CHARACTERISTICS OF WOLF AND COUGAR KILL SITES IN THE SOUTHERN YELLOWSTONE ECOSYSTEM

by
Susannah Woodruff

A thesis submitted in partial fulfillment of the
requirements for the degree of
Master of Arts from Prescott College in
Environmental Studies-Wildlife Biology

Approved as to style and content by:

David R. Parsons (Graduate advisor)	Howard Quigley (Second reader)	Paul Sneed (Third reader)
Date:	Date:	Date:

December 2006

ACKNOWLEDGMENTS

I am grateful for the help of countless people on the completion of my thesis. Without their help, I could never have done it! First, I would like to thank Dave Parsons. I could not have imagined having a better advisor and mentor for my master's. His guidance and patience over the past 3+ years was unshakable, even as I never seemed to do things the easy way. Thanks also to Mike Jimenez for friendship, support, and direction when I was straying from the task at hand; to Court Smith who explained, and explained again, and again, the ins and outs of GIS analysis and statistics; and to Howard Quigley, thanks for knowledgeable advice and the opportunity to do this project. I would also like to thank the USFWS, Beringia South, Wyoming Game and Fish, Sarah Dewey and Steve Cain at Grand Teton National Park, Bridger-Teton National Forest, all of whom contributed data, equipment, time, financial assistance and the proofreading of thesis drafts! To all the people with whom I have had the privilege to work alongside in the field, a huge thanks: Rose Jaffe, Karen Colclough, Dylan Taylor, Lydia Dixon, Rebecca Hansen, Ronnie Hegemann, and Leah Samberg.

And finally to my husband, Brian Woodruff, who has been with me through this whole process…and we made it! It has been a long time in the making. Thanks for unfailing support through the stories, the tears, and the long field days when I was hardly home for long enough to say hello.

This thesis is dedicated to my parents, Chuck and Betsey Phillips, for giving me the courage to think for myself and inspiring passion for the outdoors and all things wild.

TABLE OF CONTENTS

List of tables

List of figures

ABSTRACT

We examined kill site habitat characteristics of sympatric wolves (*Canis lupus*) and cougars (*Puma concolor*) in the southern Yellowstone ecosystem. We tracked radio-collared wolves and cougars to locate and describe kill sites from December 1999-May 2006. Using computer mapping techniques, we: 1) identified kill site characteristics (elk density, vegetation cover type, distance to waterways, slope, aspect, elevation, and terrain roughness) associated with wolf and cougar kill sites; 2) compared and contrasted characteristics between wolf and cougar kill sites; and 3) compared and contrasted winter versus spring kill site characteristics. Analysis indicated wolf kill sites were not randomly selected; cougar kill sites generally did not differ from random sites. Wolf kills occurred on less steep slopes in more open areas, and in areas with mid to high elk density. Cougar kill sites were characterized by rougher terrain and greater canopy cover and appear unaffected by elk density. We concluded that variation in kill site habitat likely stems from differences in hunting techniques.

INTRODUCTION

Wolves and cougars are becoming re-established in much of their former ranges in the American West. Understanding the ecological interactions of wolves and cougars in the Greater Yellowstone Ecosystem (GYE) may provide insight into their ecological roles, the predator-prey dynamics of the system, and the long-term management and conservation of these carnivores.

In the early 1900's, perceived as a threat to wild ungulate populations and domestic livestock, predators were poisoned, shot, and trapped in a variety of systematically conducted eradication programs. The western movement of humans in the late 1800's brought about dramatic reductions of elk (*Cervus elaphus*), deer (*Odocoileus* spp.), and bison (*Bison bison*) populations (McIntyre 1995), replacing wild ungulates with domestic livestock. Declining prey populations and increasing abundance of livestock fostered increasing predator-livestock conflicts. However, even in remote areas, far from livestock, wolves were heavily persecuted (McIntyre 1995). By the 1930's wolves were extirpated from nearly all of the contiguous United States; Minnesota remained the only state with a remnant population of wolves. Cougar populations in the West were also significantly reduced as a result of predator eradication efforts, and they were exterminated in most regions east of the Mississippi.

Attitudes toward predators began to shift in the late 1960's as the scientific community and the environmental movement emphasized the important role predation may play in maintaining healthy ecosystems (McIntyre 1995; Mech 1995; Ripple and Beschta 2003, 2004a and 2004b). Cougar bounties were eliminated in most western states during this time (Riley et al. 2004); cougar populations have rebounded since the 1970's as a result of changes in state management practices and increased prey populations (Berger et al. 2001; Bunnell et al. 2002). Idaho Fish and Game Department personnel conservatively estimate the cougar population in Idaho to be around two thousand (S. Nadeau, personal communication); estimates from Wyoming and Montana are not available. While cougar populations recovered under more protective management approaches, wolf recovery required federally mandated actions following the listing of the wolf as endangered under the Endangered Species Act (ESA) of 1973 (Clark et al 1994). As part of the ESA directive, a recovery plan was developed to restore wolves to the northern Rocky Mountain region of the U.S. (USFWS 1987). By the mid 1980's wolves began recolonizing northwestern Montana by natural dispersal from Canada; however, low survival rates and lack of reproduction prevented the wolves from establishing viable populations further south and west into Idaho and Wyoming (Ream et al. 1991). In 1995 and 1996, the United States Fish and Wildlife Service (USFWS) released 35 wolves from Canada into central Idaho and 31 wolves into Yellowstone National Park (YNP) (Bangs and Fritts 1996). In 2006, an estimated total of 1020 wolves occupied Idaho, Montana and Wyoming (US Fish and Wildlife Service et al. 2005).

Wolves and cougars are considered “habitat generalists” occupying a wide variety of terrain and vegetative types (Mladenoff et al 1995; Wydeven et al. 2001; Parsons 2003). However, significant habitat preference for travel routes and kill sites has been documented for both wolves and cougars (Kunkel and Pletscher 2001; Husseman et al. 2003; Kunkel et al. 2004). While wolf populations have been shown to decline above a threshold for mean road density (approximately 0.6 km/km^2) (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Mech 1989; Wydeven et al. 2001), Mladenoff et al. (1995) contend that roads were generally not a major hindrance to wolves. Roads increase human access and typically increase wolf mortality (Mladenoff et al. 1995; Paquet et al. 1997; Wydeven et al. 2000). Dickson and Beier (2002) found proximity to roads has been shown to affect cougar movements and home ranges, as density of roads was lower within cougar home ranges than within their study area. In general, as distance to paved roads increase, so does cougars’ use of areas (Van Dyke et al. 1986; Sweanor et al. 2000; Dickson and Beier 2002). Type of vegetation seems insignificant; still, cougars do indicate a preference for areas of heavier cover (Busch 1996).

Differing prey response behavior (e.g., running, tree climbing) and mode of predation (e.g., land vs. flight and pursuit vs. ambush) influence the ideal habitat characteristics for predation (Kruuk 1968; Walker and Craighead 1997). Typically, ambush predators depend on prey moving within close proximity for chance encounters, while coursing predators hunt by pursuit and range widely to find potential prey (Kruuk 1968; Greene 1986). Wolves are group hunting, coursing predators often relying on pursuit of disadvantaged animals over open terrain (Estes and Goddard 1967; Mech 1970). As longer chases often ensue, the kill site location is dependent not only on habitat characteristics, but also on flight behavior (Husseman et al. 2003). Thus, habitat characteristics of the actual kill site could be different from the habitat at the origin of the chase. Kunkel and Pletscher (2001) suggest wolves prefer areas with significant cover, which presumably enhances their ability to remain undetected while approaching prey. Kunkel (1997) found that as cover increased, wolves and cougars killed more deer, possibly due to a decreased chance of the predator being detected by their prey. Other research indicated the element of surprise was not a significant factor for predation success for canids (Wells and Bekoff 1982; Murray et al. 1995). Cougars, on the other hand, are solitary hunters depending on hiding cover to ambush their prey (Kruuk 1968; Kunkel et al. 1999; Husseman et al. 2003). Cougars tend to favor steep terrain (Busch 1996), heavy cover in conifer (Williams et al. 1995) and riparian vegetation types (Busch 1996; Dickson and Beier 2002). They also tend to avoid developed landscapes and grasslands (Dickson and Beier 2002).

Concurrent wolf and cougar research in northwestern Wyoming offered an opportunity to compare a variety of behavioral and ecological characteristics of these two species. Jimenez et al. (2005) examined prey selection of wolves and the behavioral response of elk to the presence of wolves in the Gros Ventre, Buffalo Fork, and Snake River drainages. Simultaneously, cougar habitat use, prey selection, and demographics were being examined in the same study area (Teton Cougar Project 2004). The purpose of our research was to determine how habitat characteristics and topography define kill sites for each species in this area. We described and compared habitat characteristics of wolf and cougar kill sites to determine how kill sites differ between wolves and cougars, how kill sites vary from typical elk habitat, and how kill site location and characteristics vary seasonally.

We tested the hypothesis that due to different hunting strategies and prey target, kill sites differ between species. We predicted that i) habitat characteristics of wolf and cougar kill sites differ; ii) habitat factors associated with kill sites vary seasonally for wolves and cougars; and iii) wolf and cougar kill sites are associated with habitat factors that enhance hunting success based on their hunting strategies.

METHODS

To acknowledge the many collaborators on this project, I used the pronoun "we" when appropriate. I take responsibility for any errors in the data analysis and writing of this thesis.

Study area

The study area encompassed approximately 2,300 km^2 defined by the Teton Range to the west, the Gros Ventre Range to the east, the Teton Wilderness area to the north and Cache Creek drainage to the south (Figure 1). Lands within the study were mostly public and were administered by the US Forest Service (Bridger-Teton National Forest) and National Park Service (Grand Teton National Park), although some of the area was privately owned. An extensive system of US Forest Service roads (mostly unimproved roads) and snowmobile trails existed throughout the study area. Rugged mountains, ridges, deep drainages and open sage flats characterized the area. Elevations ranged from approximately 1,800 m to approximately 3,600 m. Typically snow began to accumulate in October and melted by early May to late June, depending on the elevation. Average snowfall in the area was 490 cm and average rainfall was 26 cm. Low elevations were dominated by sagebrush (*Artemisia* spp.) with smaller amounts of riparian cottonwood forests (*Populus angustifolia*) and willow (*Salix spp.*); mid-elevations were generally forested consisting mainly of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseodotsuga menziesii*), and aspen (*Populus tremuloides*), while Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) dominated the higher elevations. Primary prey species for wolves and cougars in the area were elk, mule deer, and moose (*Alces alces*), with the addition of bison (*Bison bison*) for wolves, and bighorn sheep (*Ovis canadensis*) and pronghorn (*Antilocarpa americana*) for cougars. The Wyoming Game and Fish Department managed three winter feedgrounds for elk in the Gros Ventre River drainage. The 2004 winter population of the Jackson elk herd was estimated at 13,500 head (Dean et al. 2004).

Wolf and cougar locations

We tracked and located radio-collared wolves and cougars using radio-telemetry. In the summer, we captured wolves using #7 McBride traps (Alpine, Texas) set along trails and roads frequented by wolves and also at livestock depredation sites (Mech 1974; Ream et al. 1991). Immobilization and radio collaring techniques followed Mech (1974), Ream et al. (1991) and Kreeger (2002). Collars were either VHF mortality sensing MOD500 or Global Positioning System (GPS) Gen-III Model # TGW-3590 collars (Telonics, Mesa, Arizona). In winter, wolves were darted from a helicopter following protocols referenced above and Ballard et al. (1991). We helicopter darted and fitted two wolves with GPS collars, one in March 2005 and another in April 2006. The first wolf GPS collar was programmed to take a fix once every 6 hours from deployment 18 March 2005 until 1 October 2005 when fixes switched to every hour. The locations from the GPS collar were remotely downloaded via air once every 7-14 days depending on the weather. Due to the infrequent fixes, we searched most point locations for possible kill sites avoiding den sites and rendezvous sites still in use. The second GPS collar attempted to take a fix once daily from 15th April to 14th May, and beginning 15th May, a fix was attempted every half hour. Clusters were defined as two or more points within 200m of each other in a 24-hour period (Sand et al. 2005) and were searched as described above.

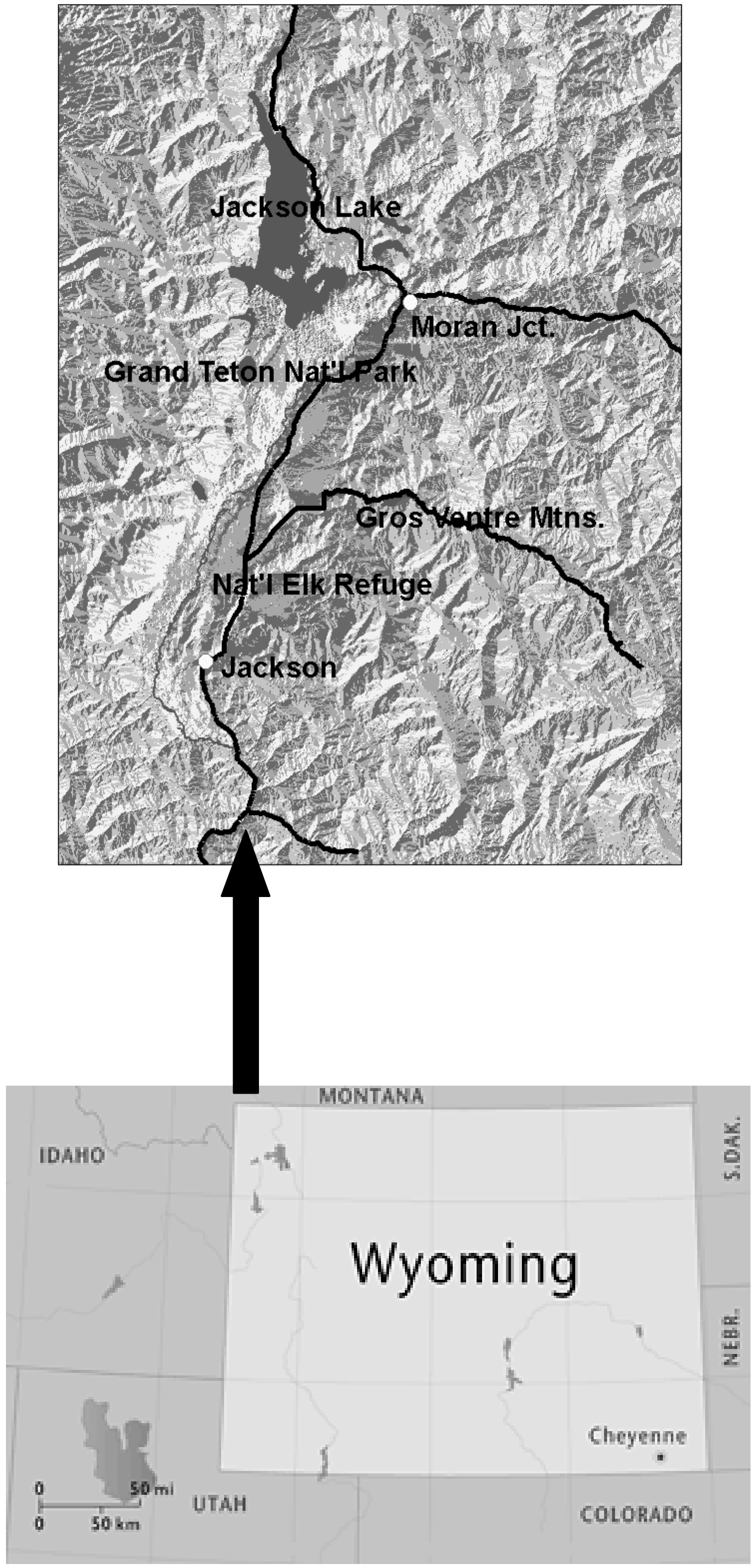


Figure 1. Greater Jackson, Wyoming study area

We captured cougars from November to April each year depending on snow conditions generally following methods developed by Quigley (1997), Murphy (1998), and Ruth (2000). Cougar handling protocols followed Hornocker Wildlife Institute guidelines (Quigley 1997) and Kreeger (2002). Cougar radio collars were either Telonics (Mesa, Arizona) VHF models MOD500, MOD400, MOD150 or MOD250, or GPS 1D Tellus (Telemetry Solutions, Sweden). Six downloadable GPS collars were deployed on cougars: winter 2005 (3 females, 1 male) and winter 2006 (2 females). These collars were programmed to acquire and store locations 6 times daily. Cougar collars were downloaded from the ground every 7-10 days and clusters of 2 locations or more within 150 m of each other during a 24-hour period were searched for possible kill sites.

We located radio-collared wolves and cougars from the air in fixed-wing aircraft and from the ground using roads and accessible trails when possible. Aerial locations were obtained using methods described by Mech (1983) and recorded in Universal Transverse Mercator coordinates (NAD27); ground locations were obtained using triangulation from at least 3 bearings (Heezen and Tester 1967; White and Garrott 1990). The accuracy of both aerial and ground locations was tested using radio-collars placed in known locations.

Prey availability

Radio-collared elk (mean: 60 ± 7 std dev.) were aerially located 1-2 times per month depending on weather. These data were collected cooperatively by the USFWS, Grand Teton National Park, and Wyoming Game and Fish Department. Additionally, in early February, Wyoming Game and Fish Department conducted aerial elk population surveys to determine age/sex structure and elk population size. All elk herd locations were recorded using a GPS. We used the ArcGIS Home Range Tool *Kernel Analysis* (ESRI, Redlands, CA) to assess elk distribution by modeling the 99% fixed kernel utilization distribution (UD) of elk telemetry locations delineated by season: winter (1 December – 31 March), and spring (1 April – 31 May) (winter: standardization: unit variance; spring: standardization: unit variance). We varied the smoothing factor using percentages of h_{ref} until they accurately fit the data. Elk distribution data were pooled across all years. We defined areas of prey (elk) availability—low, low-mid, mid, mid-high, and high—based on these UDs. For elk locations, we used available GIS layers to determine average elevation, slope, aspect, canopy cover, vegetation type, distance to nearest water (lakes, rivers, streams, ponds) and terrain roughness for each season.

Kill site location and assessment

Winter

Carcasses of ungulates killed by wolves and cougars were located using ground and aerial telemetry, downloaded GPS locations, and backtracking on skis or snowshoes. We investigated wolf-killed carcasses as soon as the wolves left the immediate area. Fresh kills (<12 hours) still containing large amounts of meat were left alone and returned to the following day to minimize disturbance and allow the wolves to resume consumption of the carcass. Non-GPS collared cougars that remained in the same location for 2-3 consecutive days were suspected to be on a kill. At this point, “close locations” were obtained using three azimuths from approximately 300 m from the study animal; every effort was made to assure the study animal was not disturbed. When the cougar left the area, the "close location" data defined the search area to determine if a kill was made. We thoroughly searched all wolf and cougar kill sites and the surrounding area for tracks, bed sites, cache sites (cougars), scats, toilets (cougars), and other indications of carnivore presence, as well as for rumen, bones and other carcass remains that may have been scattered. When possible, we skinned each carcass to examine for trauma, including hemorrhaging on the inside of the hide and tooth punctures. We searched for additional evidence of wolf and cougar kills, including signs of a chase or struggle via tracks and a blood/hair trail. Blood in the snow under and around the carcass was assessed and recorded. By examining the site around the carcass, the carcass and the hide, predator-killed carcasses were distinguished from scavenged carcasses (Wade and Brown 1982; Acorn and Dorrance 1990). Kills were classified as known, probable, possible, or scavenged carcass. Only known and probable kills were used in the analysis. If the carcass had been moved, location of rumen or copious blood in the snow determined kill site. In the case of cougars, location of cache was used in cases where actual kill site could not be determined. All kill sites were recorded in UTM coordinates using a handheld GPS unit. To reduce bias associated with winter feeding, we excluded kills found on the elk feedgrounds and the National Elk Refuge (where elk are fed hay and supplemental alfalfa pellets).

Spring

Assessment of spring kill sites was complicated by the presence of bears. Following safety protocol established by USFWS and Teton Cougar Project (TCP), a minimum of two people was present at all kill site investigations. Spring kill site location assessment for cougars followed the methods described above. For wolves, however, in the absence of snow, we relied solely on GPS locations obtained from the downloadable collars whose locations were retrieved weekly. These locations were plotted on a map and clusters of locations were presumed to indicate possible kill sites; these sites were searched for evidence of kills as described above. Potential kill sites determined from GPS locations were investigated beginning with the oldest locations to minimize bear conflict.

We identified the habitat in which elk were more likely to be killed by a wolf or a cougar by modeling the 95% fixed kernel utilization distribution for each species using kill site locations. For wolves in both winter and spring, we used unit variance standardization, fixed kernel, and a varying smoothing factor; for cougars, we again used unit variance standardization, with a varying smoothing factor in both seasons.

Habitat characterization

Using ArcGIS (ESRI, Redlands, CA), we built a Geographic Information System (GIS) basemap of the study area for terrain analyses and overlaid a prey density map and all kill site locations. The basemap included map layers (30 m pixel minimum) characterizing and defining canopy, elevation (from 10 m Digital Elevation Model (DEM) database; all 1:24,000), lakes and stream courses. Major vegetation types (70 discrete types; 30 m x 30 m) are described using the *Land Characterization of the Bridger Teton National Forest and Surrounding Area* (Homer 1998). We reclassified the vegetation types into five general categories (open terrain, conifer, mixed forest, riparian, developed). We also used the vegetation layer to create a categorical canopy cover layer—0=0-30%, 1= >30-59%, and 2 ≥ 59%. We merged 10 m DEM's from Grand Teton National Park and US Geological Survey for Wyoming to create the elevation layer for the study area. We derived slope and aspect data from DEM's using ArcGIS *Spatial Analyst* extension (ESRI, Redlands, CA); aspect was further classified into north (316^o-45^o), east (46^o - 135^o), south (136^o -225^o), and west (226^o -315^o). Terrain roughness was assessed using a moving window analysis of a DEM. We compared the elevation of each 10 m cell to the 8 surrounding cells; the sum difference is the terrain roughness value for each cell (Riley et al. 1999). Waterway data was derived from the USFS (BTNF 1997). All layers were standardized to 30 m cells. Additionally, we measured elevation (using a handheld GPS unit), slope (compass), aspect (compass), and visually estimated canopy cover as open or closed at the kill site for groundtruthing. We used spatial and attribute queries in ArcGIS to get an average value for canopy cover, elevation, slope, aspect, distance to nearest waterway, and terrain roughness at all kill sites and random locations. Within the 50 m radius and 1 km radius (discussed below), majority value was used for canopy cover and terrain roughness.

Table 1. Environmental variables and associated units measured at each wolf and cougar kill site

Variable	**Unit**
Terrain roughness	0-240 index
Canopy cover	%
Elevation	Meters
Slope	Degrees
Aspect	Degrees
Distance to water	Meters
Elk density	Individuals/km^2

Statistical analyses

Each occurrence of predation had multiple parts (i.e., chase/stalk, attack, kill, consume, and cache—for cougars) that may occur at different sites. Habitat at the site of initial prey detection was presumed to be important in the successful predation sequence. However, we often could not detect initial point of contact due to long chases or lack of sign; thus, we compared habitat at three spatial scales to account for differences in variables affecting the likelihood of a kill. The scales were: 1) actual point of kill; 2) 50 m: mean distance for ambush of prey by cougar (Ruth and Buotte 2006); and 3) 1 km: mean chase distance resulting in a successful kill by wolves (D. MacNulty and D. Smith, personal communication). We refer to the scales as kill sites, kill vicinity (50 m) and kill area (1 km). We assessed use versus available (random) habitat by generating random points within the elk utilization distribution using Hawth's *Generate Random Points* tool (Beyer 2004) (winter: 270 points--twice the number of winter wolf kill sites; spring: 98--twice the number of cougar kill sites) (J. Kie, personal communication). Habitat at random points was considered available habitat and each random point was assessed in the same manner as the kill sites. All comparisons were done on the same spatial scale (e.g., kill sites with a 50 m radius were compared to random points with a 50 m radius). Random points are referred to as random site, random vicinity, and random area, corresponding to the kill site, kill vicinity, and kill area.

We performed a Correlation and Regression Tree (CART) analysis (Brieman et al. 1984) using DTREG (Sherrod 2004) to assess broad-based differences in habitat characteristics between wolf kill sites and cougar kill sites. CART analysis performs a form of binary recursive partitioning and builds "trees" for predicting categorical predictor variables (classification) and continuous dependent variables (regression) (Brieman et al. 1984). This procedure determined the likelihood a site was a kill made by a wolf or cougar based on the input variables. This analysis identified the most significant variables for distinguishing between a wolf and cougar kill. Seven variables were included in the analysis: elk density (categorical: low, low-mid, mid, mid-high, high); canopy cover (categorical: 0, 1, 2), roughness (continuous), slope (continuous), aspect (categorical: north/south/east/west), elevation (continuous), and distance to water (continuous). Distance to water was applicable at only one spatial scale: kill site. CART "prunes" the tree to minimum cross-validated error. Initially distance to roads was also included in the analysis. However, due to the greater likelihood of detecting and investigating kills closer to roads, it was dropped from all analysis to minimize bias.

We computed a correlation matrix for the 7 variables. Slope and elevation were highly correlated, as were canopy and slope. Terrain roughness was significantly correlated with all other variables while aspect was correlated with no other variables. Due to the high levels of correlation between our variables, we used Principal Component Analysis (PCA) to condense the variables into composite values using MINITAB (1998). PCA is a widely used multivariate ordination technique, which reduces the information in multiple measured variables into a smaller set of uncorrelated components. Factor loadings (the correlations between a variable and a given principle component) describe the relationship between the composite variable (principle component) and each measured variable. Refer to McCune and Mefford (1999) for additional information on PCA. PCA allowed us to retain much of the information within our environmental variables (between 30-40% in most cases) and ensured that we did not violate the multicollinearity assumptions of binary logistic regression. We conducted separate PCA's at each spatial scale (i.e., kill/random site, kill/random vicinity, and kill/random area). Principal components were retained according to the broken-stick criterion (McCune and Mefford 1999). Retained components were then entered as independent variables (i.e., location characteristics) in binary logistic regression models, where 1 indicated a wolf or cougar kill location and 0 represented a randomly generated location. These models were used to determine if wolves and cougars were selecting for specific site attributes at kill locations versus randomly generated locations at the three spatial scales. We also used these models to assess differences between wolf and cougar kill sites and seasonal kill site differences. We used MINITAB (1998) for all statistical tests $\alpha = 0.05$. We computed a Hosmer-Lemeshow statistic to test model goodness-of-fit. A significant ($p < 0.05$) Hosmer-Lemeshow statistic suggests differences between the observed and expected frequencies in the groups, and thus, a lack of model fit; a high *p*-value is associated with a good fit. We report Goodman-Kruskal Gamma (GK-G) as a measure of the degree of association between models and data. GKG values range from –1 to 1 and are based on the difference between concordant and discordant pairs; a pair of values is concordant if the larger x value corresponds to the larger y value and discordant if the larger x value has a smaller y value. By strict definition, a relationship is "perfect" if (a) as the independent variable x increases, then the dependent variable y increases (or decreases in the case of negative relationships), and (b) if each value of x corresponds to only one y value. Similarly, as y increases, x also increases (or decreases for negative relationships), and each y value corresponds to only one x value. An implication is that there are no ties on x and no ties on y. If GKG is 0.742, it is said that knowing the independent variable reduces the error of predicting the dependent variable by 74.2% (Sheskin 2003).

Pseudoreplication can result from treating multiple samples from one experimental unit as multiple experimental units or from using experimental units that are not statistically independent (Hurlbert 1984). We were aware of the implications this has for our research, and we took precautions to avoid bias. Kill sites from multiple wolf packs and individual wolves were assessed. We used pooled samples from all wolf kill sites and additionally compared Teton Pack kill sites to non-Teton Pack kill sites. We used PCA and logistic regression for this analysis.

RESULTS

Wolf and cougar locations

A total of 42 wolves and 47 cougars were collared and monitored from 2000-2006. Number of radio collared individuals at one time ranged from 3 wolves in 2000 to a high of 14 wolves in 2006; number of individual collared cougars ranged from 4 in 2002 to 23 in 2003. Winter wolf pack size ranged from 2 – 13 individuals. Dispersing individuals and mortality caused the number of collared study animals to fluctuate. During 2005 and 2006, we monitored 2 groups of dispersing collared wolves consisting of 2-3 animals from nearby and resident packs as well as ground-tracking an uncollared pack of >10 wolves. The first wolf GPS collar successfully recorded 1157 fixes of 1315 fixes expected (88%); after only 7 months, the collar was recovered earlier than anticipated.

Success rate of the second wolf GPS collar was also 88% recording 3951 fixes of 4483 fixes expected. Cougar GPS collars deployed in 2005 were on each cat for approximately 10 months; collars from 2006 were still on cats at the end of this study for ongoing research. Average success rate for the cougar GPS collars was 63% (H. Quigley, personal communication).

Elk locations

During the study period, a total of 2,274 elk locations were recorded during winter months and 780 in spring. Elk were most often found in open terrain (52.3%) and conifer (22.3%);. They were significantly less likely to be found in riparian areas (15.4%), mixed forest (8.8%), and developed (1.1%). Elk were twice as likely to be in areas of <30% canopy cover (66.4%) than areas of 30-59% canopy cover (31.1%). Vegetation usage was similar in spring: open terrain (50.1%); conifer (24.6%); riparian (13.8%), mixed forest (8.1%); and developed (2.7%).

Kills

A total of 172 wolf kill sites (winter: 135, spring: 37), and 165 cougar kill sites (winter: 120, spring: 49) were investigated from November 1999 to May 2006. In winter, wolf kills consisted of 95% elk and 5% moose; in spring, wolf kills were composed of 92% elk and 8% moose (Jimenez et al. 2006). Cougar kills were 84% elk, 6% mule deer, 1% moose, and 9% other in winter, and 80% elk, 11% moose, and 9% other in spring (H. Quigley, personal communication).

Use vs. available

Wolf

Winter

The two most often occurring vegetation categories at wolf kill sites were open terrain and riparian. Wolves used open terrain (63.0%) and riparian areas (23.0%) more than they were available (31.1% and 10% respectively); conifer (8.1%) was used much less than available (42.2%). At the kill vicinity and kill area, again wolves used open terrain (69.4% and 73.7%) more than twice as much as it was available (30.7% and 32.2%), and conifer habitat was used (9.9% and 11.8%) less than one quarter of its availability (41.5% and 53.3%). Riparian areas were used (25.6%) more than twice as much as they were available (11.1%) within the kill vicinities and equally (6.8%) as often as they were available (6.3%) within the kill areas.

In the majority of the principal component analyses, only one principal component was retained according to the broken stick criterion. In some of the analyses, none of the principal components were retained; however, we chose to report on them nonetheless. For wolves, PC1 was retained according to broken-stick criterion at all three spatial scales. Wolf kills were most often in areas of mid-high and high elk density (69.6%; Figure 2). At the kill site, 39.7% of the total variance was explained by one principal component (Table 2). Sites with positive associations with the first component had less terrain roughness, less slope, and lower elevation. Within the kill vicinity, the first principal component accounted for 45.4% of the total variation. Primary loading of this component occurred on terrain roughness and slope. The kill vicinities were mainly positively associated with this principal component and had less rough terrain and canopy cover; lower slope and elevation; and higher elk density. Again, only one principal component, which explained 49.2% of the variation, was retained for the kill areas. Sites positively associated with this component had lower elevation; less slope, roughness, and canopy cover; and higher elk density (Table 2).

Table 2. Principal component loadings for habitat variables associated with wolf kill sites and random sites, winter and spring, greater Jackson area, 1999-2006.

	Wolf-random winter			**Wolf-random spring**		
		PC1			**PC1**	
	Pt.	50 m	1 km	Pt.	50 m	1 km
Eigenvalue	**2.78**	**2.72**	**2.95**	**2.79**	**2.89**	**3.01**
Broken stick	**2.59**	**2.45**	**2.45**	**2.28**	**2.28**	**2.45**
% Variance	39.7	45.4	49.2	39.8	48.1	50.2
Variables						
Terr. roughness	-0.487	-0.507	-0.469	0.531	-0.513	-0.438
Canopy cover	-0.383	-0.383	-0.395	0.349	-0.310	-0.333
Aspect	0.041	0.029	0.213	-0.055	0.089	0.216
Slope	-0.500	-0.520	-0.505	0.545	-0.528	-0.510
Elevation	-0.480	-0.488	-0.511	0.478	-0.494	-0.517
Dist. To water	-0.210	N/A	N/A	0.036	N/A	N/A
Elk density	0.301	0.294	0.250	-0.256	0.332	0.352

Bold indicates retained component according to broken-stick.
Underline indicates factor loadings that contributed >10% to a particular component

Logistic regression revealed that wolf kill sites were nearly 3 times more likely to have positive association with PC1 than random sites. Within the kill vicinity, wolf kill sites were 2.5 times more likely to be associated with PC1 than random vicinities. As indicated by the odds ratio (1.84), kill areas were nearly twice as likely to be associated with PC1 than random areas (Table 3). The Goodman-Kruskal Gamma measure of association indicated the models were good measures of association at all three spatial scales (Table 3).

Table 3. Logistic regression models presenting the PCA found to be significant in predicting wolf kill vs. random locations. Odds ratios and corresponding 95% confidence intervals for retained principal component analysis are provided; model significance determined via the likelihood ratio test.

WOLF WINTER							
Model	**Equation**	**O.R.**	**C.I.**	**p-value$_1$**	**HL**	**p-value$_2$**	**GKG**
Site							
Constant + PC1	g(x) = -1.11 + 0.98 (PC1)	2.66	2.15-3.30	0.00	9.49	0.30	0.64
Vicinity							
Constant + PC1	g(x) = -1.07 + 0.90(PC1)	2.47	2.01-3.04	0.00	12.59	0.13	0.60
Area							
Constant + PC1	g(x) = -1.05 + 0.6(PC1)	1.84	1.56-2.18	0.00	27.76	0.001	0.49
WOLF SPRING							
Site							
Constant + PC1	g(x) = -1.11 + 0.65 (PC1)	0.51	0.36-0.73	0.00	8.43	0.39	0.45
Vicinity							
Constant + PC1	g(x) = -0.95 + 0.64(PC1)	1.91	1.36-2.69	0.00	10.78	0.21	0.46
Area							
Constant + PC1	g(x) = -0.88 + 0.49(PC1)	1.64	1.23-2.19	0.00	11.86	0.16	0.41

OR= odds ratio; CI= 95% confidence interval
HL=Hosmer-Lemeshow goodness-of-fit test (degrees of freedom =8)
GKG= Goodman-Kruskal Gamma measure of association
p-value$_1$=value associated with odds ratio
p-value$_2$=value associated with Hosmer-Lemeshow test

Spring

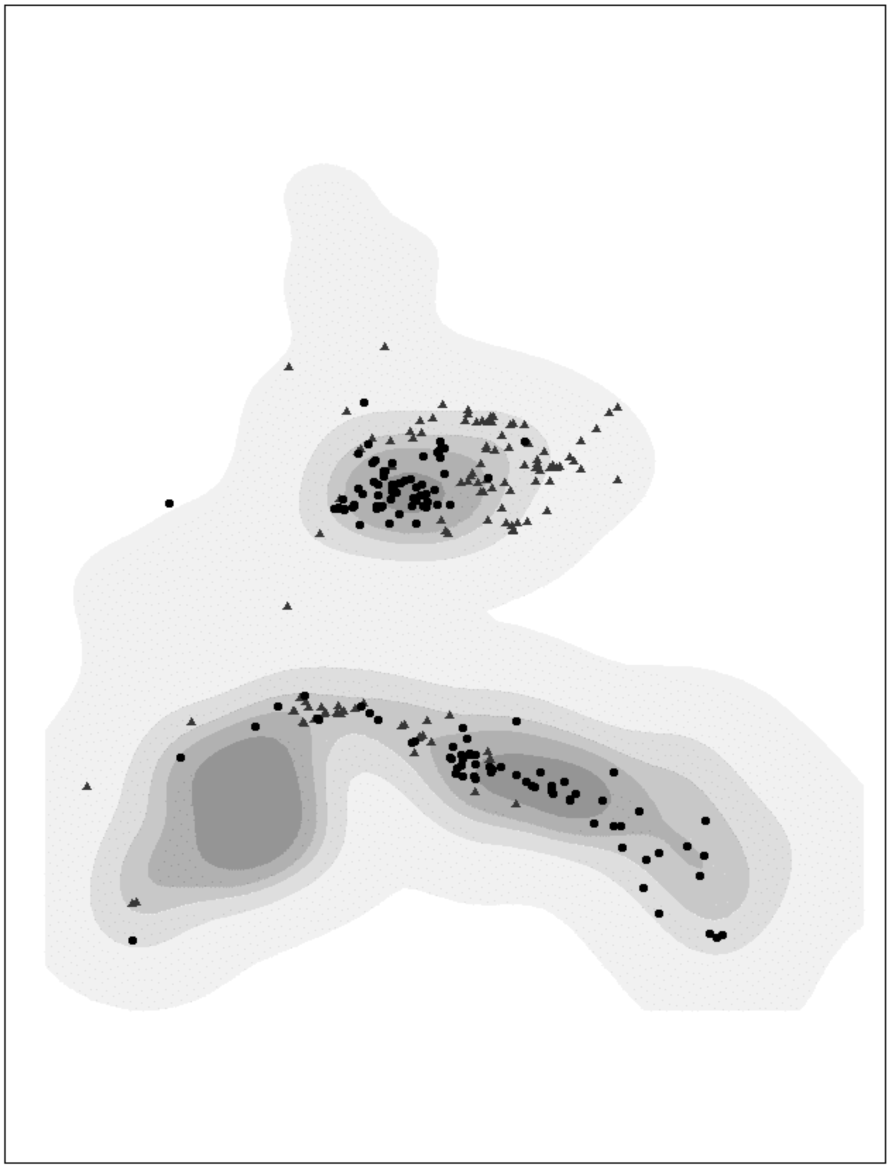
Spring wolf kills were found in a wide range of elk density with only 21% in areas of mid or high density (Figure 3). At the kill site, terrain roughness and slope were the primary loading variables in PC1 (variation 39.8%) indicating greater roughness and steeper slopes at sites associated with this component. Again, PC1 primarily loaded on terrain roughness and slope within the kill vicinities and was indicative of less roughness and slope. Within the kill areas, PC1 (variation 50.2%) loaded largely on slope and elevation indicating less slope, and lower elevation. Random areas or kill areas positively associated with PC1 had less slope, elevation, roughness and canopy cover, and higher elk density.

Wolf kill sites were only half as likely to be associated with PC1 as were random sites, but kill vicinities were nearly twice as likely to be associated with PC1 than random vicinities (Table 3). Wolf kill areas were more than 1.5 times as likely to be associated with PC1 as random areas (Table 3). Again, the Goodman-Kruskal Gamma measure of association indicated the models were good measures of association at all three spatial scales (Table 3).

Cougar

Winter

Conifer (42.2%) and open terrain (41.7%) were the most often-occurring vegetation categories at cougar kill sites. All vegetation types were used nearly equal to their availability with the exception of open terrain, which was used (41.7%) notably more than it was available (31.1%). Developed areas were not used, and were only marginally available (4.4%). Within the kill vicinities and kill areas, all vegetation categories were used nearly equal to their availability with the exception of developed areas, which were not used.



• Wolf kill sites

▲ Cougar kill sites

Figure 2. Winter wolf and cougar kill sites and elk density (0.8 h_{ref}) greater Jackson, WY. 1 December-31 March (1999-2006).

In winter, only 15% of kill sites were in mid-high or high elk density (Figure 2). At the kill site, the PC1 accounted for 31.1 % of the total variance (Table 4). Sites with positive association to this component had less terrain roughness and slope. Within the kill vicinity, the first principal component accounted for 36.6% of the variation. At the site and vicinity scales of analysis, all of the variables in the primary component were negative, except elk density, and loaded mainly on slope and terrain roughness. Areas positively with this component were had flatter, less rough terrain, lower elevation, and less canopy cover. Within the kill area, roughness, slope, and elevation largely described the first component accounting for 46.5% of the variance and were positively correlated. Thus, areas positively associated with this component tended to be rougher, steeper, and at higher elevations. Only the kill area results were significant according to the broken-stick criterion (Table 4). At all spatial scales, cougar kill sites were equally as likely to be associated with PC1 as random sites; Hosmer-Lemeshow goodness of fit tests indicate lack of fit at all three spatial scales (Table 5).

Spring

Similar to winter, elk density did not appear to be a major factor in spring cougar kill site selection with only 20% of kills found in areas with greater than low elk density (Figure 3). At the kill site and kill vicinity, PC1 loaded negatively on terrain roughness and slope indicating sites associated with this component having less roughness and slope (Table 4). Inside the kill area, slope and elevation were the primary loading variables with PC1 accounting for 47.2% of the variation (Table 4), indicating areas associated with this component having lower slope and elevation. Both the kill vicinity and kill area results were significant according to the broken-stick criterion. The logistic regression indicated cougar kill locations were approximately 1.3 times more likely to be associated with PC1 than random locations at all spatial scales (Table 5). The Goodman-Kruskal Gamma test indicated less than adequate fit for the kill site and kill vicinity and a moderate fit for the kill area (Table 5).

Table 4. Principal component loadings for habitat variables associated with cougar kill sites and random sites, winter and spring, greater Jackson area, 1999-2006.

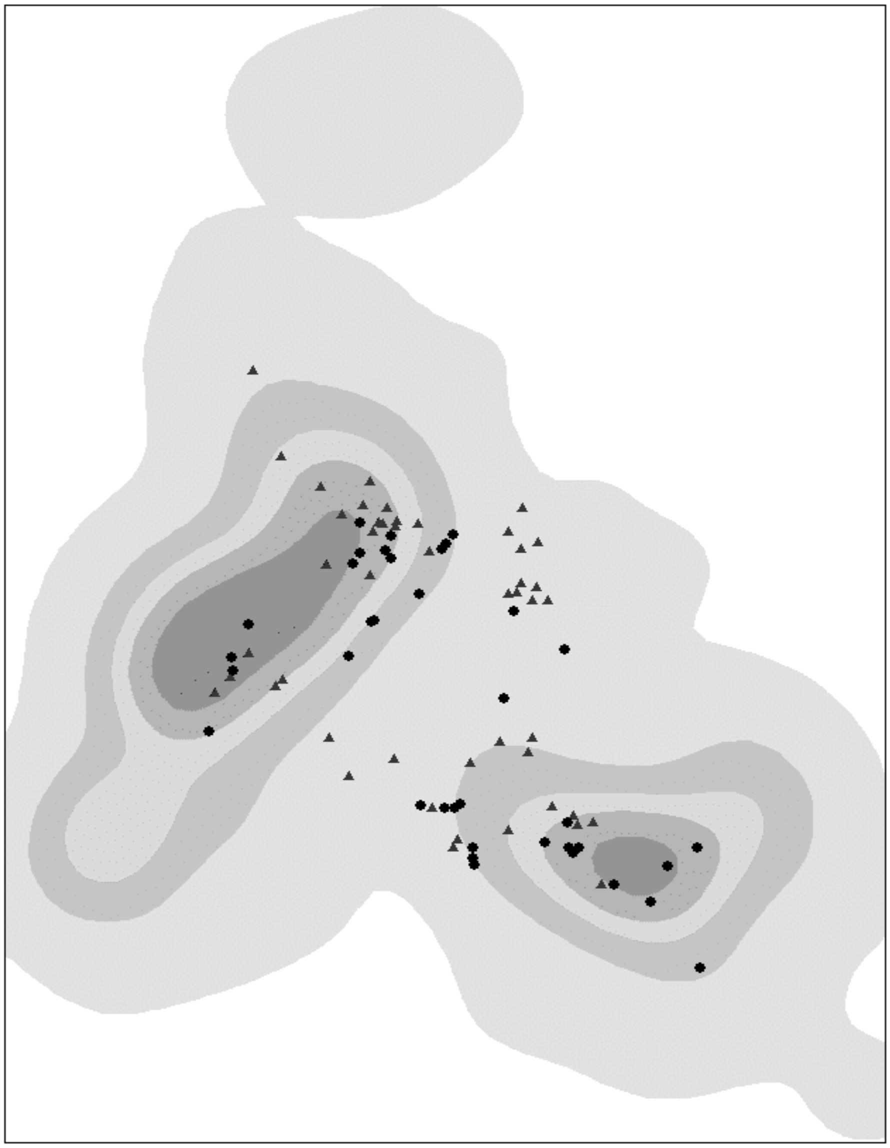
	Cougar-random winter			**Cougar-random spring**		
		PC1			**PC1**	
	Pt.	50 m	1 km	Pt.	50 m	1 km
Eigenvalue	2.18	2.20	2.79	2.55	**2.69**	**2.83**
Broken stick	2.59	2.45	**2.45**	2.59	**2.45**	**2.45**
% Variance	31.1	36.6	46.5	36.4	44.9	47.2
Variables						
Terr. roughness	-0.571	-0.575	0.492	-0.567	-0.532	-0.460
Canopy cover	-0.319	-0.307	0.342	-0.260	-0.239	-0.279
Aspect	-0.027	-0.018	-0.245	0.011	0.073	0.191
Slope	-0.599	-0.592	0.539	-0.583	-0.550	-0.530
Elevation	-0.452	-0.469	0.514	-0.477	-0.494	-0.526
Dist. To water	-0.061	N/A	N/A	0.182	N/A	N/A
Elk density	0.072	0.066	0.164	-0.102	0.329	0.342

Bold indicates retained component according to broken-stick.
Underline indicates factor loadings that contributed >10% to a particular component.

Table 5. Logistic regression models presenting the principal component analysis found to be significant in predicting cougar vs. random locations. Odds ratios and corresponding 95% confidence intervals for retained principal component analysis are provided; model significance determined via likelihood ratio test.

COUGAR WINTER							
Model	**Equation**	**O.R.**	**C.I.**	**p-value$_1$**	**HL**	**p-value$_2$**	**GKG**
Site							
Constant + PC1	g(x) = -0.81 + 0.08(PC1)	0.98	0.84-1.13	0.74	25.82	0.001	0.03
Vicinity							
Constant + PC1	g(x) = -0.81 + 0.04(PC1)	0.99	0.85-1.14	0.84	32.04	0.00	0.03
Area							
Constant + PC1	g(x) = 0.86 - 0.21(PC1)	1.12	0.98-1.27	0.10	46.14	0.00	0.14
COUGAR SPRING							
Site							
Constant + PC1	g(x) = -0.63 + 0.25(PC1)	1.29	1.00-1.65	0.04	12.67	0.12	0.19
Vicinity							
Constant + PC1	g(x) = -0.50 + 0.23 (PC1)	1.26	0.99-1.60	0.05	9.26	0.32	0.19
Area							
Constant + PC1	g(x) = -0.54 + 0.32 (PC1)	1.38	1.08-1.77	0.006	10.81	0.21	0.28

OR= odds ratio; CI= 95% confidence interval
HL=Hosmer-Lemeshow goodness-of-fit test (degrees of freedom =8)
GKG= Goodman-Kruskal Gamma measure of association
p-value$_1$=value associated with odds ratio
p-value$_2$=value associated with Hosmer-Lemeshow test



• Wolf kill sites

▲ Cougar kill sites

Figure 3. Spring wolf and cougar kill sites and elk density (0.75 h_{ref}), greater Jackson, WY. 1 April-31 May (1999-2006).

Seasonal comparison

At all landscape scales, seasonal comparisons of kill site characteristics showed few significant differences for both species. For wolves, the first principal component loaded primarily on roughness, slope, and elevation at all spatial scales (Table 6). For both species only the kill area results were significant according to broken-stick criterion. Odds ratios indicate equal likelihood of being winter or spring at all spatial scales for wolves. Cougar winter kill sites were more likely than random kill sites to be associated with PC1, but winter kill vicinities were less likely to be associated with PC1 than random vicinities. Goodman-Kruskal Gamma measures of association indicate poor model fit for wolves at all three scales. Moderate fit is indicated for cougar kill sites and kill vicinities; while within the kill areas, the measure of association indicates lack of fit (Table 7).

Table 6. Principal component loadings for habitat variables associated with winter and spring kill sites for wolves and cougars, greater Jackson area, 1999-2006.

	Wolf winter-spring			**Cougar winter-spring**		
	PC1			**PC1**		
	Pt.	50 m	1 km	Pt.	50 m	1 km
Eigenvalue	2.19	2.20	2.62	1.94	1.93	2.49
Broken stick	2.51	2.45	**2.45**	2.57	2.45	**2.45**
% Variance	31.3	36.7	43.6	27.7	32.1	41.6
Variables						
Terr. roughness	-0.590	-0.603	-0.497	0.663	-0.644	-0.488
Canopy cover	-0.152	-0.162	-0.332	-0.082	0.097	-0.345
Aspect	0.026	-0.048	0.089	0.071	-0.029	0.147
Slope	-0.597	-0.612	-0.555	0.659	-0.657	-0.522
Elevation	-0.462	-0.454	-0.542	0.276	-0.344	-0.527
Dist. To water	-0.212	N/A	N/A	0.191	N/A	N/A
Elk density	0.114	0.166	0.182	-0.043	0.158	0.266

Bold indicates retained component according to broken-stick.
Underline indicates factor loadings that contributed >10% to a particular component.

Table 7. Logistic regression models presenting the principal component analysis found to be significant in predicting wolf/cougar winter vs. spring kill sites. Odds ratios and corresponding 95% confidence intervals for retained principal component analysis are provided; model significance determined via the likelihood ratio test.

WOLF							
Model	**Equation**	**O.R.**	**C.I**	**p-value$_1$**	**HL**	**p-value$_2$**	**GKG**
Site							
Constant + PC1	g(x)=1.30-0.05(PC1)	1.05	0.83-1.34	0.69	3.89	0.87	0.04
Vicinity							
Constant + PC1	g(x)=1.28+0.06(PC1)	1.06	0.83-1.35	0.63	4.83	0.78	-0.00
Area							
Constant + PC1	g(x)=1.16+0.10(PC1)	1.10	0.88-1.38	0.39	7.07	0.53	0.03
COUGAR							
Site							
Constant + PC1	g(x)=0.92 +0.23(PC1)	1.26	0.98-1.63	0.06	10.38	0.24	0.21
Vicinity							
Constant + PC1	g(x)= 0.93–0.19(PC1)	0.82	0.64-1.06	0.13	8.35	0.40	0.19
Area							
Constant + PC1	g(x)=-0.89+0.06(PC1)	1.06	0.86-1.31	0.59	13.58	0.09	0.06

OR= odds ratio
CI= 95% confidence interval
HL=Hosmer-Lemeshow goodness-of-fit test (degrees freedom=8)
GKG=Goodman-Kruskal Gamma measure of association
p-value$_1$=value associated with odds ratio
p-value$_2$=value associated with Hosmer-Lemeshow test

Wolf to cougar

CART analysis

In the winter CART analysis, four of the seven predictor variables were deemed important in separating a wolf kill site from a cougar kill site: elk density, canopy cover, terrain roughness, and elevation (in order of importance). Elk density significantly outweighed all other variables in importance (Table 8). For example, a kill-site with mid, low-mid, or low elk density was sent to the right node (cougar kill; Figure 4). From here, roughness was evaluated; if the roughness was >30.5, the kill site was then evaluated using elevation. If the roughness was ≤ 30.5, the kill site was then again evaluated using elk density. Higher elk density and less canopy cover were indicative of a wolf kill site. The analysis correctly classified 80.5% of cougar kills and 81.1% of wolf kills.

In spring, five of the eight predictor variables were deemed important in separating wolf and cougar kill sites: elk density, terrain roughness, slope, distance to water, and canopy cover (in order of importance). Wolf kill sites were generally characterized by lower terrain roughness (≤21.5), higher elk density, lower canopy cover, and shorter distance to water compared to cougar kill sites (Table 8; Figure 5). Correct classification was 73.3% for cougars and 57.1% for wolves.

Table 8. CART analysis: Type of habitat variables and importance for wolf vs. cougar kill sites in winter and spring. Tree is pruned to minimum cross-validated error.

Variable	**Type**	**Importance winter**	**Importance spring**
Elk density	Categorical	100.00	100.00
Canopy cover	Categorical	37.51	17.45
Roughness	Continuous	25.19	96.46
Elevation	Continuous	18.26	N/A
Distance to water	Continuous	N/A	51.19
Aspect	Continuous	N/A	N/A
Slope	Continuous	N/A	51.62

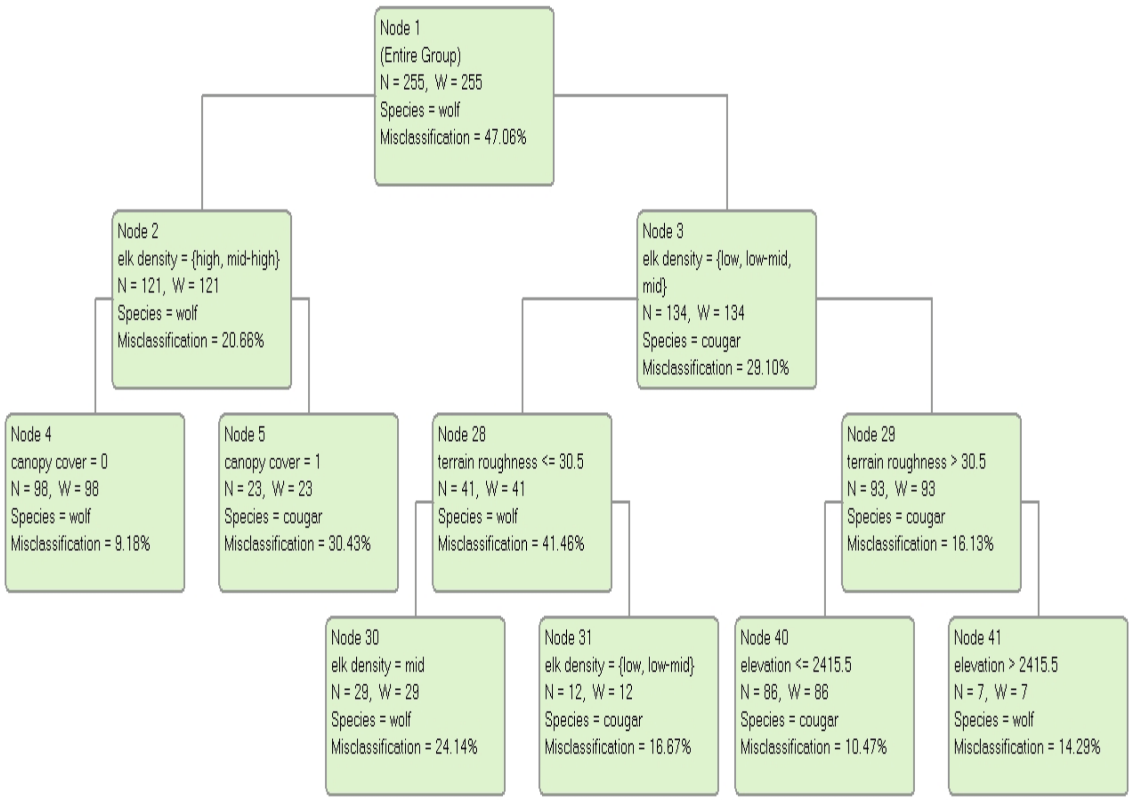


Figure 4. Single-tree CART analysis of wolf and cougar winter kill site characteristics (1 December- 31 March) greater Jackson, WY area. N= number of rows placed in node; W=sum of row weights (all rows weighted equally); Misclassification=percentage of rows misclassified

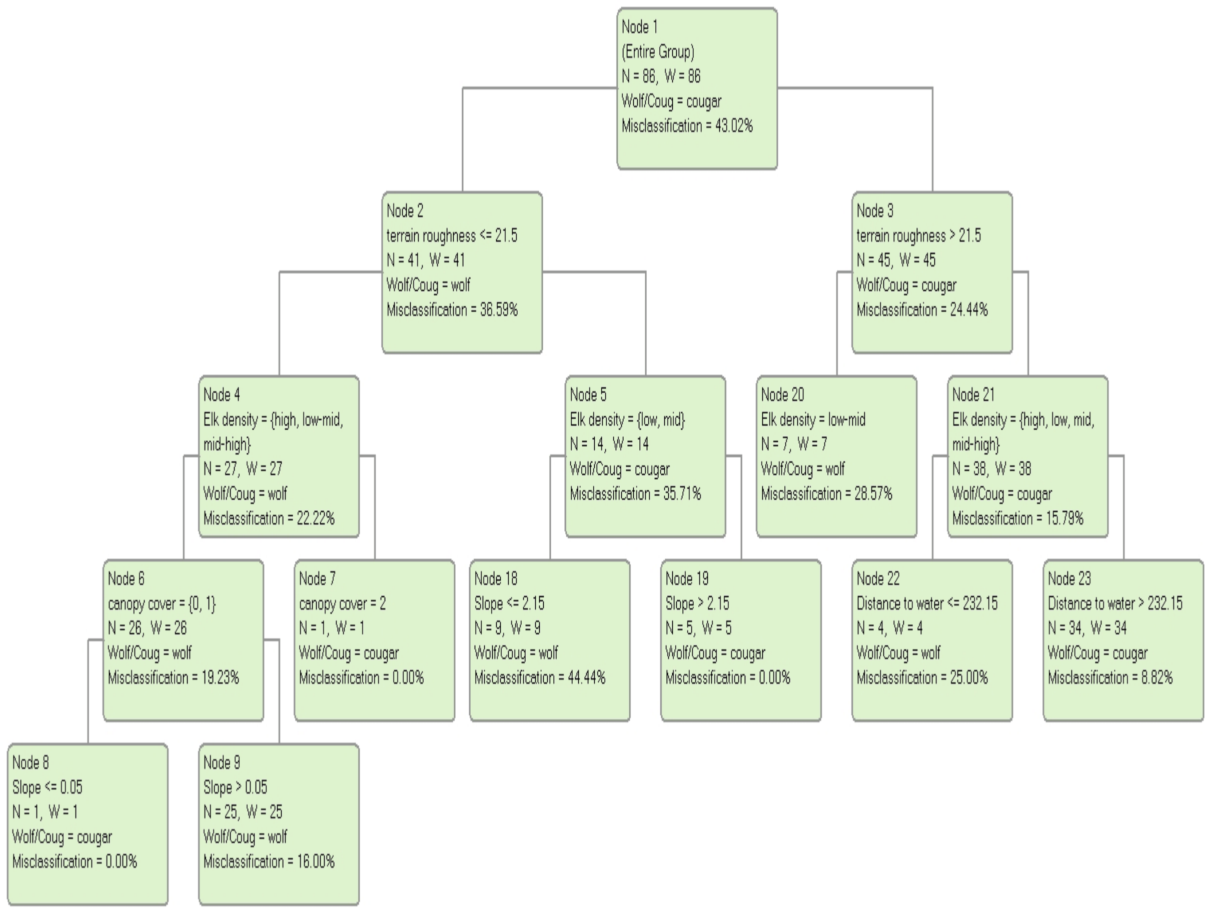


Figure 5. Single-tree CART analysis of wolf and cougar spring kill site characteristics (April 1-May 31), greater Jackson, WY area. N= number of rows placed in node; W=sum of row weights (all rows weighted equally); Misclassification=percentage of rows misclassified

Principal component analysis

Winter

When comparing wolf kill sites to cougar kill sites in winter, the first principal component accounted for 31.7% of the variation. The component loaded primarily on roughness and slope. Kill sites positively associated with this component were less rough and had higher elk density. Within the kill vicinities, PC1 explained 36.5% of the total variance; primary loading occurred on slope and terrain roughness. Sites positively associated with this component would have higher slope and elevation, more terrain roughness and canopy cover, and lower elk density. In the kill areas, PC1 primarily loaded on slope, elevation and terrain roughness and accounted for 41.3% of the total variance (Table 9). Sites positively associated with this component have lower slope, elevation, and terrain roughness. Kill area principal components were significant according to broken-stick criterion.

Wolf kill sites showed much stronger positive association with PC1 than cougar kill sites. Within the kill vicinities, wolf kill sites were only 1/3 as likely to be associated with PC1 as cougar kill sites. As indicated by the odds ratio (1.53) within the kill areas, wolf kills were 1.5 times more likely to be positively associated with PC1 as cougar kills (Table 10). Goodman-Kruskal Gamma summary measures indicate good model fit at kill sites and kill vicinities and adequate fit within kill areas (Table 10).

Table 9. Principal component loadings for habitat variables associated with wolf and cougar kill sites, winter and spring, greater Jackson area, 1999-2006.

	Wolf-cougar winter			**Wolf-cougar spring**		
		PC1			**PC1**	
	Pt.	50 m	1 km	Pt.	50 m	1 km
Eigenvalue	2.22	2.19	2.48	2.38	**2.54**	**2.97**
Broken stick	2.59	2.45	2.45	2.59	**2.45**	**2.45**
% Variance	31.7	36.5	41.3	34.0	42.2	52.2
Variables						
Terr. roughness	-0.576	0.552	-0.510	-0.592	-0.544	-0.471
Canopy cover	-0.260	0.260	-0.361	-0.125	-0.197	-0.322
Aspect	0.050	0.027	0.091	0.002	0.142	0.211
Slope	-0.604	0.600	-0.544	-0.569	-0.559	-0.498
Elevation	-0.293	0.323	-0.514	-0.469	-0.472	-0.508
Dist. To water	-0.097	N/A	N/A	0.078	N/A	N/A
Elk density	0.372	-0.403	0.203	-0.290	0.338	0.352

Bold indicates retained component according to broken-stick.
Underline indicates factor loadings that contributed >10% to a particular component.

Table 10. Logistic regression models presenting the principal component analysis found to be significant in predicting wolf vs. cougar kill sites. Odds ratios and corresponding 95% confidence intervals for retained principal component analysis are provided; and model significance determined via the likelihood ratio test.

WOLF VS COUGAR							
WINTER							
Model	**Equation**	**O.R.**	**C.I.**	**p-value$_1$**	**HL**	**p-value$_2$**	**GKG**
Site							
Constant + PC1	g(x) = 0.10 + 1.20(PC1)	3.31	2.50-4.38	<0.001	6.64	0.58	0.72
Vicinity							
Constant + PC1	g(x) = 0.10 - 1.26 (PC1)	0.28	0.21-0.38	<0.001	24.19	0.002	0.74
Area							
Constant + PC1	g(x) = -0.01 + 0.43(PC1)	1.53	1.27-1.84	<0.001	8.27	0.41	0.37
SPRING							
Site							
Constant + PC1	g(x) = -0.34 + 0.50 (PC1)	1.65	1.15-2.37	0.002	8.58	0.38	0.40
Vicinity							
Constant + PC1	g(x) = -0.30 + 0.44 (PC1)	1.56	1.12-2.17	0.004	7.67	0.47	0.39
Area							
Constant + PC1	g(x) = -0.27 + 0.17 (PC1)	1.19	0.92-1.54	0.18	11.33	0.18	0.19

OR= odds ratio; CI= 95% confidence interval
HL=Hosmer-Lemeshow goodness-of-fit test (degrees of freedom =8)
GKG= Goodman-Kruskal Gamma measure of association
p-value$_1$=value associated with odds ratio
p-value$_2$=value associated with Hosmer-Lemeshow test

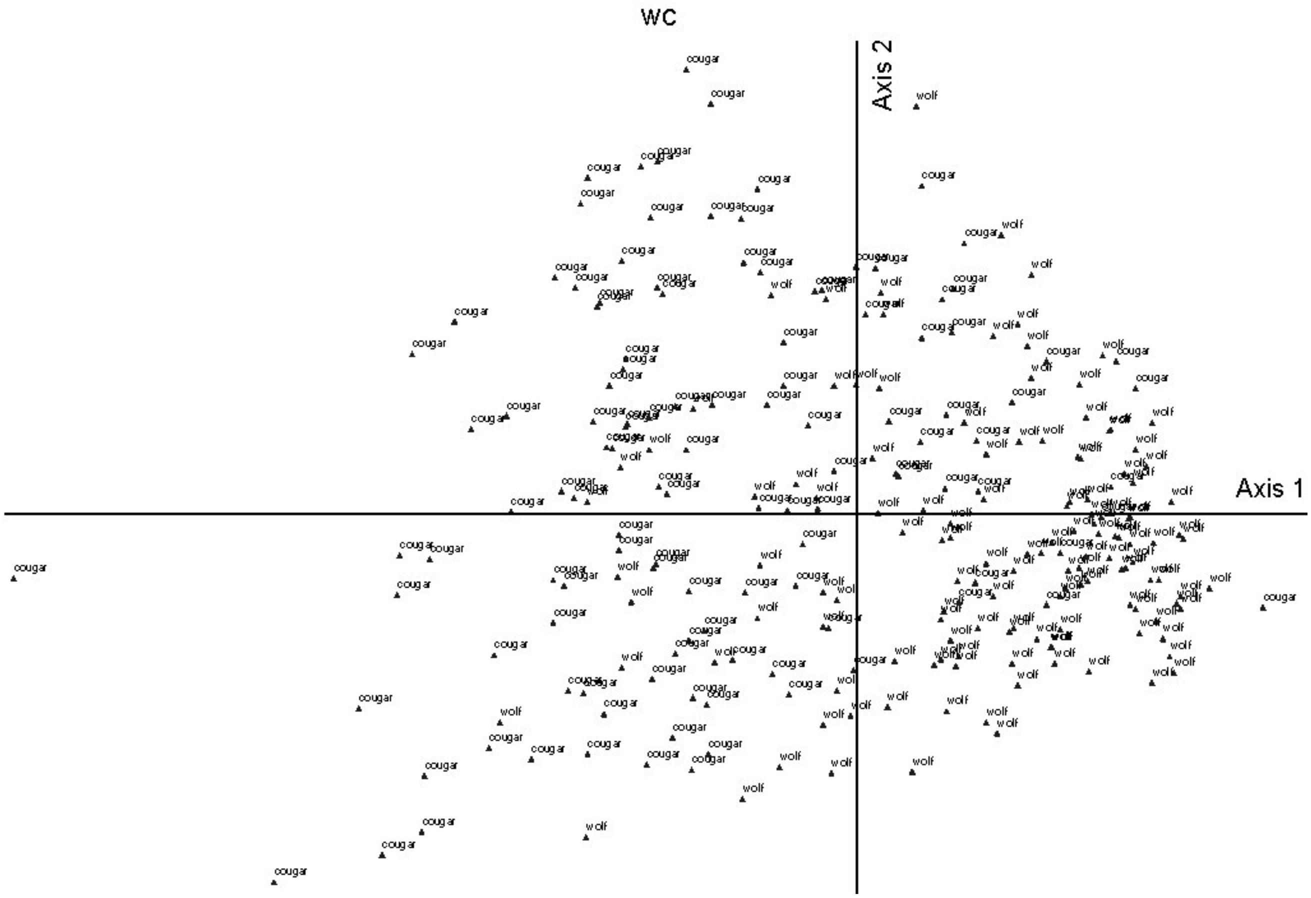


Figure 6. Scatter plot depicting the association of winter wolf and cougar kill sites with the first (x-axis) and second (y-axis) principal components, greater Jackson, WY. 1 December-31 March (1999-2006).

Spring

Comparing kill site characteristics for spring at all spatial scales, loading on PC1 was primarily on terrain roughness, slope and elevation. Sites/vicinities/areas with positive association with PC1 had less roughness, slope, elevation, and canopy cover. PC1 indicated lower elk density at sites, but higher elk density at vicinities and areas. PC1 accounted for 34.0%, 42.4%, and 52.2% of the variation at the kill site, vicinity, and area, respectively (Table 9).

At the site and vicinity, wolf kill locations were approximately 1.6 times more likely to be associated with PC1 as were cougar kill locations. At the area scale, wolf kill areas were only 1.2 times more likely to be associated with PC1 as cougar kill areas (Table 10). Goodman-Kruskal Gamma measures of association indicated good fit at kill sites and kill vicinities and moderate fit within kill areas (Table 10).

Teton pack vs. non-Teton packs

Comparing Teton pack kills and non-Teton pack kills, PC1 at all three spatial scales loaded primarily on terrain roughness, slope and elevation. At the kill site, PC1 accounted for 32.5% of the variation and was generally a positive loaded component. Within the kill vicinities and kill areas, the first principal components loaded negatively on terrain roughness, slope, and elevation and accounted for 36.2% and 41.5% of the variation (Table 11).

Table 11. Principal component loadings for habitat variables associated with Teton pack and non-Teton pack kill sites, winter and spring, greater Jackson area, 1999-2006.

	Teton vs. non-Teton		
	PC1		
	Pt.	50 m	1 km
Eigenvalue	2.27	2.17	2.49
Broken stick	2.59	2.45	2.45
% Variance	32.5	36.2	41.5
Variables			
Terr. roughness	<u>0.566</u>	<u>-0.626</u>	<u>-0.539</u>
Canopy cover	-0.046	0.028	<u>-0.323</u>
Aspect	0.024	-0.109	0.007
Slope	<u>0.603</u>	<u>-0.632</u>	<u>-0.570</u>
Elevation	<u>0.429</u>	<u>-0.421</u>	<u>-0.524</u>
Dist. To water	<u>0.353</u>	N/A	N/A
Elk density	-0.061	0.137	0.076

Bold indicates retained component according to broken-stick.
Underline indicates factor loadings that contributed >10% to a particular component.

Table 12. Logistic regression models presenting the principal component analysis found to be significant in predicting Teton pack vs. non-Teton pack kill sites. Odds ratios and corresponding 95% confidence intervals for retained principal component analysis are provided; and model significance determined via the likelihood ratio test.

Teton Pack vs. non-Teton packs							
WINTER							
Model	Equation	O.R.	C.I.	p-value$_1$	HL	p-value$_2$	GKG
Site							
Constant + PC1	g(x) = 1.08 + 0.37 (PC1)	1.44	1.05-1.98	<0.001	4.66	0.79	0.26
Vicinity							
Constant + PC1	g(x) = 1.10 - 0.25 (PC1)	0.78	0.58-1.06	<0.001	3.18	0.92	0.20
Area							
Constant + PC1	g(x) = 0.99 - 0.40 (PC1)	0.67	0.49-0.93	<0.001	4.42	0.82	0.28

OR= odds ratio
CI= 95% confidence interval
HL=Hosmer-Lemeshow goodness-of-fit test (degrees of freedom =8)
GKG= Goodman-Kruskal Gamma measure of association
p-value$_1$=value associated with odds ratio
p-value$_2$=value associated with Hosmer-Lemeshow test

Teton kill sites were 1.4 times more likely as non-Teton kill sites to be associated with PC1 at the kill sites, but less than 3/4 times as likely to be associated with respective PC1's within the kill vicinities and kill areas (Table 12). Goodman-Kruskal Gamma measures indicated moderate fit for all three spatial scales. We did not have enough spring kill data to perform a similar comparison.

DISCUSSION

Our results indicate while wolves and cougars in the greater Jackson area have overlapping areas of use and share a prey base, they use different types of habitat for hunting. We found little to no difference between wolf and cougar kill sites between seasons. We know of no other studies have been published on wolf and cougar kill site habitat selection in seasons other than winter. We note that our sample size for spring kill sites was much smaller than for winter kill sites and urge caution in interpreting our results on seasonal comparisons of wolf and cougar kill sites. Unless otherwise noted, this discussion will refer to winter data.

Wolf

Similar to findings of other wolf predation studies (Kunkel and Pletscher 2000; Husseman et al. 2003; Kunkel et al. 2004), we found kill sites were not randomly selected for wolves. Wolf kills were most likely to occur in open terrain or riparian areas; wolves appear to select against conifer and mixed forest, using them much less than available. We detected a difference between wolf kill locations and random locations at all spatial scales—site, vicinity (50 m), and area (1 km). During winter, odds ratios (odds ratio of 1 indicates equal likelihood) indicated wolves used habitat with higher elk density, less terrain roughness, slope and canopy cover, and lower elevation compared to random habitat. Generally, these were areas of lower elevation with higher elk density. Wolves' coursing, cooperative hunting strategy of running prey to find and pursue the vulnerable individual is made easier by this type of habitat. We speculate that areas of high elk density were furthermore areas of high risk of predation by wolves. Our evidence suggests prey are less likely to be killed by wolves in areas of heavier cover, in more rough terrain, away from other prey (for elk), and on steeper slopes.

The CART analysis indicates elk density is a significant factor influencing kill site selection for wolves. This suggests kill site selection is perhaps influenced more strongly by prey availability than by other elements of the available habitat. Oakleaf et al. (2005) found a positive relationship between elk density and incidence of wolf kills; Paquet (1993), Jedrzejewska and Jedrzejewski (1998), and Alexander et al. (2006) suggest that density of elk/red deer drives prey selection by wolves. At the landscape level, wolves exhibit preference for areas of high elk density. However, within areas of high elk density, wolves tend to select terrain features that facilitate their pursuit style of hunting.

Teton Pack vs. non-Teton Packs

Until winter 2005-2006, we largely followed only one wolf pack (Teton pack) and located 80-85% of the winter kills made by that pack; most of the kill sites were from this pack. As number of wolf packs increased in 2006, we located as many kills as possible made by all accessible packs. Twenty-seven percent (*n*=36) of the total winter kills found were from other (non-Teton) packs. Due to known locations of radio-collared wolves, we were often able to determine which wolves made the kill and conclude that it was not always the same wolves. Thus, we can infer that the habitat selection of the kill sites reflects the tendencies of more than just a single pack, or even specific wolves in that pack. Additionally, comparisons of wolf kill sites not associated with a pack show similarities in kill site habitat, indicating habitat selection. Due to the few significant differences found between Teton and non-Teton kill sites, we believe we are justified in our characterization of wolf kill site habitat within our study area.

Cougar

We found little difference at any scale between cougar kill locations and random locations suggesting there may be other variables important to cougars, which were not included in our study. Ruth (2004) found cougars used vegetation types within their home ranges equal to their availability. Contrary to our predictions, cougar kills were nearly equally as likely to occur in open terrain (41.7%) as conifer (42.2%). While conifer areas were used in proportion to availability, open terrain was used considerably more. The nearly equal occurrence of cougar kills in conifer forest, as compared to open terrain, indicates cougars are not likely selecting for high elk density, as elk are less likely to be found in conifer forest and more likely to be found in open terrain. Jedrzejewska and Jedrzejewski (1998) suggest tiger kill sites in Poland exhibited no pattern of higher ungulate density. We conclude prey are more likely to be killed by cougars away from other prey, on rougher, steeper terrain.

At all spatial scales, odds ratios in spring indicated cougar kill sites had somewhat *less* roughness, slope, and elevation than random sites, contrary to our predictions. Seasonal comparison indicated small differences between winter and spring kill sites and vicinities; winter kill sites and vicinities had slightly higher terrain roughness, more slope, and were found at higher elevation than spring kill sites. We surmised winter kill locations would be found at lower elevation due to ungulates selecting lower elevations with shallower snow (Miller et al. 1981; Kauffman et al., in review; Greenwood, date unknown).

Due to cougars' solitary, stalk and ambush hunting strategy and relatively short kill sequence, we expected to find considerable differences in habitat at kill locations compared to random locations, especially at the site scale. However, we did not detect a difference between cougar kill locations and random locations at any spatial scale. We presumed surprising and killing prey was made easier by greater canopy cover, steeper slopes, and more rough terrain. Cougars are possibly selecting at micro-habitat scale, smaller than what we measured.

Wolf vs. cougar

Spatially, wolf and cougar kills occurred in close proximity (see Figures 4 and 5), and study animals of both species were regularly found near each other. Ruth et al. (2003) found wolves use areas with more open canopy and less rough terrain, while cougars generally use areas with more closed canopy, rougher terrain, and even cliffs. Although we found little difference between cougar kill locations and random locations, differences between wolf and cougar kill habitats were significant. We conclude that within our study area, sympatric wolves and cougars do not use the same habitat types for hunting. As we speculated, wolf kills were more likely to be found in less rough, open canopy areas conducive to extended chases. Likewise, areas of rougher terrain with greater canopy cover afford cougars the advantage for their ambush style of hunting.

Similar to other studies, (Ruth and Hornocker 1996; Murphy et al. 1999), we found indications of wolves scavenging, usurping, or investigating cougar kills (9% of winter kills); conversely, there were a few instances of cougars visiting wolf kills (<1%). The differing hunting habitat for wolves and cougars may be an avoidance mechanism. Interactions between wolves and cougars generally favor wolves (Ruth and Hornocker 1996; Murphy et al. 1999). Due to the higher incidence of wolves killing cougars, than cougars killing wolves, (White and Boyd 1989; Boyd and Neale 1992; Boyd et al. 1994; Jimenez et al. in review), cougars may hunt in different habitat to avoid wolves. In a track density study, Alexander et al. (2006) suggest wolves and cougars directly avoid one another.

We removed all kill sites on the Wyoming Game and Fish elk feedgrounds to minimize bias. Our assumption was elk choose the feedgrounds for the available food and not for habitat purposes; thus predators are also not selecting for habitat, but for large gatherings of habituated elk. Habitat preference models for elk in the Rocky Mountains indicate as snow depths increase in winter, elk move from the higher elevations to valleys and foothills where there is increased forage and typically less snow. Year-round, elk favor sagebrush flats and grassland/forest vegetation areas out of sight of major roads (Miller et al. 1981; Kauffman et al., in review; Greenwood, date unknown). In spring, elk density at kill sites decreased for both species. Increased access to grazing areas due to snow melt, coupled with new spring vegetation growth likely causes the decreased elk concentration. Elk also begin to migrate toward calving grounds during this time.

In the course of the seven-year study, we noted patterns in wolf and elk behavior. Multiple elk would be killed before the herd moved out of the area for a short time. At this point the wolves also left in search of other prey. The elk eventually returned, as did the wolves. In some winters this occurred almost weekly, while in others wolves would spend nearly a month in an area before the elk would move out. This pattern is similar to findings by Greenwood and Swingland (1983) and Bergman et al. (2006) in which predators vacate a recently hunted area to allow prey behavior to return to normal. Murie (1944) and Bibikov (1982) maintain that wolves do not give chase when prey runs uphill. We also observed a general tendency for prey to run downhill and toward areas of greater cover when pursued by wolves. Often snow is deeper at the bottom of the hill, due to reduced wind scouring and increased snow deposition there, resulting in conditions more conducive to prey capture. On the other hand, prey pursued by cats tend to run toward open areas (P. Buotte, personal communication). It has been suggested that wolves have had insufficient time (1995-2006) to become wholly integrated into the Yellowstone ecosystem, particularly in the behavioral responses of prey and competitors. Tests conducted on moose in Alaska and Wyoming from 1995-2000 indicated a greater fear response in Alaska where wolves were never extirpated (Berger et al. 2001). In the

Gallatin drainage of Yellowstone National Park, Creel et al. (2005) found elk move to areas of greater cover and protection when wolves are in the vicinity. This evidence of anti-predator behavior in elk indicates some progress toward the integration of wolves into the predator-prey dynamics of the greater Yellowstone ecosystem.

Continued research

This study was an initial step in understanding wolf and cougar habitat preferences in the southern Yellowstone ecosystem. Continued experimentation with GPS collars will likely fill significant missing gaps in our understanding (i.e., year round data collection). Specific home range data for individual cougars would greatly increase the accuracy of use vs. availability data as well. Additionally, a resource selection function specific to the prey base would provide greater understanding of predator behavior as it pertains to hunting and habitat selection. Given the overlapping use of habitat and prey, interspecific competition between sympatric wolves and cougars is inevitable and warrants greater study. Only with more intensive studies, will we better understand the full extent of interactions between these sympatric predators.

LITERATURE CITED

Acorn, R.C. and M.J. Dorrance. 1990. Methods of investigating predation of livestock. Alberta Agriculture Crop Protection Branch. Edmonton, Alberta.

Ballard W.B., L.A. Ayres, K.E. Roney, and T.H. Spraker. 1991. Immobilization of gray wolves with a combination of tiletamine hydrochloride and zolazepam hydrochloride. Journal of Wildlife Management 55:71-74.

Bangs, E.E. and S.H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin 24(3):402-413.

Berger, J., P.B. Stacey, L. Bellis, and M.P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications 11(4):947-960.

Berger, J., J.E. Swenson, and I.L. Persson. 2001. Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. Science 9(291):1036-1039.

Bergman, E.J., R.A. Garrott, S. Creel, J.J. Borkowski, R. Jaffe and F.G.R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16(1):273-284.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Bibikov, D.I. 1982. Wolf ecology and management in the USSR. Pages 120-133 in F.H. Harrington and P.C. Paquet, editors. Wolves of the world. Noyes Publications, Park Ridge, New Jersey.

Boyd, D.K. and G.K. Neale. 1992. An adult cougar, Felis concolor, killed by gray wolves, Canis lupus, in Glacier National Park, Montana. Canadian Field-Naturalist 106:524-525.

Boyd, D.K., R.R. Ream, D.H. Pletscher, and M.W. Fairchild. 1994. Prey taken by colonizing wolves and hunters in the Glacier National Park area. Journal of Wildlife Management 58:289-295.

Breiman, L., J.H. Friedman, R.A. Olshen, and C.J. Stone. 1984. Classification and regression trees. Chapman & Hall, New York.

Bunnell, S.D., G.J. Wolfe, and D.K Crockett. 2002. Recreational use of elk. Pages 701-748 *in* D.E. Towell and J.W. Thomas, editors. North American elk; ecology and management. Smithsonian Institution Press and Wildlife Management Institute, Washington, D.C.

Busch, R.H. 1996. The cougar almanac: a complete natural history of the mountain lion. Lyons and Burford Publishers, New York, NY.

Clark, T.W., R.P. Reading, and A.L. Clarke. 1994. Endangered species recovery: finding the lessons, improving the process. Island Press, Washington D.C.

Creel, S. J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86(12):3387-3397.

Dickson, B.J. and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66(4):1235-1245.

Dean, R., M. Gocke, B. Holz, S. Kilpatrick, T. Kreeger, DVM, B. Scurlock, S. Smith, E.T. Thorne, DVM, and S. Werbelow. 2004. Elk feedgrounds in Wyoming. Wyoming Game and Fish Department, Cheyenne, WY.

Estes, R.D. and J. Goddard. 1967. Prey selection and hunting behavior of the African wild dog. Journal of Wildlife Management 31:52-70.

Greene, C.H. 1986. Patterns of prey selection: implications of foraging tactics. American Naturalist 128:825-839.

Greenwood, D. Date unknown. Cattle and elk interaction: Competition and possible benefits. http://www.cnr.uidaho.edu/range456/hot-topics/elk-cattle.htm#Habitat%20Preferences

Greenwood, P.J. and I.R. Swingland. 1983. The ecology of animal movement. Oxford University Press, New York, New York.

Heezen, K. L. and J. R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. Journal of Wildlife Management 31:124-141.

Homer, C.G. 1998. Idaho/western Wyoming landcover classification raster digital data. Department of geography and earth resources, Utah State University, Logan, Utah.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54(2):187-211.

Husseman, J.S., D.L Murray, G. Power, C. Mack, C.R. Wegner, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101:591-601.

Jedrzejewska, B. and W. Jedrzejewski. 1998. Predation in vertebrate communities: The Bialowieza Primeval Forest as a case study. Springer-Verlag, New York, New York.

Jimenez, M.D., S.P. Woodruff, S. Cain, and S. Dewey. 2005. Wolf/elk interaction on winter range and state managed feed grounds in Wyoming. 2005 Progress Report. US Fish and Wildlife Service, Washington, DC.

Jimenez, M.D., S.P. Woodruff, E.E. Bangs, S. Cain, and S. Dewey. 2006. Annual predation patterns of wolves near Jackson, Wyoming. Proceedings of Wildlife Society Annual Meeting, Laramie, WY.

Jimenez, M.D., V.J. Asher, E.E. Bangs, and S.P. Woodruff. In review. Wolves killed by cougars and a grizzly bear in the northern Rocky Mountains, U.S.A. Canadian Field-Naturalist.

Kauffman, M.J., J.N. Varley, D.W. Smith, D.R. Stahler, D.R. MacNulty, and M.S. Boyce. In review. Competition for optimal hunting grounds decouples predation risk from predator distribution in a wolf-elk system.

Kreeger, T.J., Arnemo, J.M., and J.P. Raath. 2002. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins, Colorado, U.S.A.

Kruuk, H. 1968. Interactions between felidae and their prey species: a review. Pages 353-374 in Miller, S.D. and D.D. Everett (eds.), Cats of the world. National Wildlife Federation, Washington, D.C. pp 353-374.

Kunkel, K.E. 1997. Predation by wolves and other large carnivores in northwestern Montana and southeastern British Columbia. Ph.D. thesis, University of Montana, Missoula.

Kunkel, KE, and DH Pletscher. 2000. Habitat factors affecting vulnerability of moose predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78:150-157.

Kunkel, K.E., and D.H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65(3):520-530.

Kunkel, K.E , D.H. Pletscher, D.K. Boyd, R.R. Ream, and M.W. Fairchild. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park. Journal of Wildlife Management 68(1):167-178.

Kunkel, K.E., T.K. Ruth, D.H. Pletscher, and M.G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. Journal of Wildlife Management 63:901-910.

McCune, B. and M.J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MJM Software Design, Glenden Beach, OR.

McIntyre, R. 1995. War against the wolf: America's campaign to exterminate the wolf. Voyageur Press, Stillwater, Minnesota.

Mech. L.D. 1970. The wolf: the ecology and behavior of an endangered species. Natural history press, Garden City, New York.

Mech, L. D. 1974. Current techniques in the study of elusive wilderness carnivores. Pages 315-322 in Proceedings of XIth International Congress of Game Biologists, Stockholm, Sweden, 3-7 September 1973. Edited by I. Kjerner and P. Bjurholm. Swedish National Environment Protection Board, Stockholm.

Mech, L.D. 1983. A handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, MN. Mech, L.D. 1996. A new era for carnivore conservation. Wildlife Society Bulletin 24(3):397-401.

Mech, L.D. 1989. Wolf population survival in an area of high road density. American Midland Naturalist 121:387-389.

Mech, L.D. 1995. The challenge and opportunity of recovering wild populations. Conservation Biology 9:270-278.

Mech, L.D., S.H. Fritts, G.L. Radde, and W.J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin 16:85-87.

Mech, L.D., D.W. Smith, K.M. Murphy, and D.R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65(4):998-1003.

Miller, R.F., W.C. Krueger, and M. Vavra. 1981. Deer and elk use on foothill rangelands in northeastern Oregon. Journal of Range Management 34(3):201-204.

Minitab. 1998. Release 12.1 for Windows. Minitab Inc., State College, Pennsylvania.

Mladenoff, D.A., T.A. Sickley, R.G. Haight, and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9(2):279-294.

Murie, A. 1944. The wolves of Mount McKinley. Fauna of the national parks of the U.S., Fauna Series, No. 5. U.S. Government Printing Office, Washington, D.C.

Murphy, K.M. 1998. The ecology of the cougar (*Puma concolor*) in the Northern Yellowstone Ecosystem: interactions with prey, bears, and humans. Dissertation. University of Idaho, Moscow, Id.

Murphy, K. M., P. I. Ross, and M. G. Hornocker. 1999. The ecology of anthropogenic influences on cougars. Pages 77–101 in T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Murray, D.L. S. Boutin, M. O'Donoghue, and V.O. Nams. 1995. Hunting behavior of a sympatric felid and canid in relation to vegetative cover. Animal Behavior 50:1203-1210.

Parsons, D.R. 2003. Natural history characteristics of focal species in the New Mexico highlands wildland network. Wildlands Project, Richmond, VT.

Paquet, P. C. 1993. Ecological studies of recolonizing wolves in the central Canadian Rocky Mountains. Unpublished report by John/Paul and Associates for the Canadian Parks Service, Banff, Alberta.

Paquet, P., C., J. Wierczhowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 *in* Green, J., C. Pacas, S. Bayley, and L. Cornwell. (eds.). A cumulative effects assessment and futures outlook for the Banff Bow Valley. Department of Canadian Heritage, Ottawa, ON.

Quigley, K. 1997. Immobilization and biological sampling protocols. Hornocker Wildlife Institute, Moscow, Idaho.

Ream, R. R., M. W. Fairchild, D. K. Boyd, and D. H. Pletscher. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349-366 in R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone ecosystem, redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut.

Riley, S.J., S.D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23-27.

Riley, S.J., G.M. Nesslage and B.A Maurer. 2004. Dynamics of early wolf and cougar eradication efforts in Montana: implications for conservation. Biological Conservation, In press.

Ripple, W.J. and R.L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299-313.

Ripple, W.J. and R.L. Beschta. 2004a. Wolves and the ecology of fear: can predation risk structure ecosystems? Bioscience 54(8):755-766.

Ripple, W.J. and R.L. Beschta. 2004b. Wolves, elk, willows and trophic cascades in the Upper Gallatin Range of southwestern Montana, USA. Forest Ecology and Management 200:161-181.

Ruth, T.K. 2000. Cougar-wolf interactions in Yellowstone National Park: competition, demographics, and spatial relationships. Annual progress report, Hornocker Wildlife Institute, Bozeman, MT.

Ruth, T.K. 2004. Patterns of resource use among cougars and wolves in northwestern Montana and southeastern British Columbia. Dissertation, University of Idaho, Moscow, Idaho.

Ruth, T.K. and M.G. Hornocker. 1996. Interactions between cougars and wolves (and a bear or two) in the north fork of the Flathead River, Montana. [Abstract]. Fifth Mountain Lion Workshop. Organized by the California Department of Fish and Game and the Southern California Chapter of the Wildlife Society, San Diego, California, February 27 - March 1, 1996.

Ruth, T.K., D.W. Smith, M.A. Haroldson, P.C. Buotte, C.C. Schwartz, H.B. Quigley, S. Cherry, K.M. Murphy, D. Tyers, and K. Frey. 2003. Large-carnivore response to

recreational big-game hunting along the Yellowstone National park and Absaroka-Beartooth Wilderness boundary. Wildlife Society Bulletin 31(4):1-12.
Sand, H, B. Zimmerman, P. Wabakken, H. Andren and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate systems. Wildlife Society Bulletin 33: 914-925.
Sherrod, P.H. 2004. DTREG: Classification and regression trees and support vector machines for predictive modeling and forecasting. www.dtreg.com
Sheskin, D.J. 2003. Handbook of parametric and nonparametric statistical procedures, 3rd edition. Taylor and Francis CRC Press.
Sweanor, L.L., K.A. Logan, and M.G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798-808.
Teton Cougar Project. 2004. 2003 Annual report. Beringia South, Kelly, WY.
US Fish and Wildlife Service. 1987. Northern rocky mountain wolf recovery plan. US Fish and Wildlife Service, Denver, CO.
US Fish and Wildlife Service, Nez Perce Tribe, National Park Service, Montana Fish, Wildlife, and Parks, Idaho Fish and Game, and USDA wildlife Services. 2005. Rocky mountain wolf recovery 2004 annual report. D. Boyd, ed. USFWS Ecological Services, Helena, MT.
Van Dyke, F.G., R.H. Brocke, and H.G. Shaw. 1986. Use of road track counts as indices of mountain lion presence. Journal of Wildlife Management 50:102-109.
Wade, D.A. and J.E. Brown. 1982. Procedures for evaluating predation of livestock and wildlife. Texas Agricultural Extension Service, San Angelo, Texas.
Walker, R. and L. Craighead. 1997. Least-cost-path corridor analysis: Analyzing wildlife movement corridors in Montana using GIS. Proceedings for the 1997 ESRI User's conference.
Wells, M.C. and M. Bekoff. 1982. Predation by wild coyotes: behavioral and ecological analyses. Journal of Mammalogy 63:118-127.
White, P.A. and D.K. Boyd. 1989. A cougar, Felis concolor, kitten killed and eaten by gray wolves, Canis lupus, in Glacier National Park, Montana. Canadian Field-Naturalist 103:408-409.
White, G. C. and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc., San Diego.
Williams, J.S., J.J. McCarthy, and H.D. Picton. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. Intermountain Journal of Sciences 1:16-28.
Wydeven, A.P., D.J. Mladenoff, T.A. Sickley, B.E. Kohn, R.P. Thiel and J.L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great lakes region. Endangered Species Update 18(4):110-114.