INVESTIGATING COUGAR PREDATION HABITS IN THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

by

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Dedication

I wish to dedicate this thesis to my
grandfather, who was a remarkable person,
and a great inspiration in my life. He opened
up my eyes to the natural world and beyond.
Also, this is dedicated to my mother, who has
always been there for me and raised me to be
the person I am today.

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ABSTRACT

I examined predation habits of cougars (*Puma concolor*) following the recent recovery of gray wolves (*Canis lupus*) in the southern Greater Yellowstone Ecosystem. With the extirpation of wolves in the early 20th century, cougars likely expanded their niche space to include niche space made vacant in the absence of wolves, increasing use of habitat better suited to the foraging of a coursing predator like wolves. Cougars were intensively radiotracked, and kill sites were examined from winter 2000-2001 through summer 2009. I found evidence of changes in cougar foraging habits associated with increasing wolf presence on the landscape. As the number of wolves and the proximity of wolf packs to cougar kill sites increased in the study area, cougars tended to make kills at higher elevations in summer and winter months, on more north-facing slopes in the summer and in more rugged areas in the winter. In addition, cougars preyed on a higher proportion of mule deer, consistent with exploitative competition with wolves. Observed changes in predation characteristics reflect the difference 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 by agencies when planning management strategies in systems where the recolonization of wolves may eventually take place.

INTRODUCTION

Populations of cougars (*Puma concolor*) and wolves (*Canis lupus*) have been recovering throughout many regions of western North America, primarily as a result of successful conservation efforts, reintroduction programs, and improved management practices by wildlife professionals (Bangs 1998, Smith et al. 2003, Group 2005, U.S. Fish and Wildlife Service 2008). Population recovery has varied regionally and through different degrees of effort. This varying rate of recolonization has allowed some populations of cougars to occupy former ranges as the apex predator in the absence of wolves. 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).

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 species, and generally occur in remote areas, at relatively low densities (Gese 2001). In the western U.S., cougars and wolves occupy vast expanses of undeveloped, rugged terrain which usually is difficult for human access and the application of research methods. However, recent advances in technology and non-invasive 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 methods of DNA analyses) have enabled researchers to record 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).

Wolves and cougars were nearly extirpated from the contiguous 48 states in the late 1800s and early 1900s (Mech 1970, Kellert et al. 1996). During early European settlement, fear and a general lack of understanding of ecological processes led to unregulated harvest and bounty programs implemented as the European settler population expanded westward in the mid-late 1800s (Kellert et al. 1996, Riley et al. 2004). Predators were, and continue to be viewed as a nuisance, a major competitor for food (e.g., large game species), and a threat to livestock.

Wolves in the western United States are limited currently (2009) to the central and northern Rocky Mountain regions of Idaho, Montana, and Wyoming, and restricted locally to lands within and adjacent to national forests and national parks (Bangs 1996;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.

In recent decades, the Rocky Mountain region has held a relatively healthy cougar population (Cougar Management Guidelines Working Group 2005). The cougar population in Wyoming has been stable or increasing over the past 30 years (Wyoming Game & Fish Department 2006). The Wyoming Game and Fish Department (WGFD) bases their cougar population trends on hunter harvest, sightings by hunters and non-hunters, and non-hunting mortality events. However, Wyoming state officials currently do not have a standardized scientific method of estimating the size of the cougar population. Cougars, as with other carnivore species, are difficult to census and monitor (Gese 2001, Robinson et al. 2008). One reason for the lack of information on the size of the cougar population is that it is difficult logistically to survey adequately areas occupied by cougars because of their adaptation to very rugged terrain (Lambert et al. 2006). Cougars are also difficult to monitor because they are generally a solitary, elusive, wide-ranging species occurring at low densities (Hornocker 1970, Seidensticker et al. 1973, Beier 1993, Murphy 1998).

Recent studies of cougar and wolf interactions

Intensive studies conducted in the northern range of Yellowstone National Park suggested that wolves tended to use areas with more open canopy and less rough terrain, while cougars generally used areas with more closed canopy, and steeper, rougher terrain, and even cliff faces (Murphy 1998, Ruth 2000, Ruth et al. 2003). Furthermore, in Montana and areas surrounding Banff National Park (Alberta, Canada) studies found that differences in hunting styles and adaptations for different habitats has 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 can more effectively test herds of elk and 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).

In the absence of large carnivores, prey within Rocky Mountain ecosystems may become naïve and in some cases, more vulnerable, if only temporarily, to reestablishing predator populations (Berger et al. 2001, Atwood et al. 2007). This may negatively impact the prey population if the prey species exhibits an avoidance response to the recolonizing predator by seeking refuge in adjacent habitat. The movement of naïve prey into habitat adjacent to their typical feeding habitat may decrease the risk of a recolonizing predator, but may increase the risk of predation by another predator species (Atwood et al. 2007, Atwood et al. 2009).

Woodruff (2006) investigated winter kill site characteristics of wolves and cougars within the Southern Greater Yellowstone Ecosystem (SGYE). Her results indicate that while wolves and cougars in the SGYE have overlapping areas of use and share a prey base, they use different types of habitat for hunting. In particular, Woodruff found that wolves frequented open areas with less topographical relief, whereas cougars occurred in areas of rougher terrain, and more complex vegetative structure.

Few studies have conducted long-term, daily, year-round radiotracking of cougars. Data acquired through intensive telemetry studies could be used to investigate more fine-scale changes in cougar predation ecology associated with a recolonizing wolf population. Additional insights into interactions between cougars and wolves could be established through implementing a year-round analysis of predation and spatial patterns of habitat use. The increased use of GPS collars and year-round data collection is essential to improve current knowledge of habitat preferences of sympatric cougars and wolves (Woodruff 2006).

The level of competition for resources between sympatric predators is fundamentally determined by the extent of spatial overlap (Kitchen et al. 1999). In multi-predator, multi-prey 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). Investigating factors which may be impacting cougar populations as wolves reestablish former ranges is essential to the development of effective management strategies. In the absence of wolves during the mid-late twentieth century, cougars presumably expanded their foraging niche and filled some areas of the vacated wolf niche, utilizing resources that were not previously available due to competitive interactions. Cougars 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, wolf recolonization likely resulted in increased competition for prey and similar resources with cougars (Woodruff 2006). As wolves continue to re-occupy 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). The process of increasing interactions between sympatric predators leading to altered behaviors such as resource partitioning and prey switching provides an opportunity for further research in predator-predator and predator-prey interactions within this ecosystem.

I investigated whether changes in the predation characteristics of cougars could be attributed to the increasing presence of wolves on the landscape using both population and spatial measures. I analyzed the characteristics of cougar kill sites from winter 2000 through summer 2009 during the expansion of the wolf population within a study area in northwestern Wyoming. My goal was to investigate the following predictions: 1) cougars will exhibit shifts in habitat use in the direction of habitat more favorable for ambush predation (i.e., denser cover, more-rugged terrain, higher elevation) in the presence of an expanding wolf population; 2) cougars will exhibit shifts in the overall composition of prey items killed (i.e., preying on a wider variety of prey) as an effect of increasing wolf presence on the landscape.

Study area

My study was conducted as part of a large study of cougar ecology known as the Teton Cougar Project (TCP). The TCP study area covered approximately 2,300 km^2 and was located within the Southern Greater Yellowstone Ecosystem (SGYE). Study area boundaries included Grand Teton National Park 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 Grand Teton National Park near Grassy Lake (Figure 1).

The topography of the study area varied from vast sagebrush (*Artemisia spp.*)-dominated flatlands to rolling hills, buttes, rocky cliffs, steep drainages, and rugged mountains. Elevation ranged from 1,800 m in the valley bottom to > 3,500 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 typically dominated by sagebrush and riparian areas which consisted of cottonwood (*Populus angustifolia*) and willow (*Salix spp.*) thickets. Mid-elevations were forested and consisted mainly of quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseodotsuga menziesii*). Higher elevations were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

Four of North America's largest carnivore species occupied the region: cougars, wolves, black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*). The region contained one of the highest concentrations of elk (*Cervus elaphus*) in North America, as well as populations of mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bison (*Bison bison*), and pronghorn antelope (*Antilicapra americana*). White-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*) were also present, though in relatively small numbers.

Much of the study area (~97%) was public land which was regulated and (or) managed by a number of federal and state agencies. Big game hunting was allowed throughout the study area, except in some restricted areas of Grand Teton National Park. In addition, there was an established hunting season for cougars in the Bridger-Teton National Forest (BTNF). Since 1999 the 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 1996). Although wolves were present in the northern region of the study area since the onset of the project, wolf numbers increased rapidly and several new pack territories were established since winter 2004-2005 (U.S. Fish and Wildlife Service 2008).

Throughout much of the western U.S., cougars prey primarily on deer (Ackerman et al. 1984, Kunkel et al. 1999, Cruickshank 2004, Cooley et al. 2008, Laundre 2008), which is likely associated with the habitat characteristics and relative abundance of prey species in these western landscapes. Several studies conducted in the western United States described elk to be the primary prey for cougars (Hornocker 1970, Murphy 1998, Kortello et al. 2007). Historically within the TCP study area elk have been the primary prey for cougars. Intensive management for large elk herds by state and federal agencies likely contributes to a large percentage of elk in the diets of TCP cougars. The WGFD manages for a large elk population by maintaining supplemental feeding grounds during winter. Furthermore, the USFWS manages the National Elk Refuge north of Jackson, Wyoming, which also provides supplemental feeding grounds through the winter. These management practices have allowed the elk population to be maintained at high levels to support the large number of elk harvested by hunters each year (WGFD JCR 2007).

Project background

The TCP was initiated in 2000 by H. Quigley and M. Hornocker with the Hornocker Wildlife Institute, and was adopted by Craighead Beringia South (CBS), a private, non-profit wildlife research organization in 2003 (http://www.bswy.us/). Together, D. Craighead, president and co-principal investigator, and H. Quigley, executive director and principal investigator, developed the project to study the ecology of the cougar population in the SGYE. The primary objectives of the TCP consist of:

1) Characterizing predation habits of cougars;
2) Characterizing the demographics of the cougar population;
3) Studying inter/intraspecific competition of cougars within the region;
4) Providing a comprehensive picture of cougar ecology for the study area that includes important aspects of cougar activities and dynamics in the study area, along with descriptions of cougar interactions with other carnivores and

> humans, thus creating a framework for cougar and carnivore conservation in the southern Yellowstone ecosystem.

Intensive field efforts since the onset of the project have yielded a rich dataset including abundant data on cougar movements, social organization, home range, reproduction, dispersal, density, competition, and predation. The project has opened up opportunities for large-scale ecological studies of interspecific effects with the cooperation of various other research projects being conducted within the region by state and federal agencies. In 2008, the Panthera Foundation partnered with CBS in project operations, providing additional logistical and financial support.

METHODS

Capture

*****I use the pronoun "we" in this section because the captures and field work were conducted as a team of biologists working on the TCP and I wish to acknowledge their contributions to the project. I am solely responsible for the analysis section.

We captured most cougars during winter (approximately late October through early April) using trained trailing hounds. The extent of each capture season depended on snow conditions and varied from year to year. Capture efforts followed Hornocker (1970) and Murphy (1998). Our capture crew consisted of 3 – 6 individuals. Prime conditions for searching for fresh tracks were generally in the early morning, several hours after a recent snowfall.

We fitted dogs with VHF radio collars and released them on cougar tracks as we approached the target animals. Dogs typically treed the cougar within 10 minutes of their release from the leash. In the event of longer pursuits, we used VHF receivers to locate the dogs.

When a cougar treed in a situation suitable for immobilization, we used immobilization protocols which followed Hornocker Wildlife Institute guidelines (Quigley 1997, Kreeger 2002). We used a digital range finder to estimate distance from the ground to the treed cougar, allowing proper calibration of dart velocity. Once the first dart (4.0-9.0 mg/kg @ 100mg/ml Ketamine using a DanInject® dart gun with DanInject® 3 cc darts) was administered and 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 injection (0.07 mg/kg @ 1.0 mg/ml Medetomidine) by hand. When the cougar was fully immobilized, we recorded heart rate, breathing rate, and temperature (^{O}F) every 2-5 minutes. Standard body measurements were recorded, and neck circumference was used to aid in proper fit of a VHF or GPS radio collar on the animal.

Immobilized cougars were weighed, sexed, and aged. We examined pelage color and condition and tooth color and condition to assess health. We examined each cougar for broken bones and (or) recent wounds. We aged adults based on gum recession (Laundre 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 a tissue sample from the sterilized ear tag punch, which was then placed into a sterile vial and catalogued for further lab processing. Blood samples were collected in the field and later spun in a centrifuge to extract serum. We sent these samples to the Wyoming state veterinary lab for pathological analysis. Any unique scars or physical features (e.g., frostbitten ears or tail) were recorded.

After approximately 45 – 50 minutes had passed from the time of the first injection, we administered an antagonist (0.3 mg/kg @ 5.0 mg/ml Atipamezole) and observed the cougar for 20 – 30 minutes until it was mobile. If we had observed recent wolf activity in the area, we monitored the cougar until we were confident that it would have the strength and mobility to avoid direct confrontation with wolves. 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.

Collars

We used several models of VHF radio and GPS collars during the study. VHF radio collars were used most often during the early years of the project (winter 2000-2001 through winter 2004-2005). Use of GPS collars increased starting in winter 2005-2006. After winter 2006-2007 we attempted to apply GPS collars exclusively to resident adult cougars captured in the study area.

VHF radio collar models included: Telonics (Mesa, Arizona) VHF models MOD500, MOD400, MOD225, and MOD125. GPS collar models included: Telonics/Argos global positioning system (GPS) models 348 and 458; Tellus/Televilt (Telemetry Solutions, Sweden) GPS model T5H; Northstar/Globalstar models. The GPS collar used most often was the Tellus GPS model 348. All models of GPS collars were programmed to acquire a minimum of 1 location daily. The Tellus models generally acquired 4 – 6 locations per day.

Obtaining locations

We located cougars fitted with standard VHF collars or GPS collars that were not functioning properly for the target data collection daily from roads, trails, and backcountry travel using triangulation methods (Heezen and Tester 1967, White and Garrott 1990). We attempted to get within 500 m of each collared cougar and to obtain a minimum of 3 azimuths for each location. We noted levels of accuracy and signal strength for azimuths in the field to help interpret triangulations.

Locations for cougars outfitted with GPS collars were acquired using several methods, depending on the make and model of the collar. Tellus collars required a manual download in the field using a remote transceiver. We attempted downloads every 7 – 10 days. We accessed locations from Northstar collars via a secure internet website. These location estimates were acquired daily and were available for review within 6 hours of each acquired estimate being uploaded to the server. These location estimates were automatically plotted onto a Google Earth® map layer. We downloaded all points to the database for analysis. Telonics/Argos GPS collars were deployed primarily on dispersing sub-adults. Data from these collars were accessed remotely and downloaded once every 2 – 4 weeks.

We used aerial telemetry to locate cougars that had not been detected for several consecutive days (Mech 1983). We also used aerial telemetry to track the locations of dispersing sub-adult cougars as they moved out of our study area. In addition, we used aerial tracking methods to locate cougars with GPS collars for obtaining remote downloads of the store-on-board location data.

We plotted location data with Geographic Information Systems (GIS) software, ArcView 3.3 (ESRI, Redlands, CA). We estimated final locations from VHF radio collar coordinates using the Location On A Signal (LOAS) software (Ecological Software Solutions, Sacramento, CA). The LOAS software allowed for accurate digital plotting of cougar locations and the software output included error polygons as measures of precision. All Universal Transverse Mercator projection (UTM) coordinates obtained from the analysis of location data were plotted on a digitized, georeferenced United States Geological Survey (USGS) 1:24,000 quadrangle topographic map layer using ArcView.

Locating and investigating kill sites

We defined a kill site as the location where a cougar presumably killed, consumed, and (or) cached a prey item. Our goal was to investigate each predation event that occurred during the project. Both GPS and VHF locations were used to locate kill sites. In addition, we investigated kill sites that were found opportunistically.

When we determined that a radio-collared cougar had stopped moving (localized) for more than 24 hrs (2 consecutive daily locations in the same area), a crew member would obtain a more precise location on the potential kill site. This involved getting within 300 m of the collared cougar and using triangulation methods with a minimum of 4 azimuths (whose outermost azimuths differed by > 74 degrees) on the location.

For cougars with GPS collars, clusters consisting of ≥ 2 GPS fixes within 100 m of each other within a 24-hour period were searched for possible kill sites (Anderson and Lindzey 2003, Kortello et al. 2007). We used the Hawth's tools extension (Beyer 2004) in ArcView 3.3 to select clusters and derive a centroid location where we would begin the kill site investigation.

For safety and as a way to increase efficiency of searching for signs of predation events, kill site investigations were completed by 2 researchers. We did not approach the kill site to perform an investigation if we had any indication that the cougar was within 1 km of the assumed location to minimize the amount of disturbance to cougars and their natural habits. Our goal was to be at the kill site immediately after the cougar had vacated, thus reducing the amount of time for scavengers to disrupt or disturb the kill site.

We thoroughly investigated the area within 100 m of each kill site. We searched for any evidence indicating a predation event such as sign of struggle, tufts of hair, drag marks, broken branches, blood, bones, toilets, bed sites, or a cache. When a prey item was located, we followed Ruth's kill evaluation and categorization chart (Ruth and Buotte 2007) to identify the carnivore species most likely responsible for the making kill. Telemetry location of subject animals was indicative, but to rule out scavenging behavior we had to perform a thorough search of the immediate area, and perform a necropsy on the prey item. Evidence of a predation event included tracks leading to a possible chase sequence or struggle, indicated by broken branches, or disturbed foliage. Further evidence indicative of cougar kills included claw marks and (or) canine punctures with associated subcutaneous hemorrhaging in the back, neck, and head regions as well as caching of prey items. We collected a section of the femur from each prey item for analysis of fat content (Hunt 1979, Neiland 2007), and collected the incisors and a mandible from each prey item for age determination. At each kill site, we recorded habitat characteristics and a general description of the immediate area.

Data analysis

In the Rocky Mountain region of the western U.S., prey species (i.e., elk and mule deer) generally 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). To account for the possible seasonal variation in the distribution of prey throughout the landscape attributed to fidelity to discrete winter and summer ranges, I divided the kill site characteristics data set into two distinct seasonal subsets: winter (November through April) and summer (May through October). This allowed for quantification of season-specific effects.

I formulated regression models designed to quantify the effects of increasing wolf presence on cougar kill site characteristics and prey composition. I used 2 measures of wolf presence in the analysis. The first measure was the estimated wolf population (W_POP) for each year, which I extracted from the annual wolf status reports published by the USFWS. I also used a direct spatial measure of wolf presence, defined as the distance (m) from each cougar kill site to the nearest wolf pack activity center (W_DIST). I obtained seasonal (i.e., winter, summer) wolf pack activity center estimates for all wolf packs monitored by the NPS and USFWS in the study area (Jimenez, M., USFWS and S. Dewey, NPS 2010, personal correspondence). The mean centers were derived using ArcGIS from 90% fixed-kernel home range estimates based on VHF and GPS collar locations of wolves in each of the wolf packs. Of the wolf pack data I received, I was confident that only those data representing the northern half of the study area would be suitable for the analysis, due to low numbers of monitored wolves and wolf locations in the southern half of the study area. Thus, I restricted my analysis of W_DIST as a covariate to only those cougar kill sites from the northern region, which reduced the number of cougar kill sites used in this portion of the analysis by nearly one-half. I plotted locations of wolf pack activity centers using ArcGIS and used Hawth's tools and *spatial analyst* to derive distances from each cougar kill site to the nearest wolf pack activity center.

I used ArcGIS to construct a topographical base map of the study area using USGS 1:24,000 quadrangle maps (WY GIS Clearinghouse). I obtained 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 from the US seamless map server (http://seamless.usgs.gov). I plotted all cougar kill site locations (Appendix A) and extracted slope (%), aspect (degrees), elevation (m, above sea level), and canopy cover (%) values from the NED and tree canopy layers using the ArcGIS *spatial analyst* extension. I transformed the circular distribution of aspect values to a linear distribution in order to be applied to a regression analysis. To do this, I first transformed aspect to radians, and subsequently decomposed aspect into to northness (cos[aspect]) and eastness (sin[aspect]) metrics (Alexander et al. 2006). Using ArcGIS, I conducted a simple random survey of 10,000 points from the tree canopy layer to obtain an estimate of the distribution of canopy cover values. I used R software (R software, Version 2.9.2, R Foundation for Statistical Computing, 2009) to create a histogram of the distribution, which displayed a significant discontinuity at the 15% value, suggesting a natural threshold for categorizing forest and non-forest. Subsequently, I 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 non-forested (open) habitat. I then used the regroup function in *spatial analyst* to classify any groups of ≤ 4 cells with a 'forest' classification as 'non-forest' to reduce the number of patches of forest determined as insufficient for cougar or prey cover. I used Hawth's raster tools (Beyer 2004) to create a line which defined the edge around each group of forest and non-forest cells. I then used the *join* function to derive the minimum distance from each cougar kill site to the forest/non-forest edge.

I 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 8 neighbors (3x3 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 3x3 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 (maximum differences relative to center + maximum differences in pixel values) and 0 being completely flat (Buotte, P., personal correspondence). I used ArcGIS *spatial analyst* extension to extract TRI values from each of the cougar kill sites and standardized the values to a range between 0 and 1.

I reviewed the WGFD annual big game herd unit job completion reports (JCRs) to examine general trends in the elk and mule deer herds within the study area. The JCRs also contain hunter success rates and various other information relating to prey herd size which can be used as a measure of herd size fluctuation over the years. Elk herds were generally stable throughout the duration of the study, at or above management goals. The mule deer population declined slightly during the study, but was generally at or near management goals (WGFD JCR 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).

Statistical approach

I conducted linear mixed effects regression analyses for all cougar kill site habitat variables using PROC MIXED (SAS 9.2, Cary N.C.). I used Akaike's information criterion (AIC) to evaluate relative support for alternate regression models (Burnham and Anderson 2002).

Regression analysis assumes the data are normally distributed and independent. Upon examination of histograms and quartile plots of the data, I determined that the elevation, ruggedness, distance to forest edge, and distance to nearest wolf pack activity center variables did not meet the assumption of normality. I then explored various power functions to achieve normality. I used a natural log transformation for elevation [ln(ELEV)], and distance to forest edge [ln(DFE)]. I used a Box-Cox transformation for the terrain ruggedness index [bc(TRI)] and converted percent canopy cover to a decimal metric [d(CC)]. I used maximum likelihood (PROC TRANSREG, SAS 9.2) to estimate the optimal Box-Cox parameter. I also performed a square root transformation to the distance to wolf pack activity center [sqrt(W_DIST)]. I used R software to compute summary statistics for all variables used in the analysis (Appendix B). In addition, summary statistics for all variables can be found in Appendix I. I used Pearson's Correlations to screen for independence using the correlation analysis function in Microsoft ® Excel. All habitat variables showed relatively low levels of collinearity ($r < 0.5$).

I defined seasonal year (S_YEAR) as the year in which each of the designated seasonal periods began (i.e., winter 2000-2001 = S_YEAR 2000) to account for the fact that the calendar year changes during winter. Many of the predation events observed at kill sites were made by the same individuals over a number of years. To improve inference beyond the unique set of characteristics in the dataset, seasonal year (S_YEAR), individual cougar identification (CAT_ID), and prey species (P_SPP) were treated as a random effects (i.e., intercept-only) (Littell et al. 2006). I formulated a suite of 5 models for each response variable using 4 different combinations of the random effects and a null model. 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, I analyzed the suite of 5 candidate mixed effects linear regression models (for the winter and summer subsets) for each habitat response variable using REML and ranked them using the AIC model selection approach (Burnham and Anderson 2002). I then chose the optimal model from each set of ranked models for each response variable (Table 2, Table 3). I used maximum likelihood (ML) to analyze the optimal mixed effects model with and without the wolf parameter. I used the coefficient estimates from the optimal REML models and model averaging techniques to obtain unconditional parameter estimates (Zuur et al. 2009). I used the evidence ratios, defined as the Akaike weights (w_i) of the models with the minimum AIC value (w_{min}), divided by the w_i of the second best model to assess the empirical support for the optimal models (Burnham and Anderson 2002). Using this approach, the evidence ratio can be used as a measure of how much more supportive evidence the best model carries than the next best model. For example, an evidence ratio of 3.0 means the best model carries 3 times the strength of evidence as the second best model.

Mule deer and elk

I used the same variables described in the kill site habitat characteristic analysis to formulate logistic regression models. I used PROC LOGISTIC (SAS 9.2) to analyze the prey composition at cougar kill sites. In particular, I was interested in understanding how the proportion of the two main prey items (i.e., elk and mule deer) was changing in cougar diet as an effect of increasing wolf presence. To address this question, I designed a logistic regression model and analyzed only elk and mule deer kill sites. The response variable in this analysis was the binary outcome mule deer = 1, elk = 0. I first created a global model, using all independent explanatory variables. I used this model to assess possible variation in the probability of encountering a mule deer or an elk kill by evaluating 2 models one with and one without a wolf presence parameter. I compared AIC values and evidence ratios to determine the relative levels of importance that wolf models had in explaining the probability of encountering mule deer compared to elk at cougar kill sites. I 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).

Forest and non-forest kill sites

I used the same logistic regression methods to model the relative occurrence of cougar kill sites made within the cover of forest (> 15% canopy cover) versus kill sites made in the open (binary response, where forest = 1, open = 0). I predicted that increasing presence of wolves would affect where cougars made their kills (open vs. 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 I replaced the mule deer/elk predictor variable (MD_N) with the forest/non-forest variable (F_NF). This model was analyzed with and without the wolf presence parameters and I used AIC to compare fit. I used the same criteria as in the MD_N models to interpret the ROC AUC values in my assessment of the predictive capabilities of the logistic regression models.

RESULTS

From winter 2000 through October 2009, we captured 88 cougars ranging in age from < 1 month to > 5 years old at first capture. Of these, 55 were females, 31 were males, and 2 (6 month old kittens) were not identified to sex. Individuals were recaptured several times during the study, primarily for collar replacement. In addition, many of the young (< 15 months old at time of capture [n=35]) individuals dropped their collars, died before reaching independence or adulthood, or dispersed from the study area before making any kills independently. Dependent young are usually unable to take down large prey (Logan and Sweanor 2001), so several cougars never reached a level of maturity where they were making kills independently.

From December 1999 through October 2009 we investigated 623 potential kill sites. Of these, 74 evidently were not predation events upon investigation and were removed from the final data set. Kill sites exhibiting evidence of scavenging (i.e., no explicit evidence that a cougar killed the prey item) were also removed from the data set. The final data set consisted of 539 confirmed cougar kills. Of these, 506 were made by 34 different collared cougars, and the remaining kills (n = 33) were made by unknown (non-collared) cougars, and were found opportunistically. Large ungulates made up the majority of prey items which consisted primarily of elk (65%, n = 350), mule deer (17%, n = 92) and moose (5%, n = 28). The remaining kills (n = 69) consisted of several other species (Figure 2). In addition, we found evidence of wolf presence at 5.4% (n = 29) of the cougar kill sites we investigated. Of these, 65.5% (n = 19) occurred between March 2006 and May 2009. Presence of wolf sign was indicated by tracks and scat upon examination of potential kill sites. Occurrence of wolf sign observed at cougar kill sites was primarily detected during winter months and the number of occurrences increased during the study (Figure 3).

Kill site habitat characteristics modeled with wolf proximity

Summer

In the northern half of the study area during summer months, models of elevation [ln(ELEV)], northness (N_ness) canopy cover [d(CC)] associated with cougar kill sites were better supported when distance to the nearest wolf pack activity center (W_DIST) was included as a covariate (Table 4a). Parameter estimates indicated decreasing W_DIST (i.e., closer proximity to cougar kills) was associated with higher cougar kill site elevations, more north-facing slopes, and lower percent canopy cover (Table 6). Models of ruggedness, distance to forest edge, and eastness associated with cougar kill sites were better supported when W_DIST was not included as a covariate (Table 4a, Table 4b).

Winter

In the northern half of the study area during winter months, models of elevation (ln(ELEV)) associated with cougar kill sites were better supported when W_DIST was included as a covariate (Table 4a). Parameter estimates indicated that decreasing W_DIST was associated with higher cougar kill site elevations in the winter (Table 6). Models of ruggedness, canopy cover, distance to forest edge, northness, and eastness associated with cougar kill sites were better supported when W_DIST was not included as a covariate (Table 4a, Table 4b).

Kill site habitat characteristics modeled with wolf population

Summer

Models of elevation (ln(ELEV)) associated with cougar kill sites were better supported when wolf population (W_POP) was included as a covariate (Table 5a). Parameter estimates for W_POP (Table 7) suggested that elevation increased as W_POP increased. Models of ruggedness, canopy cover, northness, eastness, and distance to forest edge associated with cougar kill sites were better supported when W_POP was not included as a covariate (Table 5a, Table 5b).

Winter

Models of ruggedness (bc(TRI)) associated with cougar kill sites during winter were better supported when W_POP was included as a covariate (Table 5a). Parameter estimates for W_POP indicated that ruggedness had a positive association with increasing W_POP (Table 7). Models of elevation, northness, eastness, canopy cover, and distance to forest edge were better supported when W_POP was not included as a covariate (Table 5a, Table 5b).

Logistic regression

Logistic regression indicated that that recolonizing wolves effect prey composition found at cougar kill sites in the northern half of the study area (Table 8). Parameter estimates indicated that the probability of encountering a mule deer kill increased as W_DIST decreased in the winter and summer months (Table 9, Figure 5). 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., versus an elk kill) increased as the wolf population increased throughout the entire study area in the winter and summer months (Table 9, Figure 4). The corresponding AUC value associated with the ROC curve indicated a good fit for this model (Table 8).

The results for the forest vs. open models were mixed. Logistic regression indicated that modeling the probability of a kill being found in forested habitat (i.e., closed versus open canopy cover) was better supported when including W_POP as a covariate (Table 8, Figure 6). The parameter estimates indicated that the probability of a kill being found in forested habitat increased as W_POP increased (Table 9). The ROC curve for this model displayed good prediction accuracy, with and AUC value indicating a good fit (Table 8). In the northern half of the study area, however, modeling the probability of finding a kill in forested habitat at cougar kill sites was not better supported when including W_DIST as a covariate. The AUC value corresponding with the ROC curve for this model indicated a good fit (Table 8).

DISCUSSION

For the past two decades, much research has focused on the recolonization of the Rocky Mountains 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 less-dominant species, and wolf presence may induce behavioral responses such as avoidance, altered diet, or shifts in space use (Kortello et al. 2007). My observations in this study are consistent with previous observations of competitive interactions (Kunkel et al. 1999, Kortello et al. 2007) and suggest exploitative and interference competition in that prey and habitat use shifted in the less-dominant species (i.e., cougars) and that these shifts were associated with an increasing more-dominant predator population. My results indicate that the recolonization of wolves (a coursing predator) has the potential to influence certain predation habits of cougars (an ambush predator). My results indicated that landscape characteristics observed at cougar kill sites shifted as a function of an increasing wolf population and as a function of the proximity of wolves to cougar foraging sites on the landscape. The changes observed at cougar kill sites were most prevalent in the northern half of the study area during the summer months, when I used a spatial measure of wolf proximity as a predictor of change. Additional support for this shift in foraging habitat was evident in the winter months 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 characteristics of cougar kill sites was evident in the winter and summer months as well, though to a lesser degree than in the northern half of the study area.

During the recolonization of wolves in the TCP study area, the formation of new packs and territories across the landscape likely reduced the extent of available foraging habitat for cougars. This reduction in available foraging habitat, coupled with the increasing rate of interactions (exhibited in the presence of wolf sign at cougar kill sites), correlates with a shift to foraging habitat characterized by higher elevations and more northerly facing slopes in the northern half of the study area during the summer months. Also, shifts to higher elevations in the summer and more rugged areas in the winter were evident throughout the study area as functions of the increasing wolf population.

Contrary to my predictions, cougar kill sites were characterized by reduced canopy cover and a reduced probability of finding a kill site in forest habitat as functions of increasing wolf presence in the northern half of the study area. Cougar kill sites 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 likely that the 30 m resolution canopy cover layer was not accurate enough to delineate certain micro-habitat characteristics, including secondary growth, shrubs, old-growth sagebrush, and willow thickets. These characteristics, typical of structurally complex habitat, provide suitable cover for predatory stalking behavior but may have been overlooked in my analysis. However, it is possible these observations could be attributed to an adaptation in foraging strategy as a result of cougars hunting different prey species in newly occupied habitat. For example, 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), we might expect to see this reflected in the composition of prey species found at cougar kill sites. My results supported this inference because the ratio of mule deer to elk found at cougar kill sites increased significantly as a function of increasing wolf presence, both at the population and landscape levels, and more so in the summer months than in the winter months. Thus, the higher incidence of mule deer kills may be an outcome of the increasing wolf population influencing cougars to alter space use, foraging in areas with higher densities of mule deer. Another explanation might be the prey species seeking refuge in adjacent habitat as an attempt to reduce predation risk from the newly established wolf population, consequently increasing predation risk from cougars. A caveat to my work is that the study design did not allow for a measure of how prey behavior may have been directly affected by the increasing wolf population; this could have allowed for fuller insight into these relationships.

Because my investigation of cougar kill sites was implemented continuously from the onset of the wolf population growth, my results may provide improved inference about the seasonal effects of a recolonizing predator on a complex multi-predator, multi-prey ecosystem. Recent studies investigating kill sites have implemented field seasons confined to 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. An exception is Alexander et al.’s (2006) study, which focused on month-by-month changes in spatial co-occurrence between wolves and cougars. I concur with Alexander et al. (2006) that observations of variability in ecological processes may be ambiguous at the annual or seasonal level when studying cougars. Hence, inferences made in recent research regarding predation habits of cougars and wolves could be misleading when data collection or field seasons are confined to shorter periods of the year, which might fail to consider obvious seasonal dynamics.

In my 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). I hypothesize that, given the recent findings in resource selection of cougars and mule deer (Atwood et al. 2009), space use by mule deer while occupying seasonal foraging ranges may increase 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. 2008). In contrast, Atwood et al. (2007) suggested that the risk of predation on mule deer by cougars 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. However, Atwood et al.’s study focused primarily on winter months and predation events in prey summer ranges were not considered. Moreover, their findings likely were related to the habitat characteristics, and the distribution and density of prey species within the study area, which varies considerably throughout the Rocky Mountain region. Because my work did not incorporate monitoring of relative elk and mule deer distributions or densities within my study area, it is difficult to make conclusions based on prey availability or vulnerability. Further intensive telemetry studies of mule deer and cougar space use would be required to investigate the extent of this seasonal movement relationship. Furthermore, the implementation of year-round data collection and subsequent analysis of seasonal patterns in prey and predator space use may allow for more informed inference about predator-prey dynamics.

If the contradiction between my predictions and the results of the canopy cover and the probability of cougar kill sites occurring in the forest analyses 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. Future research of vegetative and topographical structural complexity at kill 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 United States, conservation of large carnivores has been an important concern for several decades. As further insights were gained through pioneer studies in the 1960s and 1970s (Hornocker 1970, Mech 1970, Spalding and Lesowski 1971, Seidensticker et al. 1973), scientists, managers, and much of the general public became more aware of the importance of these animals to the regulation and continuity of basic ecological processes. More recently, with the increase of protective laws and regulations, we have witnessed an impressive reestablishment of these species to their former ranges (Ream 1991, Bangs 1996;1998, Smith et al. 2003). Variable recolonization rates of large carnivores provide scientists and managers with an opportunity to study and document the roles that reestablishing species perform within their respective systems. My findings have provided further insight into how changes in foraging habits of cougars have associated with the recolonization of wolves in the southern Greater Yellowstone Ecosystem. Seasonal changes are important within this ecosystem and my research has demonstrated the need to better understand seasonal patterns in order to gain a greater understanding of interactions.

MANAGEMENT IMPLICATIONS

Although advancements in technology and field research methods have enabled researchers to implement more intensive studies of large carnivores, problems with duration and timing of field seasons may cause researchers to miss important seasonal changes in predation habits. In multi-predator, multi-prey systems, the recolonization of wolves may influence cougars to shift to different foraging habitats, and subsequently prey on a wider variety of species, depending on the time of year. This change in foraging behavior may negatively impact populations of secondary prey species. Contrary to Atwood et al.'s (2009) findings, my results indicated that wolves may increase the rate of cougar predation on mule deer despite shared winter ranges with elk and the higher density of elk within the region. Within my study area, this may have lead to a greater reduction in the already declining mule deer population. If recolonization of wolves leads to increased predation of a secondary prey species such as mule deer, 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. This may include prescribed burns to reduce dense secondary growth near edge habitat used by cougars for stalking cover at higher elevations and along north-facing slopes. This is especially applicable to areas in the northern and central Rocky Mountain region where seasonal migrations of prey are common. I 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 habitat shifts by a resident predator species associated with influences from a recolonizing predator species.

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 quota 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. 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).

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TABLES

Table 1. Definitions and corresponding abbreviations of all variables and transformations performed on variables used in the statistical modeling of data associated with cougar kill sites as part of the Teton Cougar Project, from winter 2000-2001 through summer 2009.

Variable	Abbreviation	Definition	Transformation	Transformed Abbreviation
Elevation	ELEV	Elevation (m above sea level)	natural log	ln(ELEV)
Ruggedness	TRI	Terrain ruggedness index where 0.0 = flat and 1.0 = vertical topography	Box-Cox (optimal parameter = 1.2)	bc(TRI)
Canopy cover	CC	Percent canopy cover	decimal	d(CC)
Northness	N_ness	Where -1.0 is due south, and 1.0 is due north	sin(aspect)	N_ness
Eastness	E_ness	Where -1.0 is due west, and 1.0 is due east	cos(aspect)	E_ness
Distance to forest/non-forest edge	DFE	Distance (m) from kill site to nearest forest/non-forest edge	natural log	ln(DFE)
Wolf Population	W_POP	Wolf population within TCP study area		
Distance to nearest wolf pack activity center	W_DIST	Distance (m) from kill site to nearest wolf pack activity center	square root	sqrt(W_DIST)
Cougar identification	CAT_ID	Indentification number designated to individual cougars		
Prey species	P_SPP	Common name of prey items found at cougar kill sites		
Seasonal year	S_YEAR	Standardized year assigned according to season		
Mule deer or not	MD_N	Binary variable where mule deer = 1, elk = 0.		
Forested or not	F_NF	Binary variable where forested habitat = 1, open = 0		

Table 2. Model* selection for random effects structures (SAS PROC MIXED) using wolf population (W_POP) as a covariate, fit to descriptive data for cougar kill sites in the Teton Cougar Project study area (winter 2000 – 2001 through summer 2009). Models were fit using restricted maximum likelihood. See Table 1 for variable definitions.

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

***** Full model includes all other habitat variables as covariates with the wolf covariate.

[†] All boldface AIC values represent the random effect model selected for further analysis.

Table 3. Model* selection for random effects structures (SAS PROC MIXED) using distance to nearest wolf pack activity center (W_DIST) as a covariate, fit to descriptive data for cougar kill sites in the Teton Cougar Project study area (winter 2000 – 2001 through summer 2009). Models were fit using restricted maximum likelihood. See Table 1 for variable definitions.

W_DIST

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

***** Full model includes all other habitat variables as covariates with the wolf covariate.

[†] All boldface AIC values represent the random effect model selected for further analysis.

Table 4a. Model selection for models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area, winter 2000 - 2001 through summer 2009, for models with and without the sqrt(W_DIST) covariate. Models are shown with corresponding number of parameters k_i, maximum 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 obtained from dividing w_i of the best model by the w_i of the i-th model. See Table 1 for variable definitions.

Season	**Base model**	**Wolf Effect**	**k_i**	**$L(\theta_i)$**	**AIC**	**Δ_i**	**w_i**	**Ev. Ratio**
Winter	ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + S_YEAR)	W_DIST	9	260.0	-502.0	0.0	0.839	5.21
		null	8	257.4	-498.7	3.3	0.161	
Summer	ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_DIST	9	169.7	-321.4	0.0	0.634	1.73
		null	8	168.2	-320.3	1.1	0.366	
Winter	bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID)	W_DIST	8	272.9	-529.8	1.1	0.366	
		null	7	272.5	-530.9	0.0	0.634	1.73
Summer	bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(null)	W_DIST	7	213.6	-413.2	1.8	0.289	
		null	6	213.5	-415.0	0.0	0.711	2.46
Winter	d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(null)	W_DIST	7	-5.7	25.3	1.9	0.279	
		null	6	-5.7	23.4	0.0	0.721	2.58
Summer	d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_DIST	9	3.0	12.0	0.0	0.750	3.00
		null	8	0.9	14.2	2.2	0.250	

Table 4b. Model selection for models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area, winter 2000 - 2001 through summer 2009, for models with and without the sqrt(W_DIST) covariate. Models are shown with corresponding number of parameters k_i, maximum 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 obtained from dividing w_i of the best model by the w_i of the i-th model. See Table 1 for variable definitions.

Season	Base model	Wolf Effect	k_i	$L(\theta_i)$	AIC	Δ_i	w_i	Ev. Ratio
Winter	ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_DIST	7	-249.1	512.2	0.7	0.413	
		null	6	-249.8	511.5	0.0	0.587	1.42
Summer	ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_DIST	7	-177.8	369.5	1.4	0.332	
		null	6	-178.1	368.1	0.0	0.668	2.01
Winter	N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	W_DIST	8	-160.1	336.2	1.9	0.279	
		null	7	-160.2	334.3	0.0	0.721	2.58
Summer	N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	W_DIST	8	-123.3	262.6	0.0	0.928	12.89
		null	7	-126.9	267.7	5.1	0.072	
Winter	E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_DIST	7	-143.3	300.6	1.8	0.289	
		null	6	-143.4	298.8	0.0	0.711	2.46
Summer	E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_DIST	7	-123.2	260.4	0.6	0.426	
		null	6	-123.9	259.8	0.0	0.574	1.35

Table 5a. Model selection for models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area, winter 2000 - 2001 through summer 2009, for models with and without the sqrt(W_DIST) covariate. Models are shown with corresponding number of parameters k_i, maximum 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 obtained from dividing w_i of the best model by the w_i of the i-th model. See Table 1 for variable definitions.

Season	**Base Model**	**Wolf Effect**	**k_i**	**$L(\theta_i)$**	**AIC**	**Δ_i**	**w_i**	**Ev. Ratio**
Winter	ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID)	W_POP	8	455.6	-895.1	1.7	0.299	
		null	7	455.4	-896.8	0.0	0.701	2.345
Summer	ln(ELEV) ~ bc(TRI) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID+P_SPP+S_YEAR)	W_POP	10	334.8	-649.6	0.0	0.537	1.162
		null	9	333.7	-649.3	0.3	0.462	
Winter	bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	9	501.4	-984.7	0.0	0.562	1.283
		null	8	500.1	-984.2	0.5	0.438	
Summer	bc(TRI) ~ ln(ELEV) + d(CC) + ln(DFE) + N_ness + E_ness + random(null)	W_POP	7	395.8	-777.6	1.4	0.332	
		null	6	395.5	-779.0	0.0	0.668	2.012
Winter	d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	9	-21.2	60.4	0.0	0.500	1.000
		null	8	-22.2	60.4	0.0	0.500	1.000
Summer	d(CC) ~ ln(ELEV) + bc(TRI) + ln(DFE) + N_ness + E_ness + random(CAT_ID + P_SPP)	W_POP	9	-28.3	74.5	1.7	0.299	
		null	8	-28.4	72.8	0.0	0.701	2.345

Table 5b. Model selection for models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area, winter 2000 - 2001 through summer 2009, for models with and without the sqrt(W_DIST) covariate. Models are shown with corresponding number of parameters k_i, maximum 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 obtained from dividing w_i of the best model by the w_i of the i-th model. See Table 1 for variable definitions.

Season	**Base Model**	**Wolf Effect**	**k_i**	**$L(\theta_i)$**	**AIC**	**Δ_i**	**w_i**	**Ev. Ratio**
Winter	ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_POP	7	-495.7	1005.3	2.0	0.269	
		null	6	-495.7	1003.3	0.0	0.731	2.72
Summer	ln(DFE) ~ ln(ELEV) + bc(TRI) + d(CC) + N_ness + E_ness + random(null)	W_POP	7	-391.6	797.1	2.0	0.269	
		null	6	-391.6	795.1	0.0	0.731	2.72
Winter	N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID)	W_POP	8	-281.2	578.3	2.1	0.259	
		null	7	-281.1	576.2	0.0	0.741	2.86
Summer	N_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + E_ness + random(CAT_ID + S_YEAR)	W_POP	9	-238.0	494.0	0.7	0.413	
		null	8	-238.7	493.3	0.0	0.587	1.42
Winter	E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_POP	7	-280.0	574.0	2.0	0.269	
		null	6	-280.0	572.0	0.0	0.731	2.72
Summer	E_ness ~ ln(ELEV) + bc(TRI) + d(CC) + ln(DFE) + N_ness + random(null)	W_POP	7	-263.0	540.0	1.8	0.289	
		null	6	-263.1	538.2	0.0	0.711	2.46

Table 6. Unconditional parameter estimates for models fit to using the sqrt(W_DIST) covariate fit to descriptive data for cougar kill sites in the Teton Cougar Project study area (winter 2000 – 2001 through summer 2009). Models were fit using maximum likelihood. See Table 1 for variable definitions.

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	

*****Denotes parameter estimates with 95% confidence intervals excluding 0.

Table 7. Unconditional parameter estimates for models fit to using the W_POP covariate fit to descriptive data for cougar kill sites in the Teton Cougar Project study area (winter 2000 – 2001 through summer 2009). Models were fit using maximum likelihood. See Table 1 for variable definitions.

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	

*****Denotes parameter estimates with 95% confidence intervals excluding 0.

Table 8. Model selection for logistic regression models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area, winter 2000 – 2001 through summer 2009. Models were fit with and without wolf covariates. Models are shown with corresponding maximum 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 obtained from dividing w_i of the best model by the w_i of the i-th model. See Table 1 for variable definitions.

Response Variable	**Base Model**	**Wolf Effect**	**$L(\theta i)$**	**AIC**	**Δ_i**	**w_i**	**ROC[a] AUC**	**Ev. 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	0.159	0.788	5.30
		no wolves	-235.22	484.44	3.34	0.841	0.781	

[a] Area under the Receiver Operating Characteristic (ROC) curve. Values between 0.5 and 0.7 were considered low discrimination, values between 0.7 and 0.8 were considered acceptable discrimination, and values ≥ 0.8 were considered excellent discrimination (Hosmer and Lemeshow 2000).

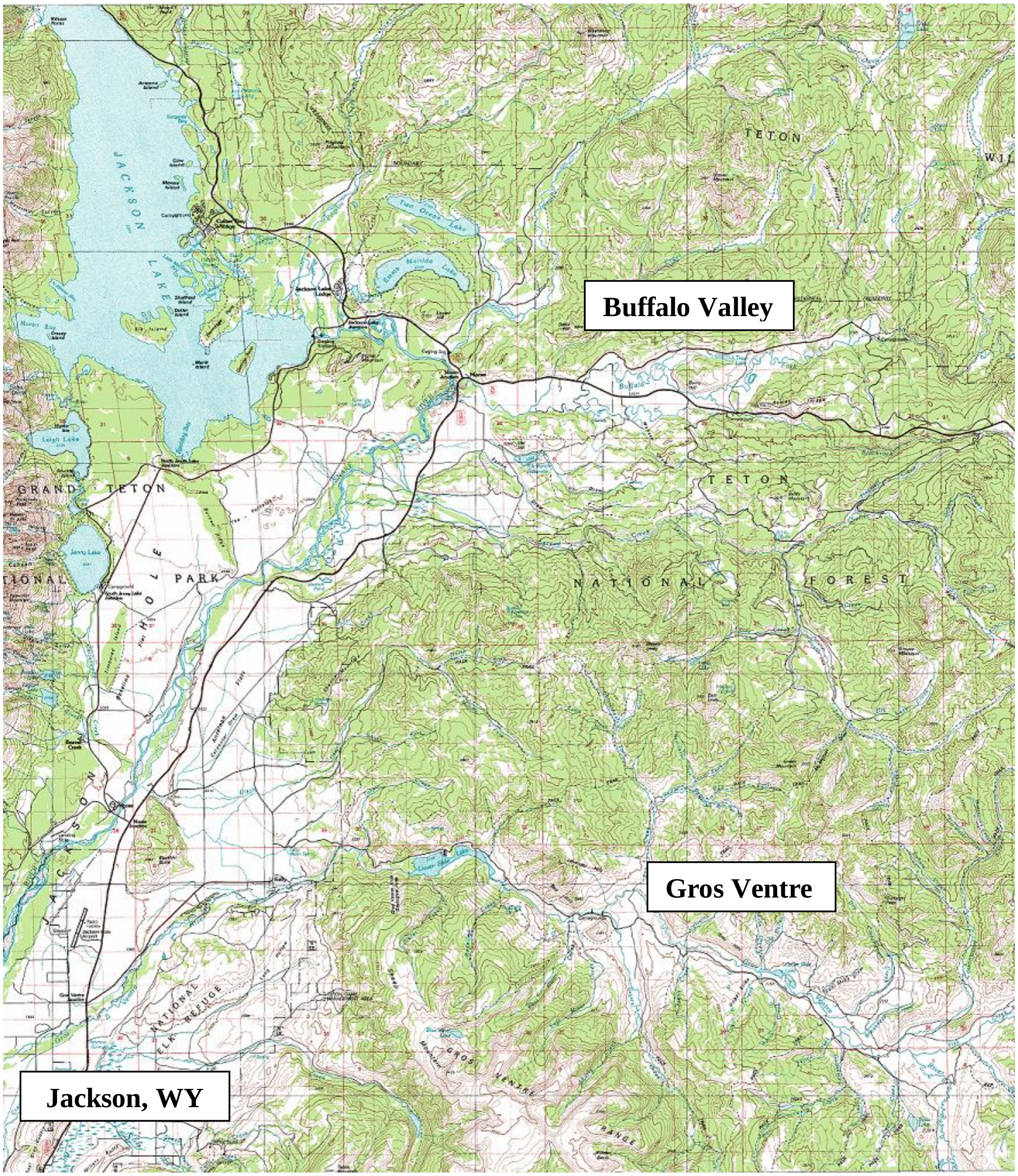
Table 9. Unconditional parameter estimates for logistic regression models fit to descriptive data for cougar kill sites in the Teton Cougar Project study area (winter 2000 – 2001 through summer 2009). Models were fit using maximum likelihood. See Table 1 for variable definitions.

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	0.0000		4.2423*	0.0000	0.5195*	1.3092*	-0.0450
F_NF	W_POP	-0.0137*		1.8035*	-0.0003	0.0775	1.3919*	-0.1199

*****Denotes parameter estimates with 95% confidence intervals excluding 0

FIGURES

Figure 1. Map of the Teton Cougar Project study area (~ 2,300 km^2) in northwestern Wyoming, USA with an outline of the approximate boundary of field monitoring efforts from winter 2000-2001 through summer 2009.



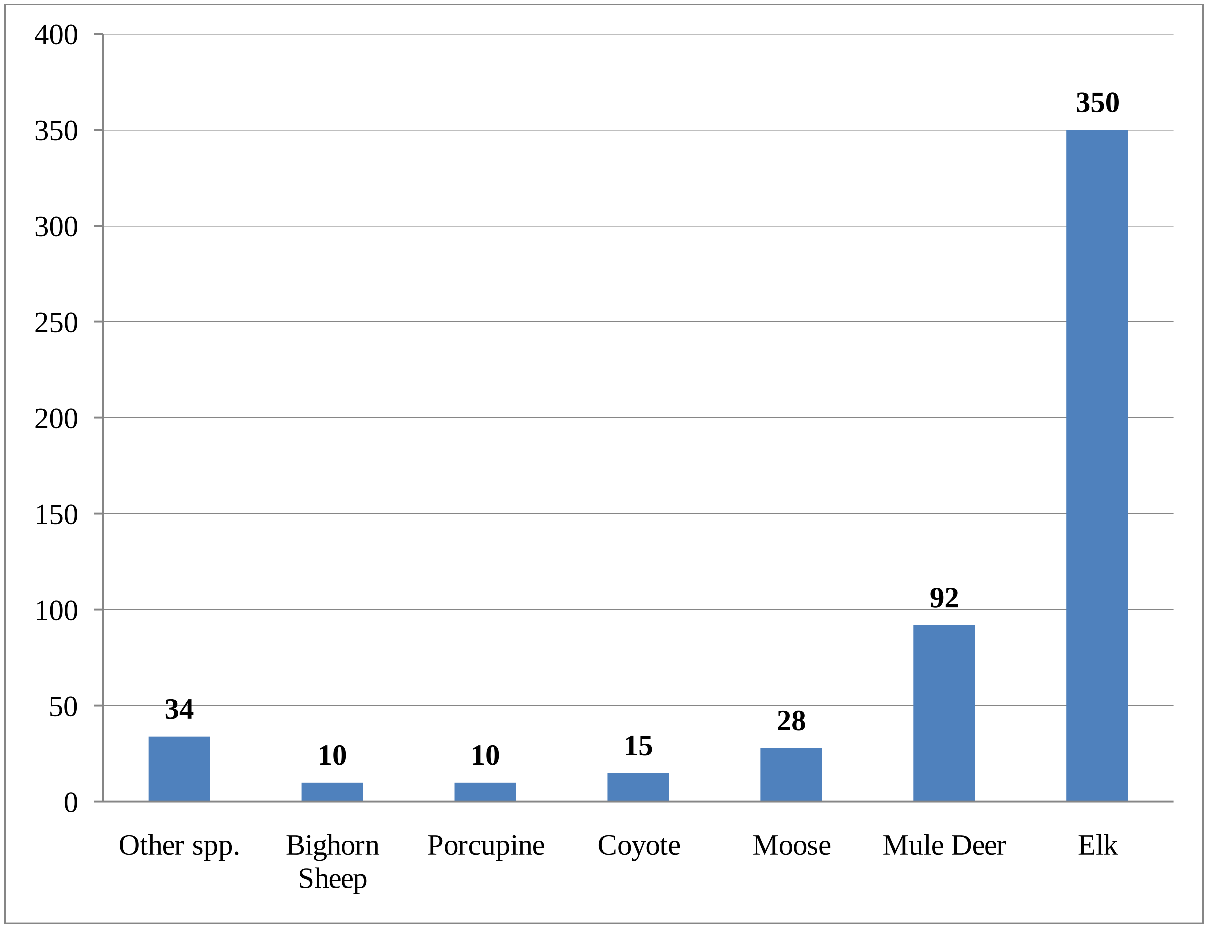


Figure 2. Prey species and their corresponding totals found at cougar kill site investigations in the Teton Cougar Project study area, Wyoming, USA from winter 2000 2001 through summer 2009.

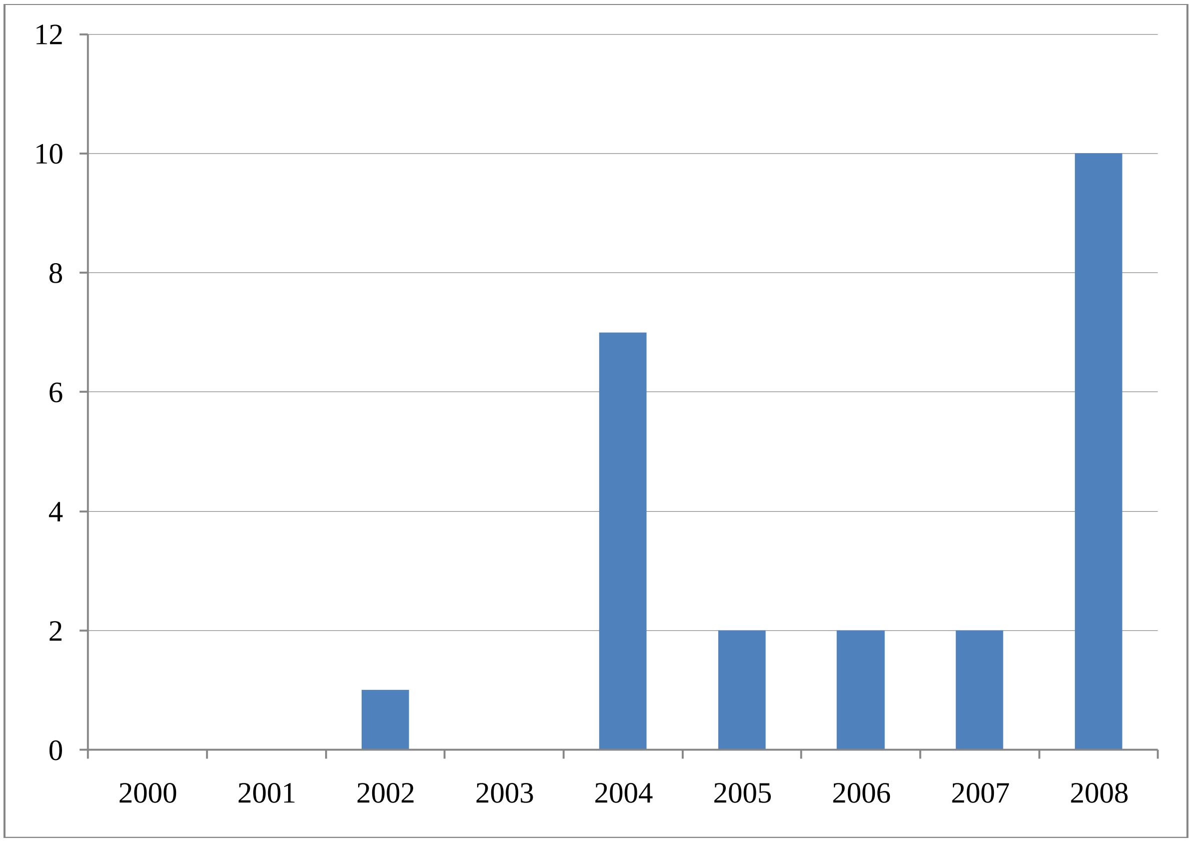


Figure 3. Number of investigated cougar kill sites documented with wolf sign present in the Teton Cougar Project study area, Wyoming, USA, from winter 2000-2001 through summer 2009.

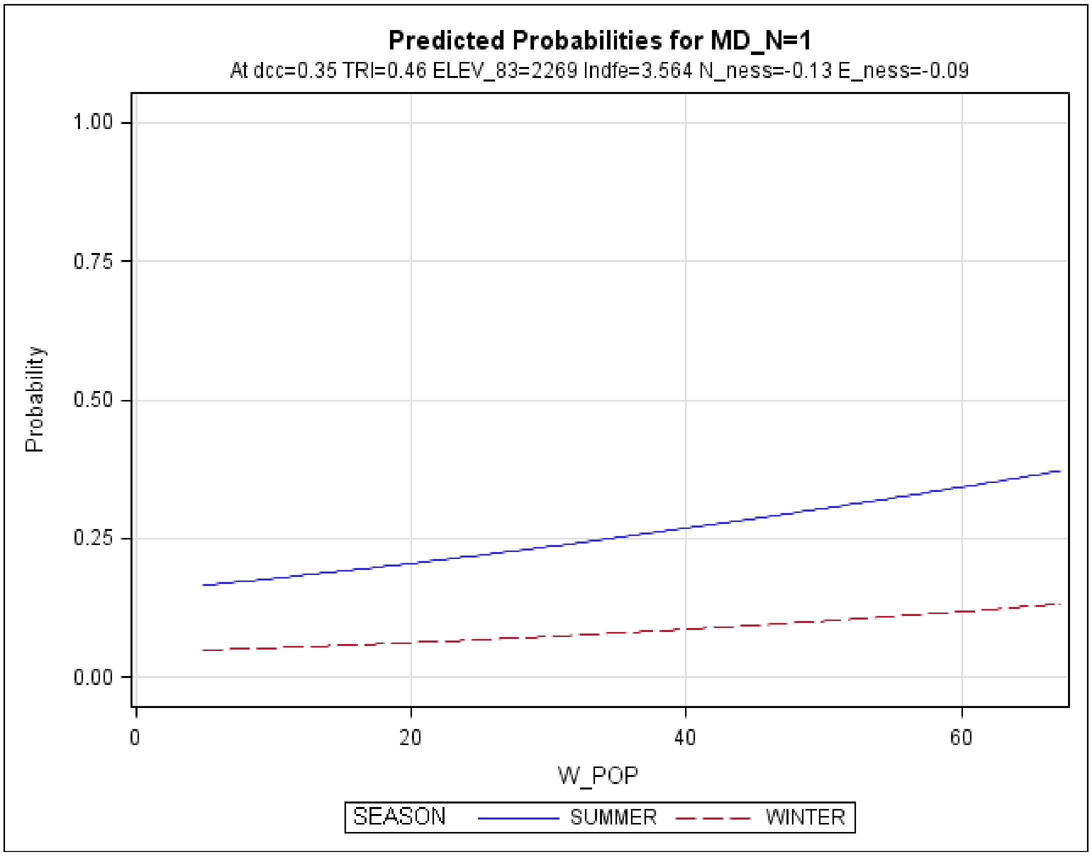


Figure 4. Predicted probabilities of encountering a mule deer kill versus an elk kill, separated by season, for logistic regression models fit to descriptive data from cougar kill sites in the Teton Cougar Project study area, winter 2000-2001 through summer 2009. Probability of encountering a mule deer (y-axis) increases as the wolf population increases.

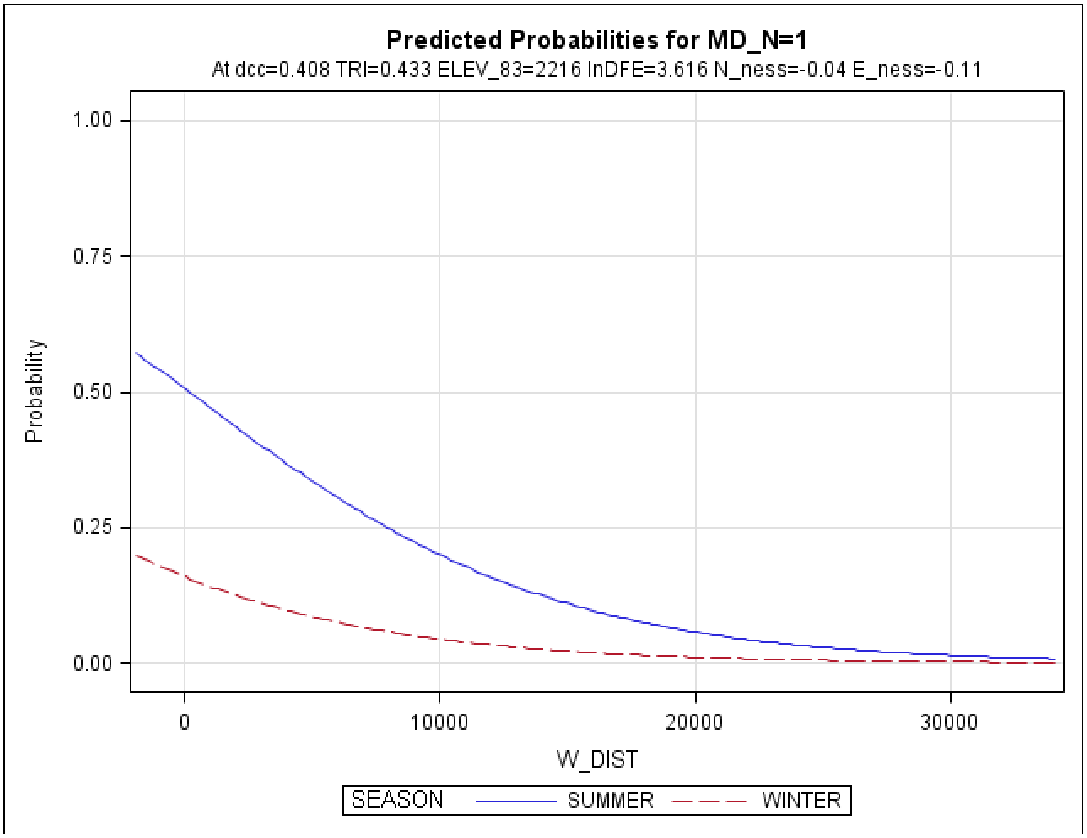


Figure 5. Predicted probabilities of encountering a mule deer kill versus an elk kill, separated by season, for logistic regression models fit to descriptive data from cougar kill sites in the Teton Cougar Project study area, winter 2000-2001 through summer 2009. Probability of encountering a mule deer (y-axis) increases as the distance from cougar kill sites to the nearest wolf pack activity center decreases.

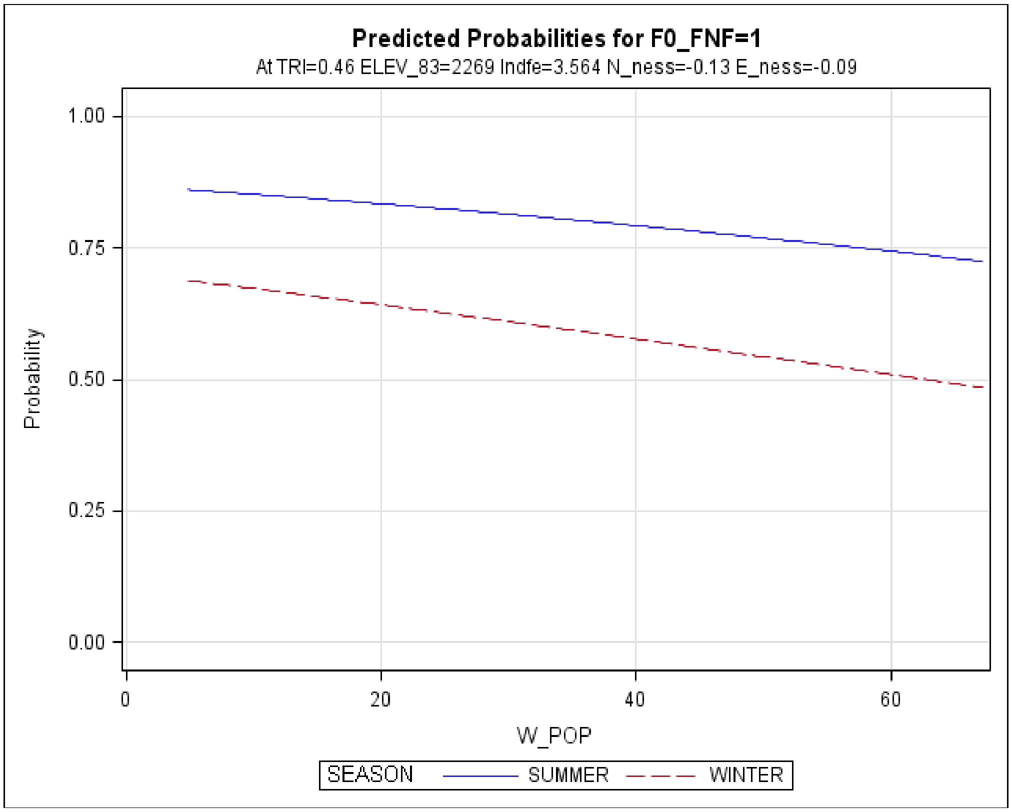
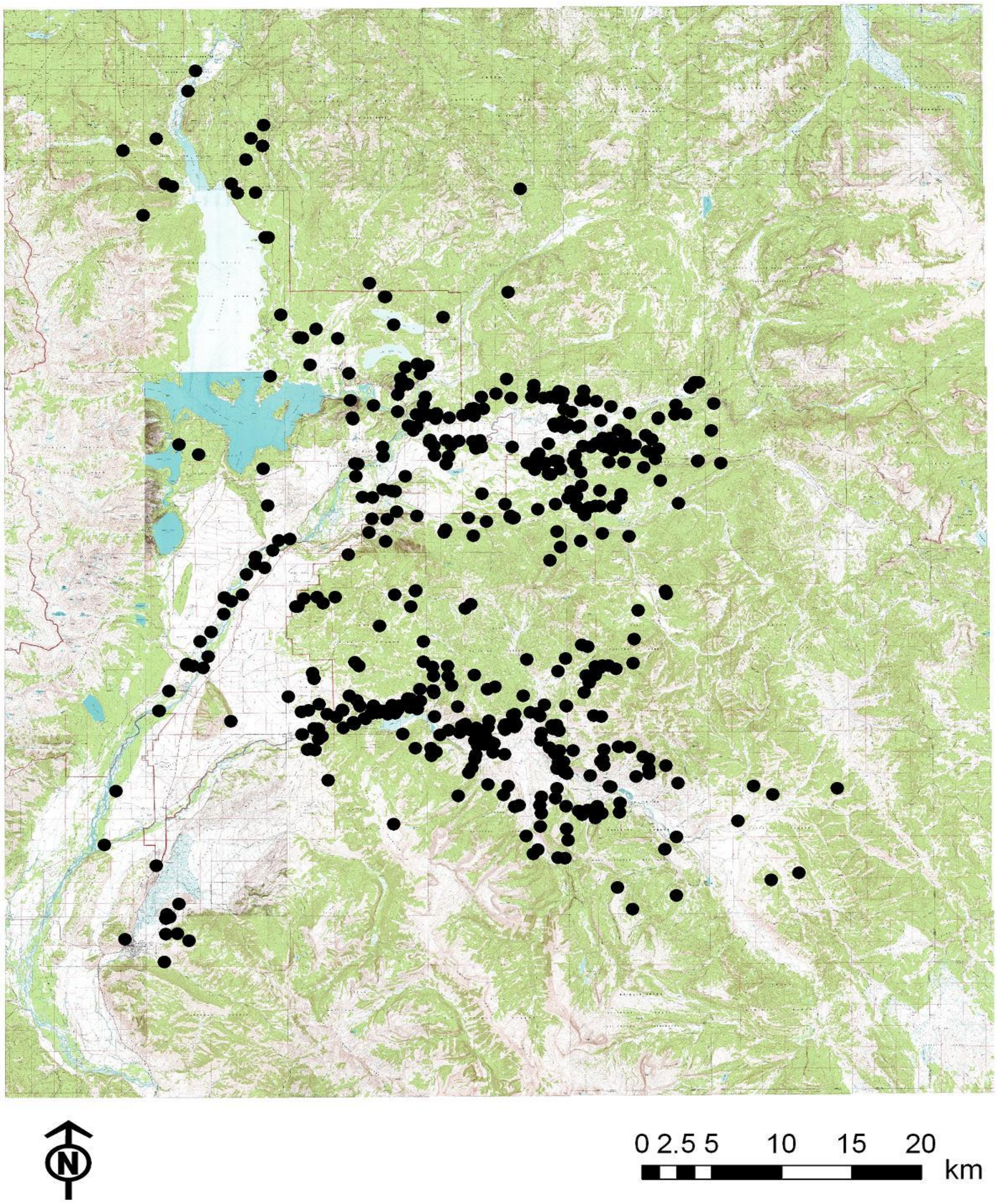


Figure 6. Predicted probabilities of finding a kill in forested habitat versus in the open, separated by season, for logistic regression models fit to descriptive data from cougar kill sites in the Teton Cougar Project study area, winter 2000-2001 through summer 2009. Probability of finding a kill in forested habitat (y-axis) decreases as wolf population increases.

APPENDIX A

Distribution of cougar kill sites (n = 539) throughout the Teton Cougar Project study area, from winter 2000-2001 through summer 2009.



APPENDIX B

Summary statistics for variables used in the statistical analysis derived from cougar kill sites in the Teton Cougar Project study area, winter 2000-2001 through summer 2009. See Table 1 for variable definitions.

Variable	Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
CC	0.00	0.00	30.00	36.21	66.00	99.00
ELEV	1905	2122	2243	2261	2376	3179
N_ness	-1.000	-0.832	-0.194	-0.099	0.635	1.000
E_ness	-1.000	-0.744	-0.087	-0.082	0.497	1.000
TRI	0.017	0.404	0.477	0.450	0.538	0.774
DFE	0.18	15.26	40.63	72.59	94.50	718.79
W_DIST	1073	6695	11140	11611	15459	31114

Transformed variables

Variable	Minimum	1st Quartile	Median	Mean	3rd Quartile	Maximum
d(CC)	0.00	0.00	0.30	0.36	0.66	0.99
ln(ELEV)	7.552	7.660	7.716	7.721	7.773	8.064
bc(TRI)	-0.500	-0.418	-0.386	-0.389	-0.355	-0.201
ln(DFE)	-1.690	2.725	3.700	3.562	4.550	6.580
sqrt(W_DIST)	32.75	81.82	105.55	103.63	124.33	176.39