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ARTICLE

Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem

T.D. Bartnick, T.R. Van Deelen, H.B. Quigley, and D. Craighead

Abstract: We examined predation habits of cougars (*Puma concolor* (L., 1771)) following the recent recovery of gray wolves (*Canis lupus* L., 1758) in the southern Greater Yellowstone Ecosystem. With the extirpation of wolves in the early 20th century, cougars likely expanded their niche space to include space vacated by wolves, and increased use of habitat better suited to the foraging of a coursing predator, like wolves. We predicted that as wolves recolonized their former range, competitive exclusion would compel cougars to cede portions of niche space occupied in the absence of wolves. To examine this hypothesis, we radio-tracked cougars and examined their predation sites from winter 2000–2001 through summer 2009. Variation in foraging by cougars was associated with increasing wolf presence. As wolf numbers increased and the mean distance between wolf pack activity centers and cougar predation sites decreased, cougars made kills at higher elevations on more north-facing slopes during summer and in more rugged areas during winter. In addition, cougars preyed on a higher proportion of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), consistent with predictions of exploitative competition with wolves. Observed changes in predation characteristics reflect differences in predation strategy between cougars and wolves, given that wolves are coursing predators and cougars are ambush predators. These possible predation effects should be considered when developing management strategies in systems where the recolonization of wolves may occur.

Key words: *Canis lupus*, cougars, competition, predation, *Puma concolor*, radio telemetry, recolonization, wolves, Wyoming.

Résumé : Nous avons examiné les habitudes de prédation des pumas (*Puma concolor* (L., 1771)) dans la foulée de la découverte récente de loups gris (*Canis lupus* L., 1758) dans la partie sud de l'écosystème du Grand Yellowstone. La disparition des loups au début du 20e siècle a vraisemblablement permis aux pumas d'élargir leur niche pour y inclure des aires laissées libres par les loups et d'accroître leur utilisation d'habitats mieux adaptés à un prédateur privilégiant la poursuite, comme le loup. Nous avons prédit que, à mesure que les loups se rétablissent dans leur aire de répartition antérieure, l'exclusion concurrentielle obligerait les pumas à céder des parties de leur niche occupées en l'absence des loups. Pour évaluer cette hypothèse, nous avons suivi des pumas par radiotélémétrie et examiné leurs lieux de prédation de l'hiver 2000–2001 à l'été 2009. Des variations sur le plan de la quête de nourriture par les pumas sont associées à la présence croissante des loups. À mesure que le nombre de ces derniers augmente et que la distance moyenne entre les centres d'activité de meutes de loups et les lieux de prédation des pumas diminue, ces derniers tuent leurs proies à plus grande élévation, sur des pentes d'orientation plus septentrionale durant l'été et dans des secteurs plus accidentés en hiver. En outre, les cerfs mulets (*Odocoileus hemionus* (Rafinesque, 1817)) représentent une proportion croissante des proies des pumas, ce qui concorde avec la prédiction d'une concurrence avec les loups pour l'exploitation des ressources. Les changements des caractéristiques de prédation observés reflètent les différentes stratégies de prédation des pumas et des loups, ces derniers étant des prédateurs qui poursuivent leurs proies alors que les pumas chassent par embuscade. Ces effets possibles de la prédation devraient être pris en considération dans l'élaboration de stratégies de gestion dans les systèmes où un rétablissement des loups pourrait avoir lieu. [Traduit par la Rédaction]

Mots-clés : *Canis lupus*, pumas, concurrence, prédation, *Puma concolor*, radiotélémétrie, rétablissement, loups, Wyoming.

Introduction

Populations of cougars (*Puma concolor* (L., 1771)) and wolves (*Canis lupus* L., 1758) have been recovering in many regions of western North America because of successful conservation efforts, reintroduction programs, and improved management practices by wildlife professionals (Bangs et al. 1998; Smith et al. 2003; Cougar Management Guidelines Working Group 2005; USFWS et al. 2008). Population recovery has varied regionally and through different degrees of effort. Varying rates of recolonization have allowed some populations of cougars to occupy formerly sympatric ranges as the sole apex predator in the absence of wolves. In addition, the expansion of formally absent predators into areas with naïve prey could cause some prey species to be more susceptible to predation risk (Berger et al. 2001). Heterogeneous recovery patterns of large predator populations provides natural experiments allowing researchers to observe dynamic ecosystems and gain further understanding of predator–prey and predator–predator relationships (Kunkel et al. 1999; Ruth 2000; Husseman et al. 2003; Kortello et al. 2007). Additional research efforts are needed to clarify responses of resident carnivores following wolf recolonization and expansion at the population level (Kortello et al. 2007).

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The dynamics of potentially competitive interactions between populations of large predators and their importance to conservation are largely unknown (Riley et al. 2004). Comprehensive, long-term studies of interspecific competition among large sympatric carnivores are difficult because large carnivores typically are elusive, wide-ranging, and generally occur in remote areas at relatively low densities (Beier 1993; Gese 2001). In the western US, cougars and wolves occupy vast, undeveloped, rugged terrain that makes research difficult. However, recent advances in technology and noninvasive sampling methods (e.g., global positioning system (GPS) telemetry, smaller, faster, and more reliable electronic field tracking devices, remote cameras, advanced computer mapping software, and DNA analyses) have enabled researchers to study these species, their prey, and their ecological relationships in unprecedented detail (Gese 2001; Anderson and Lindzey 2003; Evans et al. 2006; Onorato et al. 2006; Stoner et al. 2006; Barber-Meyer et al. 2008; Knopff et al. 2009).

Research in the northern range of Yellowstone National Park suggests that wolves use areas with more open canopy and less rugged terrain, while sympatric cougars generally use areas with more closed canopy, and steeper, more rugged terrain, and even cliff faces (Murphy 1998; Ruth 2000; Ruth et al. 2003). Furthermore, in Montana and areas surrounding Banff National Park (Alberta, Canada), differences in hunting styles and adaptations for different habitats allowed sympatric wolves and cougars to occupy separate niches (Kunkel et al. 1999; Atwood et al. 2007; Kortello et al. 2007). Wolves use a coursing hunting strategy adapted to open areas where they encounter more prey and can effectively test herds of prey to assess vulnerability (Mech 1970). Cougars are ambush predators, and thus do not necessarily test their prey before an attack, and generally take as large a prey item as possible while reducing the amount of energy expenditure in the predation event (Murphy 1998; Kunkel et al. 1999; Husseman et al. 2003).

Previous studies in northwestern Wyoming have compared the characteristics of wolf and cougar kill sites to gain a better understanding of the different habitats used for hunting by ambush and coursing predators. Woodruff (2006) investigated winter kill site characteristics of wolves and cougars within the southern Greater Yellowstone Ecosystem (SGYE) and found that while wolves and cougars in the SGYE have overlapping areas of use and share a prey base, they use different habitat types for hunting. In particular, Woodruff found that wolves tend to frequent open areas with less topographical relief, whereas cougars occur in areas of rugged terrain and more complex vegetative structure.

The level of competition for resources between sympatric predators is fundamentally determined by the extent of spatial overlap (Kitchen et al. 1999). In multipredator, multiprey systems experiencing the reestablishment of a former top predator, the less-dominant predator may exhibit behavioral changes such as avoidance, niche or resource partitioning, changes in space-use patterns, and prey switching (Kunkel et al. 1999; Husseman et al. 2003; Kortello et al. 2007). Creel and Creel (1996) observed that the density of African wild dogs (*Lycaon pictus* (Temminck, 1820)) was limited in areas where spotted hyenas (*Crocuta crocuta* (Erxleben, 1777)) and lions (*Panthera leo* (L., 1758)) thrived. Less-able competitors, such as cheetahs (*Acinonyx jubatus* (Schreber, 1775)) in the African Serengeti, are more likely to seek out spatiotemporal refuges that may contain lower prey density, depending on the relative density and extent of competition with a higher ability competitor (Durant 1998).

In the absence of wolves during the middle to late 20th century, cougars presumably expanded their foraging niche and filled some areas of the vacated wolf niche, using resources previously unavailable due to competitive exclusion. Cougars likely did not abandon their ambush predatory strategy, but presumably were more apt to use some of the more-open, less-rugged habitat in the absence of wolves—the former top competitor. However, as wolves continue to reoccupy their stereotypical niche, competitive exclusion, resulting from exploitative and (or) interference competition should compel cougars to cede portions of their former range and contract their realized niche to one more typical of cougars (e.g., more structurally complex). Exploitive competition would be detectable as an increase in the effort cougars must expend for each prey item obtained in the presence of wolves, whereas interference competition would be evidenced by a change in foraging niche and prey composition associated with increasing wolf presence. The resulting shift in niche space may lead to changes in where and how often cougars spend their time hunting, and could also lead to a shift in their primary prey species, which would be reflected upon examination of their predation sites. We investigated whether changes in the predation characteristics of cougars could be attributed to the increasing presence of wolves on the landscape by analyzing population and spatial measures. We analyzed the characteristics of cougar predation sites from winter 2000 through summer 2009 during the expansion of the wolf population within a study area in northwestern Wyoming. Our goal was to investigate the following predictions: (i) cougars will exhibit shifts in the use of foraging habitat in the direction of habitat more favorable for ambush predation (i.e., denser cover, more-rugged terrain) in the presence of an expanding wolf population; (ii) cougars will exhibit shifts in the overall composition of prey items killed (i.e., preying disproportionately on a secondary prey species) as an effect of increasing wolf presence on the landscape.

Study area

Our study was part of a larger study of cougar ecology known as the Teton Cougar Project (TCP). The TCP study area covered approximately 2300 km² within the SGYE. Study area boundaries included Grand Teton National Park (GTNP) and the Teton mountain range representing the western border; a southern boundary extending from Wilson, Wyoming, east to the Cache Creek drainage and continuing northeast of Cache Creek into the upper Gros Ventre drainage; an eastern boundary beginning around Soda Lake and continuing north to the Togwotee Pass area; and a northern boundary of the study area extending north of the upper Buffalo Valley to the northwestern extent of GTNP near Grassy Lake.

Topography varied from vast sagebrush (genus *Artemisia* L.) dominated flatlands to rolling hills, buttes, rocky cliffs, steep drainages, and rugged mountains. Elevation ranged from 1800 m in the valley bottom to >3500 m in the mountains. Climate was characterized by short, dry summers typically with a rainy (monsoon) season during late summer consisting of sometimes violent afternoon thundershowers. Summers were followed by a short fall season, when freezing temperatures and snow flurries were common, followed by long, cold, windy winters with frequent snowfall. Vegetation at lower elevations was dominated by sagebrush and riparian areas that consisted of narrowleaf cottonwood (*Populus angustifolia* E. James) and willow (genus *Salix* L.) thickets. Mid-elevations were forested and consisted mainly of quaking aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Higher elevations were dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

Four of North America's largest carnivores occupied the region: cougars, wolves, black bears (*Ursus americanus* Pallas, 1780), and grizzly bears (*Ursus arctos* L., 1758). The region contained one of the highest concentrations of elk (*Cervus elaphus* L., 1758) in North America, as well as populations of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), moose (*Alces alces* (L., 1758)), bison (*Bison bison* (L., 1758)), and pronghorn antelope (*Antilocapra americana* (Ord, 1815)). White-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), bighorn sheep (*Ovis canadensis* Shaw, 1804)), and mountain

goats (*Oreamnos americanus* (Blainville, 1816)) were also present, though in relatively small numbers.

Wolves in the western US range throughout the central and northern Rocky Mountain regions of Idaho, Montana, and Wyoming, and are generally restricted to lands within and adjacent to national forests and national parks (Bangs and Fritts 1996, Bangs et al. 1998; Jimenez et al. 2009). In 2008, the wolf population in Wyoming was estimated at >302 wolves in >42 packs (Jimenez et al. 2009). This was one of the higher wolf population estimates since the onset of the reintroduction program in the Greater Yellowstone Ecosystem, which includes portions of Wyoming, Idaho, and Montana. Since 1999, the TCP study area has encompassed a developing and mostly increasing wolf population (Jimenez et al. 2009). This expanding wolf population was the result of a reintroduction program in Yellowstone National Park and central Idaho in the mid-1990s (Bangs and Fritts 1996). Although wolves were present in the northern region of the study area since the onset of the project, wolf numbers increased steadily and several new pack territories were established since winter 2004–2005 (USFWS et al. 2008). From 1999 to 2005, the USFWS identified a mean of two wolf packs ranging exclusively in the northern half of the TCP study area with a population estimate averaging 17 wolves. From 2006 to 2008, the USFWS identified a mean of seven wolf packs ranging throughout the study area with a population estimate averaging 67 wolves (USFWS et al. 2008).

Since the 1980s, the Rocky Mountain region has maintained a stable cougar population (Cougar Management Guidelines Working Group 2005). The cougar population in Wyoming has been stable or increasing over the past 30 years (WGFD 2006) based on trends in hunter harvest, sightings by hunters and nonhunters, and nonhunting mortality events.

In much of the western US, cougars prey primarily on deer (Ackerman et al. 1984; Kunkel et al. 1999; Cruickshank 2004; Cooley et al. 2008; Laundre 2008); however, other studies described elk as the primary prey for cougars (Hornocker 1970; Murphy 1998; Kortello et al. 2007). Prior to the recolonization of wolves, elk were the primary prey for cougars in the TCP study area (H. Quigley, unpublished data). Elk herds were generally stable throughout the duration of the study (i.e., at or above management goals). The mule deer population declined slightly during the study, but was generally at or near management goals (WGFD 2007). The decline of mule deer in the TCP study area may be related to mule deer population declines throughout the western states (Gill 1999; Ballard et al. 2001, Robinson et al. 2002).

Materials and methods

Capture

We captured most cougars during winter (approximately late October through early April) using trained trailing hounds (Hornocker 1970; Murphy 1998). When a cougar was treed in a situation suitable for immobilization, we administered a first intramuscular injection (IM) (4.0–9.0 mg/kg at 100 mg/mL Ketamine) using a DanInjec® dart gun with DanInject® 3 cc (1 cc = 1 mL) darts. When the Ketamine began taking effect, a member of the capture crew would advance up the tree and use ropes to lower the cougar to the ground. We then administered a second IM injection (0.07 mg/kg at 1.0 mg/mL Medetomidine) by hand. When the cougar was fully immobilized, we recorded heart rate, breathing rate, and temperature (°F; 33.8 °F = 1 °C) every 2–5 m (Quigley 1997; Kreeger et al. 2002).

We weighed, sexed, and aged all individuals. We recorded pelage color and condition, tooth color and condition, and examined each cougar for broken bones and (or) recent wounds to assess health. We aged adults based on gum recession (Laundre et al. 2000) and tooth color. Immature cougars were aged based on birth date (if known, based on den site and radio-telemetry data), size, and pelage. We fitted females with red ear tags on the right ear

and applied a tattoo to the inside of the left ear. We fitted males with yellow ear tags on the left ear and applied a tattoo to the inside of the right ear. We collected blood and tissue samples and recorded any observed unique scars or physical features (e.g., frostbitten ears or tail). We fitted immobilized cougars with a variety of models of VHF and GPS collars throughout the study. Whether we used a VHF collar or a GPS collar depended on which collars we had available at the time of capture. We attempted to outfit all adult resident cougars with GPS collars after 2006.

After approximately 45–50 m had passed from the time of the first injection, we administered an antagonist (0.3 mg/kg at 5.0 mg/mL Atipamezole) either through IM or intravenous injection and observed the cougar for 20–30 m or until mobile. We monitored the cougar until we were confident that it would have the strength and mobility to avoid direct confrontation with other predators in the area. We conducted intensive radio-tracking for a week following each successful capture event to ensure each cougar was continuing normal daily movements and each collar was working properly. We captured 88 cougars from winter 2000 through October 2009. Of these we identified 55 females, 31 males, and did not identify 2 (6-month-old kittens) to sex. We recaptured individuals every 1–3 years for collar replacement.

Obtaining locations

We located cougars fitted with standard VHF transmitters daily from roads, trails, and backcountry travel using triangulation (Heezen and Tester 1967; White and Garrott 1990). We estimated locations from VHF radio collar coordinates using the Location On A Signal (LOAS) software (Ecological Software Solutions, Sacramento, California, USA). LOAS enabled accurate digital plotting of cougar locations collected in the field, and the program output included error polygons as measures of precision. We plotted all Universal Transverse Mercator (UTM) projection coordinates obtained from the analysis of location data on a digitized, georeferenced United States Geological Survey (USGS) 1 : 24 000 quadrangle topographic map layer using ArcView version 3.3 (ESRI 2000).

We programmed GPS collars to collect 1–6 locations daily. The number of location fixes depended on the model of GPS collar. We downloaded locations for cougars outfitted with GPS collars once every 7–10 days. We used aerial telemetry to locate cougars that had not been detected for several consecutive days (Mech 1983).

Locating and investigating predation sites

We defined a predation site as a location where a cougar presumably killed, consumed, and (or) cached a prey item. All GPS and VHF telemetry locations were used to locate potential predation sites. In addition, we investigated predation sites found opportunistically. We would obtain additional, more precise locations on potential predation sites if a radio-collared cougar appeared to have stopped moving (i.e., localized) for more than 24 h (i.e., two consecutive daily locations in the same area). This involved approaching within 300 m of the collared cougar and using triangulation methods with ≥4 azimuths, whose outermost azimuths differed by >74°. We searched for predation sites whenever we observed clusters consisting of ≥2 GPS fixes within 100 m of each other within a 24 h period (Anderson and Lindzey 2003; Kortello et al. 2007) for all cougars fitted with GPS collars. We used the Hawth's tools extension (Beyer 2004) in ArcView version 3.3 to select clusters and derive a centroid location where we would begin the investigation of the potential predation site.

We avoided investigating predation sites if we detected a collared cougar within 1 km of the estimated location. We did not want to influence the natural behavior of the study animals at their predation sites. Our goal was to investigate predation sites immediately after cougars had vacated, thereby reducing the amount of time for scavengers to disrupt or disturb evidence of a predation event.

We thoroughly searched an area ≥100 m of each potential predation site for evidence indicating predation such as signs of struggle, tufts of hair, drag marks, broken branches, blood, bones, toilets, bed sites, or caches. When a prey item was located, we followed Ruth and Buotte's (2007) kill evaluation and categorization chart to infer the carnivore species most likely responsible for the making kill. The telemetry location of a collared cougar at the predation site was indicative, but to rule out scavenging behavior, we searched the area for sign of other large predators and performed a field necropsy on the prey item. Evidence of predation included tracks indicating chase or struggle characterized by broken branches or disturbed foliage. Further evidence of cougar kills included claw marks and (or) canine punctures associated with subcutaneous hemorrhaging in the back, neck, and head regions, as well as caching of prey items.

Data analysis

In the Rocky Mountain region of the western US, prey species (i.e., elk and mule deer) exhibit high fidelity to seasonal foraging grounds (Julander et al. 1961; Brown 1992; Mao et al. 2005; Sawyer et al. 2005; Kauffman et al. 2007). We divided the data set of characteristics of predation sites into two distinct seasonal subsets—winter (November through April) and summer (May through October)—to account for seasonal variation in the distribution of prey throughout the landscape attributed to fidelity to discrete winter and summer ranges. This allowed for quantification of season-specific effects.

We used an approach that generated multiple comparisons (i.e., several dependent variables) rather than a higher dimensional approach that incorporated all of our dependent variables into a single model because we thought that our approach was more focused on discrete mechanisms that relate to differences in the predation habits of wolves and cougars. We formulated regression models using two measures of wolf presence to evaluate our prediction that the presence of wolves influenced cougar predation characteristics. We designed these models to quantify the effects of increasing wolf presence on characteristics of cougar predation sites and prey composition. Our first measure was the estimated wolf population, which was the averaged high and low estimate within our study area for each year (USFWS et al. 2008). Our second measure was the mean distance (m) from each cougar predation site to the nearest wolf pack activity center. We obtained estimates of the seasonal (i.e., winter, summer) activity centers for all wolf packs monitored by the NPS and USFWS in the study area (M. Jimenez, USFWS, and S. Dewey, NPS, 2010, unpublished data). We estimated each mean centroid of wolf pack activity using ArcGIS version 9.2 (ESRI 2006) by first calculating 90% fixed-kernel home-range estimates based on VHF and GPS collar locations of instrumented wolves in each wolf pack, and then using ArcGIS Spatial Analyst to derive the center of each home-range polygon. Only those data representing the northern half of the study area were suitable for the distance to wolf pack activity center analysis, because of low numbers of monitored wolves and wolf locations in the southern half of the study area. Thus, analysis of the mean distance from cougar predation sites to the nearest wolf pack activity center as a covariate was restricted to cougar predation sites in the northern region.

We used a National Elevation Dataset (NED), projected to UTM-12, North American Datum of 1983 (NAD83), 10 m resolution, and a National Land Cover Database (NLCD) Zone 21 Tree Canopy Layer, projected to UTM-12, NAD83, 30 m resolution obtained from the US seamless map server (available from http://seamless.usgs.gov, accessed 8 April 2009). We plotted all cougar predation site locations and extracted slope (%), aspect (°), elevation (m, above sea level), and canopy cover (%) values using the ArcGIS Spatial Analyst extension. We transformed the circular distribution of aspect values to a linear distribution to be applied to a regression analysis by first transforming aspect to radians,

and subsequently decomposing aspect into to northness (cosine(aspect)) and eastness (sine(aspect)) metrics (Alexander et al. 2006). We used ArcGIS to generate a simple random sample of 10 000 points from the tree canopy layer to obtain an estimate of the distribution of canopy cover values. We used R software (version 2.9.2; R Development Core Team 2009) to create a histogram of the tree canopy distribution, which displayed a significant discontinuity at the 15% value, suggesting a natural threshold for categorizing forest and nonforest cells. We used the ArcGIS Spatial Analyst extension to reclassify every cell with a value of ≥15% to represent forest cover within the study area. Cells with a value ≤14% canopy cover represented nonforested (i.e., open) habitat. We then used the regroup function in Spatial Analyst to classify any groups of ≤4 cells with a "forest" classification as "nonforest" to reduce the number of patches of forest determined as insufficient for cougar or prey cover. We used Hawth's raster tools (Beyer 2004) to create a line that defined the edge around each group of forest and nonforest cells. We then used the Join function to derive the minimum distance from each cougar predation site to the nearest forest edge.

We obtained a terrain ruggedness index (TRI) of the entire Greater Yellowstone Ecosystem from P. Buotte (Yellowstone Cougar Project, unpublished data). To derive the TRI layer, Buotte used the sum of the absolute value of the differences in elevation from one center cell to its surrounding eight neighbors (3 × 3 window). This was standardized to range between 0 and 1, with 1 being sheer vertical cliff and 0 being completely flat. Buotte also calculated the number of different aspect values in a 3 × 3 window, and standardized them to range between 0 and 1. Therefore, the final grid ranged in values from 0 to 2, with 2 being the maximum topographical roughness possible (i.e., maximum differences relative to center + maximum differences in pixel values) and 0 being completely flat (P. Buotte, personal correspondence). We used ArcGIS Spatial Analyst extension to extract TRI values from each of the cougar predation sites and standardized the values to a range between 0 and 1. Examination of histograms and quartile plots suggested that the elevation, ruggedness, distance to forest edge, and distance to nearest wolf pack activity center variables were non-normal. We used various transformations to achieve normality (Table 1). We used R software to compute summary statistics for all variables used in the analysis. We used Pearson's correlations to screen for independence using the correlation analysis function in R. All habitat variables showed relatively low levels of collinearity ($r < 0.5$). Diagnostic techniques for multicollinearity problems in mixed models are poorly developed (Littell et al. 2006). We screened for multicollinearity using variance inflation factors (VIFs) associated with fixed effect variables in each of our saturated models when fit without their random effects. Screening for multicollinearity among our fixed effect variables indicated that all VIFs were ≤1.58, and were well below threshold values suggesting problems with multicollinearity in multiple regression models (Hair et al. 1998; Rogerson 2001).

We conducted linear mixed effects regression analyses of response variables reflecting characteristics of cougar predation sites using PROC MIXED in SAS version 9.2 (SAS Institute, Inc. 2008). We used predictor variable and model structures to evaluate support for effects of wolves relative to null models without wolf effects (Tables 4, 5). We used Akaike's information criterion (AIC) to evaluate relative support for alternate regression models (Burnham and Anderson 2002). We defined seasonal year (S_YEAR) as the year in which each seasonal period began (i.e., for winter 2000–2001, S_YEAR = 2000) to account for the fact that the calendar year changes during winter. Many predation sites were attributed to the same individuals over a number of years. We treated seasonal year, individual cougar identification, and prey species as random effects to improve inference beyond the unique set of characteristics in the data set (Littell et al. 2006). All candidate

Table 1. Variables and transformations used to model variation associated with cougar (*Puma concolor*) predation sites from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Variable	Abbreviation*	Transformation	Transformed abbreviation†
Elevation	ELEV	Natural log	ln(ELEV)
Ruggedness	TRI	Box–Cox	bc(TRI)
Canopy cover	CC	Decimal	d(CC)
Northness	N_ness	Sine(aspect)	N_ness
Eastness	E_ness	Cosine(aspect)	E_ness
Distance to forest edge	DFE	Natural log	ln(DFE)
Wolf population	W_POP	—	—
Distance to nearest wolf pack activity center	W_DIST	Square root	sqrt(W_DIST)
Cougar ID	CAT_ID	—	—
Prey species	P_SPP	—	—
Seasonal year	S_YEAR	—	—
Mule deer or not	MD_N	—	—
Forested or not	F_NF	—	—

Note: Descriptions (with units) of variables are as follows: elevation is metres above sea level; ruggedness is terrain ruggedness index where flat topography = 0.0 and vertical topography = 1.0; canopy cover is percent overhead canopy cover at the predation site; northness is a measure of north–south slope aspect where due south facing slopes = –1.0 and due north facing slopes = 1.0; eastness is a measure of east–west slope aspect where due west facing slopes = –1.0 and due east facing slopes = 1.0; distance to forest edge is distance (metres) from the predation site to the nearest forest edge; wolf population is total estimate of the wolf population within the Teton Cougar Project study area as reported in the annual wolf report (U.S. Fish and Wildlife Service 2008); distance to nearest wolf pack activity center is distance (metres) from the predation site to the nearest center of wolf pack activity; cougar ID is the designated identification number of an individual cougar; prey species is the common name of prey items observed at cougar predation sites; seasonal year is the standardized year that is labeled according to season; mule deer (*Odocoileus hemionus*) or not is a binary variable where mule deer = 1 and elk (*Cervus elaphus*) = 0; forested or not is a binary variable where forested habitat = 1 and open canopy (≤14% canopy cover) = 0.

*Abbreviations of the response variables used in the statistical model structures.

†Descriptions of transformed abbreviations are as follows: ln(ELEV) is the natural logarithm of the elevation (metres) at the predation site; bc(TRI) is a power transformation of the terrain ruggedness index value with an optimal parameter = 1.2; d(CC) is percent canopy cover transformed to a decimal value between 0 and 1.0 by dividing the value by 100; N_ness is a sine transformation of the aspect value of the slope, which standardizes north–south aspects to values from –1.0 to 1.0; E_ness is a cosine transformation of the aspect value, which standardizes east–west aspects to values from –1.0 to 1.0; ln(DFE) is the natural logarithm of the distance (metres) from the predation site to the nearest forest edge; sqrt(W_DIST) is a square-root transformation of the distance (metres) from the predation site to the nearest wolf pack activity center.

random effects were categorical and were included in the mixed model fitting as additive terms. We formulated a suite of five models for each response variable using four different combinations of the random effects and a null model (Tables 2, 3). Mixed models fit using restricted maximum likelihood (REML) estimation (default for PROC MIXED) generate parameter estimates that are more nearly unbiased. However, models with different fixed effects cannot be compared using AICs estimated using REML (Littell et al. 2006). To cope with this issue, we analyzed the suite of five candidate mixed effects linear regression models (for the winter and summer subsets) for each habitat response variable using REML and ranked them using AIC model selection (Burnham and Anderson 2002). We then chose the optimal random model structure from each set of ranked models for each response variable (Tables 2, 3). We used maximum likelihood (ML) to estimate the optimal fixed effects model with and without the wolf parameter. Finally, we generated coefficient estimates using REML and model averaging techniques to obtain unconditional parameter estimates (Zuur et al. 2009). We used the evidence ratios (Burnham and Anderson 2002), calculated from Akaike weights to assess the empirical support for the optimal models relative to competing models (Burnham and Anderson 2002).

We used PROC LOGISTIC in SAS version 9.2 (SAS Institute, Inc. 2008) to analyze the prey composition at cougar predation sites. In particular, we were interested in understanding how the proportion of the two main prey items (i.e., elk and mule deer) was changing in cougar diet in association with increasing wolf presence. The response variable in this analysis was the binary outcome mule deer = 1 and elk = 0. We first created a global model using all independent explanatory variables, and used this model to assess possible variation in the probability of encountering a mule deer or an elk kill by evaluating two models: one with and one without a wolf presence parameter. We compared AIC values and evidence ratios to determine the relative levels of importance that models including the wolf parameters had in explaining the probability of encountering mule deer compared with elk at cougar predation sites. We examined the corresponding response and the area under the receiver operating characteristic (ROC) curves to assess the predictive capabilities of logistic regression models. Area under the curve (AUC) values ≥0.8 were considered excellent discrimination and values ≤0.5 indicated that model predictive capabilities were no better than random (Hosmer and Lemeshow 2000). We used the same analytical approach to model occurrence of cougar predation sites made within forests (>15% canopy cover) versus predation sites made in the open. The response variable in this analysis was the binary outcome forest = 1 and open = 0. We predicted that increasing presence of wolves would affect where cougars made their kills (open versus forested habitat), and that increasing presence of wolves would force cougars into hunting in more forested areas. The structure of these models was similar to logistic regression models of prey composition logistic regression, except we replaced the mule deer or elk predictor variable (MD_N) with the forest or nonforest variable (F_NF). We analyzed this model with and without the wolf presence parameters and we used AIC to compare fit. We used the same criteria to interpret the ROC AUC values in the assessment of the predictive capabilities of the logistic regression models.

Table 2. Akaike's information criterion (AIC) values for seasonal random effects structures (SAS PROC MIXED) using gray wolf (*Canis lupus*) population as a covariate (W_POP) to predict variation in cougar (*Puma concolor*) predation site characteristics from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Response variables	Random effect structure				
	Null	CAT_ID	CAT_ID + S_YEAR	CAT_ID + P_SPP	CAT_ID + S_YEAR + P_SPP
Summer					
ln(ELEV)	−510.1	−586.4	−598.6	−598.7	**−606.8**
bc(TRI)	**−726.3**	−726.3	−726.3	−726.3	−726.3
d(CC)	99.9	97.1	97.4	**95.9**	96.7
ln(DFE)	**797.4**	797.4	799.2	797.4	799.2
N_ness	510.6	501.5	**501.0**	502.6	501.1
E_ness	**548.9**	548.9	548.9	548.9	548.9
Winter					
ln(ELEV)	−803.5	**−846.4**	−845.8	−846.4	−845.8
bc(TRI)	−912.8	−927.3	−926.1	**−933.7**	−932.3
d(CC)	89.3	88.9	90.5	**82.6**	84.3
ln(DFE)	**1004.5**	1006.1	1008.0	1006.1	1008.0
N_ness	591.2	**588.4**	588.4	589.5	589.5
E_ness	**585.0**	585.0	585.0	586.2	586.2

Note: Models were fit using restricted maximum likelihood (PROC MIXED, SAS version 9.2; SAS Institute Inc., Cary, North Carolina, USA). For definitions of response variables see Table 1. Null models contained no random effects. AIC values in boldface type represent the random effects structure with the best fit.

Table 3. Akaike's information criterion (AIC) values for seasonal random effects structures (SAS PROC MIXED) using the mean distance from cougar (*Puma concolor*) predation sites to the nearest wolf (*Canis lupus*) pack activity center as a covariate (W_DIST) to predict variation in cougar predation site characteristics from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Response variables	Random effect structure				
	Null	CAT_ID	CAT_ID + S_YEAR	CAT_ID + P_SPP	CAT_ID + S_YEAR + P_SPP
Summer					
ln(ELEV)	−279.0	−306.8	−305.6	**−306.9**	−305.8
bc(TRI)	**−364.9**	−364.9	−364.9	−364.9	−364.9
d(CC)	34.8	31.7	32.4	**31.2**	32.7
ln(DFE)	**367.4**	369.1	371.0	369.1	371.0
N_ness	**267.3**	268.8	268.8	270.3	272.3
E_ness	**265.3**	267.2	267.2	268.3	268.3
Winter					
ln(ELEV)	−441.7	−446.9	**−456.3**	−446.9	−456.3
bc(TRI)	−479.8	**−480.2**	−479.2	−479.6	−478.6
d(CC)	**46.5**	46.5	48.4	48.2	50.1
ln(DFE)	**507.9**	508.9	508.9	508.9	508.9
N_ness	341.6	**340.6**	340.6	340.6	340.6
E_ness	**307.4**	309.4	309.4	309.4	309.4

Note: Models were fit using restricted maximum likelihood (PROC MIXED, SAS version 9.2; SAS Institute Inc., Cary, North Carolina, USA). AIC values in boldface type represent the random effects structure with the best fit. For definitions of response variables see Table 1. Null models contained no random effects. AIC values in boldface type represent the random effects structure with the best fit.

Results

We investigated 623 potential predation sites from December 1999 through October 2009. We classified 74 predation sites as having insufficient evidence of cougar predation and 10 predation sites as exhibiting evidence of scavenging, and we removed them from the data set. The final data set consisted of 539 confirmed cougar predation events. We determined 506 of the predation events were made by 34 individual collared cougars. We found the remaining predation events (*n* = 33) opportunistically and could not be attributed to collared cougars. Primary prey species consisted of elk (65%, *n* = 350), mule deer (17%, *n* = 92), and moose (5%, *n* = 28). The remaining predation events (*n* = 69) consisted of several other species. We found evidence of wolf presence (e.g., tracks and scat) at 5.4% (*n* = 29) of the cougar predation sites that we investigated. Of these, 65.5% (*n* = 19) occurred between March 2006 and May 2009, indicating an increase in the occurrence of wolf sign at cougar predation sites during the study.

Predation site habitat characteristics modeled with wolf proximity

In the northern half of the study area during summer, models predicting elevation, northness, and canopy cover were better supported when distance to the nearest wolf pack activity center was included as a covariate. In particular, the models predicting elevation and canopy cover were marginally better than the null

Table 4. Model selection with and without (null) the mean distance from cougar (*Puma concolor*) predation sites to the nearest wolf (*Canis lupus*) pack activity center (sqrt(W_DIST)) for models fit to descriptive data from cougar predation sites by season from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Base model	Wolf effect	Season	k_i	$L(\theta_i)$	AIC	Δ_i	w_i	Evidence ratio
ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + S_YEAR)	sqrt(W_DIST)	Winter	9	260.0	−502.0	0	0.839	5.21
	Null		8	257.4	−498.7	3.3	0.161	
ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	sqrt(W_DIST)	Summer	9	169.7	−321.4	0	0.634	1.73
	Null		8	168.2	−320.3	1.1	0.366	
bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID)	sqrt(W_DIST)	Winter	8	272.9	−529.8	1.1	0.366	
	Null		7	272.5	−530.9	0	0.634	1.73
bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(null)	sqrt(W_DIST)	Summer	7	213.6	−413.2	1.8	0.289	
	Null		6	213.5	−415.0	0	0.711	2.46
d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(null)	sqrt(W_DIST)	Winter	7	−5.7	25.3	1.9	0.279	
	Null		6	−5.7	23.4	0	0.721	2.58
d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	sqrt(W_DIST)	Summer	9	3.0	12.0	0	0.75	3.00
	Null		8	0.9	14.2	2.2	0.25	
ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	sqrt(W_DIST)	Winter	7	−249.1	512.2	0.7	0.413	
	Null		6	−249.8	511.5	0	0.587	1.42
ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	sqrt(W_DIST)	Summer	7	−177.8	369.5	1.4	0.332	
	Null		6	−178.1	368.1	0	0.668	2.01
N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	sqrt(W_DIST)	Winter	8	−160.1	336.2	1.9	0.279	
	Null		7	−160.2	334.3	0	0.721	2.58
N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	sqrt(W_DIST)	Summer	8	−123.3	262.6	0	0.928	12.89
	Null		7	−126.9	267.7	5.1	0.072	
E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	sqrt(W_DIST)	Winter	7	−143.3	300.6	1.8	0.289	
	Null		6	−143.4	298.8	0	0.711	2.46
E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	sqrt(W_DIST)	Summer	7	−123.2	260.4	0.6	0.426	
	Null		6	−123.9	259.8	0	0.574	1.35

Note: Base models use the random effect identified as Akaike's information criterion (AIC) optimal model in the previous analysis (Table 1, 2; Burnham and Anderson 2002). The seasons are winter (November through April) and summer (May through October). k_i is the number of parameters. $L(\theta_i)$ is the maximum log-likelihood value. Δ_i is the difference between the minimum AIC and the *i*-th model. w_i is the Akaike weight. The evidence ratio shows the model that favors the AIC-optimal model for each pair (Burnham and Anderson 2002).

model when using wolf proximity, whereas there was 12.89 times more support for the model predicting northness when using wolf proximity relative to the null model (Table 4). Parameter estimates indicated that closer mean proximity of wolf pack activity centers to summer cougar predation sites was associated with higher mean elevations, more north-facing slopes, and lower percent canopy cover (Table 6). Models of ruggedness, distance to forest edge, and eastness at summer cougar predation sites were marginally better supported when distance to the nearest wolf pack activity center was not included as a covariate (Table 4).

In the northern half of the study area during winter, models predicting elevation as a response variable had 5.71 times more support than the null model when distance to the nearest wolf pack activity center was included as a covariate (Table 4). Parameter estimates indicated that decreasing mean distance to the nearest wolf pack activity center was associated with higher elevations at winter cougar predation sites (Table 6). Models of ruggedness, canopy cover, distance to forest edge, northness, and eastness associated with winter cougar predation sites were marginally better supported when distance to the nearest wolf pack activity center was not included as a covariate (Table 4).

Predation site habitat characteristics modeled with wolf population

Models of elevation associated with cougar predation sites in summer were marginally supported relative to the null model when the wolf population estimation was included as a covariate (Table 5). Parameter estimates suggested that mean elevation of

summer cougar predation sites increased as the wolf population increased (Table 7). Models of ruggedness, canopy cover, northness, eastness, and distance to forest edge associated with summer cougar predation sites were marginally better supported when W_POP was not included as a covariate (Table 5).

Models of ruggedness (bc(TRI)) associated with cougar predation sites during winter were marginally supported relative to the null model when W_POP was included as a covariate (Table 5). Parameter estimates indicated that ruggedness had a positive association with an increasing wolf population (Table 7). Models of elevation, northness, eastness, canopy cover, and distance to forest edge were marginally better supported when W_POP was not included as a covariate (Table 5).

Logistic regression indicated that recolonizing wolves were associated with changes in prey composition found at cougar predation sites in the northern half of the study area. In particular, support for the model predicting the probability of encountering a mule deer kill had 134.14 times more support relative to the null model when using the mean proximity of wolves as a covariate and 6.72 times more support relative to the null model when using wolf population as a covariate (Table 8). Parameter estimates indicated that the probability of encountering a mule deer kill at a predation site increased as W_DIST decreased during winter and summer (Table 9). The specificity of this logistic regression model, assessed by the resulting ROC curve and the associated AUC value, indicated a good fit (Table 8). Parameter estimates also indicated that the probability of finding a mule deer kill (i.e.,

Table 5. Model selection with and without (null) the wolf (*Canis lupus*) population covariate (W_POP) for models fit to descriptive data from cougar (*Puma concolor*) predation sites by season from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Base model	Wolf effect	Season	k_i	$L(\theta_i)$	AIC	Δ_i	w_i	Evidence ratio
ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID)	W_POP	Winter	8	455.6	−895.1	1.7	0.299	
	Null		7	455.4	−896.8	0	0.701	2.34
ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP + S_YEAR)	W_POP	Summer	10	334.8	−649.6	0	0.537	1.16
	Null		9	333.7	−649.3	0.3	0.462	
bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	Winter	9	501.4	−984.7	0	0.562	1.28
	Null		8	500.1	−984.2	0.5	0.438	
bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(null)	W_POP	Summer	7	395.8	−777.6	1.4	0.332	
	Null		6	395.5	−779.0	0	0.668	2.01
d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	Winter	9	−21.2	60.4	0	0.5	1.00
	Null		8	−22.2	60.4	0	0.5	1.00
d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	Summer	9	−28.3	74.5	1.7	0.299	
	Null		8	−28.4	72.8	0	0.701	2.34
ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_POP	Winter	7	−495.7	1005.3	2.0	0.269	
	Null		6	−495.7	1003.3	0	0.731	2.72
ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_POP	Summer	7	−391.6	797.1	2.0	0.269	
	Null		6	−391.6	795.1	0	0.731	2.72
N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	W_POP	Winter	8	−281.2	578.3	2.1	0.259	
	Null		7	−281.1	576.2	0	0.741	2.86
N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID + S_YEAR)	W_POP	Summer	9	−238.0	494.0	0.7	0.413	
	Null		8	−238.7	493.3	0	0.587	1.42
E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_POP	Winter	7	−280.0	574.0	2.0	0.269	
	Null		6	−280.0	572.0	0	0.731	2.72
E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_POP	Summer	7	−263.0	540.0	1.8	0.289	
	Null		6	−263.1	538.2	0	0.711	2.46

Note: Base models use the random effect identified as Akaike's information criterion (AIC) optimal model in the previous analysis (Table 1, 2; Burnham and Anderson 2002). The seasons are winter (November through April) and summer (May through October). k_i is the number of parameters. $L(\theta_i)$ is the maximum log-likelihood value. Δ_i is the difference between the minimum AIC and the *i*-th model. w_i is the Akaike weight. The evidence ratio shows the model that favors the AIC-optimal model for each pair (Burnham and Anderson 2002).

Table 6. Unconditional parameter estimates for models using the mean distance from cougar (*Puma concolor*) predation sites to the nearest wolf (*Canis lupus*) pack activity center covariate (sqrt(W_DIST)).

Response variable	Season	sqrt(W_DIST)	ln(ELEV)	bc(TRI)	d(CC)	ln(DFE)	N_ness	E_ness
ln(ELEV)	Winter	−0.0006*		0.3572*	0.0004	0.0020	−0.0011	0.0025
	Summer	−0.0004		0.8196*	−0.2582*	0.0076	−0.0069	−0.0101
bc(TRI)	Winter	−0.0001	0.3611*		0.0240	−0.0022	0.0023	−0.0084
	Summer	−0.0001	0.3891*		0.0366*	−0.0056	0.0093	0.0080
d(CC)	Winter	0.0002	−0.1587	1.0219*		0.0780*	0.1411*	−0.0201
	Summer	0.0017*	−0.3113	1.2396*		0.1200*	0.0781*	−0.0570
ln(DFE)	Winter	−0.0038	−0.7182	−2.0470	1.8889*		−0.1360	−0.2201
	Summer	0.0024	1.9340	−3.0798	2.0433*		0.1638	0.2959*
N_ness	Winter	0.0006	−0.5747	0.5611	1.0676*	−0.0342		0.1702
	Summer	−0.0057*	−0.8756	2.0779	0.6463*	0.0752		0.0328
E_ness	Winter	−0.0007	0.5257	−1.9507	−0.1214	−0.0548	0.1188	
	Summer	−0.0026	−0.6377	1.8297	−0.3641	0.1236*	0.0451	

Note: Models were fit using maximum likelihood to the descriptive data from cougar predation sites from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA. For definitions of variables see Table 1.
*Parameter estimates with 95% confidence intervals excluding 0.

versus an elk kill) increased as the wolf population increased throughout the entire study area during winter and summer (Table 9). The corresponding AUC value associated with the ROC curve indicated a good fit for this model (Table 8).

The results for the forest versus open models varied. Logistic regression indicated that the probability of a predation site being found in forested habitat (i.e., closed versus open canopy cover) had 5.3 times more support relative to the null model when including W_POP as a covariate (Table 8). Parameter estimates indicated that the probability of a predation site being found in forested habitat decreased as W_POP increased (Table 9). The ROC curve for this model displayed good prediction accuracy, with an

Table 7. Unconditional parameter estimates for models using the wolf (*Canis lupus*) population covariate (W_POP).

Response variable	Season	W_POP	ln(ELEV)	bc(TRI)	d(CC)	ln(DFE)	N_ness	E_ness
ln(ELEV)	Winter	−0.0001		0.4961*	0.0045	−0.0016	−0.0019	0.0081
	Summer	0.0007		0.2961*	0.0187	−0.0021	−0.0107	0.0088
bc(TRI)	Winter	0.0002	0.3634*		0.0120	−0.0022	0.0009	−0.0107*
	Summer	−0.0001	0.2660*		−0.0001	−0.0018	0.0091	−0.0053
d(CC)	Winter	−0.0013	0.2051	0.4479		0.0401*	0.2022*	−0.0385
	Summer	−0.0008	0.1082	0.1651		0.0923*	0.1224*	−0.0181
ln(DFE)	Winter	0.0002	−2.2538	−1.7678	0.9857*		−0.1879	0.1006
	Summer	−0.0006	−0.6515	−1.0454	1.7065*		0.0490	0.1695
N_ness	Winter	0.0006	0.0283	0.2104	1.1521*	−0.0428		0.0413
	Summer	−0.0048	−0.8008	0.6120	0.6981*	0.0080		0.0528
E_ness	Winter	0.0002	0.5775	−2.3414*	−0.1876	−0.0230	0.0330	
	Summer	−0.0007	1.1526*	−1.1053	−0.0463	0.0599	0.0751	

Note: Models were fit using maximum likelihood to the descriptive data from cougar (*Puma concolor*) predation sites from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA. For definitions of variables see Table 1.
*Parameter estimates with 95% confidence intervals excluding 0.

Table 8. Model selection for logistic regression models fit to descriptive data from cougar (*Puma concolor*) predation sites from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Response variable	Base model	Wolf effect	$L(\theta_i)$	AIC	Δ_i	w_i	ROC AUC	Evidence ratio
MD_N	dCC + TRI + ELEV_83 + lnDFE + N_ness + E_ness + season	W_DIST	−69.11	156.23	0.00	0.993	0.838	134.14
		No wolves	−75.02	166.04	9.81	0.007	0.803	
MD_N	dCC + TRI + ELEV_83 + lnDFE + N_ness + E_ness + season	W_POP	−177.51	373.02	0.00	0.870	0.810	6.72
		No wolves	−180.41	376.83	3.81	0.130	0.798	
F_NF	TRI + ELEV_83 + lnDFE + N_ness + E_ness + season	W_DIST	−99.81	215.62	0.01	0.498	0.829	
		No wolves	−100.81	215.61	0.00	0.502	0.824	1.01
F_NF	TRI + ELEV_83 + lnDFE + N_ness + E_ness + season	W_POP	−232.55	481.10	0.00	0.841	0.788	5.30
		No wolves	−235.22	484.44	3.34	0.159	0.781	

Note: Models were fit with and without wolf covariates. Fit statistics include log likelihood ($L(\theta_i)$), Akaike's information criterion (AIC), the difference between the model with the lowest AIC value and the *i*-th model (Δ_i), Akaike weight (w_i), and the evidence ratio in favor of the AIC-optimal model. ROC AUC is the area under the receiver operating characteristic (ROC) curve. For definitions of variables see Table 1.

Table 9. Unconditional parameter estimates for logistic regression models fit to descriptive data for cougar (*Puma concolor*) predation sites from winter 2000–2001 through summer 2009 in the Grand Teton region of northwestern Wyoming, USA.

Response variable	Wolf covariate	Wolf	dCC	TRI	ELEV_83	lnDFE	N_ness	E_ness
MD_N	W_DIST	−0.0001*	2.7260*	−0.0116	0.0028*	−0.0683	−0.0425	0.5419
MD_N	W_POP	0.0175*	0.9581	−1.5071	0.0035*	0.0328	0.1234	0.3803*
F_NF	W_DIST	0		4.2423*	0	0.5195*	1.3092*	−0.045
F_NF	W_POP	−0.0137*		1.8035*	−0.0003	0.0775	1.3919*	−0.1199

Note: Models were fit using maximum likelihood. For definitions of variables see Table 1.
*Parameter estimates with 95% confidence intervals excluding 0.

AUC value indicating a good fit (Table 8). In the northern half of the study area, however, modeling the probability of finding a predation site in forested habitat had marginal support when W_DIST was not used as a covariate. The AUC value corresponding with the ROC curve for this model indicated a good fit (Table 8). Parameter estimates indicated no change in the probability of finding a cougar predation site in forested habitat as the mean distance to wolf pack activity centers decreased (Table 9).

Discussion

Recent research has focused on recolonization of the Rocky Mountain region of North America by wolves and the subsequent effects on their prey (Kunkel et al. 1999; Husseman et al. 2003; Atwood et al. 2007; Atwood et al. 2009) and sympatric predators (Murphy 1998; Kortello et al. 2007). In cougar–wolf interactions, cougars tend to be the subordinate species, and wolf presence may induce behavioral responses such as avoidance, altered diets, or shifts in space use (Kortello et al. 2007). Our observations are consistent with previous observations of competitive interactions (Kunkel et al. 1999; Kortello et al. 2007) and suggest exploitative and interference competition because composition of prey and habitat characteristics at predation sites shifted in the subordinate species (i.e., cougars) and these shifts were associated with an increasing population and mean proximity of the dominant predator (i.e., wolves). The changes observed at cougar predation sites were most prevalent in the northern half of the study area during summer when we used a measure of wolf proximity as a predictor. Although we did not have access to the wolf pack home site locations, it is likely that the center of wolf pack activity was centered at the pack home site in the summer months. These results may have been influenced by wolves utilizing a home site throughout summer. Additional support for a shift in foraging habitat was evident during winter in the northern half of

the study area. Furthermore, upon examination of the entire study area and using wolf population as a measure of increasing wolf presence, a shift in the characteristics of cougar predation sites was evident in both winter and summer.

During wolf recolonization in the TCP study area, formation of new packs and territories and the subsequent avoidance by cougars likely reduced the extent of available foraging habitat for cougars. This reduction in available foraging habitat, coupled with increasing rates of interactions exhibited in the presence of wolf sign at cougar predation sites, was associated with a shift in predation site characteristics that included higher elevations and more northerly facing slopes in the northern half of the study area during summer. Similarly, shifts in the characteristics of cougar predation sites to higher elevations in summer and more rugged areas in the winter was evident throughout the study area and were associated with the increasing wolf population.

Contrary to our predictions, cougar predation sites were characterized by more open canopy cover and a reduced probability of finding a predation site in forested habitat when associated with increasing wolf presence. Cougar predation sites located in smaller patches of forest may have been misclassified when extracting values from the canopy cover layer using ArcGIS at the 30 m scale. It is possible that the 30 m resolution canopy cover layer was not accurate enough to delineate certain microhabitat characteristics (e.g., secondary growth, shrubs, old-growth sagebrush, and willow thickets). These characteristics, as well as others typical of more structurally complex habitat, could provide suitable cover for predatory stalking behavior but may have been overlooked in the analysis.

Success of cougar hunting tends to be influenced by habitat features to a higher degree in comparison with wolves (Mech 1970; Seidensticker et al. 1973; Kunkel et al. 1999; Kortello et al. 2007). If the changes found in cougar foraging habits led to increased encounters with other prey species (e.g., mule deer), this would likely be reflected in the composition of prey species found at cougar predation sites. Our results supported this inference by indicating that the ratio of mule deer to elk found at cougar predation sites increased as a function of increasing wolf presence, both at the population and landscape levels. Thus, higher incidence of cougar predation on mule deer within our study area may reflect an increasing wolf population, influencing cougars to alter space use and forage in areas with higher densities of mule deer. Similarly, mule deer may be seeking refuge in adjacent habitat as an attempt to reduce predation risk from the newly established wolf population, consequently increasing predation risk from cougars.

Since our investigation of cougar predation sites occurred continuously from the onset of growth of the wolf population in our study area, our results may provide improved inference about the effects of a recolonizing predator on a complex multipredator, multiprey ecosystem. Recent studies investigating predation sites have implemented field seasons confined to relatively short sampling periods of 1–6 months (Hebblewhite et al. 2005; Alexander et al. 2006; Atwood et al. 2007; Kauffman et al. 2007; Atwood et al. 2009) and primarily during winter. Hence, inferences made in recent research regarding predation habits of cougars and wolves could fail to consider important seasonal or temporal dynamics. Although the number of wolves with tracking collars in the study area started very low and increased during the study, the wolf location data that we had to work with was limited. Consequently, we used a coarse spatial and temporal resolution in estimating the wolf effect because of the sparseness of the data. The key limitation with this approach is that we might have been unable to detect more subtle effects. In addition to limited location data, the estimate of the number of wolves in each pack fluctuated over the duration of the study. We did not feel confident in attempting to model any effects that wolf pack size may have had on cougar predation habits because of the fluctuation and uncertainty in the

estimated pack size over time and instead took the more coarse approach of modeling seasonal wolf pack center points.

In our study area, cougars tended to prey on a greater proportion of mule deer during late summer. Typically, mule deer throughout much of the Rocky Mountain region migrate to and from summer and winter foraging ranges (Brown 1992). We hypothesize that space use by mule deer while occupying seasonal foraging ranges may increase their vulnerability to predation by cougars in regions where recent colonization of wolves has occurred. As cougars frequent higher elevations to avoid colonizing wolves, they may encounter mule deer at a higher rate if mule deer also are using higher elevations during summer (Armleder et al. 1994; Cooley et al. 2008). This increased rate of encounters may cause cougars to prey on mule deer disproportionately during summer (Cooley et al. 2008; Robinson et al. 2002). In contrast, Atwood et al (2007) suggested that the risk of cougar predation on mule deer could have been reduced in Montana's Madison Range as an effect of habitat shifts by elk into structurally complex refugia in response to recolonizing wolves. The contrast between our results and those of Atwood et al. (2007) is likely attributed to regional differences in prey ratios and migration dynamics.

If the contradiction between our predictions and the analysis of the probability of cougar predation sites occurring in the forest were attributed to an issue of spatial scale, one solution for future research would be to follow methods used by Atwood et al. (2007), who implemented a cover complexity index (CCI). The CCI was calculated using various attributes associated with the habitat and topography at wolf and cougar kill sites and provided an informative measure associated with resource use by wolves and cougars rather than relying on the extraction of values of the parameters from GIS layers as we did. Future research on vegetative and topographical structural complexity at predation sites should implement a standardized estimate of the surrounding vegetative structure, whether it is a simple standardized canopy closure estimate, an estimate of the percent hiding cover, or a CCI.

In the US, conservation of large carnivores has been an important concern for several decades (Hornocker 1970; Mech 1970; Spalding and Lesowski 1971; Seidensticker et al. 1973), because of the importance of these animals to the regulation and continuity of basic ecological processes. More recently, with increased laws and regulations, conservationists have witnessed an impressive reestablishment of these species to their former ranges (Ream et al. 1991; Bangs and Fritts 1996, Bangs et al. 1998; Smith et al. 2003). Variable recolonization rates of large carnivores provide scientists and managers with opportunities to study and document the roles that reestablishing species perform within their respective systems. Our findings provide further insight into how changes in foraging habits of cougars are associated with the recolonization of wolves in the SGYE. Seasonal changes are important within this ecosystem and our research has demonstrated the need to better understand seasonal patterns to gain a greater understanding of interactions.

Management implications

Our results indicated that recolonizing wolves may lead to an increase in cougar predation on mule deer. If recolonization of wolves leads to increased predation of a secondary prey species such as mule deer, then managers may consider limiting harvest of the secondary prey species in certain game management units to alleviate the added pressure of increased predation risk from cougars. Another strategy may include the management of available cover to reduce predation risk from cougars. We suggest managers consider careful monitoring of predator and prey distributions throughout the year as opposed to only during the winter. Year-round monitoring of prey and predator interactions may provide useful knowledge of when and where prey species are most vulnerable to shifts in space use and prey composition by a resident predator species associated with in-

fluences from a recolonizing predator species. In addition, the impacts of recolonizing predator species on resident predator populations may be better understood with the continued use of intensive, year-round daily tracking, and (or) the increased implementation of GPS collar use (Ruth et al. 2010). As wolves reestablish former ranges, partitioning of or competition for available resources may reduce available habitat for cougars, potentially resulting in a reduced carrying capacity for cougars. Managers confronted with these potential situations could consider temporary reduction in the cougar harvest in regions experiencing wolf recolonization until improved cougar population assessments are established. Agencies currently using indirect methods of obtaining population estimates based on hunter success, sightings, etc., should consider the implementation of standardized population indices.

Acknowledgements

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