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FORAGING ECOLOGY OF COUGARS IN THE PRYOR MOUNTAINS OF

WYOMING AND MONTANA

by

Linsey W. Blake

A thesis submitted in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

Eric M. Gese Major Professor Michael L. Wolfe Committee Member

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UTAH STATE UNIVERSITY Logan, Utah

2014

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ABSTRACT

Foraging Ecology of Cougars in the Pryor Mountains of Wyoming and Montana

by

Linsey W. Blake, Master of Science

Utah State University, 2014

Major Professor: Eric M. Gese Department: Wildland Resources

Cougars (*Puma concolor*) are elusive top-level predators and their predation patterns, particularly upon sensitive species, can be a source of concern to wildlife managers. Predation patterns, however, vary widely in accordance with differing landscape attributes, prey community composition, and preferences of individual cougars. The objective of this study was to better understand the impact of cougars upon their prey in the Pryor Mountains of Wyoming and Montana. Managers were concerned that cougar predation was having a negative impact upon a small, isolated Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) population and were hoping predation might be limiting a burgeoning feral horse population (*Equus caballus*).

With GPS collar data, we examined cougar kills (n = 200) to determine kill rates, prey composition, and selection for prey. Our findings indicated this population of cougars preyed primarily on mule deer (*Odocoileus hemionus*; 71.5%) but also included a substantial amount of bighorn sheep (8.0%) and other prey items (19.5%) in their diet. All bighorn kills were attributable to a specialist individual and we found no evidence of predation upon feral horses. Results showed that, while cougar predation was not limiting the feral horse population, at times, predation could be one of a host of factors limiting the bighorn sheep population.

To better understand the link between the risk of cougar predation and landscape attributes, we examined predation-specific resource selection by cougars. We first compared our set of confirmed kill sites to random sites at a fine scale (within 25 m of kill sites). We then built resource selection functions to conduct a coarse-scale analysis by using the 95% upper cut-off point of the known distances-dragged (94.9 m) to buffer caches sites, thereby creating zones of risk which had high probabilities of containing kill sites. We found that risk of cougar predation was associated with vegetation class and increased with decreasing horizontal visibility. For bighorn sheep, risk of predation was associated with juniper-mountain mahogany (*Juniperus spp., Cercocarpus ledifolius*) woodlands. We recommend managers thin junipers to increase horizontal visibility in areas where the juniper-mountain mahogany vegetation class intersects bighorn sheep habitat.

(112 pages)

PUBLIC ABSTRACT

Foraging Ecology of Cougars in the Pryor Mountains of Wyoming and Montana

by

Linsey W. Blake, Master of Science

Utah State University, 2014

Major Professor: Eric M. Gese Department: Wildland Resources

We conducted this study to better understand the impact of cougar (*Puma concolor*) predation in the Pryor Mountains of Wyoming and Montana. Managers of the Bighorn Canyon National Recreation Area and the Pryor Mountain Wild Horse Range were concerned that cougars were having a negative impact upon a small, isolated Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) population and were hoping predation might be limiting a feral horse population (*Equus caballus*) that was in excess of the Appropriate Management Level set by the Bureau of Land Management. Wildlife tourism brings revenue to the park and the surrounding communities making the status of these herds an economic, as well as an ecological and social, concern.

We captured and GPS-collared cougars and examined their kills to determine kill rates, prey composition, and selection for prey. Our findings indicated this population of cougars preyed primarily on mule deer (*Odocoileus hemionus*) but also included a substantial amount of bighorn sheep and other prey items in their diet. All bighorn kills were attributable to a specialist individual and we found no evidence of predation upon feral horses. These results showed that, while cougar predation was not limiting the feral horse population, at times, predation could be one of a host of factors limiting the bighorn sheep population.

Cougars are an ambush predator and must approach to within a close distance of prey items undetected to achieve a successful kill. Consequently, there is a relationship between cougar predation and landscape attributes such as horizontal visibility, slope, vegetation class, and ruggedness. To better understand the link between the risk of cougar predation and landscape attributes we examined predation-specific habitat selection by cougars at fine and coarse scales. After making a kill, cougars typically drag their prey items to a cache site where they consume their kill and, therefore, it is often impossible to identify specific kill sites. When possible we backtracked from cache sites to kill sites and used a fine-scale analysis to compare landscape characteristics within the immediate vicinity of these confirmed kill sites to those of random sites. For our coarsescale analysis of predation risk we utilized our entire dataset of kills by using the typical distances-dragged to buffer caches sites, thereby creating zones of risk which had high probabilities of containing kill sites. We modeled risk of cougar predation by constructing resource selection functions for these zones of risk. We found that risk of predation was associated with vegetation class and increased with decreasing horizontal visibility. For bighorn sheep, risk of cougar predation was associated with junipermountain mahogany (Juniperus spp., Cercocarpus ledifolius) woodlands. We recommend managers thin junipers to increase horizontal visibility in areas where the juniper-mountain mahogany vegetation class intersects bighorn sheep habitat.

ACKNOWLEDGMENTS

I would like to first express my sincere thanks to my advisor, Dr. Eric Gese. He provided crucial guidance and support when I needed it the most as well as the freedom to follow my own lines of inquiry. I could not have asked for a better mentor to guide me through this rewarding and challenging journey. I would also like to thank my committee members, Dr. Mike Wolfe and Dr. Toni K. Ruth. Both are experts in cougar ecology and it was an honor to work under their guidance. Despite busy schedules they made themselves available to answer my questions and provide valuable advice, especially regarding the design of my research questions and field logistic strategies. Thank you also to Dr. Dan Thompson with the Wyoming Game and Fish Department for advice and encouragement, especially regarding captures. I would also like to thank my fellow graduate students who provided valuable feedback, creative insights, and the necessary non-academic distractions. In particular I'd like to acknowledge Michel Kohl, who was always enthusiastic to chat about spatial ecology and resource selection functions. Your help was invaluable.

I had excellent help in the field and I cannot imagine how I would have pulled this project off without the following people. Jenny Dowd, thank you for introducing me to the magic of tracking and capturing cougars, and for all of your hard work and friendship out there. Lauren Satterfield, you were an outstanding assistant with your insatiable appetite for difficult terrain, working 14-hour days and, of course, talking statistical theory. Thank you. Gavin Cotterhill, I appreciate all of your hard work and your oversight of the project when I needed to return to campus. I could not have left it in better hands. Of course, a cougar project only works if you can capture cougars, a difficult task in an expansive, rugged study site with a low density of cats. Tanner Allen, my houndsman turned husband, the talent and passion you have for what you do is something special. I know you and your dogs could have caught more cats elsewhere and words cannot express my gratitude for your commitment to this project. And personally, your patience through this process as well as the support and encouragement you've provided along the way has been critical. Thank you. Boone and Sam Smith also briefly provided hound work and some entertaining stories.

I am grateful to the Bighorn Canyon National Recreation Area staff for the opportunity to conduct this project as well as financial and logistical support. In particular, Cassity Bromley, thank you for your guidance, flexibility, and participation while this project took its twists and turns. Bill Pickett, Ryan Felkins, Patti Martin, Randy Townsend, Scott Butler, Tyler Ennis, and Doug Butler, thank you for your field and logistical assistance. I'd like to thank Jared Bybee of the Bureau of Land Management for providing housing and information about the feral horse herd. I would also like to thank the USDA APHIS National Wildlife Research Center for their funding and support, particularly Dr. Toni Piaggio and Matt Hopken for their hard work on the genetic samples. Also, thank you to helicopter pilot Eric Waldorf for your safe flying during the aerial surveys. Additional educational funding was provided by Utah State University.

Our study area spanned many jurisdictions, and access to the Crow Indian Reservation proved critical. I would like to recognize, in particular, Larry Tobacco and Bill Schnell. Various private landowners graciously allowed us access to their properties, particularly, Hip and Loretta Tillet, Jerri Tillett, Abbie Tillett, and the Bassett family.

Finally, I would like to thank my family and friends. In particular, my parents offered endless support throughout my educational process. They also provided me with a healthy dose of outside time at young age. Thanks for helping me get my priorities straight from the start.

Linsey W. Blake

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CHAPTER 1

INTRODUCTION

The interactions between predators and their prey species have long held the interest of scientists, managers, and the general public. Cougars (*Puma concolor*) are elusive top-level predators and their predation patterns, particularly upon sensitive species, can be a source of concern to wildlife managers. Cougar predation varies regionally and even between individuals (Ross 1997, Murphy and Ruth 2010), therefore it is difficult to understand local predation patterns and impacts in the absence of an actual study. Cougars have been implicated in predation upon Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), feral horses (*Equus caballus*), and mule deer (*Odocoileus hemionus*) in the Pryor Mountains of north-central Wyoming and south-central Montana, particularly in the Bighorn Canyon National Recreation Area (BCNRA) and the Pryor Mountain Wild Horse Range (PMWHR). The bighorn sheep and feral horse populations are well-known and highly-valued symbols of the area. Tourism brings revenue to the park and the surrounding communities making the sustainability of these herds an economic, as well as an ecological and social, concern.

During the 20th century, the historic range of bighorn sheep was drastically reduced throughout the western United States, largely due to human encroachment including habitat fragmentation and modification, and disease transferred from livestock (Krausman and Shackleton 2000). Since the 1950s, many translocations have met with success (Krausman and Shackleton 2000). However, translocations involving smaller, more isolated populations, such as the population at BCNRA, have proven less successful (Berger 1990, Singer et al. 2001). The BCNRA bighorn population was extirpated in the 1800s and subsequently reintroduced between 1971 - 1974 (Kissell et al. 1996). It is a small population, estimated to be at 107 ewes and lambs (95% CI: 75 - 172) in 2012 with a mark-recapture study (Kissell 2013). In addition to being small, the bighorn population is also isolated, and so particularly vulnerable to stochastic events, disease outbreaks, or predation. Although bighorns typically are not a primary prey species for cougars, it has been observed that an individual or group of cougars that selectively prey on bighorn can have a significant impact on a small population (Wehausen 1996, Logan and Sweanor 2001).

While feral horses are not their principal prey, cougars can learn to prey on foals (Turner and Morrison 2001) and were implicated in taking a portion of the PMWHR foal crop in 2004. The current feral horse population exceeds the Appropriate Management Level of 90-120 individuals (Bureau of Land Management 2009) and managers have an interest in knowing if cougar predation could serve as a limiting factor. Mule deer, traditionally a primary prey of cougars, live in sympatry with the bighorn sheep and feral horses. It has been reported that the status of a primary prey species population can influence predation upon secondary prey species (Logan and Sweanor 2001, Cooley et al. 2008).

Cougar predation on ungulates is intertwined with landscape characteristics (Husseman et al. 2003, Laundre and Hernandez 2003). Rugged topography or dense vegetation with low visibility can increase hunting opportunities for an ambush predator like the cougar. Land managers at BCNRA have been improving bighorn sheep habitat by increasing horizontal visibility through controlled burns and the mechanical removal of vegetation. BCNRA staff has a direct interest in knowing if their efforts are likely to decrease cougar predation on bighorn sheep.

The goal of this project was to examine the relationships between the cougars and ungulate populations of the BCNRA and the Pryor Mountains and to determine how landscape characteristics might influence predation risk. We intend to provide information for future management decisions aimed at sustaining viable populations of all three ungulates and their primary predator. In chapter 2 we describe cougar predation patterns in the Pryor Mountains including composition of cougar kills, selection for prey species or sex-age classes of prey, kill rates, and handling times. We looked for differences in predation patterns as related to seasons and the sex or social class of cougars. In chapter 3 we examine cougar selection for kill site attributes at two scales (fine and coarse). In our fine-scale analysis we examined those characteristics in the immediate vicinity of confirmed kill sites (i.e., elevation, slope, aspect, vegetation class, horizontal visibility) that enabled a cougar to make a successful ambush and kill. In our coarse-scale analysis, we built resource selection functions (RSF; Manly et al. 2002) to describe the relative probability of use (i.e., kill site selection) across the study area with respect to several landscape characteristics (distance-to-roads, distance-to-water, slope, elevation, ruggedness, aspect, vegetation class). We analyzed characteristics within the larger (94.9 m radius) zones of risk created by buffering cache sites with the typical distance a prey item was dragged from a cougar kill site. By doing so, we were able to

utilize our full dataset of kills and analyze the features of polygons which had high probabilities of containing kill sites. In chapter 4 we summarize our findings and describe actions managers could take to manipulate predation pressure and achieve their wildlife management objectives.

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CHAPTER 2

PREDATION PATTERNS OF COUGARS IN THE PRYOR MOUNTAINS OF WYOMING AND MONTANA

ABSTRACT

The impact of cougars (*Puma concolor*) on their prey species varies regionally. To document the relationships between cougar predation and the Rocky Mountain bighorn sheep (Ovis canadensis canadensis), mule deer (Odocoileus hemionus), and feral horse (Equus caballus) populations of the Bighorn Canyon National Recreation Area and the Pryor Mountains, we deployed GPS collars on 6 cougars and visited their location clusters to determine their kill rates and foraging patterns. We examined the composition of cougar kills by species, mule deer sex and age classes, prey size classes, season, as well as the sex or social class of the cougar. As a measure of prey selection, we examined the composition of prey killed relative to the composition of the ungulate population obtained during an aerial survey. We found mule deer were the primary prey killed by cougars in the Pryor Mountains, while bighorn sheep constituted a secondary prey species. While cougars selected for bighorn sheep, this was all attributable to a single individual that specialized on bighorn sheep. This cougar population also selected for adult male and juvenile mule deer. Female cougars killed more does and male cougars killed more bucks. Family groups had the highest kill rates (i.e., the shortest time intervals between kills), while adult males had the lowest. Reducing cougar predation risk through habitat manipulation for bighorn sheep should be considered. In addition, at the time of this study, the cougar population was not depredating any feral

horses; therefore managers will need to continue management actions to reach their objective of reducing the feral horse population.

INTRODUCTION

Predators can have profound impacts upon their prey populations. Cougar (*Puma concolor*) predation has been implicated as a regulating factor in some ungulate populations (Ballard et al. 2001, Logan and Sweanor 2001, Robinson et al. 2002). However, the influence of predation can be difficult to understand when compounded by complicating factors such as the presence of other predator species, availability of secondary prey, or demographic vulnerability inherently present within small, isolated ungulate populations (Festa-Bianchet et al. 2006, Atwood et al. 2007, Cooley et al. 2008). Managers concerned with the dynamics of prey populations under their auspices need information about the extent and impact of predation in those ecosystems if they are to make sound management decisions. Specifically, they need reliable estimates of predation indices, including composition of cougar kills and kill rates.

Due to their nocturnal, secretive hunting and prey consumption habits, cougar predation is almost impossible to observe directly. The advent of GPS collars has allowed us to better understand cougar predation patterns by enabling 24-hour monitoring of a cougar's location, thereby allowing scientists to identify cache sites and locate prey remains (Anderson and Lindzey 2003). With this advance, biologists have been able to more accurately estimate cougar predation metrics (Monroy-Vilchis et al. 2009, Knopff et al. 2010, Kunkel et al. 2013, Mitchell 2013). An understanding of the role of cougar predation is enhanced by knowledge of their selection for certain prey species and for sex-age classes within a prey population. For instance, if the composition of cougar kills reveals they disproportionately prey upon sex-age classes with higher reproductive values (often adult females), it could have a more significant impact than if they do not select for particular prey classes (Rubin et al. 2002, Boukal et al. 2008). Some research has supported the reproductive vulnerability hypothesis (Lima and Dill 1990, Knopff et al. 2010, Mitchell 2013) which proposes that sex-age classes of prey should vary in their vulnerability to predation based upon their reproductive state. That is, male ungulates should be most vulnerable during and after the rut, females during late gestation and shortly after giving birth while tending neonates, and juvenile ungulates shortly after their birth when they are inexperienced and less mobile. Researchers have also examined the interplay between predation patterns and the sex or social class of cougars. In most instances, females supporting dependent kittens tend to kill more frequently than solitary adult females or males (Anderson and Lindzey 2003, Knopff et al. 2010, Mitchell 2013) thus having a greater impact on prey populations in terms of the number of individuals killed. Kill rates and handling times are also generally influenced by the biomass of prey (Mattson et al. 2007, Cavalcanti and Gese 2010). A cougar killing large-bodied ungulates, for example, should go longer between kills than a cougar taking neonates. Finally, it has been demonstrated that dominant predators such as brown bears (Ursus arctos), black bears (Ursus americanus), and wolves (Canis lupus) may engage in kleptoparasitism by displacing subordinate felids from their kills (Ruth and Murphy 2010b, Krofel et al. 2012, Allen et al. 2014). Prey loss due to kleptoparasitism should increase the kill rates of cougars as they compensate for lost biomass of prey by resuming

hunting earlier following usurped kills. The resulting increased total off-take of prey has implications for wildlife managers.

Previous studies have found cougar predation upon feral horses (*Equus caballus*) varies widely. Turner and Morrison (2001) found cougars limited feral horse populations in the White Mountains of California and Nevada, while in other studies cougar predation has been negligible, or attributable to a specialist individual (Knopff and Boyce 2007). While bighorn sheep are typically thought to be a secondary prey item, cougar predation has been shown to impact small, isolated populations, sometimes even driving them to extinction (Wehausen 1996, Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004, Festa-Bianchet et al. 2006). Predation pressures upon bighorn sheep (Ovis canadensis) vary between cougar populations and even among individual cougars (Ross et al. 1997, Logan and Sweanor 2001). The presence of cougars does not necessarily imply a threat to a bighorn sheep population (Hornocker 1970, Rominger et al. 2004), although there are indications that predation pressures may increase with a change in the population of a primary prey species, or if an individual cougar learns to specialize in killing bighorn sheep. Cougars have sometimes been blamed for mule deer population declines, but the influence of cougar predation on a mule deer (Odocoileus hemionus) population is often complicated by the presence of secondary prey species, additional predators such as black bears or coyotes (*Canis latrans*), and by whether the nature of predation is additive or compensatory (Ballard et al. 2001, Robinson et al. 2002).

Cougars have been implicated in predation upon mule deer, bighorn sheep, and feral horses in the southern Pryor Mountains of Montana and Wyoming (Schoenecker 2004; C. Bromley, National Park Service, personal communication). Managers who have an interest in maintaining healthy herds of all three prey species and their predator need insight into cougar predation patterns. Our objectives were to: (1) estimate kill rates and handling times for all cougars and by cougar social classes, seasons, and prey size classes, (2) document composition of cougar kills and determine differences in the proportion of prey species, prey sex-age classes, or prey size classes, killed by different social classes of cougars and by season, and (3) examine if cougars are selective for certain prey species or prey sex-age classes as compared to the composition of ungulates observed in an aerial survey.

We hypothesized ungulate prey killed by cougars in our study area would be composed primarily of mule deer with smaller percentages of bighorn sheep and feral horses. We anticipated some predation of feral horses during the foaling season (Turner et al. 1992). We expected higher kill rates among females with kittens than with solitary cougars. We expected shorter inter-kill intervals to follow those kills that were detected by black bears. We also expected handling time to be shorter for adult males (Mattson et al. 2007). Lastly, we hypothesized differential prey use with selection for larger prey (mule deer bucks and bighorn rams) among male cougars, while female cougars would select for smaller prey (female and young mule deer and bighorn ewes and lambs; Anderson and Lindzey 2003, Knopff et al. 2010, White et al. 2011).

STUDY AREA

We conducted this study in the southern portion of the Pryor Mountains of northcentral Wyoming and south-central Montana. The 2,553 km² study area included the Bighorn Canyon National Recreation Area (BCNRA), the Pryor Mountain Wild Horse Range (PMWHR), a portion of the Crow Indian Reservation, the Custer National Forest, Bureau of Land Management (BLM) property, and private properties (Fig. 2.1).

The habitat and topography of the Pryor Mountains was extremely variable. One notable feature was Bighorn Canyon itself with cliffs up to 300 m high. Several riparian systems flowed through the study area: Bighorn River, Crooked Creek, Dryhead Creek, and Sage Creek. Additional water sources included several other seasonal creeks, natural springs and anthropogenic water sources. The southern portion of the study area consisted of desert badlands, expanses of sagebrush (*Artemisia spp.*), and desert shrublands. The northern portion was characterized by steep timbered slopes, high alpine meadows, and sagebrush steppes. Rugged, incised canyons were prevalent throughout the study area. Using the vegetation community classifications developed for the BCNRA (Knight 1987) and the nearby Bighorn Mountains (Logan and Irwin 1985), we classified vegetation as sagebrush, coniferous forest, juniper-mountain mahogany (*Juniperus spp., Cercocarpus ledifolius*) woodland, desert shrubland, grassland, deciduous shrubland, riparian, or developed.

Elevations ranged from 950 to 2,900 m. The climate was characterized by very hot summers with temperatures exceeding 32° C and very cold winters with temperatures below -15° C. There was a north-south precipitation gradient with an average total annual precipitation of 16.9 cm in the south and 45.8 cm in the north, with most precipitation falling as rain during May and June (Western Regional Climate Center). Because the study site exhibited strong seasonality, we defined two seasons: summer (April 16 - October 15) and winter (October 16 - April 15).

Cougars and black bears were the apex predators of the area. While they existed in the nearby Absaroka Mountain Range, grizzly bears (*Ursus arctos horriblis*) and wolves had not re-established in the study site. Other mammals in the study area included coyote, red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), beaver (*Castor canadensis*), and porcupine (*Erethizon dorsatum*). The main ungulate species were mule deer, feral horses in the PMWHR, and domestic cattle (*Bos primigenius*). Additional ungulates included a small population of Rocky Mountain bighorn sheep and a few white-tailed deer (*Odocoileus virginianus*). The bighorn sheep population was estimated to be 107 ewes and lambs (95% CI: 75 - 172) in 2012 (Kissell 2013) and the feral horse population was approximately 170 individuals (J. Bybee, Bureau of Land Management, personal communication) exceeding the BLM's Appropriate Management Level of 90-120 individuals (Bureau of Land Management 2009).

METHODS

Cougar Capture and GPS Collaring

We captured resident adult cougars using hounds (Hornocker 1970) or box traps (Shuler 1992) between January 2011 and March 2012. We immobilized cougars with ketamine hydrochloride and xylazine hydrochloride, and fitted them with Telonics GEN3 GPS collars (Telonics Inc., Mesa, AZ). We programmed the collars to record 8 GPS locations per 24-hour period with locations recorded at 2-hour intervals during nocturnal periods and 6-hour intervals during diurnal periods. We retrieved collars following automatic drop-off. Animal capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees of the National Wildlife Research Center (QA-1811) and Utah State University (#1516).

GPS Locations and Cluster Investigation

The GPS collars transferred their GPS locations through the Argos satellite system to the Argos Processing Center (CLS America Inc., Lanham, MD). Every 3 days, we downloaded the raw data from the Argos website and converted it into Universal Transverse Mercator (UTM) coordinates with the Telonics Data Converter (Telonics Inc., Mesa, AZ). Not all locations were successfully transmitted while the collars were on the animals. We acquired remaining locations from the collars at the time of an animal's death, or after the pre-programmed collars dropped off. We used a data screening protocol to minimize error by eliminating all locations within 48 hours of capture events or with only 2D accuracy.

Cougars typically stay and feed on their kills for several days. Consequently, cougar kill sites can be identified by spatially and temporally clustered GPS locations (Beier et al. 1995, Anderson and Lindzey 2003). We examined our location data sequentially to identify clusters. Following the protocol from Anderson and Lindzey (2003), we initially defined a cluster as 2 or more locations within 200 m during the same or consecutive nights. Because we were not having success finding prey remains at 2 or 3-location clusters, we modified our cluster definition to 4 or more locations within 150 m during the same or consecutive nights. To decrease our likelihood of missing a kill of a neonate ungulate, we still investigated 2 and 3-location clusters between May 23 and

September 30 when fawns and lambs would be small and consumed quickly. We visited these clusters and, if we did not find a kill immediately, searched a circle at least 100 m in diameter centered on the mean UTMs of the GPS locations of the cluster. We searched in concentric circles approximately 5 - 10 m apart depending upon visibility, with the goal of visually examining all of the ground within the search area. When we found prey remains, we recorded species, age, and sex. We divided prey into juvenile (<1 year) or adult (\geq 1 year) classes based on dentition. When sex or species could not be determined by physical characteristics, muscle, hide, or hair samples were collected and sent to the National Wildlife Research Center (Fort Collins, CO) for analysis of DNA using a polymerase chain reaction (Yamamoto et al. 2002). We examined sites for evidence of black bear activity (scat or tracks) within 100 m of prey remains. If black bear sign was of a similar age to the cluster, we considered the cluster to have been detected and possibly usurped by a black bear.

Composition of Cougar Kills

We determined composition of cougar kills as the percent frequency of total prey by species. We used Pearson's chi-square tests to determine statistically significant ($P \le 0.10$) differences in the proportion of prey species (deer, sheep, other), prey size classes (small: <40 kg, medium: 40 - 90 kg, or large: >90 kg), or sex-age classes of mule deer (<1 yr old, adult female, adult male) killed as a function of cougar sex and season. Due to small sample sizes, we were unable to examine the effect of cougar social classes beyond cougar sex. We also tested for increased proportions of sex-age classes of mule deer killed by all cougars during their vulnerable seasons as predicted by the reproductive vulnerability hypothesis (bucks: September – December, does: April – June, juveniles: June – August). We were unable to consider the social classes of bighorn sheep killed in our analyses due to insufficient sample sizes.

Ungulate Surveys

We conducted a winter aerial helicopter survey to determine herd size and composition of the ungulate species in the study area. We surveyed the study area as we initially defined it. This boundary, however, turned out to be a subset of the ultimate study area which we defined as the minimum convex polygon of all cougar locations (Fig. 2.2). We divided the study site into 2.59 km^2 guadrats and randomly selected and surveyed approximately 10% of these quadrats. Perimeters of the quadrats were flown initially to 'capture' any animals leaving the quadrats due to the survey disturbance. Several transect lines were flown within each quadrat to ensure thorough coverage (Gill 1969, Freddy 2004). Counts of ungulate species, their age and sex, and a relative measure of habitat openness (1 = most open, 3 = most visually obscured) was recorded for each quadrat. Helicopter aerial surveys, while generally more accurate than ground surveys, are subject to bias associated with imperfect detection (Caughley 1974). To address this, we used existing sightability correction factors from prior surveys conducted under similar conditions in similar habitats to derive population estimates (Keegan et al. 2011, Flesch and Garrott 2013).

Prey Selection

Relative to our mule deer and bighorn population estimates, we looked for statistically significant ($P \le 0.10$) selection of prey species (mule deer versus bighorn)

and of different demographic classes of mule deer killed by cougars with Pearson's chisquare tests. We compared the proportion of species, or sex-age classes of mule deer derived from our aerial surveys (the expected proportion) to the observed counts of animals killed by cougars. Because our aerial surveys were conducted on a subset of what would ultimately become our study area, we only included those mule deer and bighorn sheep kills within the area covered by the aerial survey. We were unable to examine differences in selection between bighorn social classes, or between different sex or social classes of cougars, due to insufficient sample sizes.

Kill Rates

To determine kill rates, we calculated the inter-kill interval between the first GPS location at a confirmed kill site cluster and the first GPS location at the next confirmed kill site cluster. In 2 instances we were unable to visit a cluster due to safety or logistical issues so we eliminated the interval in which it occurred (White 2009, Cavalcanti and Gese 2010). We only used intervals during which the collar had a \geq 45% fix rate (Knopff et al. 2009) of nocturnal locations. We eliminated any intervals for which a cougar was collared \leq 4 weeks in a given season and social class (Knopff et al. 2010), intervals in which we disturbed cougars on kills, or when they scavenged our bait carcasses. We removed 2 intervals because they were extreme outliers and intervals after which an adult male cougar sustained a non-capture related trapping injury that eventually led to his starvation and death. We used a natural log transformation to normalize the data and then analyzed kill rates with a 1-way ANOVA to examine significant differences ($P \leq 0.10$)

season, and between prey size classes. To examine how possible kleptoparasitism by black bears influenced kill rates, we used a square root transformation to normalize the data and then tested for significant differences ($P \le 0.10$) in inter-kill intervals following kills with and without indications of possible kleptoparasitism. Due to a small sample size, we pooled all possible kleptoparasitism events and therefore were able to include intervals in which cougars were collared ≤ 4 weeks in a given season and social class.

Handling Time

To determine handling time (i.e., the amount of time a cougar spent on a kill), we subtracted the time of the last nocturnal location at a kill cluster from the first nocturnal location at the same cluster. To be consistent with the kill rate analysis, we removed any clusters for which a cougar was collared \leq 4 weeks in a given season and social class. We also removed 2 clusters at which a cougar consumed 2 kills simultaneously, dividing her time between them. We used a natural log transformation to normalize the data and then analyzed handling times with a 1-way ANOVA to examine differences in handling times between individual cougars, social classes of cougars, seasons, and prey size classes.

RESULTS

Cougar Capture and GPS Collaring

We spent a minimum of 188 days attempting to locate and capture cougars with hounds, box traps, and snares in the portion of our study area south of Sage and Dryhead Creeks and west of the Bighorn River. While that 929 km² area represented only 36.4% of what would become our study area (defined by the eventual home ranges of collared

cougars), it included the land management areas that were the focus of our research, BCNRA and the PMWHR. We believe we captured and collared all resident adult cougars within that zone. Investigations of cougar sign invariably led back to alreadycollared, or shortly-thereafter collared, cougars. This included numerous tracks, 5 scavenged bait carcasses, 4 kills that we found opportunistically, and 2 photographs captured with game cameras. Two exceptions included one solitary adult female whose sign we encountered several times before, but not after, a hunter reported taking a female in what we believed was her home range. The second exception was an adult female travelling with a kitten. We saw their tracks twice, but despite searching extensively for them we never re-encountered them, leading us to believe they had made an unusual foray into the study area or possibly died.

GPS Locations and Cluster Investigation

We captured and monitored 6 cougars (2 adult females, 3 adult males, 1 sub-adult male) in the study area. The minimum density of adult cougars during our study was 0.20 individuals/100 km². Cougars were collared between 98 and 416 days ($\bar{x} = 254.2 \pm 129.0$ SD) for a total of 1,525 cougar-days. Over that period of time, we acquired between 665 and 2,664 locations per cougar ($\bar{x} = 1,644.7 \pm 772.7$ SD) for a total of 9,868 locations. The overall fix rate for the GPS collars was 80.9%. Individual fix rates for the GPS collars varied between 76.0% and 89.9% (Table 2.1). In total we identified 383 clusters and searched 381 of them for kills; 190 clusters had kills and 10 had 2 prey items for a total of 200 kills. Black bears visited 18 clusters with kills (9.5%). Fifteen of those clusters (7.9%) were visited by black bears soon enough to consider them possible

kleptoparasitism events. Although they comprised a part of the cougar diet, we did not consider the scavenging of our bait carcasses as predation events.

Composition of Cougar Kills

As mentioned above, 190 of the clusters we searched had kills and 10 of these had 2 prey items generating a total of 200 kills (Table 2.2). Mule deer made up the majority of the prey killed (71.5%), with bighorn sheep accounting for 8.0%. We also found a single elk (*Cervus canadensis*) kill (0.5%), the only indication we had of elk in the study area. There was a variety of non-ungulate prey items including beavers (6.5%), raccoons (3.5%), porcupines (3.5%), and coyotes (3.0%). We found single instances of predation upon a striped skunk (Mephitis mephitis), American marten (Martes Americana), mallard (Anas platyrhynchos), and a red fox (0.5% each). Also of note was a GPS-collared female cougar (0.5%) that was killed and most likely consumed by a GPS-collared male cougar. Despite their presence in the study area, collared cougars killed no feral horses or domestic livestock. Of the mule deer kills where we could identify age, 31.6% were juveniles while 68.4% were adults. Of the mule deer kills where we could identify sex, 37.5% were male and 62.5% were female. Bighorn sheep kills with identifiable age were 25% juveniles and 75% adults. Of the bighorn sheep kills where we could identify sex, 53.3% were male and 46.7% were female.

There was a significant difference between the proportion of prey species killed $(\chi^2 = 35.38, df = 2, P < 0.001)$ by female and male cougars. Female cougars killed 16.2% bighorn sheep, 77.8% deer, and 6.1% other, while males killed 67.0% deer, and 33.0% other (Table 2.3). There was a significant difference in the proportion of prey species

between the seasons ($\chi^2 = 5.55$, df = 2, P = 0.062). In summer, cougar prey consisted of 4.0% bighorn sheep, 78.2% deer, and 17.8% other, while in winter the composition of prey was 12.2% bighorn, 66.3% deer and 21.4% other (Table 2.4).

We found a significant difference in the sex-age class of mule deer killed by male and female cougars ($\chi^2 = 5.11$, df = 2, P = 0.078), but found no significant difference in the proportion of sex-age classes of mule deer killed between seasons ($\chi^2 = 0.62$, df = 2, P = 0.734). Among mule deer killed by female cougars, 46.9% were adult females, 22.4% were adult males, and 30.6% were juveniles. Among mule deer killed by male cougars, 22.9% were adult females, 34.3% were adult males, and 42.9% were juvenile mule deer (Table 2.5). We failed to detect significant differences in the proportions of sex-age classes of mule deer killed during their vulnerable periods as indicated by the reproductive vulnerability hypothesis.

We also found a significant relationship between prey size class and the sex of the cougar ($\chi^2 = 15.52$, df = 2, *P* < 0.001). Kills by female cougars were composed of 23.5% large, 39.7% medium, and 36.8% small prey items, while kills by male cougars were 19.1% large prey, 13.2% medium prey, and 67.6% small prey items (Table 2.6). There was no influence of season on the proportion of prey size classes killed ($\chi^2 = 0.51$, df = 2, *P* = 0.777).

Ungulate Surveys

We flew 38 quadrats on January 12 and 20, 2012. Weather conditions prevented us from completing the survey in a shorter time frame. Raw counts revealed 5 bighorn sheep, 80 mule deer, and no feral horses. After applying sightability correction factors,
we calculated population estimates of 67 bighorn sheep and 1,159 mule deer (Table 2.7). The estimated fawn:doe ratio was 13.7 fawns:100 does. We did not estimate the ewe:lamb ratio because we could not distinguish between the sexes of all adult sheep and we did not observe any lambs. Our density estimates in the aerial survey area were 1.25 mule deer/km² and 0.07 bighorn sheep/km².

Prey Selection

A total of 122 ungulates were killed within the aerial survey area. By comparing these kills with our mule deer and bighorn sheep population estimates (Fig. 2.3), we found cougars disproportionally killed bighorn sheep ($\chi^2 = 13.74$, df = 1, *P* < 0.001). However all of these bighorn sheep kills were attributed to a single female cougar. We also found that cougars selected for sex-age class of mule deer when making kills ($\chi^2 =$ 86.23, df = 2, *P* < 0.001). Cougars killed more adult male and juvenile mule deer, and less adult female mule deer than were estimated to be available (Fig. 2.3).

Kill Rates

We retained 155 inter-kill intervals with which to analyze kill rates (Fig. 2.4). To examine inter-kill intervals with respect to prey size class, we eliminated 54 of these intervals because, although we knew the species of some ungulate remains, without sex or age we were unable to assign them to a size class. The mean kill rate was 7.21 ± 0.33 ($\bar{x} \pm$ SE) days. A natural log transformation normalized the dataset, meeting an underlying assumption of 1-way ANOVA. Kill rates differed significantly among individual cougars from 5.95 ± 0.47 to 9.61 ± 0.95 days ($F_{4, 150} = 3.20$, P = 0.015), and between social class of the cougar with adult females with kittens having the shortest

intervals ($\bar{x} = 6.01 \pm 0.42$ days), adult males having the longest intervals ($\bar{x} = 8.24 \pm 0.53$ days), and solitary adult females having intermediate intervals ($\bar{x} = 7.25 \pm 1.04$ days; $F_{2,152} = 1.30$, P = 0.016). Kill rates did not differ by season ($F_{1,153} = 1.23$, P = 0.270). Kill rates differed significantly based upon the size of the prey item ($F_{2,98} = 3.86$, P = 0.024). The shortest inter-kill intervals followed the consumption of the smallest prey items ($\bar{x} = 6.61 \pm 0.54$ days), mid-length inter-kill intervals followed the killing of medium size prey ($\bar{x} = 7.75 \pm 0.88$ days), and cougars went the longest between kills after killing the largest prey items ($\bar{x} = 9.68 \pm 0.94$ days). We detected no significant difference between inter-kill intervals following potential kleptoparasitism events and those with no indication of kleptoparasitism by black bears.

Handling Time

We retained 166 kills to examine with respect to handling time (Fig. 2.5). With respect to prey size class, we only used 104 kills for reasons described above. The mean handling time was 2.52 ± 0.16 ($\bar{x} \pm SE$) days. We applied a natural log transformation to normalize the dataset. Handling times differed significantly among individual cougars from 1.52 ± 0.21 to 3.11 ± 0.36 days ($F_{4, 161} = 3.34$, P = 0.012). Handling times did differ significantly by social class of the cougar ($F_{2, 163} = 5.93$, P = 0.003). Adult males displayed the shortest handling times ($\bar{x} = 2.24 \pm 0.20$ days), while solitary adult females spent the most time on their kills ($\bar{x} = 4.48 \pm 0.72$ days), and adult females with kittens had handling times only slightly longer than the adult males ($\bar{x} = 2.34 \pm 0.24$ days). Handling times also differed significantly by prey size class ($F_{2, 101} = 17.60$, P < 0.001). The smallest prey items were only handled for 1.64 ± 0.20 days, while medium prey items were handled for a mean of 3.35 ± 0.35 days, and the largest prey items were handled for a mean of 4.15 ± 0.63 days. Handling times did not differ significantly by season ($F_{1,164} = 2.02$, P = 0.157).

DISCUSSION

Composition of Cougar Kills

Congruent with other studies (Ackerman et al. 1984, Logan and Irwin 1985, Anderson and Lindzey 2003, Mitchell 2013), this cougar population subsisted primarily on the main resident ungulate species on the study area, mule deer. Bighorn sheep served as a (not insignificant) secondary prey source for one individual. The single elk that was killed was probably a lone individual that had travelled into the study area, possibly from the east side of the Bighorn River. Cougars incorporated an important amount (19%) of non-ungulate prey into their diets, including a notable amount of beavers. In most cases, the consumption of prey was near complete (in some cases, probably due to some consumption by scavengers) and, in the case of ungulate prey, often just the skeleton, hide, and rumen remained for examination. Due to this lack of evidence, we possibly classified some scavenging events as kills. As evidence, we did observe several instances (n = 5) of scavenging in our study site in which cougars scavenged deer carcasses that we had brought in for trapping efforts. Our study design was also biased towards the detection of larger kills. We could have missed smaller prey items that were either consumed within the <2 hours needed to generate a cluster, or entirely consumed and thereby classified as non-kill clusters.

We found the sex of the cougar influenced the composition of prey species killed by cougars. Male cougars killed and consumed more items from the other prey species class. In contrast, one female was responsible for all of the bighorn sheep killed (n = 16) which composed 16.2% of the diet of female cougars. Interestingly, while this female's territory had the greatest overlap with bighorn sheep range, 3 of the 4 other cougars spent significant amounts of time in bighorn sheep habitat without killing them. Similar studies have also shown that certain cougars may develop individual prey preferences (Elbroch and Wittmer 2013). Cougars specializing on bighorn sheep have been observed before and can have a profound impact upon a small bighorn population (Ross et al. 1997, Logan and Sweanor 2001).

The season of the year also influenced the species composition of prey killed by cougars with more bighorn and other prey items being taken in the winter and more mule deer being killed and consumed in the summer. While this might appear to suggest an increased vulnerability of neonate deer to cougar predation (Knopff et al. 2010, Mitchell 2013), we tested for an increased presence of juvenile mule deer among cougar prey following the mule deer birth pulse and found no effect.

The sex of the cougar also influenced selection among different prey size classes with females killing proportionally more medium-sized and less small-sized prey than males, and males killing proportionally less medium-sized and more small-sized prey than females. We found that the proportion of large-sized prey killed by males and females did not differ contrary to the differential prey use hypothesis in which the sexual dimorphism of cougars leads to females generally taking smaller prey items than males presumably because they are safer to kill (Ross and Jalkotzy 1996, Anderson and Lindzey 2003, White et al. 2011). However, our study area lacked populations of larger prey items such as elk and moose (*Alces alces*). Less killing of small-sized prey by females may be due to their increased energetic needs associated with raising kittens. The time and effort needed to hunt and kill small prey may not meet the energetic demands of family groups. It was also possible that we missed small prey items of female cougars because they would have been consumed faster and more completely by females associated with a family group. Our finding that males killed more small prey items than females is in contrast to some previous studies (Anderson and Lindzey 2003, Knopff et al. 2010). This may be a unique strategy of the male cougars in our study area if they are prey switching and supplementing their diets with small prey due to a low density deer population. Additionally, with our small sample size of cougars, the data could be influenced strongly by single individuals, for instance, one male who appeared to specialize in killing beavers (Table 2.2).

The sex class of cougars influenced the demographic composition of their mule deer prey. Of the mule deer they killed, females killed proportionally more does while male cougars killed more bucks and juveniles. In contrast to our findings amongst all prey killed, these findings amongst just mule deer kills could support the differential prey use hypothesis described above. We did not find that cougars selected differently for mule deer sex-age classes between seasons.

It is important to note that feral horses were absent from the prey killed during this study. While there is some evidence cougars have preyed on foals before in the PMWHR, our study showed that cougar predation cannot be consistently counted on to limit this horse population.

Ungulate Surveys

Our ungulate surveys showed that the mule deer population had a relatively low density with poor recruitment. A review of mule deer densities by Innes (2013) reported mule population densities between 0.1 - 29 mule deer/km². Our density of 1.25 deer/km² falls on the lower end of this spectrum. For comparison, in the prairie breaks and badlands of Montana, densities ranged from 1.4 - 4.4 mule deer/km² (Hamlin and Mackie 1989). About 16 mule deer/km² were found in the mountain-foothill areas in Utah (Robinette et al. 1977) while the mountainous pinyon pine-Utah juniper (*Pinus edulis*, *Juniperus osteosperma*) Piceane Basin of Colorado supported 14 - 24 mule deer/km² (Unsworth et al. 1999). Our fawn:doe ratio of 13.7:100 is also on the low end of reported ranges. In their review of mule deer population demographics Unsworth et al. (1999) reported fawn:doe ratios of 42-48:100 in Colorado, 49-77:100 in Idaho and 25-51:100 in Montana.

Prey Selection

Based on the kills within the aerial survey area, we did see selection by cougars for bighorn sheep over mule deer. However, as mentioned above, all of these bighorn were killed by a single cougar. While we only documented a single specialist cougar preying upon bighorn sheep, it is reasonable to assume this behavior will develop again based on past instances of cougar predation in BCNRA and the intersection of cougar and bighorn habitat. Additionally, the mule deer herd is sympatric with the bighorn sheep herd and during times when the deer herd is declining, it is possible predation on bighorn sheep will increase through prey switching (Kamler et al. 2002, Ruth and Murphy 2010a). Conversely, cougar predation on bighorn sheep could increase through apparent competition if the mule deer population increases (Roemer et al. 2002, DeCesare et al. 2010). Considering 16 bighorn were killed over a 416-day monitoring period by a single cougar, predation could be influencing this small bighorn population. However, current information on the sex-specific and age-specific vital rates of this bighorn sheep population (e.g., fecundity, recruitment, survival, etc.) in combination with the sex-age classes of all killed sheep would be needed to further understand the effect of cougar predation upon this population's long-term growth rate. It is important to note that bighorn sheep population growth rates are affected by factors aside from cougar predation including direct and indirect interspecific competition, other predator species (e.g., black bear, golden eagle [Aquila chrysaetos], coyote), disease, selenium levels, and forage availability (Risenhoover et al. 1988, Goodson et al. 1991, Sawyer et al. 2002, McKinney et al. 2006).

We observed selection by cougars for mule deer sex-age classes with cougars killing disproportionately more adult male and juvenile mule deer, and less adult female mule deer than were available to them. A lack of selection for female mule deer should be less limiting to the deer population if they are the primary reproductive class but, for reasons described above, it is difficult to understand the impact of cougar predation on mule deer without understanding the specific vital rates and additional pressures to this population (Ballard et al. 2001). We acknowledge that kills of adult deer were biased low relative to juveniles because adult deer with unknown sex were eliminated from this analysis while juvenile mule deer of unknown sex were retained.

Kill Rates

Our mean kill rates ranged from 6.01 ± 0.42 ($\bar{x} \pm SE$) to 8.24 ± 0.53 days between social classes of cougars. These rates were within the previously reported ranges of 5.4 -15.2 days (Anderson and Lindzey 2003, Mattson et al. 2007, Knopff et al. 2010, Ruth et al. 2010, Mitchell 2013). Other studies have had larger prey (i.e., elk, moose) and some included kill rates for sub-adults which may go longer between kills than adults. Expectedly, our kill rates were on the lower end of this spectrum. As expected, female cougars with dependent kittens had the highest kill rates, consistent with the greater energetic requirements of a family group (Laundre 2005). Adult males had the lowest kill rates. As we also hypothesized, we found that prey size influenced kill rates with cougars going the longest before making a kill after consuming a large prey item and making their next kill sooner after killing smaller prey. We were surprised that we did not detect shorter inter-kill intervals following kills with evidence of potential kleptoparasitism. It is likely that our small sample size of kills with evidence of potential keptoparasitism by black bears (n = 15) prevented us from detecting a difference.

Handling Time

As anticipated, adult males were the cougar social class with the shortest handling times, while solitary females displayed the longest handling time. This is consistent with findings of Mattson et al. (2007) that adult males had a life strategy focused on travelling long distances quickly and spending less time on kills. Also expected was that cougars

handled larger prey items for longer periods of time than smaller prey items. We expected to see shorter handling times in summer than winter due to increased spoilage, scavenging, and displacement from black bears, but we did not.

MANAGEMENT IMPLICATIONS

Our ungulate survey suggested low density and low recruitment of mule deer (Innes 2013). Increased predation upon a secondary species, like this bighorn population, is consistent with the prey switching that can occur when a primary prey species, here mule deer, experiences a population decline. While one approach would be to investigate ways to enhance the mule deer population, we recommend this approach with caution, as the relationships between two prey species' densities and their predator can be complicated and shift over time. Another approach might be to examine those habitat factors whose alteration could reduce predation pressures on bighorn sheep (see chapter 3). Regardless, managers should be aware that maintaining small isolated populations of bighorn sheep is often difficult and costly, and may require management interventions (e.g., translocations of sheep). Unfortunately, the feral horse population, over the course of this study, was not experiencing any predation pressure from the resident cougars. This trend could change if certain cougars learn to specialize on horses (Turner and Morrison 2001). In the meantime, the BLM will need to continue management action to keep this population within their stated management goal.

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Table 2.1. Social class, monitoring duration, GPS location acquisition rates, number of kills, and kill rates of GPS-collared cougars, Pryor Mountains of Wyoming and Montana, 2011-2012.

Cougar ID	Social class ¹	Days monitored	Number of GPS locations	Acquisition rate	Number of kills	Number of kill intervals used	Kill rates (days) ± SD
F1	AF/AFK	416	2664	80.0%	67	52	5.95 (±3.41)
F2	AFK	210	1510	89.9%	33	29	6.86 (±3.86)
M1	AM	404	2456	76.0%	38	28	9.61 (±5.04)
M2	SM	98	665	84.8%	6 ²	0	-
M3	AM	230	1450	78.8%	30	25	7.62 (±4.06)
M4	AM	167	1123	84.1%	26	21	7.14 (±4.10)

 ^{1}AF = solitary adult female, AFK = adult female with kittens, AM = adult male, SM = subadult male.

²M2 was F1's dependent kitten. We only analyzed kills from the period after he dispersed.

Prey Species	F1	F2	M1	M2	M3	M4	Total
Mule deer	47 (70.1)	30 (90.9)	27 (71.1)	3 (50.0)	14 (46.7)	22 (84.6)	143 (71.5)
Deer (spp. unknown)	0	0	0	0	1 (3.3)	0	1 (0.5)
Bighorn sheep	16 (23.9)	0	0	0	0	0	16 (8.0)
Unknown (mule deer or bighorn sheep)	1 (1.5)	0	0	0	0	0	1 (0.5)
Elk	0	0	1 (2.6)	0	0	0	1 (0.5)
Coyote	1 (1.5)	1 (3.0)	1 (2.6)	0	3 (10.0)	0	6 (3.0)
Raccoon	1 (1.5)	0	3 (7.9)	0	0	3 (11.5)	7 (3.5)
Beaver	0	0	3 (7.9)	0	9 (30.0)	1 (3.8)	13 (6.5)
Porcupine	0	1 (3.0)	1 (2.6)	3 (50.0)	2 (6.7)	0	7 (3.5)
Red fox	0	1 (3.0)	0	0	0	0	1 (0.5)
Striped skunk	0	0	1 (2.6)	0	0	0	1 (0.5)
American marten	1 (1.5)	0	0	0	0	0	1 (0.5)
Mallard	0	0	1 (2.6)	0	0	0	1 (0.5)
Cougar	0	0	0	0	1 (3.3)	0	1 (0.5)
Totals	67	33	38	6	30	26	200 (100.0)

Table 2.2. Number of prey items killed by each cougar in the Pryor Mountains of Wyoming and Montana, 2011-2012. Percentage of total diet for each cougar is indicated in parentheses.

Table 2.3. Species composition of prey killed by male and female cougars in the Pryor Mountains
of Montana and Wyoming, 2011-2012.

	Female cougars		Male cougars			
Prey species	n	%	n	%		
Mule deer	77 ¹	77.8	67	67.0		
Bighorn sheep	16	16.2	0	0.0		
Other	6	6.1	33	33.0		

¹Includes one *Odocoileus spp*.

Mountains of Wyoming and Montana, 2011-2012.								
	Su	nmer	W					
Prey species	n	%	n	%				
Mule deer	79^{1}	78.2	65	66.3				
Bighorn sheep	4	4.0	12	12.2				
Other	18	17.8	21	21.4				

Table 2.4. Species composition of prey killed by cougars during summer and winter in the Pryor Mountains of Wyoming and Montana, 2011-2012.

¹Includes one *Odocoileus spp*.

	Fema	le cougars	Male cougar		
Sex-age class of mule deer	n	%	n	%	
Adult female	23	46.9	8	22.9	
Adult male	11	22.4	12	34.2	
Juvenile	15	30.6	15	42.9	

Table 2.5. Sex–age class of mule deer killed by male and female cougars in the Pryor Mountains of Wyoming and Montana, 2011-2012.

Table 2.6. S	Size class	of prey	killed by	male	and	female	cougars	in th	ne Pryor	Mountair	ns of

Wyoming and Montana, 2011-2012.

	Female cougars		Male	cougars
Prey size class	n	%	n	%
Large	16	23.5	13	19.1
Medium	27	39.7	9	13.2
Small	25	36.8	46	67.6

					Total			
	Sightability	Population	Raw	Corrected	Number	population	Total herd	
	factor	segment	count	count	per km ²	estimate	estimate	
Bighorn high visibility	0.90	All	0	0.00	0.00	0		
Bighorn intermediate visibility	0.7	All	5	7.14	0.07	67	67	
		Bucks	3	4.00	0.04	38		
Mule deer high visibility	0.75	Does	7	9.33	0.09	88		
		Fawns	2	2.67	0.03	25		
		Bucks	4	5.97	0.06	56		
Mule deer intermediate visibility	0.67	Does	55	82.09	0.83	772	1159	
		Fawns	7	10.45	0.11	98		
		Bucks	1	4.35	0.04	41		
Mule deer low visibility	0.23	Does	1	4.35	0.04	41		
		Fawns	0	0.00	0.00	0		

Table 2.7. Aerial ungulate survey data from the Pryor Mountains of Wyoming and Montana, January 2012. Raw counts of ungulates were corrected for sightability bias with sightability factors.



Fig. 2.1. The 2,553 km² study area in the southern Pryor Mountains of Wyoming and Montana. The study area was formed by creating a minimum convex polygon of all recorded cougar locations.



Fig. 2.2. The 2,553 km² study area in the southern Pryor Mountains of Wyoming and Montana with the 925 km² aerial ungulate survey area.



Fig. 2.3. Percentages of (A) bighorn sheep and mule deer, (B) and mule deer sex-age classes, available and killed within the aerial survey area, Pryor Mountains of Wyoming and Montana, 2011-2012.

Killed

0%

Available



Fig. 2.4. Kill rates of (A) individual cougars, (B) cougar social classes, (C) seasons, and (D) prey size classes, Pryor Mountains of Wyoming and Montana, 2011-2012. Means and standard errors are indicated by the blue bars.



Fig. 2.5. Handling times of (A) individual cougars, (B) cougar social classes, (C) seasons, and (D) prey size classes, Pryor Mountains of Wyoming and Montana, 2011-2012. Means and standard errors are indicated by the blue bars.

CHAPTER 3

PREDATION-SPECIFIC RESOURCE SELECTION BY COUGARS IN THE PRYOR MOUNTAINS OF WYOMING AND MONTANA

ABSTRACT

A spatial understanding of predation risk can assist managers in devising management approaches to reduce predation risk to sensitive species. To model predation risk with respect to landscape characteristics in the Pryor Mountains of Wyoming and Montana, we collected locations from GPS-collared cougars (Puma concolor) from January 2011 – August 2012 to determine resource selection at cougar kill sites. We examined this predation-specific resource selection at two different scales (fine and coarse). When possible we backtracked from cache sites to kill sites and used a fine-scale analysis to examine landscape characteristics within 25 m of these confirmed kill sites. At this scale, kill sites had lower horizontal visibility than random sites, and were more likely to be in juniper-mountain mahogany (Juniperus spp., Cercocarpus *ledifolius*) and less likely to be in grassland vegetation. For our coarse-scale analysis of predation risk we utilized our entire dataset of kills (n = 194) by using the 95% upper cutoff point of the known distances-dragged (94.9 m) to buffer caches sites, thereby creating zones of risk which had a high probabilities of containing kill sites. We modeled seasonal cougar predation site selection by constructing resource selection functions for these zones of risk. The top model for predation risk during the summer consisted of

vegetation class, distance-to-water and a quadratic term for slope, while the top model for predation risk during the winter included vegetation class and elevation. Local wildlife managers interested in reducing predation to Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) will be able to intersect the predation risk resource selection function with bighorn sheep habitat to guide habitat modification efforts aimed at increasing horizontal visibility to potentially reduce the risk of cougar predation.

INTRODUCTION

The interactions between a predator and their prey have long been of interest to ecologists and managers. Conservation and management planning often benefit from an understanding of predator-prey relationships (Ballard et al. 2001). It is well-documented that, through predation, cougars (*Puma concolor*) can exert strong pressures on their prey populations (Bleich and Taylor 1998, Hayes et al. 2000, Robinson et al. 2002, Cooley et al. 2008). A population of cougars in Nevada nearly caused a local extinction of porcupines (*Erethizon dorsatum*; Schweitzer et al. 1997) and in British Columbia, Wittmer et al. (2005) found cougar predation to be limiting caribou (*Rangifer tarandus caribou*) survival. In Nevada and California, cougar populations have driven small populations of bighorn sheep (*Ovis canadensis*) towards extirpation (Wehausen 1996). While cougars do not consistently prey upon feral horses (*Equus caballus*), in some instances they have influenced horse population growth rates, particularly via predation upon foals (Turner and Morrison 2001).

Cougars are an elusive ambush predator whose habitat selection and predation patterns intertwine (Husseman et al. 2003, Laundre and Hernandez 2003, Holmes and Laundre 2006). As an ambush predator evolved for short bursts of speed, cougars must approach their prey undetected to within relatively close distances to make a successful kill (Hornocker 1970). Cougars are unlikely to complete a kill if they initiate the ambush attempt >25 m from their potential prey (Young and Goldman 1946, Wilson 1984, Holmes and Laundre 2006). Previous research has shown cougars select for certain landscape features (e.g., thick vegetation, rock outcroppings), presumably because these features provide cover and facilitate the successful stalking and killing of prey (Holmes and Laundre 2006, Atwood et al. 2009, Kunkel et al. 2013). Atwood et al. (2009) found cougars used areas with more structural complexity, while Kunkel et al. (2013) found cougars selected for more rugged terrain. In southern California, Dickson and Beier (2002) found cougars selected for riparian habitats, against grasslands, and against human-dominated habitats. Husseman et al. (2003) reported that sites with cougar kills had lower horizontal visibility than random sites.

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

Cougars have been implicated in preying on bighorn sheep, mule deer, and feral horses in the Pryor Mountains of Montana and Wyoming (Schoenecker 2004; C. Bromley, National Park Service, personal communication). Area land managers have an interest in increasing the bighorn sheep herd while reducing feral horse numbers. Understanding the factors influencing cougar predation is fundamental to making sound management decisions. While cougar predation and habitat use has been described in other areas, little is known with regards to cougar predation in the Pryor Mountains and surrounding region. If cougar predation is influenced by landscape characteristics, managers may have an opportunity to manipulate predation by changing these habitat features. For example, if cover provided by Utah juniper (*Juniperus osteosperma*) is linked to an increased likelihood of cougar predation, then juniper removal through controlled burns or mechanical methods may present an opportunity to lessen predation to this small bighorn sheep population.

Our first objective was to examine and compare the characteristics of cougar kill sites to randomly generated sites at a fine scale (i.e., within 25 m of the kill site; as described above, the distance in which a cougar would likely have been to initiate a successful ambush). For this analysis, we only used the subset of our kill sites that we could confidently distinguish from cache sites. Through field visits, we determined horizontal visibility, vegetation class, slope, and aspect of each kill and random site. We determined elevation by intersecting kill and random sites with a digital elevation model (DEM) in a Geographic Information System (GIS).

Our second objective was to analyze kill site selection on a coarse-scale by using the upper cut-off point of the known distances-dragged (94.9 m) to buffer cache sites, thereby creating circular zones of risk which each had a 95% chance of containing a kill site. For this analysis, we were able to work with the complete set of kills to enhance our analysis and level of inference. This larger dataset enabled us to model predation risk separately by season, a distinction important to cougar habitat use (Koehler and Hornocker 1991). We included the same landscape characteristics we measured for our fine-scale analysis with the addition of distance-to-low-use roads, distance-to-high-use roads, distance to-water, ruggedness, and with the exception of horizontal visibility. In contrast to the fine-scale analysis, this data was not collected through field visits; all data was collected by intersecting zones of risk with GIS layers. We built seasonal resource selection functions (RSF; Manley et al. 2002) to understand the impact of landscape covariates on the relative probability of kill site selection by cougars. We then projected the RSFs across the study area to create seasonal layers visually depicting the relative probability of predation risk by cougars.

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

STUDY AREA

We conducted this study in the southern portion of the Pryor Mountains of northcentral Wyoming and south-central Montana. The 2,553 km² study area included the Bighorn Canyon National Recreation Area (BCNRA), the Pryor Mountain Wild Horse Range (PMWHR), a portion of the Crow Reservation, the Custer National Forest, Bureau of Land Management (BLM) property, and private properties (Fig. 3.1).

The habitat and topography of the Pryor Mountains was extremely variable. One notable feature was Bighorn Canyon itself with cliffs up to 300 m high. Several notable riparian systems flowed through the study area: Bighorn River, Crooked Creek, Dryhead Creek, and Sage Creek. Additional water sources included several other seasonal creeks, natural springs and anthropogenic water sources. The southern portion of the study area consisted of desert badlands, expanses of sagebrush (*Artemisia spp.*), and desert shrublands. The northern portion was characterized by steep timbered slopes, high alpine meadows, and sagebrush steppes. Rugged, incised canyons were prevalent throughout the study area. Using the vegetation community classifications developed for the BCNRA (Knight et al. 1987) and the nearby Bighorn Mountains (Logan and Irwin 1985), we classified vegetation as sagebrush, coniferous forest, juniper-mountain mahogany (*Juniperus spp., Cercocarpus ledifolius*) woodland, desert shrubland, grassland, deciduous shrubland, riparian, or developed.

Elevations ranged from 950 to 2,900 m. The climate was characterized by very hot summers with temperatures exceeding 32° C and very cold winters with temperatures below -15° C. There was a north-south precipitation gradient with an average total annual precipitation of 16.9 cm in the south and 45.8 cm in the north, with most precipitation falling as rain during May and June (Western Regional Climate Center). Because the study site exhibited strong seasonality, we defined two seasons: summer (April 16 - October 15) and winter (October 16 - April 15).

Cougars and black bears (*Ursus americanus*) were the apex predators of the area. While they exist in the nearby Absaroka Mountain Range, grizzly bears (*Ursus arctos horriblis*) and wolves (*Canis lupus*) had not re-established in the study site. Other mammals in the study area included coyote (*Canis latrans*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), beaver (*Castor canadensis*), and porcupine (*Erethizon dorsatum*). The main ungulate species were mule deer, feral horses in the PMWHR, and domestic cattle (*Bos primigenius*). Additional ungulates included a small population of Rocky Mountain bighorn sheep and a few white-tailed deer (*Odocoileus virginianus*). The bighorn sheep population was estimated to be 107 ewes and lambs (95% CI: 75 – 172) in 2012 (Kissell 2013 and personal communication) and the feral horse population was approximately 170 individuals (J. Bybee, Bureau of Land Management, personal communication) exceeding the BLM's Appropriate Management Level of 90-120 individuals (Bureau of Land Management 2009).
METHODS

Cougar Capture and GPS Collaring

We captured resident adult cougars using hounds (Hornocker 1970) or box traps (Shuler 1992) between January 2011 and March 2012. We immobilized cougars with ketamine hydrochloride and xylazine hydrochloride, and fitted them with Telonics GEN3 GPS collars (Telonics Inc., Mesa, AZ). We programmed the collars to record 8 GPS locations per 24-hour period with locations recorded at 2-hour intervals during nocturnal periods and 6-hour intervals during diurnal periods. We retrieved collars following automatic drop-off. Animal capture and handling protocols were reviewed and approved by the Institutional Animal Care and Use Committees of the National Wildlife Research Center (QA-1811) and Utah State University (#1516).

Fine-Scale Kill Site Analyses

The first stage of our analysis was a fine-scale (within 25 m of confirmed kill locations) comparison of characteristics of kill sites to random sites. Clusters of GPS locations were visited to identify cougar kills (Anderson and Lindzey 2003; chapter 2). Once prey carcasses were located, field personnel attempted to back-track to the location where the cougar first made physical contact with the prey item. We called this location the kill site, although in some cases it would be more accurately termed the ambush site (i.e., if the prey animal travelled farther before succumbing to the attack). When we located a possible kill site we assigned it a confidence level: 1 = denoting extreme confidence, and 3 = indicating only moderate confidence. Determinations of confidence levels were based upon the presence of compelling characteristics including signs of

impact or struggle, blood, clumps of hair, or drag marks. After censuring the potential kill sites with the lowest confidence level, we retained 30 kill sites for fine-scale analysis. We generated random sites (n = 218) in a GIS and visited them to compare to the kill sites. We measured slope and aspect on a fine-grained scale (within 5 m of the kill site). During our analysis we treated aspect as a categorical variable, binning it based on degrees: north (0 - 44.99, 315 - 360), east (45 - 134.99), south (135 - 224.99), and west (225 - 314.99). We recorded the dominant vegetation class within 25 m of the kill site. We obtained horizontal visibility measures at 14 m and 25 m using the staff-ball method (Collins and Becker 2001, Greene 2010). For consistency with prior studies conducted in this region, we also recorded visibility at 14 m with the checkerboard method (Smith and Flinders 1991, Johnson 1995, Schoenecker 2004). In addition to comparing horizontal visibility between kill sites and random sites, we examined differences in horizontal visibility specifically in the juniper-mountain mahogany vegetation class. The junipermountain mahogany class was the only vegetation class that contained a useful sample size of kill sites and Bighorn Canyon National Recreation Area staff has been focusing their habitat modification efforts in this vegetation class. We obtained elevations by intersecting the kill sites with a 30 m DEM (United States Geological Survey 2011). We compared means of continuous variables with Welch's 2-sample t-tests. We used 1-sided t-tests to test whether horizontal visibility was lower at kill than at random sites, and 2sided t-tests to test for differences in the means of other continuous variables. We analyzed the categorical variables, aspect and vegetation class, with 2-sample proportion tests. We used a significance level of $P \le 0.10$.

Coarse-Scale Kill Site Analysis with Resource Selection Functions

In the second phase of our analysis, we constructed RSFs (Manley et. al. 2002) to analyze kill site selection by cougars at a coarse-scale (within 94.9 m of cache site). We again examined selection by comparing used kill sites to randomly-generated (i.e., available) sites with respect to several landscape covariates. RSFs operate within a logistic regression framework making them ideal to explore data with a binary response, such as used versus available. We developed a summer and a winter predation risk RSF with a fixed-effect logistic regression model.

Landscape covariates.—We used ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) to store, manipulate, and analyze all spatial data. We used 30 m resolution DEMs from the United States Geological Survey (2011) National Elevation Dataset to derive elevation, slope, and aspect layers. We derived a ruggedness layer from these 30 m DEMs following the procedure described by Sappington et al. (2007). We used road layers from the 2012 TIGER/Line Shapefiles (United States Census Bureau 2012). We subdivided roads into high and low use classes based on the MAF/TIGER (Master Address File/Topologically Integrated Geographic Encoding and Referencing) Feature Classification Codes. We adjusted the road class assignments based on our personal knowledge. We obtained stream data from the United States Geological Survey (2007) National Hydrography Dataset and used the Feature-Code classification system to retain only perennial water sources. We calculated distance-toroads and distance-to-water layers using the Euclidean Distance tool in ArcMap. We developed a vegetation class layer by downloading and joining data tiles from the

Northwest GAP Analysis Program (NWGAP; 2007). We collapsed the NWGAP vegetation types into our coarser classification system (Appendix A); unknown or rare vegetation types were excluded from our analyses. To determine the NWGAP-derived layer classification accuracy, we compared the GIS-assigned class to the vegetation class recorded at each site visited (194 cache sites, 35 kill sites, 218 random sites). These observations were 40.5% accurate when compared to the NWGAP-derived layer. These low accuracy rates were due to the coarser analysis by NWGAP that would have missed smaller patches of habitat, an imperfect alignment of the two classifications systems, and different coverage cut-offs used to determine vegetation class assignment. We were able to improve upon the NWGAP-derived layer in the BCNRA by using an updated vegetation layer developed for the park in 2013 by the Colorado Natural Heritage Program (CHNP; J. Stevens, Colorado Natural Heritage Program, unpublished data). Again, we collapsed the CHNP vegetation types into our classification system (Appendix B) excluding unknown or rare vegetation types. We ground-truthed the CHNP-derived layer against the 110 visited sites (43 caches sites, 22 kill sites, 30 random sites) that fell within the layer. The vegetation types we recorded at these sites had an 80.0% match with the CHNP-derived layer. The final combined vegetation layer had an accuracy of 55.7%. All layers were projected into NAD83 Zone 12N. We resampled all layers to insure they were orthogonal and then clipped them to the study area boundary.

Used and available zones of risk.—We used the distances-dragged from the highconfidence kill sites to cache sites as a measure with which to buffer all cache sites, thereby creating zones of risk. These zones of risk enabled us to examine the habitat characteristics in an area which was highly likely to have contained the kill site allowing us to use the full dataset of cache sites (as opposed to our fine-scale kill site analysis where we were limited to a smaller sample of confirmed kill sites) to build a set of seasonal RSFs modeling the risk of cougar predation. We used 95% kernel density estimations (KDE) to define availability within cougar home ranges. We generated 3 available zones of risk for every used zone of risk, stratified by cougar and season. Used and available zones of risk were intersected with each landscape covariate layer in Geospatial Modeling Environment (Geospatial Modeling Environment Version 0.7.2.0, www.spatialecology.com, accessed 5 April 2013) using the Isectpolyrst tool. For continuous variables (i.e., elevation, slope, ruggedness, distance-to-low-use roads, distance-to-high-use roads, distance-to-water) the Isectpolyrst tool calculated the mean of the raster cell values contained in each zone of risk polygon. For categorical variables (i.e., aspect, vegetation class), the Isectpolyrst tool calculated the proportion of different raster cell values (e.g., 0.60 south, 0.40 east) within each zone of risk polygon. We assigned aspect and vegetation classes based on the proportionally dominant class. In the case of a tie between 2 aspects, one was randomly assigned. In the case of a tie between 2 vegetation classes, we examined aerial imagery and site notes to make a decision. We exported this dataset to conduct analysis in R (R Version 2.13.2, www.r-project.org, accessed 30 Sept 2011).

Exploratory analyses.—To look for patterns in kill site selection, we first performed exploratory analyses for summer and winter zones of predation risk. We

performed univariate logistic regression with the following equation (Hosmer and Lemeshow 2000):

$$g(x) = \beta_0 + \beta_1 x \tag{1}$$

where the logit, g(x), is the relative probability of selection for a resource unit (i.e., a pixel) and is dependent upon the intercept, β_0 , and the slope, or beta coefficient, β_1 , as related to the landscape covariate x. The resulting beta coefficients indicate the direction of selection for the associated landscape covariate; positive values indicate selection for a covariate, while negative values indicated selection against a covariate. To perform univariate logistic regression on the categorical variables, we assigned one class as a reference category. The resulting beta coefficients are interpreted relative to this reference category. In other words, a negative beta coefficient does not necessarily mean that a class was selected for less than proportionate to its availability, but only that it was selected for less than the reference class. This provided preliminary information regarding the effect of each landscape covariate on the probability of use (i.e., kill site selection; see Appendix C) and assisted us in developing our sets of candidate models.

We tested for collinearity between the landscape covariates of each RSF by conducting Variance Inflation Factor (VIF) tests for each pair of covariates. We tested for collinearity between pairs of covariates containing at least one categorical covariate with Generalized Variance Inflation (GVIF) tests. All scores were between 1 and 2 indicating that there were no issues with collinearity (Neter et al. 1996). *Fitting and selecting the RSF models.*—Based on knowledge of cougar ecology and the results of the exploratory univariate analyses, plausible lists of candidate models were developed *a priori* for the summer and winter zones of predation risk datasets.

To fit and select the risk models we used the following exponential fixed-effects RSF (Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$
(2)

where relative probability of use, w(x), is described by landscape covariate, x_n , and betacoeffecient, β_n . We dropped the intercept, β_0 , from the equation because it is meaningless in our use-availability study design (Manly et al. 2002) and unnecessary without the inclusion of a random intercept.

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

Model validation.—We evaluated our top performing models with the *k*-fold cross validation technique (Boyce et al. 2002, Fernández et al. 2003). This process entailed randomly splitting the datasets into *k* partitions (folds) and using n - 1 folds (the training set) to fit the model and then testing the model by its ability to predict the remaining fold (the testing set). We used 5 folds and this process was repeated 5 times so that each fold

served as the training fold a single time. The results from these cross-validations were averaged to produce a single cross-validation estimate of accuracy. Because the estimates can be variable (Maindonald 2007), we iterated this process 100 times to calculate the mean cross-validation estimate of accuracy (between 0 and 1) for the topperforming summer and winter zones of risk models.

Projecting the RSFs.—Using the Raster Calculator in ArcMap, the top summer and winter models were projected across the study site for the predation risk RSFs. We entered the beta-coefficients from the top model of each RSF along with the landscape covariate layers into equation 2 to project the relative probabilities of kill site use, w(x), spatially across the landscape.

RESULTS

Capture and GPS Collaring

We captured, GPS-collared, and monitored 5 cougars for between 168 and 417 days for a total of 1,432 cougar-days. Excluded from this analysis was a sub-adult male who was GPS-collared but later found to be travelling with his mother whom was GPScollared as well.

Fine-Scale Kill Site Analysis

Over the course of the study we visited 388 clusters and located 194 prey remains and 35 kill sites. We censured the lowest confidence level kill sites and retained 30 sites in which we were able to confidently identify a kill site. We visited 218 random sites for comparison (Table 3.1). At 14 m the mean percent horizontal visibility was significantly lower (P = 0.022) at kill sites ($\bar{x} = 56.4\%$) than at random sites ($\bar{x} = 68.5\%$). At 25 m, the mean percent horizontal visibility was also significantly lower (P = 0.008) at kill sites $(\bar{x} = 37.8\%)$ than at random sites $(\bar{x} = 53.3\%)$. While not significant, mean horizontal visibility of juniper-mountain mahogany vegetation was lower at kill sites than random sites at 14 m and especially 25 m; our small sample likely prevented us from detecting a difference. Random sites had significantly (P = 0.020) higher elevations ($\bar{x} = 1,743$ m) than kill sites ($\bar{x} = 1,581$ m). Kill sites were not significantly different from random sites in their slopes. We assessed for significant differences in kill sites and available random sites amongst aspect and vegetation classes with 2-sample proportion tests (Fig. 3.2, Table 3.1). There were no significant differences between the aspects of kill and random sites. The grassland and juniper-mountain mahogany classes were the only vegetation classes to have significant differences between kill sites and random sites. Significantly (P = 0.045) more random sites were in the grassland class ($\bar{x} = 22.5\%$) than kill sites ($\bar{x} =$ 6.7%). Significantly (P <0.001) more kill sites ($\bar{x} = 56.7\%$) than random sites ($\bar{x} =$ 27.1%) were in the juniper-mountain mahogany vegetation class.

Coarse-Scale Kill Site Analysis with Resource Selection Functions

Used and available zones of risk.—The distance-dragged from the highconfidence kill sites (n = 30) to the primary cache sites was 43.7 ± 31.1 ($\bar{x} \pm$ SD) m. We used a 95% upper cut-point (94.9 m, Z = 1.644) as the radius with which to buffer all cache sites creating 194 (2.83 ha) zones of risk. These distances-dragged are similar to results from Beier et al. (1995). We generated 582 available zones of risk for comparison (Fig. 3.3).

Fitting and selecting the summer zones of risk RSF model.—There were seven well-performing candidate models for the summer zones of risk dataset with ΔAIC_c scores of <2 (Table 3.2). They had 3 landscape covariates in common: distance-to-water, a quadratic term for slope, and vegetation. Although it ranked second with a ΔAIC_c of 0.104, we retained the most parsimonious model as our top model. Other models had very similar ΔAIC_c scores, including one with a smaller score, but they all included additional parameters. When parameters are added without a ≥ 2 drop in ΔAIC_c , they can be considered uninformative. That is, there is not a sufficient addition of explanatory power to warrant their inclusion (Arnold 2010). The beta-coefficients of the top summer zones of risk model (Table 3.4) indicated that cougars selected kill sites closer to water sources ($\beta = -0.315$) and exhibited a quadratic selection for slope. This quadratic slope relationship was concave and curvilinear indicating increasing selection for slope up to a certain threshold after which slope is selected against. Cougars selected most strongly for the riparian vegetation class when making kills, and against coniferous forest ($\beta = -$ 1.558), juniper-mountain mahogany ($\beta = -1.840$), desert shrubland ($\beta = -1.984$), and especially sagebrush ($\beta = -2.050$), and grassland ($\beta = -2.432$) vegetation classes.

Fitting and selecting the winter zones of risk RSF model.—The top winter zones of risk model included only the elevation and vegetation class covariates (Table 3.3). The next 4 models performed well with ΔAIC_c scores <2, but they all took the form of the top model with additional covariates. As above, we retained the top model in the interest of parsimony and avoidance of uninformative parameters. The beta-coefficients of the top winter zones of risk model (Table 3.4) showed that cougars selected for lower

elevations (β = -2.166). Kills were most apt to be made in riparian habitats. Relative to riparian, kill sites were less apt to be in juniper-mountain mahogany (β = -1.677), desert shrubland (β = -1.899), sagebrush (β = -2.328), and grassland (β = -2.595) habitats.

Model validation.—The top summer zones of risk RSF model had a mean cross-validation estimate of accuracy of 0.763 ± 0.005 SD while the top winter model had a mean cross-validation estimate of accuracy of 0.778 ± 0.004 SD.

Projecting the Resource Selection Functions.—Following equation 2, we entered the beta-coefficients from the top performing predation risk models for summer and winter (Table 3.4) and the landscape covariate raster layers, into the Raster Calculator in ArcMap. This produced a visual output of the relative probability of summer cougar kill site selection for each pixel across the study area (Fig. 3.4). To scale the resulting raster pixel values between 0 and 1, we divided these raster layers by the maximum pixel value of each RSF. Pixels with unknown or extremely rare habitat classes (e.g., open water) were excluded from this analysis (Fig. 3.4).

DISCUSSION

Fine-Scale Kill Site Analysis

Our fine-scale kill site analysis produced results similar to those from past studies (Logan and Irwin 1985, Laundre and Hernandez 2003) that reported cougars selected for kill sites in more obscuring vegetation classes (i.e., juniper-mountain mahogany) and they selected against kill sites in the more open grassland vegetation class. The selection for lower elevation kill sites was anticipated and has been reported before (Pierce et al. 1999,

Rieth 2010), likely because for a good portion of the year most cougars and their prey are avoiding the deep snows and suboptimal foraging conditions of the upper elevations.

Our results confirmed our hypothesis that kill sites would have lower horizontal visibility than random sites. This was in agreement with previous research which suggested cougars need effective hiding cover to successfully stalk, approach, and kill prey (Beier et al. 1995, Husseman et al. 2003). While horizontal visibility was lower in the juniper-mountain mahogany vegetation class, the difference was not significant, but was likely obscured by our small sample size. However, 100% of kills of bighorn sheep were in the juniper-mountain mahogany class and, consequently, sheep represented a greater percentage of prey items in just the juniper-mountain mahogany class (29.4%) than in all vegetation classes combined (16.7%). Considering that juniper-mountain mahogany was the vegetation class where bighorn sheep were frequently killed, and that predation events were more apt to happen in sites with lower horizontal visibility, management efforts aimed at increasing horizontal visibility in this vegetation class appear well-targeted.

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

Coarse-Scale Kill Site Analysis with Resource Selection Functions

Our relatively high frequencies of correct classifications during the k-folds crossvalidation analysis suggests that our top predation risk models were useful in predicting kill site locations for this population of cougars. The top predation risk model during summer was composed of distance-to-water, a quadratic term for slope, and vegetation class. Distance-to-water was selected against probably indicating cougars were significantly influenced by their biological requirement for water, or by their prey's, in the summer. A quadratic relationship with slope seems obvious given that cougars have previously shown preference for (steeper) slopes, but they use steep terrain up to a certain threshold after which its usability declines. Not surprisingly, vegetation class was significant. Vegetation class was also the only covariate common to both the top summer and winter predation risk models. Previous studies have uncovered the important link between kill or cache site selection and vegetation type (Laundre and Hernandez 2003, Rieth 2010, Kunkel et al. 2013). Vegetation can be assumed to influence cover, horizontal visibility, and the distribution of prey. Vegetation classes with more obscuring vegetation experienced positive selection relative to more open classes. Riparian vegetation was favored in the top summer and winter predation risk models.

The top model for the predation risk RSF during winter included just the elevation and vegetation class covariates. Not surprisingly, elevation was selected against at winter kill sites. In mountainous areas, ungulate populations typically migrate to lower elevations in the winter to forage and avoid deep snows (D'eon and Serrouya 2005). Kunkel et al. (2013) also found selection for lower elevations at winter kill sites, while Rieth (2010) and Elbroch et al. (2013) found selection for lower elevations at kill sites year-round. Riparian was still the preferred vegetation class, although coniferous forest was not strongly selected against relative to riparian.

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

Our sample size led us to examine risk to all prey species combined and we acknowledge that this approach glosses over the details of risk to any one particular species. For example, bighorn sheep were killed exclusively in the juniper-mountain mahogany habitat but, because mule deer were killed in other habitats, the risk value of juniper-mountain mahogany to just bighorn was biased low. Furthermore, we recognize that our realm of inference is our sample population of cougars. Unfortunately our sample size of 5 individual cougars precluded us from incorporating mixed effects which would have allowed us to account for individual effects and extrapolate to the entire cougar population of the study area. We do believe, however, that our study was close to a census and we are confident we had a very high (if not the entire proportion) of the adult resident cougars collared (see chapter 2) in the BCNRA and PMWHR.

MANAGEMENT IMPLICATIONS

While not much can be done to alter certain landscape characteristics (e.g., slope, elevation) associated with increased predation risk from cougars, our results indicated that habitat modifications with the goal of increasing horizontal visibility in the junipermountain mahogany class may well be worth the efforts. Juniper-mountain mahogany was the vegetation class where we discovered all of our bighorn sheep kills and, across all vegetation classes, lower measures of horizontal visibility were associated with higher predation risk. In addition to a possible reduction in predation pressure, opening up juniper-mountain mahogany areas would likely confer other advantages to sheep such as a reduced need for energetically costly vigilance behavior (Risenhoover and Bailey 1985). The predation risk RSFs should help managers target their juniper removal activity by working in those places where areas of high predation risk intersect bighorn sheep habitat. We caution that mountain mahogany is a primary browse species for bighorn sheep in the Pryor Mountains, especially during the fall and winter (Kissell et al. 1996) so vegetation removal in the juniper-mountain mahogany class should focus on juniper removal. Manual removal of juniper may be preferable to controlled burns in areas with mountain mahogany. While the bighorn sheep herd may respond positively to manipulation of predation levels, it appears that cougar predation cannot be counted on as a management tool to limit the feral horse population (i.e., cougars killed no horses). The BLM will need to continue population reduction efforts using fertility control and gathers in order to keep this population within its stated population objective.

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Table 3.1. Fine-scale analysis of landscape covariates at kill and random sites of cougars in the Pryor Mountains of Wyoming and Montana, 2011-2012. Differences in means were tested with Welch's 2-sample t-tests for continuous variables and with 2-sample proportion tests for categorical variables. Dashes indicate instances where it was not possible to generate a p-value due to low expected values. Significant results are in bold.

Landscape covariates	Kill sites	Random sites	P-value
Continuous covariates			
Slope (degrees)	16.90	14.03	0.231
Horizontal visibility at 14m (percent)	56.37	68.50	0.022
Horizontal visibility at 25m (percent)	37.85	53.32	0.008
JM* Horizontal visibility at 14m (percent)	49.51	50.12	0.465
JM Horizontal visibility at 25m (percent)	27.90	33.90	0.191
Elevation (m)	1581.05	1742.99	0.020
Aspect			
Flat	0.00%	1.38%	-
North	10.35%	14.68%	-
East	41.38%	29.36%	0.188
South	27.59%	27.52%	0.994
West	20.69%	27.06%	0.464
Vegetation			
Coniferous forest	16.67%	24.77%	0.328
Deciduous shrubland	0.00%	0.92%	-
Desert shrubland	3.33%	2.29%	-
Grassland	6.67%	22.48%	0.045
Juniper - mountain mahogany	56.67%	27.06%	<0.001
Riparian	0.00%	1.84%	-
Sagebrush	16.67%	20.64%	0.611

*JM = juniper-mountain mahogany.

Model Description	n	K	d.f.	Log Likelihood	AICc	ΔAICc
water + $slope^2$ + $aspect$ + veg	380	12	368	-192.431	409.713	0.000
water $+$ slope ² $+$ veg	380	9	371	-195.665	409.816	0.104
low-use $rds + water + slope^2 + veg$	380	10	370	-194.798	410.193	0.480
water + elev + rugged + $slope^2$ + $aspect$ + veg	380	14	366	-190.540	410.231	0.519
water + rugged + $slope^2$ + $aspect$ + veg	380	13	367	-191.693	410.380	0.667
$full^* + slope^2$	380	16	364	-188.505	410.509	0.796
water + elev + $slope^2 + veg$	380	10	370	-195.235	411.067	1.354
$full + rugged^2 + slope^2$	380	17	363	-188.505	412.700	2.988
full - $rds + slope^2$ - $rugged + elev^2$	380	14	366	-191.799	412.749	3.036
full - high-use $rds + elev^2 + slope^2$	380	16	364	-189.775	413.049	3.337
water + $elev^2 + slope^2 + veg$	380	11	369	-195.202	413.121	3.408
$full + elev^2 - rugged + slope^2$	380	16	364	-189.894	413.286	3.573
water + veg	380	7	373	-199.669	413.638	3.926
$slope^2 + veg$	380	8	372	-198.687	413.761	4.049
full - low-use $rds + elev^2 + rugged^2 + slope^2$	380	17	363	-189.318	414.326	4.614
$full + elev^2 - rugged + slope^2 - aspect$	380	13	367	-193.725	414.444	4.731
full - $rds + elev^2 + rugged^2 + slope^2$	380	16	364	-190.507	414.512	4.799
$full + elev^2 + rugged^2 + slope^2$	380	18	362	-188.405	414.704	4.991
low-use rds + water + veg	380	8	372	-199.282	414.952	5.239
low-use rds + water + aspect + veg	380	11	369	-196.223	415.163	5.451
full - high-use $rds + elev^2 + rugged^2 + slope^2$	380	17	363	-189.772	415.235	5.522
water + elev + veg	380	8	372	-199.553	415.494	5.781
veg	380	6	374	-201.686	415.596	5.884
$full + elev^2 + rugged^2 + slope^2 - aspect$	380	15	365	-192.276	415.870	6.158

Table 3.2. Top 25 candidate models for zones of cougar predation risk during summer in

the Pryor Mountains of Wyoming and Montana, 2011-2012; top model is in bold.

*full model = distance-to-high-use roads + distance-to-low-use roads + distance-to-water + elevation + ruggedness + slope + aspect + vegetation class

Table 3.3. Top 25 candidate models for zones of cougar predation risk during winter in the
Pryor Mountains of Wyoming and Montana, 2011-2012; top model is in bold.

Model Description	n	K	d.f.	Log Likelihood	AICc	ΔAICc
elev + veg	396	7	389	-191 128	396 544	0 000
full* + rugged ² - aspect	396	13	383	-184 980	396 913	0.369
$elev^2 + veg$	396	8	388	-190 312	396 997	0.263
full + rugged ²	396	16	380	-182,190	397 816	1 272
high-use rds + $elev + veg$	396	8	388	-191.068	398.508	1.964
water $+$ elev $+$ veg	396	8	388	-191.124	398.620	2.076
high-use rds + $elev^2$ + veg	396	9	387	-190.145	398.757	2.213
water + $elev^2$ + veg	396	9	387	-190.232	398.930	2.386
full + $elev^2$ + $rugged^2$	396	17	379	-181.740	399.099	2.556
full - high-use $rds + elev^2 + rugged^2 + slope^2$	396	17	379	-181.929	399.477	2.933
full - roads + $elev^2$ + $rugged^2$ + $slope^2$	396	16	380	-183.056	399.547	3.004
full + $rugged^2$ + $slope^2$	396	17	379	-182.189	399.997	3.453
full + $elev^2$ + $rugged^2$ + $slope^2$ - $aspect$	396	15	381	-184.492	400.247	3.704
water + elev + slope ² + veg	396	10	386	-189.976	400.523	3.980
high-use rds + water + elev + veg	396	9	387	-191.067	400.600	4.056
water $+$ elev $+$ rugged $+$ veg	396	9	387	-191.119	400.704	4.161
high-use rds + water + $elev^2$ + veg	396	10	386	-190.084	400.740	4.196
water + $elev^2 + slope^2 + veg$	396	11	385	-189.200	401.087	4.543
water + $elev^2$ + $slope^2$ + $aspect$ + veg	396	14	382	-186.033	401.168	4.624
$full + elev^2 + rugged^2 + slope^2$	396	18	378	-181.740	401.294	4.751
full - low-use $rds + elev^2 + rugged^2 + slope^2$	396	17	379	-182.971	401.561	5.017
full - roads	396	13	383	-187.665	402.282	5.739
full - roads + $slope^2$	396	14	382	-186.741	402.584	6.040
full - roads + $elev^2$	396	14	382	-186.769	402.641	6.098
$full + elev^2 - rugged + slope^2$	396	16	380	-184.734	402.904	6.360

*full model = distance to high-use roads + distance to low-use roads + distance to water + elevation + ruggedness + slope + aspect + vegetation class

Table 3.4. Beta-coefficients and standard errors from the top generalized linear (fixed effects) models fit to zones of cougar predation risk during summer and winter in the Pryor Mountains of Wyoming and Montana, 2011-2012. The top summer model consisted of distance-to-water, a quadratic term for slope, and vegetation class. The top winter model consisted of elevation and vegetation class.

Landscape Covariate	Summer	Winter
Distance-to-high-use roads	-	-
Distance-to-low-use roads	-	-
Distance-to-water	-0.315 (0.137)**	-
Elevation	-	-2.166 (0.519)***
Ruggedness	-	-
Slope	14.270 (5.864)**	-
Slope ²	-41.708 (16.831)**	-
North	-	-
South	-	-
West	-	-
Coniferous forest	-1.558 (0.556)***	-0.266 (0.524)
Desert shrubland	-1.984 (0.766)***	-1.899 (0.655)***
Grassland	-2.432 (0.579)***	-2.595 (0.542)***
Juniper - mountain mahogany	-1.840 (0.547)***	-1.677 (0.450)***
Sagebrush steppe	-2.050 (0.563)***	-2.328 (0.508)***

Standard errors in parentheses. *Significant at 10%, **significant at 5%, ***significant at 1%. Dashes signify covariates that are not included in the models.



Fig. 3.1. The 2,553 km² study area in the southern Pryor Mountains of Wyoming and Montana. The study area was formed by creating a minimum convex polygon of all recorded cougar locations.



Fig. 3.2. Percentages of random and kill sites in different (A) aspect categories, and (B)
vegetation classes, for cougars in the Pryor Mountains of Wyoming and Montana, 2011-2012.
CF = coniferous forest, DEC = deciduous shrubland, DES = desert shrubland, GR = grassland,
JM = juniper – mountain mahogany, RI = riparian, SS = sagebrush.



Fig. 3.3. Two cougar home ranges (95% kernel density estimates) showing used and available zones of risk, Pryor Mountains of Wyoming and Montana, 2011-2012.



Fig. 3.4. Maps of summer (A) and winter (B) RSFs of zones of cougar predation risk, Pryor Mountains of Wyoming and Montana, 2011-2012. No data areas are displayed in white.

CHAPTER 4

CONCLUSIONS

Our research provided valuable insights into prey use by cougars (Puma *concolor*), as well as the relationships between cougar predation and landscape characteristics, in the Pryor Mountains of Wyoming and Montana. In our examination of cougar foraging patterns (chapter 2), we found that in addition to mule deer (Odocoileus hemionus), cougars consumed a variety of other prey items, including Rocky Mountain bighorn sheep (Ovis canadensis canadensis), but not feral horses (Equus caballus) or domestic livestock. We found not all cougars preyed on bighorn sheep, even when their territories exhibited spatial overlap with areas used by sheep. In line with prior studies that have reported specialist individuals, all sheep predation was the work of one individual cougar (Ross et al. 1997, Logan and Sweanor 2001). Predation of bighorn sheep by cougars has been confirmed in the recent past in Bighorn Canyon National Recreation Area (BCNRA; Schoenecker 2004) and there is reason to believe it will occur again. While removing a specialist cougar might decrease predation pressure to bighorn sheep, this was not a desirable option in the BCNRA and, in the future, without collared cougars, it would be difficult to confirm removal of the offending individual. In fact, accidental removal of a cougar that does not prey on sheep could have deleterious effects, opening up a territory to new cougars that may prey on bighorn. Over the course of this study, we found no cougar-killed horses. Cougars have, however, been implicated in predation of feral horse foals in the Pryor Mountain Wild Horse Range (PMWHR) in the recent past (J. Bybee, Bureau of Land Management, personal communication). Unless

the cougar population resumes sufficient horse predation, the BLM will most likely need to continue management efforts to keep the horse herd numbers close to their Appropriate Management Level goal of 90-120 individuals (Bureau of Land Management 2009).

We found that the social class of cougars influenced their kill rates with females with dependent kittens having the highest kill rates. This is congruent with what is expected based on the greater energetic requirements of a family group (Laundre 2005) and has been reported in other studies measuring kill rates (Cooley et al. 2008, Knopff et al. 2010, Mitchell 2013). Managers should take this into account when considering the impact of cougar predation upon ungulate herds.

An aerial ungulate survey suggested the mule deer population was at a low density and experiencing low recruitment. The status of a primary prey population can influence predation to a secondary prey species, often in complex and indirect ways and can be influenced by population densities, spatial ecology, seasonal movements, the presence of specialist individuals, and other predators (Holt 1997, Ruth and Murphy 2010). An increase in the mule deer population might counteract predation pressure to a secondary prey due to prey switching in which consumption of a prey species increases with its relative abundance (Turner et al. 1992, Sweitzer et al. 1997). However we recommend managers approach this tactic cautiously and with further study. In fact, an abundance of primary prey may increase a predator species population and thereby negatively impact a secondary prey species through apparent competition (Roemer et al. 2002). Perhaps a better option to decrease the potential of cougar predation upon bighorn sheep is to modify those landscape characteristics that increased predation risk. In line with previous studies (Laundre and Hernandez 2003) we found cougars did select for certain landscape and habitat characteristics when making kills. Many of these characteristics (e.g., slope, elevation, aspect, ruggedness, distances-to-roads, and water) cannot reasonably be altered to reduce predation risk. Vegetation type and horizontal visibility, however, represent landscape characteristics that can be manipulated. We found evidence that lower horizontal visibilities increased predation risk, suggesting that management efforts such as controlled burns and mechanical removal of dense vegetation may help reduce predation. We recommend managers continue to focus these efforts in bighorn sheep habitat indicated in past studies (Schoenecker 2004) that intersects habitat management areas with high predation risk. Because all of the cougar kills of bighorn sheep occurred in the juniper-mountain mahogany vegetation class, we recommend further targeting juniper removals within this vegetation class.

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APPENDICES
Appendix A. Vegetation reclassification of the NWGAP vegetation layer for the Pryor

Mountains of Wyoming and Montana.

Vegetation Class	NWGAP Classification		
Agriculture	Cultivated Cropland		
Coniferous	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest		
forest	Rocky Mountain Lodgepole Pine Forest Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland		
	Southern Rocky Mountain Ponderosa Pine Woodland		
	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland		
	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland		
	Northwestern Great Plains - Black Hills Ponderosa Pine Woodland and Savanna		
Deciduous	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland		
shrubland	Western Great Plains Wooded Draw and Ravine		
Desert	Western Great Plains Badland		
shrubland	Inter-Mountain Basins Shale Badland		
	Inter-Mountain Basins Mat Saltbush Shrubland		
	Inter-Mountain Basins Mixed Salt Desert Scrub		
	Inter-Mountain Basins Greasewood Flat		
Developed	Developed, Open Space		
	Developed, Low Intensity		
	Developed, Medium Intensity		
	Developed, High Intensity		
	Quarries, Mines and Gravel Pits		
Grassland	Northern Rocky Mountain Lower Montane, Foothill and Valley Grassland		
	Northwestern Great Plains Mixedgrass Prairie		
	Southern Rocky Mountain Montane-Subalpine Grassland		
	Western Great Plains Sand Prairie		
	Pasture/Hay		
	Introduced Upland Vegetation - Annual Grassland		
Juniper -	Rocky Mountain Foothill Limber Pine-Juniper Woodland		
mountain	Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland		
mahogany	Rocky Mountain Lower Montane-Foothill Shrubland		
Riparian	Introduced Riparian and Wetland Vegetation		
	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland		
	Rocky Mountain Subalpine-Montane Riparian Shrubland		
	Western Great Plains Open Freshwater Depression Wetland		
	North American Arid West Emergent Marsh		
	Rocky Mountain Subalpine-Montane Fen		
	Western Great Plains Closed Depression Wetland		
	Western Great Plains Saline Depression Wetland		
	Northwestern Great Plains Riparian		
	Western Great Plains Riparian Woodland and Shrubland		
	Western Great Plains Floodplain		
	Northwestern Great Plains Floodplain		

Sagebrush	Wyoming Basins Dwarf Sagebrush Shrubland and Steppe		
steppe	Inter-Mountain Basins Big Sagebrush Steppe		
	Inter-Mountain Basins Montane Sagebrush Steppe		
	Inter-Mountain Basins Big Sagebrush Shrubland		
Unknown	No Data		
or rare	Rocky Mountain Cliff, Canyon and Massive Bedrock		
	Rocky Mountain Alpine Bedrock and Scree		
	Inter-Mountain Basins Active and Stabilized Dune		
	Inter-Mountain Basins Cliff and Canyon		
	Open Water		

Appendix B. Vegetation reclassification of the CHNP vegetation layer for the Pryor Mountains

of Wyoming and Montana.

Vegetation	CUND Classification		
	CHNP Classification		
Agriculture	Agricultural Land		
Confierous forest	Pinus ponderosa woodiand		
	Pseudotsuga menziesii / Acer giabrum Forest		
	Pseudotsuga menziesii Forest		
	Pseudotsuga menziesii Scree woodland		
	Pseudotsuga menziesii Woodland		
Deciduous	Acer negundo / Prunus virginian Forest		
shrubland	Acer negundo / Rhus trilobata Wooded Shrubland		
	Prunus virginiana - (Prunus americana) Shrubland		
	Rhus trilobata / Pseudoroegneria spicata Shrub Herbaceous Vegetation		
Desert shrubland	Atriplex gardneri Dwarf-shrubland		
	Sarcobatus vermiculatus Shrubland		
	Yucca glauca / Pseudoroegneria spicata Shrub Herbaceous Vegetation		
Developed	Landscaped Urban Vegetation		
	Urban		
Grassland	Agropyron cristatum - (Pascopyrum smithii, Hesperostipa comata) Semi-natural Herbaceous Vegetation		
	Bouteloua gracilis Herbaceous Vegetation (Blue Grama Herbaceous Vegetation)		
	Bromus inermis - (Pascopyrum smithii) Semi-natural Herbaceous Vegetation		
	Bromus tectorum Semi-natural Herbaceous Vegetation		
	Disturbed Annual and Perennial Weedy Herbaceous Vegetation		
	Leucopoa kingii Herbaceous Vegetation		
	Pascopyrum smithii Herbaceous Vegetation		
	Pseudoroegneria spicata - Eriogonum brevicaule Sparse Vegetation		
	Pseudoroegneria spicata - Hesperostipa comata Grassland		
	Sporobolus spp. Herbaceous Vegetation		
Juniper -	Cercocarpus ledifolius / Pseudoroegneria spicata Scrub		
mountain	Juniperus osteosperma (Juniperus scopulorum) / Cercocarpus ledifolius Woodland		
mahogany	Juniperus osteosperma Woodland		
	Juniperus scopulorum Intermittently Flooded Woodland		
	Pinus flexilis / Juniperus spp. Woodland		
Riparian	Elaeagnus angustifolia Semi-natural Woodland		
	Phalaris arundinacea Western Herbaceous Vegetation		
	Populus angustifolia Temporarily Flooded Woodland		
	Populus deltoides ssp. wislizeni / Disturbed Understory Woodland		
	Rhus trilobata Intermittently Flooded Shrubland		
	Tamarix spp. Temporarily Flooded Semi-natural Shrubland		
	Typha (latifolia, angustifolia) Western Herbaceous Vegetation		
Sagebrush steppe	Artemisia cana ssp. cana / Pascopyrum smithii Shrub Herbaceous Vegetation		
C 11	Artemisia nova Shrubland		
	Artemisia tridentata - (Ericameria nauseosa) / Bromus tectorum Semi-natural Shrubland		
	Artemisia tridentata ssp. wyomingensis / vaseyana Shrubland		

Unknown or rare	Barren and Sparsely Vegetated Cliff
	Borrow Pit - Disturbed
	Cut Bank
	Non-vegetated / Barren Land
	Reservoir Edge
	Water

Appendix C. Beta (regression) coefficients from univariate logistic regression of landscape covariates and zones of risk by season for cougars in the Pryor Mountains of Wyoming and Montana. East and riparian were chosen as reference categories for the categorical variables aspect and vegetation class.

Landscape Covariate	Summer	Winter
Distance-to-high-use roads	0.006 (0.049)	-0.164 (0.070)**
Distance-to-low-use roads	2.319 (1.326)*	0.114 (1.538)
Distance-to-water	-0.335 (0.127)***	-0.287 (0.121)**
Elevation	-0.430 (0.336)	-1.249 (0.353)***
Ruggedness (mean)	-14.712 (15.239)	4.814 (10.684)
Ruggedness (max)	-1.599 (4.979)	1.074 (3.748)
Slope	-0.490 (0.969)	-0.542 (1.373)
North	-0.551 (0.380)	-0.201 (0.373)
South	0.131 (0.301)	0.269 (0.297)
West	-0.464 (0.323)	0.248 (0.314)
Coniferous forest	-1.531 (0.492)***	-1.333 (0.438)***
Desert shrubland	-2.076 (0.707)***	-1.589 (0.634)**
Grassland	-2.374 (0.546)***	-2.700 (0.520)***
Juniper - mountain mahogany	-1.699 (0.498)***	-1.502 (0.421)***
Sagebrush	-2.124 (0.535)***	-2.466 (0.485)***

Standard errors in parentheses. *Significant at 10%, **significant at 5%, ***significant at 1%.