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ORIGINAL PAPER

# Cougar den site selection in the Southern Yellowstone Ecosystem

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**Abstract** Den sites are critical resources that ultimately influence the population dynamics of many species. Little is known about cougar den selection, even though dens likely play important roles in cougar fitness and kitten survivorship. Thus, we aimed to describe cougar den site selection in the Southern Yellowstone Ecosystem (SYE) at two scales (third- and fourth-order resource selection) and within an ecological framework that included environmental characteristics, as well as some measure of prey availability and anthropogenic landscape features. We documented 25 unique dens between 2002 and 2013, and gathered data on microsite characteristics and paired random points for 20 dens. The timing of dens was clumped in summer, with 56 % of 25 dens beginning in June or July. Unexpectedly, female cougars in our study system exhibited third-order selection for den areas in less rugged terrain, but did not exhibit selection for greater or lesser access to hunting opportunity, roads, water, or specific habitat classes, as compared with the remainder of their home ranges. Instead, our findings suggested that third-order selection for den areas was much less important than fourth-order selection: cougar den sites were characterized by high concealment and substantial protective structure. Therefore, our results provided evidence in support of land practices that promote and protect downed wood and heavy structure on forest floors—these will best provide opportunities for cougars to find suitable den sites and maintain parturition behaviors.

**Keywords** Cougar · Den site · *Puma concolor* · Resource selection · Yellowstone

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## Introduction

Carnivores are a diverse group of mammals that often live in sympatry with additional carnivore species (Vanak et al. 2013). Thus, behavioral decisions and resource selection driving fitness for many carnivores reflect both prey availability (Durant 1998; Grigione et al. 2002; Vanak et al. 2013) and the mitigation of risks associated with interactions with dominant competitors (Hutchinson 1957; Vanak et al. 2013; Lendrum et al. 2014). Animals select resources at different scales. For example, carnivore distributions (first-order resource selection; Johnson 1980) and home ranges or territories (second-order resource selection) are explained by prey availability (Grigione et al. 2002), the distributions of conspecifics and competitors (e.g., Vanak et al. 2013; Lendrum et al. 2014), and refugia (Elbroch and Wittmer 2012; van der Meer et al. 2013).

Den sites are critical resources that influence the survivorship of young and ultimately population dynamics of many species (Fernández and Palomares 2000; Laack et al. 2005; Ross et al. 2010; van der Meer et al. 2013). Den selection exhibited by female carnivores also occurs at multiple scales (Squires et al. 2008) and generally reflects third- and fourth-order resource selection. Third-order resource selection describes habitat or patch selection within home ranges, whereas the behavioral decisions made within specific habitats that decide microsite characteristics reflect fourth-order resource selection (Johnson 1980). Subordinate carnivores, including many wild felids, are typically at risk from both dominant carnivores and humans (Lendrum et al. 2014), and therefore typically select fortified den sites. For example, Pallas's cat (*Otocolobus manul*), Iberian lynx (*Lynx pardinus*), and ocelot (*Leopardus pardalis*) dens provide essential thermoregulation, as well as refugia from other carnivores and humans (Fernández and Palomares 2000; Laack et al. 2005; Ross et al. 2010). Kit foxes (*Vulpes macrotis* Pruss 1999) and African wild dogs (*Lycaon pictus* van der Meer et al. 2013) have also been observed to select den sites that reflect their subordinate status and provide protection from dominant competitors.

Cougars (*Puma concolor*) are a large, solitary felid and the most widespread terrestrial carnivore in the western hemisphere (Sunquist and Sunquist 2002). Cougars are induced ovulators (Bonney et al. 1981) and may exhibit courtship and parturition at any time of the year. Nevertheless, evidence suggests that cougars exhibit a birth pulse in summer (Ruth 2004; Jansen and Jenks 2012) that researchers speculate allows cougars access to increased prey availability during the ungulate birth pulse (Logan and Sweanor 2001; Jansen and Jenks 2012). Cougars are also subordinate to gray wolves (*Canis lupus*), American black bears (*Ursus americana*), brown bears (*Ursus arctos*), and jaguars (*Panthera onca*) across most of their range (Ruth and Murphy 2010; Foster et al. 2013; Elbroch et al. 2014). Second-order resource selection exhibited by cougars balances prey availability, refugia, and an awareness of competition with dominant carnivores (Grigione et al. 2002; Elbroch and Wittmer 2012; Lendrum et al. 2014). In fact, research in the Southern Yellowstone Ecosystem (SYE) in northwest Wyoming, USA, showed that cougars selected home ranges that provided high hunting opportunity but mitigated encounters with gray wolves (Lendrum et al. 2014).

Little is known about cougar den selection, even though dens likely play important roles in cougar fitness and population dynamics. Dens serve as shelter for females and their defenseless kittens for up to 8 weeks (Maehr et al. 1990; Beier et al. 1995), and most kitten mortality occurs between birth and 3 months of age (Logan and Sweanor 2001; Benson et al. 2008). In Florida, research on third-order resource selection has shown that Florida panthers select for dens closer to upland hardwoods and mixed conifers, and further from freshwater marshes and wet prairies (Maehr et al. 1990). In the Sierra Nevada Mountains of California, fourth-order resource selection analysis revealed that cougar dens offer thermal regulation and protection from thermal extremes (Bleich et al. 1996). Otherwise, all fourth-order assessments of cougar den selection remain descriptive. Consistently, cougar dens are described as found in "nearly impenetrable vegetation" (Maehr et al. 1989; Beier et al. 1995).

New GPS technology has increasingly facilitated the discovery of cougar dens (Quigley and Hornocker 2010). Thus, we aimed to describe cougar den site selection in the SYE at two scales (third and fourth order) and within an ecological framework that included environmental characteristics, as well as some measure of prey availability and anthropogenic landscape features. We tested whether ecological attributes associated with third-order resource selection of den areas, including hunt opportunity (Elbroch et al. 2013), distance to roads, habitat cover class, and terrain ruggedness, differed from the remainder of their home ranges. Then, we tested whether the physical characteristics of actual den sites associated with fourth-order resource selection differed from random locations throughout their home ranges. As subordinate carnivores and trophy game species subject to human hunting in the state of Wyoming, we hypothesized that cougars would select dens in rugged terrain, and away from roads, offering them refugia from dominant competitors and human hunters. Further, we predicted cougar dens would be in thickets and other physical refugia that would prevent potential kitten predators from entering the actual den or from watching females enter and exit the area (Podgórski et al. 2008; Ross et al. 2010; van de Meer et al. 2013).

## Materials and methods

### Study area

Our study area encompassed approximately 2300 km$^2$ of the Southern Yellowstone Ecosystem (SYE) in southern Teton County, Wyoming, and included portions of the Bridger-Teton National Forest, Grand Teton National Park, and National Elk Refuge (Fig. 1). Elevations in the study area ranged from 1800 m in the valleys to >3600 m in the mountains. The area was characterized by short, cool summers and long, cold winters with frequent snowstorms. Average summer temperatures were 6.9 °C, and average winter temperatures were −7.2 °C (Gros Ventre SNOTEL weather station). Precipitation occurred mostly as snow, and maximum snow depths ranged from 100 cm at lower elevations to >245 cm at intermediate and higher elevations (2000 m+).

Habitats included foothill grasslands, big sagebrush (*Artemisia tridentate*) dominated shrub-steppe, Douglas-fir forests, aspen (*Populus tremuloides*) forests, and higher elevation coniferous forests, composed of lodge pole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and white bark pine (*Pinus albicaulis*). Riparian corridors were dominated by cottonwood (*Populus ungustifolia*, *Populus balsamifera*, and *Populus trichocarpa*) and willow (*Salix* spp.) communities (Marston & Anderson 1991). In addition to cougars, the SYE was inhabited by numerous other carnivores, including brown bears, American black bears, wolves, coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). Ungulate prey included elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), Shiras moose (*Alces alces shirasi*), bighorn sheep (*Ovis canadensis*), and North American pronghorn (*Antilocapra americana*).

### Cougar capture, collar programming, and identifying den sites

From late-November through March, we used trailing hounds to force cougars to retreat to a tree or rocky outcrop where we could safely approach them. Cougars were immobilized with ketamine (2.5–3.0 mg/kg) and medetomidine (0.075 mg/kg), before they were processed. We recorded age using tooth condition

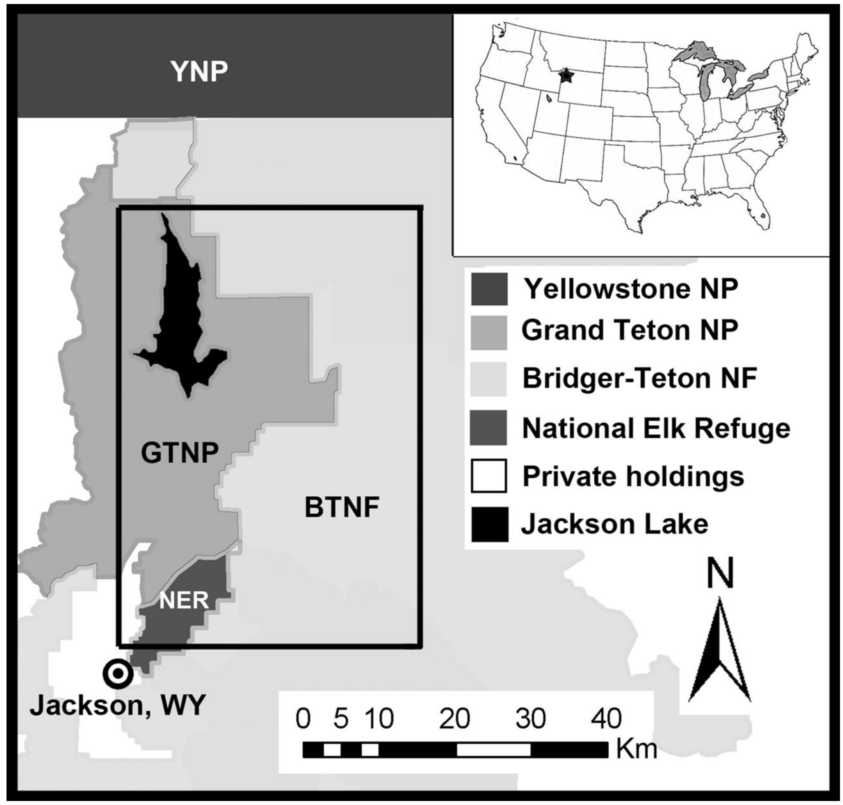


**Fig. 1** Location of the study area in northwest Wyoming, USA, and a close up of land ownership within the area of focus. The smaller rectangle delineated by a *black line* was the area in which we focused capture efforts and our cougar den study

(Heffelfinger 2010) or gum line recession (Laundré et al. 2000), gender, weight, and standardized body measurements. Cougars were fitted with either VHF (Telonics, Mesa, AZ) or GPS collar (Telonics, Mesa, AZ, Televilt, Bandygatan, Sweden, or Vectronics, Berlin, Germany). GPS collars were programmed to acquire location data between 4 and 8 times per day. All collars were equipped with mortality sensors that activated after 8 h of inactivity. Our capture protocols for cougars followed those outlined in Quigley (2000) adhered to the guidelines outlined by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210).

As part of research on cougar foraging ecology (Elbroch et al. 2013), we conducted site searches of areas where triangulation of cougars wearing VHF collars revealed that they had not moved for 24+ h, or spatially aggregated GPS points, called GPS clusters (Anderson and Lindzey 2003), indicated a cougar had remained in place for 8+ h. This protocol opportunistically identified cougar dens when we discovered newborn kittens.

## Third-order selection: comparing den area attributes to home range attributes

Following the methods outlined for our study system in Lendrum et al. (2014), we quantified 95 % kernel density estimators (KDE; Worton 1989; Kie et al. 2010) and isopleths in the Geospatial Modeling Environment (GME plug-in method; Beyer 2009-2012) to obtain annual home ranges for adult female cougars for which we had recorded dens. Based on observed distances moved by hunting females attending dens (Fig. 2), we placed a 2 km buffer around den sites which we defined as the "den area". In ArcGIS 10, we assigned 200 random points within each den area and 400 random points within the remaining portions of their 95 % KDE home ranges (the home range minus the den area). We then assigned the following attributes to each random point: cougar ID, terrain ruggedness (a 3-dimensional vector ruggedness measure (VRM) Sappington et al. 2007), habitat type, distance to forest edge, and aspect of location (transformed into categories of North, East, South, West), hunt opportunity (described below), distance to nearest road, and distance to nearest river or lake.

We derived aspect and VRM from the digital-elevation model (http://datagateway.nrcs.usda.gov/) following the method of Sappington et al. (2007). We reclassified 87 land cover classes described in a Gap Analysis Program (GAP) land cover (gapanalysis.usgs.gov/gaplandcover) at 30 m resolution, into five general land cover classes, by lumping similar cover classes together (Elbroch et al. 2013): (1) open meadows or crop lands, (2) barren habitats and open water bodies, (3) shrub-steppe, (4) forest, and (5) riparian zones. We converted all forested lands from the GAP into a polygon layer in ArcGIS, and then created an edge layer from the

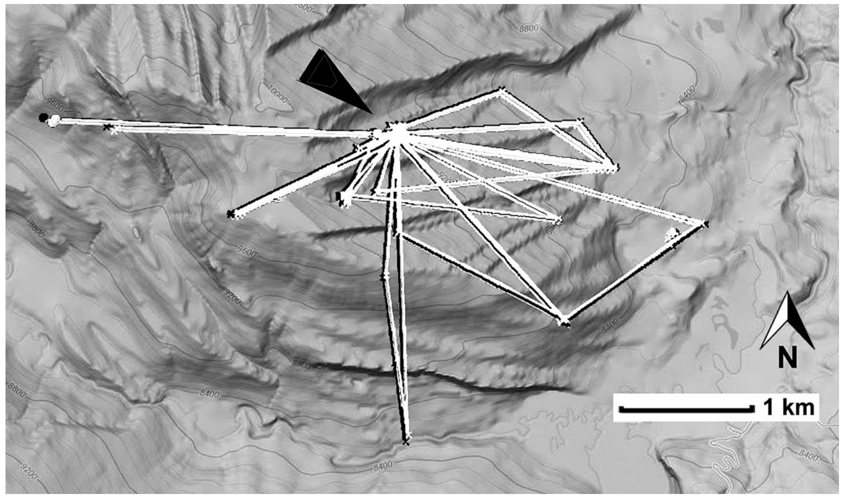


**Fig. 2** The GPS locations and associated movements of a female cougar utilizing a den in the SYE. The den is marked with a *black arrow*

perimeter of each forested section. We included roads and water sources as provided by the United States Department of Agriculture (http://datagateway.nrcs.usda.gov/).

We also employed results of earlier seasonal resource selection function analyses based on 687 verified cougar kills and 2719 random points (Elbroch et al. 2013), in which we calculated the relative probability of a cougar making a kill in any location in the study area. The resulting odds ratio expression for a given landscape location was calculated using the spatial distribution of actual cougar kills to generate a probability surface that then served as a template to identify landscape heterogeneity (Kauffman et al. 2007); cells with a higher value indicated a higher relative probability of kill occurrence. Contributing point attributes included in this analysis were distance to forest edge (m), distance to nearest water (m), aspect (transformed to North, East, South,West), slope (%), and elevation (m) (Elbroch et al. 2013).

Prior to any statistical analyses, we used a correlation matrix to evaluate collinearity ($|r|>0.5$) among predictor variables. Distance to forest edge and hunt opportunity was highly correlated ($|r|=0.7$), so we removed distance to forest edge from further analyses. Other predictor variables were not correlated (all $|r|<0.50$). We employed a series of generalized linear mixed models (GLIMMIX; SAS Institute, Cary, NC, USA) with a binomial distribution (logit link function), to test whether cougars selected den sites at coarse scales based on terrain ruggedness, habitat type, aspect, hunt opportunity, distance to nearest road, distance to nearest water body, or some combination of these attributes. We also included cougar ID as a random effect in the analysis to account for potential bias introduced by unequal sampling across individuals: we documented two dens each for five individuals.

To reduce the number of explanatory variables and the likeliness of over fitting the top model, we first ran a global model containing all variables. We retained only variables with a $p$ value ≤0.1 for model selection. Hunt opportunity was the only variable with a $p$ value >0.1, and therefore, we removed it from any further modeling. We then ran all possible combinations of remaining variables and calculated Akaike's Information Criterion adjusted for small sample size ($AIC_c$, $\Delta AIC_c$, and Akaike weight $w_i$; Burnham and Anderson 2002) for each model to determine variables that influenced den site selection relative to the attributes of the home range. Models that had ≥2 $\Delta AIC_c$ were considered to have predictive power of significant difference from the next model (Burnham and Anderson 2002).

### Fourth-order selection: Microsite characteristics of den sites

We conducted site investigations and recorded microhabitat features of verified den sites plus 5-27 random locations assigned in the GME dispersed throughout unique home ranges associated with each individual den. At each site, we conducted 10 m transects in each cardinal direction, along which we measured the diameter of downed woody debris and rocks ≥8 cm in diameter, and the diameter at breast height (DBH) of trees ≥ 3 cm diameter that intersected with the line. We summed diameters for logs, rocks, and trees for each cardinal direction to create one value for each variable. We then averaged values for each environmental variable across random points associated with a particular den, to account for variable numbers of random points investigated in each home range.

We also measured canopy cover and concealment (Noon 1981) in each cardinal direction, from the center of each location (e.g., the den site if one were present). Canopy cover was measured with a convex spherical crown densiometer (Forestry Supplier, Kackson, MS, USA). Each densiometer delineated 24 squares with which to quantify canopy cover, and we subdivided each square into 4 quarters, allowing for a potential of 96 total units. While standing in the center of each location, we quantified the canopy as % canopy cover, calculated as the variable number of 96 sections in which vegetation was visible. Concealment was measured with a concealment board (Noon 1981) measuring 2 m tall and 50 cm wide. We subdivided the board into three sections. The first subdivision was 0–0.5 m above ground, the second was

**Fig. 3** A characteristic cougar den site in the SYE, inside a criss-cross of downed wood

0.5–1.0 m above ground, and the third was 1–2 m above ground. We assumed that 0.5 m of cover provided sufficient cover to conceal an adult cougar. Each 0.5 m subdivision contained a grid of 25 10×10 cm squares, and the 1 m subdivision contained 50 squares. The concealment board was held at the center of each site, and we recorded the percent of the concealment board that was obscured by natural features when viewed from 10 m away in each cardinal direction.

Prior to any statistical analyses, we employed a correlation matrix to evaluate collinearity among predictor variables. All three levels from the concealment board were highly correlated with each other ($|r|>0.7$), so we combined the three values to create one measure of concealment. Due to small sample size ($n=20$ dens), we did not have the statistical power to employ multivariate analyses to assess fourth-order selection. Instead, we employed separate Mann–Whitney U tests (Mann and Whitney 1947) to compare microsite characteristics at den sites with microsite characteristics at random sites within female home ranges. For females for which we had recorded multiple dens in multiple years, we averaged values for microsite characteristics to remove biases associated with unequal sampling across individuals.

## Results

### Dens

We documented 20 unique dens from 15 female cougars between 2002 and June 2012, for which we gathered data on microsite characteristics and paired random points. We documented an additional five dens after June 2012, which we have included here for our discussion of birth timing and gross microsite descriptions. For 23 of the 25 total dens, we recorded general microsite descriptions: 17 were in deadfall (horizontal log structure; Fig. 3), two were in caves created by boulders in scree slopes, three were in brushy thickets, and one was in a relatively open clump of young fir trees in forested habitat.

The timing of dens was clumped (Fig. 4), with 56 % of 25 dens beginning in June or July. The earliest parturition recorded between 2001 and 2013 was May 20th and the latest parturition was November 3rd, suggesting a courtship period beginning in late February and ending in early August (Fig. 4).

### Third-order selection: comparing den attributes to home range attributes

The top model explaining third-order selection included only terrain ruggedness (Appendix A). Terrain ruggedness was > 13 $\Delta AIC_c$ less than the next model and contained 99.8 % of the Akaike weight (Appendix A). Cougars selected den areas in less rugged terrain when compared to the remainder of the

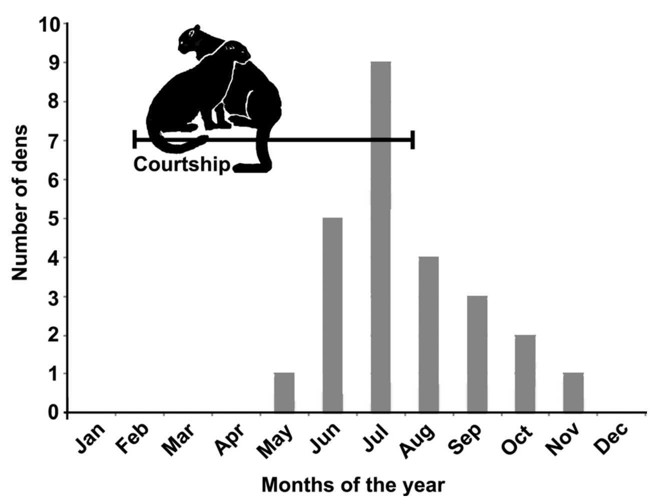


**Fig. 4** The frequency of parturitions by month of the year, and the associated breeding season inferred from parturition dates

**Table 1** Least square descriptive statistics (mean±SE) for third-order dens site selection. We compared the attributes of 1750 random locations within a 2 km buffer around the den sites to those of 3555 points in the remainder of their respective 95 % KDE home ranges; mean±standard deviation displayed for terrain ruggedness (VRM), distance to nearest road, distance to nearest river or lake (Water), distance to nearest forest Edge, and hunting opportunity; mode displayed for categorical variables of Aspect (1=North) and Habitat type (1=forest)

| | VRM | Roads | Water | Edge | HuntOppo | Aspect | Habitat |
|---|---|---|---|---|---|---|---|
| Dens | 0.151±0.007 | 2321.291±198.766 | 478.936±17.113 | 91.998±9.087 | 2.853±0.049 | 1 | 1 |
| Home range | 0.161±0.006 | 2287.650±195.938 | 507.244±15.841 | 98.802±8.842 | 2.839±0.048 | 1 | 1 |

home range ($F_{1,5291}$=3.95, $p$=0.046; ß=−0.3257), but did not select den area with greater access to hunt opportunity or water, further from roads, or of a particular habitat or aspect as compared to the remainder of their home ranges (Table 1).

Fourth-order selection: Microsite characteristics of dens

At the fourth order, we compared microsite characteristics of den sites for 15 individuals and 366 random locations. The percent canopy cover ($U_A$=17.5, $p$<0.001), downed logs ($U_A$=14.0, $p$<0.001), and concealment cover ($U_A$=24.0, $p$=0.002) were all higher at den sites than a random sites. The amount of rocks ($U_A$=77.5, $p$=0.74) and size of trees ($U_A$=75.0, $p$=0.65) did not differ between den sites and random locations (Table 2).

## Discussion

Our results suggested that fourth-order selection exhibited by cougars for den sites was much stronger than third-order selection for den areas. In contrast, other carnivore studies have found den site selection to occur at multiple scales (Maehr et al. 1990; Squires et al. 2008). Our results also supported the birth pulse hypothesis reported for other cougar populations (Ruth 2004; Jansen and Jenks 2012), as well as assertions that cougar dens are characterized by “impenetrable vegetation” (Maehr et al. 1989; Beier et al. 1995).

The results of our analysis of third-order selection for den areas were less compelling. We did have a strong top model, as determined with Akaike’s Information Criterion, which revealed that cougars selected den areas in less rugged terrain. These results contradicted our hypothesis that den areas would be in more rugged terrain to offer females and their vulnerable kittens increased protection from competitors and potential predators, including wolves, bears, and human hunters. Den areas were not further from roads than the remainder of the home range, nor did they offer increased resource availability, in terms of hunting opportunity or water. Either female cougars in the SYE do not select den areas very different from the remainder of their home ranges, or we did not detect important characteristics of den areas because we did not select the right variables to test.

Other researchers found evidence that cougars in Florida exhibited third-order selection for upland hardwood and mixed conifer habitats around dens (Maehr et al. 1990), and thus our findings may not apply beyond the northern Rocky Mountain region; however, our study system was less diverse than in Florida, in terms of habitat classes. Further, our definition of third-order selection, which employed a circular buffer around the den site, included multiple habitat types, whereas the research in Florida was specifically focused on the single habitat in which the den site was located. Thus, future work in the Rocky Mountains may want to consider new definitions for third-order selection in order to test additional questions about den selection at this scale.

The results of our analysis of female fourth-order den selection were much clearer. Den sites were characterized by high concealment and were most often in forests with high structure (e.g., logs and increased canopy cover). Forests may extend “concealment” surrounding den sites, as compared with more open habitats. In this way, forests provide additional protection to cougars as they enter and depart den sites, and reduce their chances of being detected by dominant competitors moving in the area (sensu van der Meer et al. 2013). The criss-crossing downed logs and thickets characteristic of cougar dens in the SYE appeared to provide structural protection from predators, weather, and temperature extremes (Bleich et al. 1996).

In summary, our work described cougar den selection at two scales. Our findings suggested that third-order selection for den

**Table 2** Descriptive statistics (mean±SD) for fourth-order dens site selection. We compared microsite characteristics of 20 den sites to 366 random locations in 95 % KDE home ranges; mean±standard deviation of canopy cover, summed diameter of logs, summed diameter of rocks, summed diameter of trees, and total concealment. *Asterisk* indicates a significant difference.

| | Canopy (%)* | Logs (cm)* | Rocks (cm) | Trees (cm)* | Concealment (#)* |
|---|---|---|---|---|---|
| Den sites | 64.69±20.74 | 511.42±323.25 | 177.50±509.19 | 12.44±15.70 | 295.08±120.19 |
| Random sites | 34.14±33.16 | 136.28±204.21 | 15.25±45.99 | 2.12±6.75 | 129.90±116.64 |

areas was much less important than fourth-order selection for den sites characterized by concealment and protective structure. An important next step to this work is to link kitten survivorship to den site and den area selection to better understand why cougars select specific sites and whether some den sites are better than others. If indeed kitten survivorship is lower in dens with less concealment, which may correlate with other environmental variables (e.g., forest thinning, fire suppression, and weather patterns), wildlife managers can incorporate these characteristics into land management practices. Our current results suggest complex den site characteristics are most important for female cougars selecting dens, and therefore, that land practices that promote and protect downed wood and heavy structure on forest floors will best provide opportunities for cougars to find suitable den sites and maintain parturition behaviors. Similar recommendations have been made to aid in the conservation of other felids (Podgórski et al. 2008).

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## Appendix A

**Table 3** Ranked model comparisons, including number of parameters (K), $AIC_c$ scores, delta $AIC_c$, and model weight ($w_i$) for third-order resource selection; including VRM (terrain ruggeness), RoadDist (distance to nearest road), WaterDist (distance to nearest water river or lake), Aspect, and Veg (habitat type)

| Model # | K | Model | AIC*c* | AIC*c* | W*i* |
|---|---|---|---|---|---|
| 1 | 1 | {VRM} | 23080.11 | 0.00 | 0.9987 |
| 2 | 1 | {RoadDist} | 23093.68 | 13.57 | 0.0011 |
| 3 | 1 | {WaterDist} | 23097.58 | 17.47 | 0.0002 |
| 4 | 2 | {RoadDist+VRM} | 23107.07 | 26.96 | 0.0000 |
| 5 | 1 | {Aspect} | 23110.33 | 30.22 | 0.0000 |
| 6 | 2 | {WaterDist+VRM} | 23111.44 | 31.33 | 0.0000 |
| 7 | 2 | {Aspect+VRM} | 23122.53 | 42.42 | 0.0000 |
| 8 | 2 | {WaterDist+RoadDist} | 23124.84 | 44.73 | 0.0000 |
| 9 | 2 | {RoadDist+Aspect} | 23,137.16 | 57.04 | 0.0000 |
| 10 | 3 | {WaterDist+RoadDist+VRM} | 23,138.57 | 58.46 | 0.0000 |
| 11 | 2 | {WaterDist+Aspect} | 23,139.01 | 58.89 | 0.0000 |
| 12 | 3 | {RoadDist+Aspect+VRM} | 23,149.31 | 69.20 | 0.0000 |
| 13 | 3 | {WaterDist+Aspect+VRM} | 23,151.35 | 71.24 | 0.0000 |
| 14 | 3 | {WaterDist+RoadDist+Aspect} | 23,165.89 | 85.78 | 0.0000 |
| 15 | 4 | {WaterDist+RoadDist+Aspect+VRM} | 23,178.16 | 98.05 | 0.0000 |
| 16 | 1 | {VegClass} | 23,303.73 | 223.61 | 0.0000 |
| 17 | 2 | {VegClass+VRM} | 23,313.77 | 233.65 | 0.0000 |
| 18 | 2 | {RoadDist+VegClass} | 23,339.47 | 259.36 | 0.0000 |
| 19 | 3 | {RoadDist+VegClass+VRM} | 23,350.13 | 270.02 | 0.0000 |
| 20 | 2 | {WaterDist+VegClass} | 23,351.98 | 271.87 | 0.0000 |
| 21 | 2 | {Aspect+VegClass} | 23360.23 | 280.12 | 0.0000 |
| 22 | 3 | {WaterDist+VegClass+VRM} | 23,362.73 | 282.62 | 0.0000 |
| 23 | 3 | {Aspect+VegClass+VRM} | 23,368.94 | 288.83 | 0.0000 |
| 24 | 3 | {WaterDist+RoadDist+VegClass} | 23,387.24 | 307.12 | 0.0000 |
| 25 | 4 | {WaterDist+RoadDist+VegClass+VRM} | 233,98.87 | 318.75 | 0.0000 |
| 26 | 3 | {RoadDist+Aspect+VegClass} | 23,399.89 | 319.77 | 0.0000 |
| 27 | 3 | {WaterDist+Aspect+VegClass} | 23,404.28 | 324.17 | 0.0000 |
| 28 | 4 | {RoadDist+Aspect+VegClass+VRM} | 23,409.26 | 329.14 | 0.0000 |
| 29 | 4 | {WaterDist+Aspect+VegClass+VRM} | 23,413.61 | 333.50 | 0.0000 |
| 30 | 4 | {WaterDist+RoadDist+Aspect+VegClass} | 23,443.40 | 363.29 | 0.0000 |
| 31 | 5 | {WaterDist+RoadDist+Aspect+Veg+VRM} | 23,453.74 | 373.63 | 0.0000 |

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