + aspect + vegetation class (veg).

visibility was lower ($P = 0.022$) at kill sites ($\bar{x} = 56.4\%$) than at random sites ($\bar{x} = 68.5\%$). At 25 m, the mean percent horizontal visibility was also lower ($P = 0.008$) at kill sites ($\bar{x} = 37.8\%$) than at random sites ($\bar{x} = 53.3\%$). Although not significant, mean horizontal visibility of juniper-mountain mahogany vegetation was lower at kill sites than random sites at 14 m and especially 25 m; our small sample likely prevented us from detecting a difference. Random sites had ($P = 0.020$) higher elevations ($\bar{x} = 1{,}743$ m) than kill sites ($\bar{x} = 1{,}581$ m). Kill sites were not different from random sites in slope. There were no differences between the aspects of kill and random sites (Fig. 2 and Table 1). The grassland and juniper-mountain mahogany classes were the only vegetation classes that were different between kill sites and random sites. More random sites were in the grassland class ($\bar{x} = 22.5\%$) than kill sites ($\bar{x} = 6.7\%$; $P = 0.045$). More kill sites ($\bar{x} = 56.7\%$) than random sites ($\bar{x} = 27.1\%$) were in the juniper-mountain mahogany vegetation class ($P < 0.001$).

Coarse-Scale Kill Site Analysis Using Resource Selection Functions

The mean distance dragged from the high-confidence kill sites ($n = 30$) to cache sites was 43.7 ± 31.1 ($\bar{x} \pm$ SD) m. These distances are similar to results from Beier et al. (1995). We used a 95% upper cut-point (94.9 m, $Z = 1.644$) as the radius with which to buffer all cache sites. We generated 582 available buffered cache sites for comparison (Fig. 3) to the 194 cache sites.

The top summer predation risk model included distance to water, a quadratic term for slope, and vegetation class (Table 2). The coefficients of the top summer risk model (Table 3) indicated cougars selected most strongly for the riparian vegetation class when making kills and relative to riparian, against coniferous forest ($\beta = -1.558$), juniper-mountain mahogany ($\beta = -1.840$), desert shrubland ($\beta = -1.984$), and especially sagebrush ($\beta = -2.050$), and grassland ($\beta = -2.432$) vegetation classes. Cougars selected kill sites closer to water sources ($\beta = -0.315$), and exhibited a quadratic selection for slope. This quadratic slope relationship was concave and curvilinear indicating increasing selection for slope up to a certain threshold after which slope was selected against.

There were 7 candidate models for summer predation risk with ΔAIC_c scores of <2 (Table 2), which all contained covariates for distance to water, a quadratic term for slope, and vegetation. Although it ranked second with a ΔAIC_c of 0.104, we retained the most parsimonious model as our top model. Other models had very similar ΔAIC_c scores, including one with a smaller score, but they all included additional parameters. When parameters are added without a $\geq$2 drop in ΔAIC_c, they can be considered uninformative. That is, there is not a sufficient addition of explanatory power to warrant their inclusion (Arnold 2010). The top summer predation risk model had a mean cross-validation estimate of accuracy of 0.763 ± 0.005 (SD). The top winter predation risk model included only the elevation and vegetation class covariates (Table 4). Cougars selected most strongly for kill sites in riparian habitat. Relative to riparian, kill sites were less likely to be in juniper-mountain mahogany ($\beta = -1.677$), desert shrubland ($\beta = -1.899$), sagebrush ($\beta = -2.328$), and grassland ($\beta = -2.595$) vegetation. The coefficients of the top winter risk model (Table 3) showed cougars also selected for lower elevations ($\beta = -2.166$). The next 4 models performed well with ΔAIC_c scores <2, but

Table 3. Coefficients and standard errors from the top generalized linear (fixed effects) models fit to cougar predation risk determined from buffered cache sites during summer and winter in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012.

Landscape covariate	Summer[a]	Winter[a]
Distance to water	−0.315 (0.137)**	
Elevation		−2.166 (0.519)***
Slope	14.270 (5.864)**	
Slope^2	−41.708 (16.831)**	
Coniferous forest	−1.558 (0.556)***	−0.266 (0.524)
Desert shrubland	−1.984 (0.766)***	−1.899 (0.655)***
Grassland	−2.432 (0.579)***	−2.595 (0.542)***
Juniper-mountain mahogany	−1.840 (0.547)***	−1.677 (0.450)***
Riparian[b]		
Sagebrush	−2.050 (0.563)***	−2.328 (0.508)***

[a] Standard errors in parentheses.
[b] Riparian is the reference class for vegetation.
Significance: 0.05 (**), 0.01 (***).

Table 4. Top 10 candidate models for cougar predation risk determined from buffered cache sites during winter in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012; top model is indicated with an asterisk.

Model description	K[a]	Log likelihood	AIC_c[b]	ΔAIC_c
Elev + veg*	7	−191.13	396.54	0.00
Full[c] + rugged^2 − aspect	13	−184.98	396.91	0.37
Elev^2 + veg	8	−190.31	397.00	0.45
Full + rugged^2	16	−182.19	397.82	1.27
High-use roads + elev + veg	8	−191.07	398.51	1.96
Water + elev + veg	8	−191.12	398.62	2.08
High-use roads + elev^2 + veg	9	−190.14	398.76	2.21
Water + elev^2 + veg	9	−190.23	398.93	2.39
Full + elev^2 + rugged^2	17	−181.74	399.10	2.56
Full − high-use roads + elev^2 + rugged^2 + slope^2	17	−181.929	399.477	2.933

[a] K = number of parameters.
[b] AIC_c = Akaike's Information Criterion with a correction for small sample sizes.
[c] Full model = distance to high-use roads + distance to low-use roads + distance to water (water) + elevation (elev) + ruggedness (rugged) + slope + aspect + vegetation class (veg).

they all took the form of the top model with additional covariates. As above, we retained the top model in the interest of parsimony and avoidance of uninformative parameters. The top winter model had a mean cross-validation estimate of accuracy of 0.778 ± 0.004 (SD).

Movement Analysis Using Resource Selection Functions

We retained 4,830 used locations for analysis (2,617 summer and 2,213 winter) and generated 14,490 available locations (7,851 summer and 6,639 winter) for comparison. The top model for cougar movement during the summer included all landscape covariates except aspect. Terms for elevation, ruggedness, and slope were quadratic (Table 5). The coefficients of this model (Table 6) indicated that during summer, cougars selected most strongly for the riparian vegetation class. Relative to the riparian vegetation class, cougars selected against deciduous shrubland ($\beta = -1.034$), coniferous forest ($\beta = -1.052$), juniper-mountain mahogany ($\beta = -1.193$), grassland ($\beta = -1.342$), sagebrush ($\beta = -1.464$), desert shrubland ($\beta = -1.696$), and especially developed ($\beta = -2.025$) vegetation classes. Cougars selected for locations farther from high-use ($\beta = 0.043$) and low-use roads ($\beta = 0.959$) and closer to water ($\beta = -0.088$). Elevation, ruggedness, and slope all had positive coefficients for their base terms and negative coefficients for their squared terms indicting concave curvilinear relationships in selection. In other words, while moving, cougars selected for these features up to a certain threshold, after which they selected against them. We had 2 well-performing models for summer cougar movements with $\Delta AIC_c < 2$ (Table 5). Although it ranked second with a ΔAIC_c of 1.45, we retained the simpler model as our top model. The top summer movement model had a mean cross-validation estimate of accuracy of 0.743 ± 0.001 (SD).

The top model for winter movements contained all landscape covariates expect distance to high-use roads; terms for elevation, ruggedness, and slope were quadratic (Table 7). Coefficients (Table 6) indicated that, in winter, riparian was again the preferred vegetation class. Relative to the riparian vegetation class, cougars selected against coniferous forest ($\beta = -0.546$), juniper-mountain mahogany ($\beta = -0.603$), sagebrush ($\beta = -0.983$), grassland ($\beta = -1.165$), and desert shrubland ($\beta = -1.272$) vegetation classes. In winter, cougars selected for locations that were closer to water ($\beta = -0.060$) and closer to low-use roads ($\beta = -0.844$). As with the summer movement model, the quadratic terms for elevation, ruggedness, and slope all indicated positive selection for these attributes up to a

Table 5. Top 10 candidate models for cougar movement locations during summer in the Pryor Mountains of Wyoming and Montana, 2011–2012; top model is indicated with an asterisk.

Model description	K[a]	Log likelihood	AIC_c[b]	ΔAIC_c
Full[c] + elev^2 + rugged^2 + slope^2	20	−5,563.86	11,167.81	0.00
Full + elev^2 + rugged^2 + slope^2 − aspect*	17	−5,567.60	11,169.26	1.45
Full − low-use roads + elev^2 + rugged^2 + slope^2	19	−5,567.13	11,172.33	4.52
Full + rugged^2 + slope^2	19	−5,569.96	11,178.00	10.19
Full − low-use roads + rugged^2 + slope^2	18	−5,572.11	11,180.28	12.47
Full − high-use roads + elev^2 + rugged^2 + slope^2	19	−5,573.33	11,184.73	16.92
Full − water + elev^2 + rugged^2 + slope^2	19	−5,573.33	11,184.74	16.93
Water + elev^2 + rugged^2 + slope^2 + aspect + veg	18	−5,575.72	11,187.51	19.70
Full + elev^2 + rugged^2	19	−5,580.32	11,198.72	30.91
Full − high-use roads + rugged^2 + slope^2	18	−5,582.66	11,201.38	33.57

[a] K = number of parameters.
[b] AIC_c = Akaike's Information Criterion with a correction for small sample sizes.
[c] Full model = distance to high-use roads + distance to low-use roads + distance to water (water) + elevation (elev) + ruggedness (rugged) + slope + aspect + vegetation class (veg).

Table 6. Coefficients and standard errors from the top generalized linear (fixed effects) models fit to cougar movement during summer and winter in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012.

Landscape covariate	Summer[a]	Winter[a]
Distance to high-use roads	0.043 (0.100)***	
Distance to low-use roads	0.959 (0.351)***	−0.844 (0.366)**
Distance to water	−0.088 (0.020)***	−0.060 (0.024)**
Elevation	2.872 (0.688)***	3.461 (0.875)***
Elevation^2	−0.655 (0.187)***	−1.372 (0.254)***
Ruggedness	29.763 (3.358)***	25.389 (3.639)***
Ruggedness^2	−211.827 (38.621)***	−198.983 (41.003)***
Slope	4.755 (0.771)***	8.518 (0.821)***
Slope^2	−9.576 (1.720)***	−14.906 (1.815)***
East[b] North		−0.317 (0.082)***
South		0.496 (0.067)***
West		0.098 (0.072)
Coniferous forest	−1.052 (0.117)***	−0.546 (0.122)***
Deciduous shrubland	−1.034 (0.428)**	−0.630 (0.440)
Desert shrubland	−1.696 (0.155)***	−1.272 (0.156)***
Developed	−2.025 (0.538)***	−0.759 (0.475)
Grassland	−1.342 (0.116)***	−1.165 (0.116)***
Juniper-mountain mahogany	−1.193 (0.116)***	−0.603 (0.111)***
Riparian[c] Sagebrush	−1.464 (0.115)***	−0.983 (0.116)***

[a] Standard errors in parentheses.
[b] East is the reference class for aspect.
[c] Riparian is the reference class for vegetation.
Significance: 0.05 (**), 0.01 (***).

threshold, after which they were selected against. Relative to east, cougars selected against north ($\beta = -0.317$), but selected for south ($\beta = 0.496$) aspects. The top winter movement model had a mean cross-validation estimate of accuracy of 0.747 ± 0.001 (SD).

DISCUSSION

Fine-Scale Kill Site Analysis

Although our study population was limited to 5 animals, we are confident we had a near, if not complete, census of cougar predation within our study area, with the exception of the impact of transients. Our work advances cougar management approaches by providing an alternative framework in which to consider responses to undesirable impacts of cougar predation. Although removal through hunting or agency actions has often been used to affect levels of cougar predation, there are situations in which lethal control of cougars is not biologically or socially desirable. An understanding of the interactions between habitat characteristics and cougar predation could offer biologists a tool to alter the latter by manipulating the former. On occasion, habitat modification, if it is in the form of habitat restoration, may provide additional ecosystem benefits.

Our fine-scale kill site analysis produced results similar to those from past studies (Logan and Irwin 1985, Laundré and Hernandez 2003) reporting cougars selected for kill sites in more obscuring vegetation classes (i.e., riparian, coniferous forest, juniper-mountain mahogany) and against kill sites in the more open grassland vegetation class. Our results confirmed the hypothesis that kill sites would have lower horizontal visibility than random sites and was in agreement with previous research suggesting cougars need effective hiding cover to successfully stalk, approach, and kill prey (Beier et al. 1995, Husseman et al. 2003). Although horizontal visibility was lower in the juniper-mountain mahogany vegetation class kill sites than random sites, the difference was not significant, but was likely obscured by our small sample size. However, 100% of kills of bighorn sheep were in the juniper-mountain mahogany class and, consequently, sheep represented a greater percentage of prey items in the juniper-mountain mahogany class (29.4%) than in all vegetation classes combined (16.7%). Considering juniper-mountain mahogany was the vegetation class where bighorn sheep were frequently killed, and that predation events were more likely to happen in sites with lower horizontal visibility, management efforts aimed at increasing horizontal visibility in this vegetation class appear well-founded. The selection for lower elevation kill sites was anticipated and has been reported before (Pierce et al. 1999, Rieth 2010), likely because for a good portion of the year most cougars and their prey are avoiding the deep snows and suboptimal foraging conditions of the upper elevations.

Table 7. Top 10 candidate models for cougar movement locations during winter in the Pryor Mountains of Wyoming and Montana, USA, 2011–2012; top model is indicated with an asterisk.

Model description	K[a]	Log likelihood	AIC_c[b]	ΔAIC_c
Full[c] − high-use roads + elev^2 + rugged^2 + slope^2*	19	−4,594.52	9,227.13	0.00
Full + elev^2 + rugged^2 + slope^2	20	−4,594.21	9,228.51	1.38
Water + elev^2 + rugged^2 + slope^2 + aspect + veg	18	−4,597.21	9,230.49	3.36
Full − low-use roads + elev^2 + rugged^2 + slope^2	19	−4,597.09	9,232.27	5.14
Full − water + elev^2 + rugged^2 + slope^2	19	−4,597.29	9,232.66	5.54
Elev^2 + rugged^2 + slope^2 + aspect + veg	17	−4,600.74	9,235.54	8.41
Full − high-use roads + rugged^2 + slope^2	18	−4610.15	9,256.38	29.25
Full + rugged^2 + slope^2	19	−4,610.11	9,258.30	31.17
Full − high-use roads + elev^2 + slope^2	18	−4,612.06	9,260.19	33.06
Full + elev^2 + slope^2	19	−4,611.89	9,261.87	34.75

[a] K = number of parameters.
[b] AIC_c = Akaike's Information Criterion with a correction for small sample sizes.
[c] Full model = distance to high-use roads + distance to low-use roads + distance to water (water) + elevation (elev) + ruggedness (rugged) + slope + aspect + vegetation class (veg).

Cougars did not demonstrate significant selection for or against any of the other landscape characteristics, which was probably, at least in part, due to our small sample size of only 30 kill sites. Although the fine-scale kill site analysis enabled us to examine several landscape characteristics including horizontal visibility, it had some limitations. In particular the small sample size probably prevented us from detecting significant selection for or against some landscape characteristics. Sample size also prevented us from dividing this dataset into summer and winter classes, leading us to miss any seasonal variations in kill site selection. Selection for a characteristic would have been particularly obscured if selection was positive in one season and negative in the other. The coarse-scale RSF-based analyses were able to overcome some of our sample size-related limitations.

Coarse-Scale Kill Site Analysis

Our relatively high frequencies of correct classifications during the *k*-folds cross-validation analysis suggested our top predation risk models were useful in predicting kill site location for this cougar population. The top predation risk model during summer was composed of distance to water, a quadratic term for slope, and vegetation class. Vegetation class was also the only covariate common to the top summer and winter predation risk models. Previous studies have uncovered the important link between kill or cache site selection and vegetation type (Laundré and Hernandez 2003, Rieth 2010, Kunkel et al. 2013). Vegetation can be assumed to influence cover, horizontal visibility, and the distribution of prey. Vegetation classes with more obscuring vegetation experienced positive selection relative to more open classes. Riparian vegetation was favored in the top summer predation risk model followed by coniferous forest and juniper-mountain mahogany. Selection against distance to water probably indicated cougars were influenced by their biological requirement for water, or by their prey's, in the summer. A quadratic relationship with slope seems obvious given cougars have previously shown preference for (steeper) slopes, but they use steep terrain up to a certain threshold after which its usability declines.

The top model for the predation risk RSF during winter included only the elevation and vegetation class covariates. The order of selection within the vegetation classes matched that of the summer risk model; riparian was still the preferred vegetation class, although coniferous forest was not strongly selected against relative to riparian, followed by juniper-mountain mahogany. Not surprisingly, elevation was selected against at winter kill sites. In mountainous areas, ungulate populations typically migrate to lower elevations in the winter to forage and avoid deep snows (D'eon and Serrouya 2005). Kunkel et al. (2013) also reported selection for lower elevations at winter kill sites, whereas Rieth (2010) and Elbroch et al. (2013) reported selection for lower elevations at kill sites year-round.

We were surprised ruggedness, which prior researchers have suggested has a strong influence on the success of stalking and killing of prey (Logan and Irwin 1985, Kunkel et al. 2013), was absent from the summer and winter predation risk models. But similarly, Elbroch et al. (2013) did not detect a selection for ruggedness at cougar kill sites in the Southern Yellowstone Ecosystem, USA. Sample size could have prevented us from detecting a selection for ruggedness, but perhaps more likely, our study site was sufficiently rugged and, consequently, cougars did not need to select for ruggedness when making kills. Sufficient vegetative cover may also have provided enough cover for cougars to make successful ambushes and kills without having to select for rugged terrain. To ensure we did not miss selection for extreme values of ruggedness because of the zonal (i.e., multiple pixel) nature of the analysis, we also tested and found no significant selection for the maximum pixel value of ruggedness in each zone.

Our sample size led us to examine risk to all prey species combined and we acknowledge that this approach glosses over the details of risk to any one particular species. For example, bighorn sheep were killed exclusively in the juniper-mountain mahogany habitat but, because mule deer were killed in other habitats, the risk value of juniper-mountain mahogany to just bighorn was biased low.

Movement Analysis

All of the landscape covariates we considered influenced the relative probability of cougars moving through the landscape with the exception of aspect during the summer and distances to high-use roads in the winter. The top model for summer movements included distance to roads, distance to water, vegetation class, and quadratic terms for slope, elevation, and ruggedness. The top winter movement model included the same covariates with the addition of aspect and the exception of distance to high-use roads. As above, the high mean cross-validation estimates of accuracy from the *k*-folds analysis indicated our top models had useful predictive power.

Consistent with previous studies and the predation risk models, the riparian vegetation class was preferred to all others year-round (Dickson and Beier 2002, Dickson et al. 2005). This was not surprising given the thickness of vegetation and, presumably, an association with prey using riparian water sources. During the summer, cougars also selected for deciduous shrublands, coniferous forests and juniper-mountain mahogany shrublands more frequently than the remaining vegetation classes, particularly the developed class during summer, which in consistent with prior research (Dickson and Beier 2002). In winter, following the riparian class, they selected for coniferous forests and juniper-mountain mahogany. Selection against the developed class relative to riparian was not significant during winter habitat selection. As mentioned above, the study area receives less traffic and tourism in winter so an avoidance of developed areas may be less pronounced. More open vegetation classes (e.g., desert shrubland, sagebrush) ranked lower. Unfortunately, we were unable to consider selection for or against the developed or deciduous shrubland in the risk models because of samples size. Of the vegetation classes included in the predation risk and movement models, riparian, coniferous forest, and then juniper-mountain mahogany were preferred. Vegetation class was the only covariate that appeared in all 4 of the top predation and movement models, emphasizing the importance of this attribute to cougars.

As expected, distances to high- and low-use roads were selected for in summer movements (meaning cougars avoided areas closer to roads) and, during winter, cougars selected for decreased distances to low-use roads. It was probable that cougars were avoiding roads in the summer because they received increased human traffic during the tourist season. Seasonal avoidance of roads correlated with increased human activity has been reported before (Jalkotzy et al. 2000). It is possible that, during the winter, low-use roads provided some travel advantages due to snow compaction from snowmobile traffic. Not surprisingly, the top movement model included a selection for proximity to water sources in winter and especially in summer. This was consistent with the summer predation risk model. Preliminary univariate analysis revealed a summer selection for elevation, and a winter selection against it. This was consistent with the winter risk model, and was what we anticipated based on prior studies (Logan and Irwin 1985, Koehler and Hornocker 1991). Quadratic terms for ruggedness and slope were also expected given that cougars prefer these landscape attributes (Seidensticker et al. 1973, Logan and Irwin 1985, Kunkel et al. 2013), but clearly there was an upper threshold at which they must become unusable. As expected (Ashman et al. 1983), cougars exhibited a selection against northern aspects and for southern aspects during winter, presumably because of desirable thermal properties, reduced snow-depth, and increased prey. This was in line with some prior studies and our hypothesis (Koehler and Hornocker 1991). We were surprised that aspect what not a significant factor in our summer cougar movement model. Perhaps the lack of snow coupled with a primarily nocturnal activity pattern did not present the same advantages and disadvantages associated with aspect during winter.

Most of the landscape variables included in the predation models were also represented in the movement models, suggesting that cougars on our study area were in hunting mode while moving through their home range. Being an opportunistic ambush predator, we are not surprised by this conclusion. Seasons were influential on resource selection of cougars in our area with snow at higher elevations during the winter likely causing prey (mainly mule deer) to move to lower elevations bringing about a corresponding change in resource selection among cougars.

MANAGEMENT IMPLICATIONS

Our results indicated vegetation class consistently governed habitat use by cougars when making kills and during general movements through the landscape. Habitat modifications with the goal of increasing horizontal visibility in the juniper-mountain mahogany class may reduce predation risk to mule deer and bighorn sheep, and confer other advantages including a reduced need for energetically costly vigilance behavior (Risenhoover and Bailey 1985). The predation risk RSFs should help managers target their juniper removal activity by working in those places where areas of high predation risk intersect bighorn sheep habitat. We caution that mountain mahogany is a primary browse species for bighorn sheep in the Pryor Mountains, especially during fall and winter (Kissell et al. 1996), so vegetation removal in the juniper-mountain mahogany class should focus on juniper removal; manual removal of juniper may be preferable to controlled burns in areas with mountain mahogany. Beyond our study area, our findings suggest that modifying vegetation may present an opportunity to manipulate cougar predation pressure to a sensitive species when cougar removal is disadvantageous. Although lethal control of individual cougars specializing on sensitive species has proven successful, it can be difficult to identify the offending individual, particularly in the absence of GPS collars. The removal of a cougar that does not prey on a sensitive species (e.g., bighorn sheep) could have a deleterious effect by opening up a territory for a cougar that does kill bighorn sheep (Ernest et al. 2002, Knopff and Boyce 2007). In some areas, lethal control of predators receives significant public opposition. Our results suggest habitat manipulation may be an alternative solution to reduce predation pressure in those areas where lethal control of cougars is undesirable for social or biological reasons.

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