

Is niche separation between wolves and cougars realized in the Rocky Mountains?

by

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ABSTRACT

Multiple carnivore species can have greater population limiting effects than single carnivores. Two coexisting carnivores can only be similar up to a certain extent. I investigate how two carnivores, wolves (*Canis lupus*) and cougars (*Puma concolor*), coexist through niche partitioning in the central east slopes of the Alberta Rocky Mountains. Wolf packs spatio-temporally avoided other wolf packs more than they did cougars, while cougars avoided conspecifics as much as wolves. Reinforcing spatial separation, temporally wolves had two crepuscular movement peaks while cougars had just one. Male cougar movements peaked in the late evening and was high over night, while female cougar movement increased throughout the day and peaked in the evening. Female cougars selected different habitat features from male cougars and from wolves during both the day and night, while male cougars had more habitat selection differences from wolves at night. I found some evidence that cougars were more influenced by landscape features than wolves. Differences in the predators' habitat selection were primarily for prey density contingent upon habitat features, likely related to maximizing hunting efficiency. Both species killed primarily deer (*Odocoileus virginianus*, *O. hemionus*), though wolves and male cougars killed and selected more large-bodied ungulate prey, such as elk (*Cervus elaphus*), moose (*Alces alces*) and/or feral horses (*Equus caballus*) than female cougars, who strongly selected for deer. It is advantageous to consider both these species together when building management plans for both predator species as well as for their ungulate prey.

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CHAPTER ONE

GENERAL INTRODUCTION

Competition inevitably occurs when two species fill similar ecological roles; the more similar these roles, the more severe the competition (Darwin 1859). Carnivore assemblages can be structured by processes of exploitative and interference competition or a combination of the two (Park 1954). Exploitation competition occurs when a predator's access to limited prey is altered because prey are removed by another carnivore eating the prey, regardless of aggressive interactions (Wrangham, Gittleman and Chapman 1993). In contrast, interference competition among carnivores can occur when one species' access to resources is limited because the other species is larger, more aggressive or a social group that outnumbers the first species, and can successfully intimidate, injure, steal from, or kill the first species (Fanshawe and Fitzgibbon 1993; Palomares and Caro 1999; Donadio and Buskirk 2006). To limit competition species can exhibit resource partitioning with differential use of resources such as spatial habitat, food, or time (Schoener 1974), which leads to coexistence where their ranges overlap (Chesson 2000).

Identifying potential competitive interactions and niche partitioning among carnivores is important in developing programs for large carnivore conservation and in managing predator-prey systems. Indeed, multiple predator communities may have more complex effects on prey populations than single predators alone. For instance, when just cougars (*Puma concolor*), coyotes (*Canis latrans*) and black bears (*Ursus americanus*) are the large carnivores in a system, survival of neonatal elk (*Cervus elaphus*) is 23% higher than in areas with these carnivores plus wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) (Griffin et al. 2011). Similarly, roe deer (*Capreolus capreolus*) density across Europe was over 5x higher in areas with either wolves or

lynx (*Lynx lynx*) present compared to areas with both predators (Melis et al. 2009). Predators also can alter prey movements and distributions (Fortin et al. 2005; Valeix et al. 2009; Burkepile et al. 2013). In shifting their distributions or behaviors to avoid one predator, prey may make themselves vulnerable to other predators. For example, an experiment showed that when owls (*Bubo bubo*) were the sole predator, gerbils (*Gerbillus allenbyi*, *G. pyramidium*) avoided open habitats that owls have high hunting success in; however, when vipers (*Cerastes cerastes*), ambush predators that hunt most successfully from the bush, were added to the environment, gerbils increased their exposure to owls in the open (Kotler, Blaustein and Brown 1992). The potential for prey refuges that have been described in single predator system (Mech 1977; Hebblewhite, Merrill and McDonald 2005) may be even more limited in multiple predator systems (Kotler, Blaustein and Brown 1992; Thaker et al. 2011). If prey preferences of predators within a multi-predator system differ or if switching by one predator occurs, predation pressure may be distributed more evenly across prey resulting in higher prey evenness (Holt 1977; Sundell et al. 2003; Siddon and Witman 2004). For example, coyotes and red foxes (*Vulpes vulpes*) select for voles (*Microtus* spp.) and eastern cottontails (*Sylvilagus floridanus*), though they switched to consume more mice (*Peromyscus* spp.), the most abundant prey, when the availability of their preferred prey decreased (Randa et al. 2009). In contrast, where multi-predators coexist, apparent competition (Holt 1977; Schmitt 1987; DeCesare et al. 2010; Latham et al. 2013) between prey species may be strong if a dominant predator limits the subordinate predator's access to the primary prey.

Demonstrating true competition is difficult without the manipulation of predator-prey communities because of the “ghost of competition past”, where competition over the same resources in the past caused the separation of resources used today (Connell 1980). Logistically,

manipulative experiments for multiple large carnivore populations are difficult to execute, and thus few have been conducted (Trewby et al. 2008; Hurley et al. 2011). Regardless, we can still observe resource overlap and partitioning to make inferences about coexisting predators. Creel and Creel (1996) suggest that the negative relationship between African wild dog (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*) densities is due to exploitation competition because of the high overlap in their diets. However, with these species potential interference competition is also present, as the larger bodied spotted hyenas usurp African wild dogs' prey, and do so quicker as the group size of hyenas increases relative to the African wild dog pack size (Fanshawe and Fitzgibbon 1993). In addition, in northern Europe the arctic fox (*V. lagopus*) is now endangered potentially due to interference competition as large-bodied red foxes were known to kill arctic foxes when they reproduced in close proximity (Tannerfeldt, Elmhagen and Angerbjorn 2002).

Niche partitioning mechanisms may structure large carnivore communities by altering the other species' spatial distribution or hunting times to avoid direct aggression. For example, cheetah (*Acinonyx jubatus*) select for landscape features, such as thicket, and areas of low prey density, that African lions (*Panthera leo*) and packs of hyenas avoid (Durant 1998; Cristescu, Bernard and Krause 2013). In southwestern Spain, Fedriani, Palomares and Delibes (1999) suggest that the red fox's use of pastureland when active during dusk and night is to avoid lynx, who use scrubland during crepuscular periods. Additionally, in Africa, cheetahs hunt primarily in the morning and lions hunt at night (Durant 1998; Cristescu, Bernard and Krause 2013), whereas in India, dholes (*Cuon alpinus*) make > 60% of their kills in the morning and tigers (*Panthera tigris*) and leopards (*Panthera pardus*) make < 30% of their kills in the morning, more often killing prey in the evening and at night (Karanth and Sunquist 2000). Although their activity

patterns were attributed primarily to the preferred prey of dhole being diurnally active, dhole may also have been avoiding tigers and leopards because they had similar space use patterns.

Large carnivore coexistence also may be facilitated by exploiting different prey as a result of different body sizes and hunting strategies. For example, large-bodied predators, such as lions, and those that hunt socially, such as wild dogs, successfully catch and consume a larger range in prey body size compared to small-bodied or solitary carnivores such as cheetahs and leopards (Sinclair, Mduma and Brashares 2003; Woodroffe and Ginsberg 2005). Large-bodied tigers kill more large prey species than smaller-bodied leopards that hunt alone and dholes who hunt in packs (Karanth and Sunquist 2000). African golden cats (*Felis aurata*) may have limited competition with leopards as their diets consist primarily of rodents (50.9%) and ungulates (20.2%), whereas the diet of leopards consist more of ungulates (53.5%) and primates (25.4%) (Hart, Katembo and Punga 1996). However, Hart, Katembo and Punga (1996) suggest that through intraguild predation (Polis, Myers and Holt 1989) leopards limit golden cats and can limit their prey, although leopards are more likely to experience competition from hunters for ungulates.

In Alberta, two large predators, wolves and cougars, have high range overlap and both species have gone through major population changes since the early 1900s. Soon after European settlement in Alberta, wolf numbers were low as humans set bounties from the late 1800s through the 1920s for poisoning, shooting and trapping them. Plus there were low densities of ungulates at this time (Alberta Forestry, Lands, and Wildlife 1991). In the 1930s and 1940s the wolf population increased and there was the perception that they provided major competition for hunters. In 1952 a large carnivore control program was implemented due to rabies, and wolf

populations declined to between 500-1000 individuals in Alberta in 1956. To maintain ungulate populations, localized wolf control continued until 1966. Today, as a result of abundant ungulates, wolves number over 4000 in the winter in Alberta, and are locally subject to a long hunting and trapping season and continued control (Webb, Allen and Merrill 2011).

Comparatively, cougars in Alberta have had a similar population fluctuation pattern since human settlement, with their populations likely following the patterns of ungulate densities (Alberta Forestry, Lands, and Wildlife 1992). Bounties were set for cougars in 1937 until 1964, suggesting that cougar populations were high during this period as there were more cougar-human interactions than at the start of the century when there were no bounties. In the last two decades, cougar numbers have increased and they have expanded their range from the southwestern part of Alberta further north and east (Knopff, Webb and Boyce 2014). Cougars are being managed as a big-game species and are hunted with the use of dogs during a 3-month season unless quotas are filled early and the hunt is discontinued (Ross, Jalkotzy and Gunson 1996; Knopff, Knopff and Boyce 2010). The current provincial population estimate for cougars is estimated at 2050 (Alberta ESRD 2012).

In the central east slopes of the Rocky Mountains of Alberta, cougar populations have been expanding and cougars and wolves now overlap in space at relatively high densities for Alberta (Robichaud and Boyce 2010; Webb, Allen and Merrill 2011; Knopff, Webb and Boyce 2014). How these two top-level carnivores coexist in high densities is not well understood. To examine the potential mechanisms behind their coexistence, I used data collected from studies in 2004 to 2006 on wolves (Webb 2009) and 2006 to 2008 on cougars (Knopff 2010). The major focus of these 2 studies was to explore predator-prey dynamics in a human modified landscape.

Specifically, Webb (2009) focused on a new approach to survey wolf populations (Webb, Hebblewhite and Merrill 2008), demographics of a human-harvested wolf population (Webb, Allen and Merrill 2011), and factors influencing the functional response of wolves (Webb 2009). Knopff (2010) investigated cougar susceptibility to snaring at wolf bait stations when scavenging (Knopff, Knopff and Boyce 2010), the use of GPS for estimating cougar prey composition, kill rates and the multi-species functional response (Knopff et al. 2010), whether cougars were ambush predators (Knopff 2010) and more recently the temporal shifts in cougar habitat selection and tolerance to anthropogenic development (Knopff et al. 2014).

Data in the above studies were collected on wolves and cougars in the same area east of Rocky Mountain House, Alberta, which provided a unique opportunity to compare the dietary composition and spatio-temporal use patterns of these two predators in the same environment. I focused my analyses on winter, as wolf pack cohesion is greater than in summer (Metz et al. 2011), because most young of the year constrain the movements of female cougars less in the winter (Murphy 1998; Laundré and Hernández 2007) and to avoid the complexity of additional large predators, e.g., grizzly and black bears. In chapter 2, I compared the partitioning of resources by cougars and wolves to better understand the behavioural patterns that lead to their coexistence. Although data collection was sequential in years, data on the two carnivores overlapped only in the winter of 2006. I used data from all years to compare ungulate kill composition, selection and overlap among wolves, female and male cougars to assess whether differential use of ungulate prey by these predators may contribute to their coexistence. I used the data across all years because of a relatively small number of kills per individual in each year. In contrast, I limited my comparison of space use and temporal patterns by individuals to the

same winter months in 2006 to limit environmental differences and because the use of GPS collars provided sufficient data.

In chapter 3 I summarize my results and discuss their relevance for future management practices.

CHAPTER TWO

IS NICHE SEPARATION BETWEEN COUGARS AND WOLVES REALIZED IN THE ROCKY MOUNTAINS?

Large carnivores are important components of ecosystems because of their trophic interactions (Beschta and Ripple 2009; Estes et al. 2011; Ripple et al. 2014), their use as umbrella species for conservation (Noss et al. 1996), and for ecotourism (Kellert et al. 1996; Ripple et al. 2014). The favourable shift in attitude toward carnivores over the past decades (Kellert et al. 1996; Treves and Karanth 2003; Knopff 2011) has led to their conservation and reintroduction allowing their expansion in North America (Fritts et al. 1997; Gese 2001; Treves and Karanth 2003; Knopff, Webb and Boyce 2014). In ecosystems where multiple carnivores are present, understanding how they may coexist is important both for their management and because their interactions may alter the top-down influences on ecological communities (Estes et al. 2011).

Wolves (*Canis lupus*) and cougars (*Puma concolor*) are two large carnivores in North America whose range overlap has increased because of the reestablishment of wolves and expansion of cougar populations over the past several decades (Bangs et al. 1998; Riley, Nesslage and Maurer 2004; Kortello, Hurd and Murray 2007; Knopff, Webb and Boyce 2014). Research on these species where they co-occur provides some evidence for potential niche partitioning related to differences in prey selection and hunting strategies. Because they hunt in packs, particularly in winter (Metz et al. 2011), wolves may be more likely to kill large-bodied prey like moose (*Alces alces*) and elk (*Cervus elaphus*) more than cougars (Fanshawe and Fitzgibbon 1993; Creel and Creel 1995; Radloff and Du Toit 2004; Kuzyk, Kneteman and

Schmiegelow 2006), although this may depend on prey availability. For example, in Montana's Madison Range where elk comprised 72% and deer (*Odocoileus hemionus*, *O. virginianus*) 28% of the ungulate prey post-wolf recolonization; wolf kills reflected ungulate availability whereas cougars killed almost twice as many deer as elk (Atwood, Gese and Kunkel 2007). If the abundance of the preferred species is low, wolves as cursorial hunters (Kunkel et al. 1999; Husseman et al. 2003; Atwood, Gese and Kunkel 2007) may be at an advantage for maintaining encounter rates with prey compared to "stalk and ambush" hunters, which cougars are considered (Ross and Jalkotzy 1992; Kunkel et al. 1999; Husseman et al. 2003; Atwood, Gese and Kunkel 2007). For example, when the local elk population decreased in Banff National Park in the early 2000s, cougars showed a shift in their kills to other prey such as deer and bighorn sheep (*Ovis canadensis*) sooner than did wolves (Kortello, Hurd and Murray 2007).

In addition, hunting success of these two predators may be facilitated by different landscape features that influence prey distribution, detection or vulnerability. For example, cover may promote successful ambush hunting in cougars (Logan and Irwin 1985; Holmes and Laundré 2006; Atwood, Gese and Kunkel 2007; Kunkel et al. 2013), and there is evidence that cougar kill sites occur often along forest edges or in areas with high hiding cover or rugged terrain (Holmes and Laundré 2006; Atwood, Gese and Kunkel 2007; Kunkel et al. 2013; Bartnick et al. 2013). In contrast, wolf kills have been found in flat or open areas perhaps due to higher detection (McPhee, Webb and Merrill 2012a; Kunkel et al. 2013), or in forested areas where the prey may be more vulnerable (Husseman et al. 2003; Hebblewhite, Merrill and McDonald 2005). Based on snow-tracked kill sites in Montana's Madison Range, Atwood, Gese and Kunkel (2009) suggest the location of kill sites of mule deer was attributed to cougar habitat selection because cougars often selected the same habitats as mule deer, while location of elk

kills was a function of habitat characteristics that increased elk vulnerability at the wolf-elk encounter locations. Kunkel et al. (1999) attributed the inconsistency in expected differences in selection of prey by cougars and wolves consistent with prey body sizes, to the homogenous forests with few openings in Glacier National Park that may have forced wolves to adopt more of a stalking hunting strategy like that of cougars.

Alternatively, wolves may be dominant over cougars and cougars may avoid wolves, implicating interference competition. For example, in Banff National Park cougars waited longer than wolves (66.5 ± 22.9 vs. 27.2 ± 4.1 hrs) to move into areas previously used by wolves than wolves did after cougar use of an area (Kortello, Hurd and Murray 2007). In both Banff National Park and Glacier National Park cougars also scavenged less on wolf kills (0-7 and 3%, respectively) than wolves scavenged on cougar kills (16-33% and 20%) (Kunkel et al. 1999; Kortello, Hurd and Murray 2007). Wolves have also been observed to track cougars, chase and tree them, kleptoparasitize their kills, and kill cougars in the North Fork of the Flathead River in Montana (Polis, Myers and Holt 1989) with few reciprocal interactions noted (Ruth 2004). As a result, wolves may alter the prey killed by cougars where they overlap. In the southern Greater Yellowstone Ecosystem, where elk were the primary prey of cougars, cougars were more likely to kill mule deer than elk as the wolf population increased, and the cougar's proximity to wolves decreased, even though the elk population remained stable (Bartnick et al. 2013). Further, as the wolf population increased and were in closer proximity to cougars, radiocollared cougars killed prey at higher elevations and more north-facing slopes in summer than previously, and winter kill sites were found in areas of more rugged terrain (Bartnick et al. 2013). If hunting patterns of these two species follow the activity patterns of their prey (Beier, Choate and Barrett 1995;

Theuerkauf et al. 2003a), this may intensify wolf-cougar interactions unless they can spatially avoid each other.

Anthropogenic features associated with human disturbance also may contribute to how cougars and wolves interact across sympatric landscapes, but this has received only limited attention (Ruth 2004; Atwood, Gese and Kunkel 2009). Roads can influence the survival and distribution of both these carnivores. For example, cougar mortality from humans, predation or natural/accidental causes, in the Greater Yellowstone Northern Range, increased with increased road density, particularly during the hunting season (Ruth et al. 2011), whereas in southeastern Alaska wolves' risk of fall harvest also increased with road density (Person and Russell 2008). In contrast, in Alberta, wolves travel on linear features including roads, seismic lines and trails and this has been attributed to assisting travel and increasing access to prey (James and Stuart-Smith 2000; Latham et al. 2011a). Further, McKenzie et al. (2012) showed seismic lines could lead to frequent prey encounters, unless prey learned to avoid linear features in response (e.g., caribou (*Rangifer tarandus*) (Dyer et al. 2001; Latham et al. 2011a). Use of linear features also may depend on time of day. In the central east slopes of the Alberta Rocky Mountains, cougars avoided areas of high road density more during the day (Knopff et al. 2014), as did wolves in the Bialowieża Forest, Poland (Theuerkauf et al. 2003b). Cougars and wolves tend to avoid humans (Van Dyke, Brocke and Shaw 1986; Thurber et al. 1994; Whittington, St. Clair and Mercer 2005; McPhee, Webb and Merrill 2012a), but direct comparison of predator responses to humans is difficult without studies in the same areas because they likely depend not only on the density of features but amount of human traffic, cover, and alternative habitat.

Interactions between wolves and cougar also may depend on the age and sex of the individuals, particularly of cougars because they are highly sexually dimorphic in body sizes.

Male cougars weigh approximately 1.4x more than females (Logan and Sweanor 2009) and often kill larger prey than females (Ross and Jalkotzy 1996; Murphy 1998). Small-bodied female cougars are likely more vulnerable to both male cougar and wolf attacks, particularly when kittens are present (Gittleman 1985; Logan and Sweanor 2001; Holmes and Laundré 2006; Knopff et al. 2010; White et al. 2011), which can be year round (Ross and Jalkotzy 1992). Infanticide by male cougars was a major source of kitten mortality in the Greater Yellowstone Northern Range, causing 43% of kitten mortality before wolf reestablishment and 5% during wolf reestablishment (Ruth et al. 2011). Thus, female cougars may shift their distribution to avoid male cougars at the same time as wolves. For example, female cougars with kittens may use forested areas particularly with thick understory to avoid male cougars and wolves (Laing and Lindzey 1991; Holmes and Laundré 2006; Ruth et al. 2011).

In the central east slopes of the Alberta Rocky Mountains, wolf and cougar populations overlap at high densities for Alberta (Webb 2009; Knopff 2010; Robichaud and Boyce 2010; Knopff, Webb and Boyce 2014), but how they coexist in this area has not been thoroughly investigated. In this study, I examined the composition of ungulate prey at cougar and wolf kill sites, and their spatial and temporal movement patterns in an area of high range overlap. I hypothesized that cougars and wolves have distinct patterns of resource use because they kill different prey, select different habitats and/or exhibits different hunting patterns. Additionally, I predicted overlap in the prey species killed would be higher between wolf packs and male cougars than wolf packs and female cougars because of differences in prey body size (Shaw 2009). Specifically, I expected wolves and male cougars to select large prey (elk/moose/horses (*Equus callabus*)) more than female cougars such that the highest overlap in composition of ungulate prey killed would be between wolves and male cougars. I hypothesized that habitat

selection by wolves and male cougars would be more similar than female cougars and wolves because of similar prey selection, and that female cougars would avoid both male cougars and wolves in time and space than other female cougars. I used detailed data from GPS-collared individuals of both species in the same area to test these predictions. I focused on interactions in winter because pack coherence in wolves is greater in winter than summer (Metz et al. 2011), because most young of the year constrain the movements of female cougars less at this time (Murphy 1998; Laundré and Hernández 2007) and because it avoided the complexity of interactions with additional large predators, e.g., grizzly (*Ursus arctos*) and black bears (*U. americanus*). I limited the focus of kill composition to the major ungulate prey species (deer, elk, moose and feral horses) because they comprised the 92-96% of the wolf and cougar diet (Knopff, unpublished data, Merrill, unpublished data). Because wolves were monitored in 2004-2006 and cougars in 2006-2008, I assessed kill composition, overlap and selection of ungulate kills across the 3 years each species was monitored to increase the sample size, but I limited comparisons in space use and temporal movements to the same winter months in the 2006 to control for winter conditions.

STUDY AREA

The study area covers 25,000 km² located on the central east slopes of the Rocky Mountains in Alberta (Fig. 2.1). It lies primarily in Clearwater County west of Rocky Mountain House and is bordered to the west by Jasper National Park and Banff National Park. The topography consists of mountains in the west and foothills to flatlands in the east, providing an east-west gradient in terrain and elevation. The mountains expose bare rock and permanent ice, which cover nearly a quarter of the study area (~23%). The remaining area is dominated by coniferous forest (~52%), which is composed mostly of lodgepole pine (*Pinus contorta*) and

white and black spruce (*Picea glauca*, *P. mariana*). Mixed within the forest are small areas of deciduous trees (~3%), including trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The remainder of the vegetation includes meadows, wetlands, shrubs and treed bogs (~10%). Winters (October – April) are cold with mean daily temperature at the Nordegg station between 2.2 and -9.7°C (Government of Canada 2014). Snow comes as early as September with monthly snowfall averages (September – May) between 5.7 and 27.6 mm. Forestry and oil and gas industries are prominent in the area, and have created cut blocks (~6% of study area), roads, seismic lines and well sites for over 28,000 km of linear clearings (Frair et al. 2005). Recreational activities such as camping, snowmobiling, motorbikes, all-terrain vehicles, and off road all-terrain vehicles also occur.

Wolves historically were present in the study area, but were reduced soon after European settlement with a bounty program in the early 1900s and poisoning programs to reduce rabies in the 1950s and early 1960s, with localized wolf control continuing until 1966 (Alberta Forestry, Lands, and Wildlife 1991). During the study, wolves were harvested with no quotas via trapping from 1 October – 31 March and hunting from 25 August – 31 May in most of the area, with hunting until 15 June in some areas. Residents could hunt wolves on public land without a license during the hunting season and year-round on or near (within 8 km) private lands (Webb, Allen and Merrill 2011). An average of 0.97 – 2.2 wolves/100 km² were estimated in the study area during the study with 3-17 wolves per pack (mean 7.76 ± 2.8 wolves) (Webb, Hebblewhite and Merrill 2008; Webb 2009; Webb, Allen and Merrill 2011; McPhee, Webb and Merrill 2012b). Growth of cougar populations in Alberta over the last century are not as well documented as wolves (Alberta Forestry, Lands, and Wildlife 1992), but in the last two decades, cougar numbers have increased and their range has expanded from the southwestern part of

Alberta further north and east (Knopff, Webb and Boyce 2014). Cougars in the study area were managed as a big-game species and hunted with the use of dogs from 1 December - 28 February, unless the quota of 10% was filled early (Ross, Jalkotzy and Gunson 1996; Knopff, Knopff and Boyce 2010). Cougar densities were estimated at 2.67-3.49 cougars/100km² (Knopff 2010).

The primary ungulate prey are white-tailed and mule deer (0.61 ± 0.06 deer/km²), elk (0.28 ± 0.17 elk/km²), moose (0.24 ± 0.04 moose/km²), and feral horses (0.10 ± 0.02 horse/km²), with the relative abundances as reported by McPhee, Webb and Merrill (2012b). Other ungulates available include bighorn sheep and mountain goats (*Oreamnos americanus*). Other carnivores in the area include bobcat (*Lynx rufus*), lynx (*L. canadensis*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), and black bears and grizzly bears.

METHODS

Animal Capture and Collaring

Details of wolf and cougar capturing and handling are described in Webb, Hebblewhite and Merrill (2008) and Knopff et al. (2010). Briefly, 28 wolves in 14 packs were captured during 2004 to 2006 using net gunning from a helicopter in the winter and modified foot-hold traps in the summer (University of Alberta Animal Care Protocols No. 391305, 353112, and 411601). Wolves were collared with either a Lotek 3300Sw store-on-board or a 4400S remote-downloadable GPS collar (Lotek Engineering, Newmarket, Ontario, Canada) with fixes occurring at 2-hr intervals between 15 October and 14 April. Only one GPS collar from a single wolf provide locations at any given time from a pack. Pack sizes ranged from 4 – 14 wolves per pack, with > 70% of the packs having between 5 -7 wolves. In 2005 to 2008, 12 male cougars and 27 female cougars were treed by hounds and then immobilized via remote injection with

Telazol and Xylazine (University of Alberta Animal Care Protocol no. 479505). Cougars were collared with Lotek 4400S GPS radio collars set to collect locations at 3-hr intervals during the winter between 15 October and 14 April. Of the male cougars, 6 were adults at the time of capture and 6 were sub-adults (dispersed from mother to > 2.5 – 3 years of age (Knopff, Knopff and Boyce 2010)). Of the female cougars, 22 were adults at the time of capture and 5 were sub-adults with at least 52% having kittens with them at some point during the study, while at least 63% were solitary at some point during the study.

Composition, Overlap and Selection of Ungulate Kills

Composition, overlap and selection of ungulate kills were based on identifying ungulate prey at kill sites from 12 of the 14 wolf packs and the 27 female cougars and 12 male cougars. Kills were distinguished from scavenging events using signs of cougar or wolf predation, including chase or struggle, disarticulated carcasses, arrow or bullet wounds, dumped by humans at a trapper bait station or livestock dump site (Knopff, Knopff and Boyce 2010; McPhee, Webb and Merrill 2012a). Scavenging events were rare (15% of cougar kills, (Knopff, Knopff and Boyce 2010; Knopff et al. 2010) and < 3% of wolf kill clusters were scavenging events (Webb, Hebblewhite and Merrill 2008)) and were omitted from my analyses.

For the majority of wolf kills (n = 92), a space-time permutation scan statistic (STPSS) with cluster definition constrained to within 300 m and 4 days was used in SaTScan to identify potential kill clusters from telemetry locations (Kulldorff et al. 2005) and clusters were then visited to verify kill sites following Webb, Hebblewhite and Merrill (2008). Additional wolf kills (n = 70) by known packs were found using snow-tracking, aerial observations or opportunistically (Webb, Hebblewhite and Merrill 2008). Before 1 November 2007, cougar kill

sites ($n = 239$) were determined by visiting clusters of ≥ 2 telemetry locations within 200 m and 6 days of each other following (Knopff et al. 2009). After 1 November 2007, cougar kill sites ($n = 143$) were visited based on outcomes of logistic regression modeling that predicted kill presence (Knopff et al. 2009). Additional cougar kills ($n = 18$) by known cougars were found by opportunistic snow-tracking during the study. I conducted pairwise comparisons between predator groups to determine differences in the proportion of each prey species made by each individual animals using a Mann-Whitney U-test in R statistical software (R Core Team 2013).

I pooled the number of ungulate kills from each predator group to determine the percent overlap in the types of kills by the predators using Schoener's overlap index (Schoener 1970):

$$O_{jk} = 100 * \left(1 - \frac{1}{2} \sum (p_{ji} - p_{ki})\right) \quad (1)$$

where O is the percent overlap in the prey killed by predators j and k , based on the proportions, p , of prey species i found at their kill sites, ranging from 0 to 100%. I followed Wallace (1981) and used an overlap score of $> 60\%$ to indicate biologically meaningful overlap (Wallace 1981), while values of $> 75\%$ defined high overlap (Pedersen 1999).

I determined the selection ratio (w_i , Manly, McDonald and Thomas 2002) for each ungulate prey species for each GPS-collared individual predator using the proportional frequency of deer, elk, moose and horses in the winter kills of the predator (% use) and the proportional availability (% available) within the predator's individual 100% MCP home range. Relative abundance of prey within a home range was based on spring pellet group counts along 372 1-km x 2-m transects corrected for detection, interpolated across the study area, and converted to density of animals based on the ratio of pellet counts to number an animals counted in an aerial survey of a unit (see details in McPhee, Webb and Merrill 2012b). I compared the mean w_i for

each prey species between each pair of predator groups using a Mann-Whitney U-test with R statistical software (R Core Team 2013).

Habitat Selection and Spatio-temporal Avoidance

To assess space use, I tested whether predators avoided each other in space or selected different habitats on the landscape. For the habitat selection analyses I used a subset of 10 of the 14 GPS-collared wolf packs, 5 male cougars and 10 female cougars monitored during the same winter periods of January – April 2006 and October – December 2006. I compared habitat selection between wolves and male cougars and wolves and female cougars based on latent selection difference functions (LSDFs) (Czetwertynski 2008; Latham, Latham and Boyce 2011). I used this approach because wolves and cougars had high home range overlap and the means of habitat features within individual home ranges of predator groups did not differ across predator groups (Appendix II).

I compared selection of habitat features by male cougars (1) to selection by wolves (0), female cougar selection (1) to selection by wolves, and female cougar selection (1) to selection by male cougars. Rather than using model selection, I evaluated full models for both daytime and nighttime because habitat features that cougars and wolves select for in this area are known (McPhee, Webb, Merrill 2012a; Knopff et al. 2014) and my objective was to contrast differences between the species. All habitat variables were measured with a 500-m circular buffer around a 30 x 30 m pixel containing the GPS location of the predator. Habitat variables included in the model were terrain ruggedness based on a 30 m DEM (McPhee, Webb and Merrill 2012b), south aspect (proportion of slopes 135-225°), proportion of forest, residuals of density of forest edge (km/km²) regressed on proportion of forest, density of roads (km/km²), seismic lines (km/km²),

wells (# wells/km²), and the abundance (# of individual prey/buffer circle) of deer, elk, moose and horses. I used a circular buffer with a radius of 500 m because the female cougar step length, the predator group with the shortest average step length, averaged 532 m.

Landcover and density of roads, seismic lines and wells were mapped in GIS to a 30 m x 30 m resolution cover map developed using Indian Radar Satellite Imagery (Frair et al. 2005). Forest cover (1) included all coniferous and deciduous forest, and non-forest (0) was any other land cover class. Forest edge density was determined as the total length of forest edge in the buffer (km/km²). Forest edge length was determined using a Geospatial Modelling Environment (Beyer 2012). Residuals of forest edge density regressed on the proportion of forest was used to control for the relationship between amount of forest and forest edge because the two metrics are not independent (McGarigal and McComb 1995). Prey availability in the buffer was determined as described above. All landscape variables were uncorrelated ($r < |0.6|$).

I tested for differences in availability of landscape features by first averaging each landscape feature in the home range of each individual predator, and then used MANOVA with R statistical software (R Core Team 2013) to pairwise compare availabilities between wolf packs, male cougars and female cougars (Appendix II). Across landscape features there were no differences in the mean availabilities between wolves and male cougars (MANOVA, $F = 0.60$, $P = 0.77$), wolf packs and female cougars (MANOVA, $F = 0.57$, $P = 0.81$) and female cougars and male cougars (MANOVA, $F = 0.42$, $P = 0.86$), justifying the use of the latent selection difference function (LSDF) approach (Czetwertynski 2008) to assess habitat selection.

I used logistic regression to derive the sex-specific LSDFs for both day (0600 – 1600) and night (1800 – 0400) to predict the probability of a landscape variable, given the other

variables in the model, being selected by each sex of cougars (1) relative to wolves (0), and to assess female cougars (1) relative to male cougars (0) as a function of landscape features:

$$s(x) = \left(\frac{P(\text{male cougar})}{P(\text{wolf pack})} \right) = \exp(\beta_{1x1} + \beta_{2x2} + \dots + \beta_{nxn}) \quad (2)$$

$$s(x) = \left(\frac{P(\text{female cougar})}{P(\text{wolf pack})} \right) = \exp(\beta_{1x1} + \beta_{2x2} + \dots + \beta_{nxn}) \quad (3)$$

$$s(x) = \left(\frac{P(\text{female cougar})}{P(\text{male cougar})} \right) = \exp(\beta_{1x1} + \beta_{2x2} + \dots + \beta_{nxn}) \quad (4)$$

where $s(x)$ is the relative selection, x_i are the landscape variables, and β_i s are coefficients that reflect the relative difference in selection between wolves and for that variable, given all other variables in the model (Czertwytynski 2008; Latham, Latham and Boyce 2011). Huber-White sandwich estimators were used to estimate the standard errors clustered by individual using R statistical packages lme4 and sandwich (R Core Team 2013).

Because LSD does not reflect the actual avoidance of an area, but the selection of a type of habitat, I conducted a second analysis directed at actual avoidance of other animals. For this analysis I calculated pairwise distances between all GPS-collared wolf and cougar individuals that were monitored during same winter periods and were neighbours, as their 100% MCP home ranges overlapped (Appendix II). I used contrasts from 10 female cougars, 5 male cougars and 11 wolf packs monitored during January – April 2006 and October – December 2006. I derived the distance between each pair at each time they had a temporally matching (within 5 minutes) GPS location. Mann-Whitney U-tests were used to compare pairwise the distances between female cougars – female cougars, male cougars – male cougars, wolf packs – wolf packs, female cougars – wolf packs, male cougars – wolf packs, and female cougars – male cougars. Mann-Whitney U-tests were used to compare whether spatio-temporal avoidance differed between predator groups during the daytime (0600 – 1700) and nighttime (1800 – 0500).

Hourly Movement Patterns

I used the straight line distance between two consecutive GPS locations divided by the fix rate (2 hr for wolves; 3 hr for cougars) from 10 female cougars, 5 male cougars and 11 wolf packs monitored during January – April 2006 and October – December 2006. I tested for differences in the average movement rate of individuals for each predator group as the mean of all the individuals' average movement rates in a predator group paired by each hour. Movement rates were tested pairwise between the predator groups for differences using Wilcoxon signed-rank tests in R statistical software (R Core Team 2013) paired by hour. Movement patterns of predators were analysed by standardizing values to the mean movement using z-scores over the 24-hr period within each predator group and then testing pairwise for day (0600 – 1700) and for night (1800 – 0500), as well as between day and night for the same predator group using Mann-Whitney U-tests in R statistical software.

RESULTS

Composition, Overlap and Selection of Ungulate Kills

Deer comprised the largest percent of the ungulate prey at the kill sites of all 3 predator groups with deer comprising 45% more of the kills made by female cougars than wolves and almost 25% more than male cougars (Table 2.1). In contrast, large prey including moose and horses were found approximately 18% more at wolf kill sites than female cougar kill sites and approximately 10% more at male cougar kill sites than female cougar kill sites. Male cougars did not kill different proportions of elk than female cougars or wolf packs, but wolf packs did kill more elk than female cougars. As a result, there was higher overlap (87.5%) in ungulate prey

killed by wolf packs and male cougars than overlap between female cougars and male cougars (66.9%) and female cougars and wolf packs (61.9%).

Female cougars selected for deer (selection ratio > 1 , $P < 0.05$) no more or less than male cougars but more than wolf packs (1.7x), which do not select or avoid deer (Table 2.2). All three predator groups avoided killing moose (selection ratio < 1 , $P < 0.05$), but both male and particularly female cougars avoided killing moose more than wolves, whereas both male cougars and wolves selected for horse more than female cougars with no observed case of a female cougar killing a horse during this study. All of the predator groups appeared to kill elk in proportion to their abundance in the environment.

Habitat Selection

Female cougar selection of habitats relative to male cougars and wolves was consistent between day and night (Table 2.3, 2.4). Females selected for forest edge more than males, but did not select for areas of high deer densities in forest edge as strongly as males and wolves (Appendix II), and did not select for areas of abundant elk as strongly as males and wolves except when associated with forested areas. During the day, females also avoided areas of high horse density in forested areas more than males (Table 2.3).

Male, but not female, cougars showed consistently stronger selection for rugged terrain than wolves during both day and night (Table 2.4, 2.5). Male cougars differed in their habitat selection from wolves more at night than during the day, selecting for areas of high elk density at night, particularly when associated with either high forest edge or low amounts of forest (Appendix II). Further, compared to wolves, male cougars at night selected areas of low horse

density, particularly when it was associated with low forest edge; however, males selected for high horse density in highly forested areas.

Spatio-temporal Avoidance

Of the collared animals monitored during winter 2006, wolf packs had the highest spatio-temporal distances between conspecifics (Fig. 2.2, Appendix II). The average pairwise distances between wolf packs was 1.6x greater than the distances between female cougars and wolves ($P < 0.01$) and 1.3x greater than the distance male cougars and wolf packs ($P = 0.067$). In contrast, there was no evidence that female and male cougars distanced themselves within or between the sexes. Further, there was no evidence that either female or male cougars avoided wolves more than other cougars. These patterns were consistent between day and night (Table 2.6).

Hourly Movement Patterns

Overall wolves were the most active during a 24-hr period, moving on average 2.3x farther than male cougars ($P < 0.001$) and 3.1x farther than female cougars ($P < 0.001$), and male cougars moved on average 1.4x farther than female cougars ($P < 0.01$). All three predator groups displayed clear daily movement patterns with wolves exhibited a strong bimodal movement pattern distinct from the cougars with movement peaks in the late morning (1000) and in the evening (2000), and inactive periods between 0400 – 0600 and 1300 – 1600 (Fig. 2.3). Female cougars had relatively more of their movements during the day (0600 – 1700) than male cougars ($P < 0.01$) but less than male cougars during the night (1800 – 0500) ($P < 0.05$) (Appendix II). Male cougars moved more during the night than day ($P < 0.001$), while both wolves ($P = 0.06$) and female cougars ($P = 0.32$) did not.

DISCUSSION

In the central east slopes of Alberta, space use by wolves was strongly influenced by intraspecific pack interactions, whereas cougars did not avoid wolves more than other conspecifics, contrary to my hypothesis. Wolf packs actively defend their territories to the degree that wolf mortalities have been documented near the borders of their territories (Mech 1994). When densities of packs increase, there is more potential for intraspecific conflict. For example, Kauffman et al. (2007) demonstrated that as the number of wolf packs doubled over the 10 years following wolf reintroduction on the Northern Range of Yellowstone National Park, there was more than 4x as many interpack aggressive conflicts. Territorial behaviour in wolves is assumed to have evolved, in part, to partition prey (Carbyn 1981), and movement models show that scent marking by wolves may be a major mechanism by which wolves shift territory boundaries to avoid direct aggression (White, Lewis and Murray 1996). However, in a review of home range sizes, only 33% of the variation in size was due to variation in prey biomass (Fuller, Mech and Cochrane 2003) indicating that other factors, such as interspecific strife may influence territory size. In western Montana, Rich et al. (2012) reported that wolf pack territory size decreased by 33 km² with every additional surrounding pack per 1000 km². On the Kenai Peninsula, Alaska, Peterson, Woolington and Bailey (1984) reported that as territory size decreased with pack size, spatial openings initially formed creating potential areas with little predation until new packs formed (White, Lewis and Murray 1996).

Lack of evidence for cougars spatio-temporally avoiding wolves more than conspecifics that I found is consistent with cougars in Banff National Park, where cougars were not found further from wolves within a 2-hour period than random based on non-temporally matching fixes

(Kortello, Hurd and Murray 2007). Because male cougars are territorial towards other male cougars and show little home range overlap (Ross and Jalkotzy 1992; Spreadbury et al. 1996; Logan and Sweanor 2009), male cougars may not be able to avoid wolves any more than other males with this area having high wolf (0.97 – 2.2. wolves/100 km² (Webb 2009)) and cougar (2.67 – 3.49 cougars/100 km² (Knopff 2010)) densities (compare wolf densities of 1.1 and 1.2 wolves/100 km² elsewhere in Alberta (Fuller and Keith 1980; Kuzyk 2002), and ~0.13, 0.19 and 0.22 wolves/100 km² in Northwestern Montana, Greater Yellowstone Area and central Idaho, respectively (Bangs et al. 1998) and cougar densities of 0.5 cougars/100 km² in southern Utah (Hemker, Lindzey and Ackerman 1984) and 2 – 3.1 cougars /100 km² in southeastern Idaho and northwestern Utah (Holmes and Laundré 2006). In contrast, female cougars presumably avoid males because males can be infanticidal (Ross and Jalkotzy 1992; Logan and Sweanor 2001; Cooley et al. 2009; Ruth et al. 2011). I found only weak evidence for female cougars avoiding wolves and male cougars more than female conspecifics (Fig. 2.2). However, only 2 of the 11 female – male cougar pairs and 4 of the 17 female cougar – wolf pairs were ever found within 1 km, and this included less than 14 % of the female – male cougar observations, and less than 2% of the female cougar – wolf observations. In contrast, 1 of 5 female pairs were found within 1 km, and at one point were < 6 m apart and stayed in close proximity as long as a week. Similar to my results, female cougar home ranges overlapped in Utah, but the individuals were rarely close in space, with two females only recorded within 1 km of each other 4 times, and any cougar associations with other cougars occurred only during < 2% of relocations, which included 6 apparent mating sessions (Hemker, Lindzey and Ackerman 1984). Because of infanticidal males and because cougars will breed year round (Ross and Jalkotzy 1992; Quigley and Hornocker 2009), females without kittens are less likely to avoid males. Unfortunately, without the

knowledge of the date of kitten births or observing kittens, I was unable to confidently separate the fixes for females with and without kittens for my spatio-temporal avoidance analyses.

Wolves and cougars also showed distinct movement patterns that may be related to the spatio-temporal avoidance patterns I observed. Wolves moved farther and exhibited a definitive bimodal movement pattern while both male and female cougars exhibited a less pronounced unimodal pattern with male cougars more active at night than females. Similar crepuscular bimodal patterns by wolves have been noted (Vilà, Urios and Castroviego 1995; Merrill and Mech 2003; Theuerkauf et al. 2003a). Two female cougars in Florida had their highest movements between 1600 and 2100 and 1800 and 2400h, though they also had with arrivals and departures from their dens at both crepuscular periods (Maehr et al. 1989), rather than just dusk as my results would predict. In the Santa Ana Mountains in California, cougars also showed peak movement at dusk, but the researchers did not address the difference between males and females, though of the 16 females and 10 males, only 4 females did not show a tendency towards nocturnal and crepuscular movements (Beier, Choate and Barrett 1995). These latter patterns of cougar movements were determined based on GPS locations every 15 minutes indicating that because I found similar results with GPS fix rates of 3 hours, the fix rates I used are frequent enough to exhibit these differences.

I suggest that the distinction between wolf and cougar movement patterns may be related to different hunting tactics and social structures, as well as dominance by wolves. The movement data support the notion that compared to cougars, wolves are cursorial hunters (Kunkel et al. 1999; Husseman et al. 2003; Atwood, Gese and Kunkel 2007) because on average they moved 1.5 – 4.6x farther than cougars in any hour of the day or night. Increased predator movements have the potential to increase prey encounter rate (McKenzie et al. 2012). Both wolves and

cougars have increased success at killing prey when moving, as wolves killed 1.8 times more often than expected during crepuscular hours (Theuerkauf et al. 2003a), and cougars moved more right before a kill, as their winter movement rates were highly correlated ($R = 0.93$) with kills (Knopff 2010). Additionally, cougar movements were 40% longer when kills were made than during the average search movement (Knopff 2010). The difference in movement rates I found also is consistent with lower mean time to kill by wolves (118 ± 14 h [mean \pm SE] for small ungulates; 126 ± 18 h for large ungulates, $n = 6$ wolves in different packs) (McPhee, Webb and Merrill 2012a) than cougars (159 ± 207 h [mean \pm SD], $n = 27$ cougars) for all ungulates (Knopff et al. 2010) in this study area.

The movement pattern differences are also likely a reflection of social structure and associated energetic demands. Wolf packs are cohesive in winter (Metz et al. 2011) and the large sizes of packs reported for this study area (mean 7.76 ± 2.8 wolves) (Webb, Allen and Merrill 2011) may require killing larger prey or killing small prey more often than small packs (Ballard, Whitman and Gardner 1987; Jędrzejewski et al. 2002) and thus also solitary cougars. This is consistent with the negative relationship between pack size and kill rate (Ballard, Whitman and Gardner 1987) and implies that individual wolves in large packs likely are afforded less on a per individual basis as pack size increases. For example, in the Yukon, individuals in small packs were estimated to have 6.4 ± 0.8 kg/wolf daily and large packs had 4.1 ± 0.9 kg/wolf daily (Hayes et al. 2000). Given that inconspicuous deer comprise ~50% of the diet of wolves in this area, one further way to improve hunting success may be to hunt prey when they are most active (Clark 1994; Sih, Englund and Wooster 1998; Visscher 2010). Ungulates feed most actively at dawn and dusk (Collins, Urness and Austin 1978; Lowe, Patterson and Schaefer 2010; Robinson,

Hebblewhite and Merrill 2010), which roughly match the temporal peaks in wolf movement rates that I found.

As a solitary predator, cougars may on average have lower energetic requirements per hunting group (e.g., single cougar or female with kittens) than large wolf packs. Within cougars, the ~40% larger body size of male cougars than females and their associated energetic requirements (Laundré 2005) likely contribute to the higher movement rates by males than females that I observed. The reason why cougars tend to move less during the early period of ungulate activity in contrast to wolves is unclear. Their sit and wait strategy coupled with a stronger reliance on selecting habitats where they are successful at killing prey may make this a successful hunting tactic, particularly for male cougars who appear to hunt and potentially position themselves more during the darkness. In contrast, females moving less at night may reflect avoidance of wolves, but more particularly avoidance of male cougars. Because females with kittens face a greater energetic challenge, they may need to extend feeding times, increasing the risk of encountering males. Although, Hemker, Lindzey and Ackerman (1984) found solitary females move farther net distances than females with young kittens (0.3 – 10.8 km and 0.0 – 4.5 km, respectively, $P < 0.05$) and that the net displacement of cougars with kittens increased as the kittens got older. Additionally, in Idaho movements of females with kittens peaked between 1600-2200 and were away from their kittens > 80% then, whereas the time they spent with their kittens corresponded to their lowest movement rates (Laundré and Hernández 2008), indicating maternal protection.

Stronger habitat selection by cougars relative to wolves may reinforce the effectiveness of their hunting strategies and may facilitate the coexistence of wolves and cougars in the same landscape. Compared to cougars, I found wolves were less selective of habitat features than of

prey density. For example, wolves selected areas of high density elk at both night and day relative to female cougars, whereas compared to male cougars wolves selected areas of high density of horses at night, particularly near forest edges. In my study area, wolves concentrated their hunting in areas of high small and large ungulate density within their home range (McPhee, Webb and Merrill 2012b). However, wolves killed more large-bodied prey in the open, as well as further from well sites, and near natural edges than at random. In Yellowstone National Park, Bergman et al. (2006) concluded that wolves select where to both travel and kill based on factors influencing vulnerability of elk, such as proximity to edges and habitat class, and less so on elk density. Further, for an area south of my study area in the Alberta Rockies, Alexander, Logan and Paquet (2006) similarly indicated that cougar habitat use in winter fluctuated with their prey species (deer and elk), whereas wolves were consistently and positively correlated with elk and deer.

Cougars, relative to wolves, selected more for landscape features such as terrain ruggedness and there was some evidence for forest edges as well, which may facilitate successful prey capture in these areas. Knopff et al. 2014 showed cougars in this area have high selection for edge habitat and hypothesized these areas provide optimal foraging for cougars when humans are absent. Cougar selection for edge is consistent with the hunting behavior of cougars in Idaho where cougars killed prey more often at forest edges and less in the forest (Holmes and Laundré 2006). Cougars also may select these areas to avoid wolves. For example, in the Greater Yellowstone Ecosystem, cougars killed prey in more rugged terrain when wolf density increased and proximity to wolves decreased, suggesting the use of rugged terrain as an avoidance tactic (Bartnick et al. 2013). Additionally, the use of more rugged terrain by cougars compared to wolves has been reported several times in sympatric cougar and wolf study areas (Ruth et al.

2003; Alexander, Logan and Paquet 2006; Kunkel et al. 2013). Rich et al. (2012) suggest that rugged terrain decreases wolf hunting success because as coursing predators they need relatively flat land to run down prey, a habitat necessity not required for a stalk and ambush predator. In my study area, the risk of wolves killing a deer was lower when they moved through rugged terrain ($P < 0.05$) (McPhee, Webb and Merrill 2012a). Thus, selecting for prey in different areas may allow male cougars and wolves to exploit the same prey species across broad areas because of the differences in hunting tactics. I did not find any strong selection differences for cougar and wolf use of anthropogenic features, consistent with previous studies showing both cougars and wolves avoid humans more during the day than night (Hebblewhite and Merrill 2007; Robinson, Hebblewhite and Merrill 2010; Knopff et al. 2014). Both cougars and wolves are more tolerant of humans when they live in rural areas compared to wilderness areas (Thiel, Merrill and Mech 1998; Hebblewhite and Merrill 2007; Knopff et al. 2014).

The most pronounced differences in fine-scale habitat selection were between female and male cougars and these differences were consistent across the day and night. I interpreted these differences largely as females avoiding male cougars but in some cases this may also have led to avoiding wolves. For example, females selected more strongly for edges while avoiding areas of high elk densities, relative to both male cougars and wolves. Selection for forest edges or frequent kills at edges occur in this study area and others (Laundré and Hernández 2003; Holmes and Laundré 2006; Knopff et al. 2014). However, I also found several habitat X prey density interactions indicating that male and female cougars altered their prey density selection contingent on habitat conditions. Although males selected for more high elk areas, they selected for areas of high density elk when forest cover was low, potentially reflecting a poor ability of cougars to encounter prey in forested areas similar wolves (Hebblewhite, Merrill and McDonald

2005) or because females choose to hunt in the forest for protection of kittens (Holmes and Laundré 2006). Males, did however, select more for high horse density in forested areas than females during the night, perhaps because horses are less able to flee in the forest (Goodwin 2002). In contrast, female cougar selection for edge was less than males when deer densities were high, implicating females were less constrained by habitat features when there is an abundance of prey.

Consistent with my hypotheses based on body size differences, there was more overlap in the prey killed by wolves and male cougars than wolves and female cougars that also were generally consistent with hunting tactics and habitat selection. For all of the predators, deer comprised the largest number of kills, which reflects their high densities in the study area relative to other prey species (McPhee, Webb and Merrill 2012a). Wolves killed deer in proportion to their abundance, consistent with their coursing hunting tactic, where they are likely to kill what they encounter, particularly when more vulnerable than other available species like moose (Mech 1966). In contrast, female cougars killed small-bodied deer, which is consistent with my interpretation of them not needing to use edge when hunting for an abundant species. All three predator groups killed elk equal to their availability, whereas male cougars and particularly wolves selected to kill large-bodied moose and horses relative to females. Because of high overlap in what male cougars and wolves kill, differences in where the two species are most efficient in killing prey and their fine-scale habitat selection differences may be key to their coexistence. As such, MCPhee et al. (2012a) found wolf time to kill for deer to decrease in areas of rugged terrain and close to well sites. Similarly, although Knopff (2010) found cougar sex, age and weight best predicted cougar consumption rates, there was evidence that a competing

model, that included those cougar characteristics plus density of linear features, proportion of edge habitat and proportion of open habitat, also predicted cougar consumption rates.

In conclusion, I submit that niche separation of cougars and wolves is realized in the central east slopes of the Rocky Mountains, where there is a diversity ungulate prey. The different hunting strategies, prey body sizes and landscape features in the area have led to these species, as well as the different sexes of the cougars, exploiting different areas and prey during winter. While I did not find that cougar and wolves physically avoid each other more than conspecifics, differences in their temporal movement patterns and local habitat selection promote their coexistence. Highest potential dietary overlap in prey appears to be between male cougars and wolves, which previous studies have not documented. However, because male cougars and wolves select different types of habitats, particularly at night, to hunt, they may be minimizing encounters with one another. Killing in different areas affords cougars and wolves greater overlap in the prey species they kill.

Table 2.1. Winter percentage of deer (*Odocoileus virginianus*, *O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*) and feral horse (*Equus caballus*) in the ungulate kills made by individual female cougars (*Puma concolor*) and male cougars in 2006-2008 and wolf (*Canis lupus*) packs in 2003-2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Predator		Prey			
		Deer	Elk	Moose	Horse
Female cougar	Mean	93.6%	5.56%	0.79%	0.00%
	SD	13.7%	13.5%	3.30%	0.00%
Male cougar	Mean	69.8%	9.49%	11.3%	9.47%
	SD	26.3%	16.0%	21.1%	22.3%
Wolf pack	Mean	49.0%	14.6%	18.9%	17.6%
	SD	24.9%	19.7%	14.2%	32.3%
Female cougar – Wolf pack	<i>P</i> -value	< 0.001	< 0.05	< 0.001	< 0.001
Male cougar – Wolf pack	<i>P</i> -value	0.10	0.38	0.11	0.14
Female cougar – Male cougar	<i>P</i> -value	< 0.01	0.50	< 0.05	< 0.05

Note: *P* values are the result of testing for differences between predator groups using a Mann-Whitney U-test.

Table 2.2. Winter selection ratios for deer (*Odocoileus virginianus*, *O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*) and feral horse (*Equus caballus*) based on the percent of the prey genera found in the ungulate kills made by individual female cougars (*Puma concolor*) and male cougars in 2006-2008 and wolf (*Canis lupus*) packs in 2003-2006 divided by the percent of the genera available in their home range in the central east slopes of the Alberta Rocky Mountains, Canada

Predator		Prey			
		Deer	Elk	Moose	Horse
Female cougar	Mean	1.62*	1.04	0.03*	0.00
	SD	0.37	2.49	0.12	0.00
Male cougar	Mean	1.28	0.89	0.39*	1.10
	SD	0.46	1.53	0.74	2.57
Wolf pack	Mean	0.94	1.10	0.68*	1.59
	SD	0.46	1.33	0.48	2.36
Female cougar – Wolf pack	<i>P</i> -value	< 0.001	0.14	< 0.001	< 0.001
Male cougar – Wolf pack	<i>P</i> -value	0.16	0.43	0.10	0.23
Female cougar – Male cougar	<i>P</i> -value	0.07	0.72	< 0.05	< 0.05

Note: *P* values are the result of testing for differences between predator groups using a Mann-Whitney U-test.

*Indicates values whose 95% confidence limits do not include 1.

Table 2.3. Relative habitat selection during the day (0600 – 1600) and night (1800 – 0400) between female cougars (*Puma concolor*) (1) and male cougars (0) in winter 2006 using a latent selection difference function model in the central east slopes of the Alberta Rocky Mountains, Canada.

Variable	Day			Night		
	β	<i>SE</i>	<i>P</i>	β	<i>SE</i>	<i>P</i>
(Intercept)	0.281	2.174	0.897	2.239	2.484	0.367
Ruggedness	-0.025	0.015	0.100	-0.021	0.014	0.141
Aspect	0.000	0.001	0.513	0.000	0.001	0.930
Forest	0.003	0.003	0.255	0.001	0.003	0.825
Forest edge	0.494	0.180	0.006	0.404	0.203	0.047
Seismic lines	-0.032	0.125	0.798	-0.065	0.112	0.566
Wells	-0.103	0.140	0.465	-0.022	0.156	0.889
Roads	0.110	0.207	0.595	0.071	0.134	0.600
Deer	2.927	2.701	0.279	0.609	3.419	0.859
Elk	-34.293	7.194	< 0.001	-37.046	9.148	< 0.001
Moose	3.710	4.741	0.434	2.920	4.474	0.514
Horse	22.669	13.286	0.088	11.019	13.084	0.400
Deer X forest edge	-1.148	0.237	< 0.001	-1.022	0.326	0.002
Elk X forest edge	0.908	0.813	0.264	-0.140	0.970	0.885
Moose X forest edge	0.123	0.308	0.690	0.157	0.352	0.656
Horse X forest edge	0.308	0.678	0.650	0.501	0.741	0.499
Deer X forest	-0.004	0.004	0.219	-0.002	0.004	0.691
Elk X forest	0.045	0.008	< 0.001	0.051	0.012	< 0.001
Moose X forest	-0.005	0.005	0.295	-0.005	0.005	0.317
Horse X forest	-0.033	0.014	0.022	-0.019	0.014	0.190

Note: bolded values indicate significance

Table 2.4. Relative habitat selection during the day (0600 – 1600) and night (1800 – 0400) between female cougars (*Puma conolor*) (1) and wolves (*Canis lupus*) (0) in winter 2006 using a latent selection difference function model in the central east slopes of the Alberta Rocky Mountains, Canada.

Variable	Day			Night		
	β	<i>SE</i>	<i>P</i>	β	<i>SE</i>	<i>P</i>
(Intercept)	-1.544	2.092	0.461	-0.436	2.108	0.836
Ruggedness	0.005	0.014	0.738	0.010	0.015	0.520
Aspect	0.000	0.001	0.858	0.000	0.001	0.793
Forest	0.001	0.002	0.648	0.000	0.002	0.899
Forest edge	0.323	0.194	0.097	0.308	0.208	0.139
Seismic lines	0.051	0.141	0.719	0.017	0.138	0.901
Wells	-0.078	0.130	0.546	-0.043	0.111	0.697
Roads	0.188	0.100	0.061	0.054	0.092	0.556
Deer	2.308	3.071	0.452	1.440	3.382	0.670
Elk	-12.236	5.532	0.027	-14.476	5.987	0.016
Moose	3.613	2.994	0.228	2.062	2.631	0.433
Horse	-7.259	7.225	0.315	-9.113	7.266	0.210
Deer X forest edge	-0.493	0.234	0.035	-0.553	0.265	0.037
Elk X forest edge	0.844	0.732	0.249	0.767	0.795	0.335
Moose X forest edge	0.116	0.303	0.701	0.212	0.276	0.443
Horse X forest edge	-0.794	0.496	0.109	-0.749	0.508	0.140
Deer X forest	-0.003	0.003	0.423	-0.002	0.004	0.688
Elk X forest	0.013	0.007	0.055	0.016	0.008	0.050
Moose X forest	-0.004	0.003	0.236	-0.002	0.003	0.541
Horse X forest	0.006	0.008	0.409	0.009	0.008	0.251

Note: bolded values indicate significance

Table 2.5. Relative habitat selection during the day (0600 – 1600) and night (1800 – 0400) between male cougars (*Puma concolor*) (1) and wolves (*Canis lupus*) (0) in winter 2006 using a latent selection difference function model in the central east slopes of the Alberta Rocky Mountains, Canada.

Variable	Day			Night		
	β	<i>SE</i>	<i>P</i>	β	<i>SE</i>	<i>P</i>
(Intercept)	-3.901	2.333	0.094	-4.362	2.352	0.064
Ruggedness	0.025	0.009	0.006	0.031	0.011	0.007
Aspect	0.000	0.000	0.513	0.000	0.001	0.742
Forest	0.001	0.002	0.705	0.001	0.003	0.643
Forest edge	0.167	0.213	0.433	0.125	0.213	0.558
Seismic lines	0.017	0.120	0.888	0.049	0.110	0.659
Wells	-0.121	0.224	0.588	-0.145	0.264	0.582
Roads	0.092	0.186	0.619	-0.025	0.125	0.843
Deer	3.546	3.213	0.270	4.743	3.176	0.135
Elk	3.722	3.337	0.265	10.585	3.220	0.001
Moose	-0.023	3.302	0.994	-1.723	3.039	0.571
Horse	-12.833	7.795	0.100	-13.080	4.852	0.007
Deer X forest edge	0.101	0.254	0.690	0.223	0.256	0.382
Elk X forest edge	0.604	0.469	0.198	1.058	0.367	0.004
Moose X forest edge	-0.367	0.285	0.198	-0.319	0.188	0.090
Horse X forest edge	-0.877	0.493	0.075	-1.160	0.451	0.010
Deer X forest	-0.003	0.003	0.400	-0.004	0.003	0.208
Elk X forest	-0.005	0.003	0.109	-0.015	0.004	< 0.001
Moose X forest	0.001	0.003	0.728	0.004	0.003	0.274
Horse X forest	0.014	0.009	0.090	0.015	0.005	0.002

Note: bolded values indicate significance

Table 2.6. Spatio-temporal avoidance of wolf packs (*Canis lupus*), male cougars (*Puma concolor*) and female cougars, measured as the distance (km) between two individuals with overlapping MCP (100%) home ranges and temporally matching GPS fixes measured during the day (0600 – 1600) and night (1800 – 0400) in winter 2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Pair	Day		Night		<i>P</i> – value ¹
	Mean	SD	Mean	SD	
Female cougars – Female cougars	16.4	2.97	16.7	3.26	0.841
Male cougars – Male cougars	14.2	N/A ²	15.4	N/A	1.000
Wolf packs – Wolf packs	30.1	10.7	30.0	10.4	0.982
Female cougars – Wolf packs	19.5	7.58	19.2	7.45	0.946
Male cougars – Wolf packs	23.2	9.95	23.4	10.9	0.887
Female cougars – Male cougars	20.1	7.74	19.4	6.92	0.652

¹*P* - value indicates difference between night and day based on Mann-Whitney U-tests

²*n* = 1

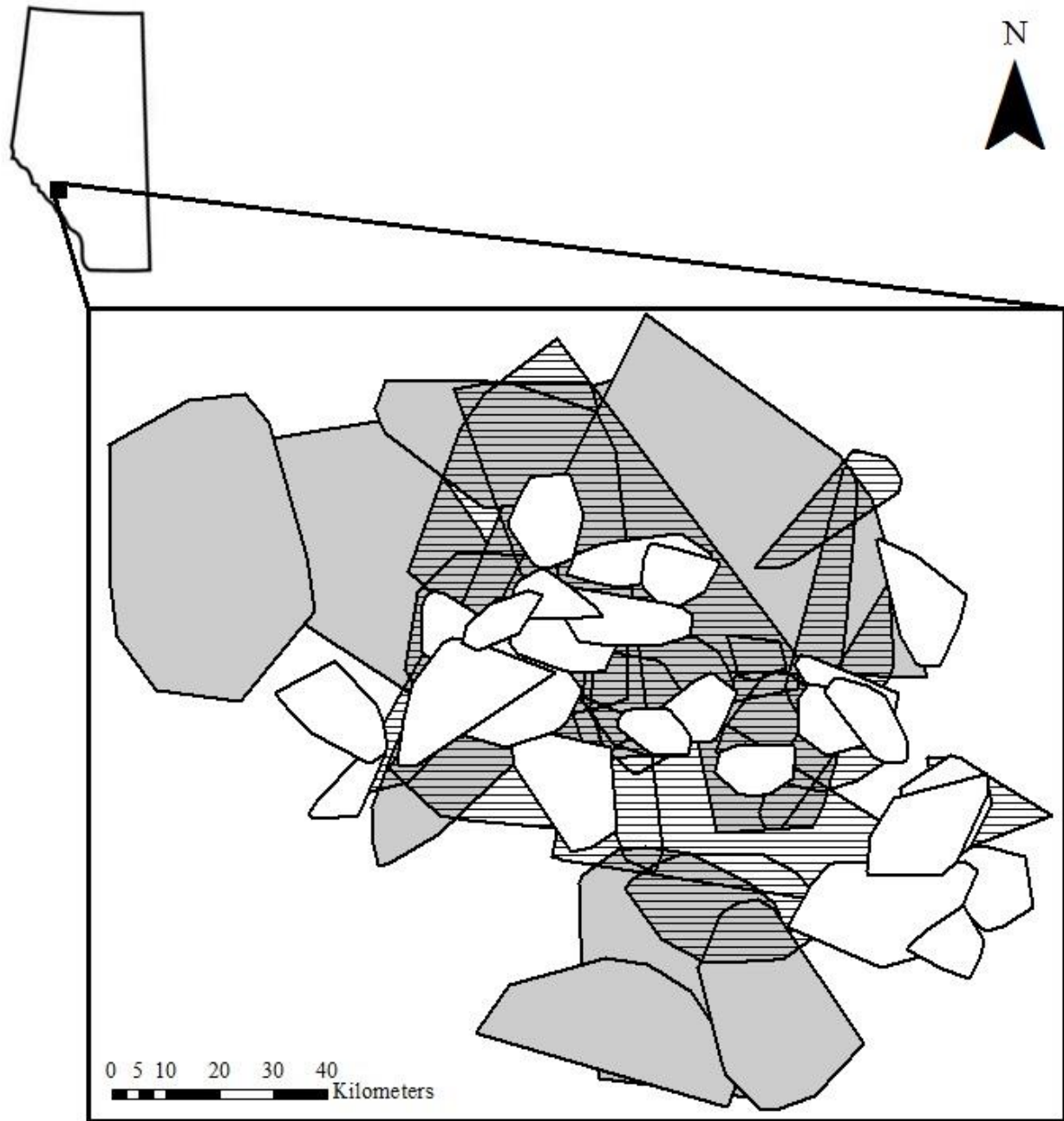


Figure 2.1. Wolf (*Canis lupus*) pack (gray polygons), male cougar (*Puma concolor*) (lined polygons) and female cougar (white polygons) 100% MCP winter home ranges from 2004-2008 in the central east slopes of the Alberta Rocky Mountains, Canada.

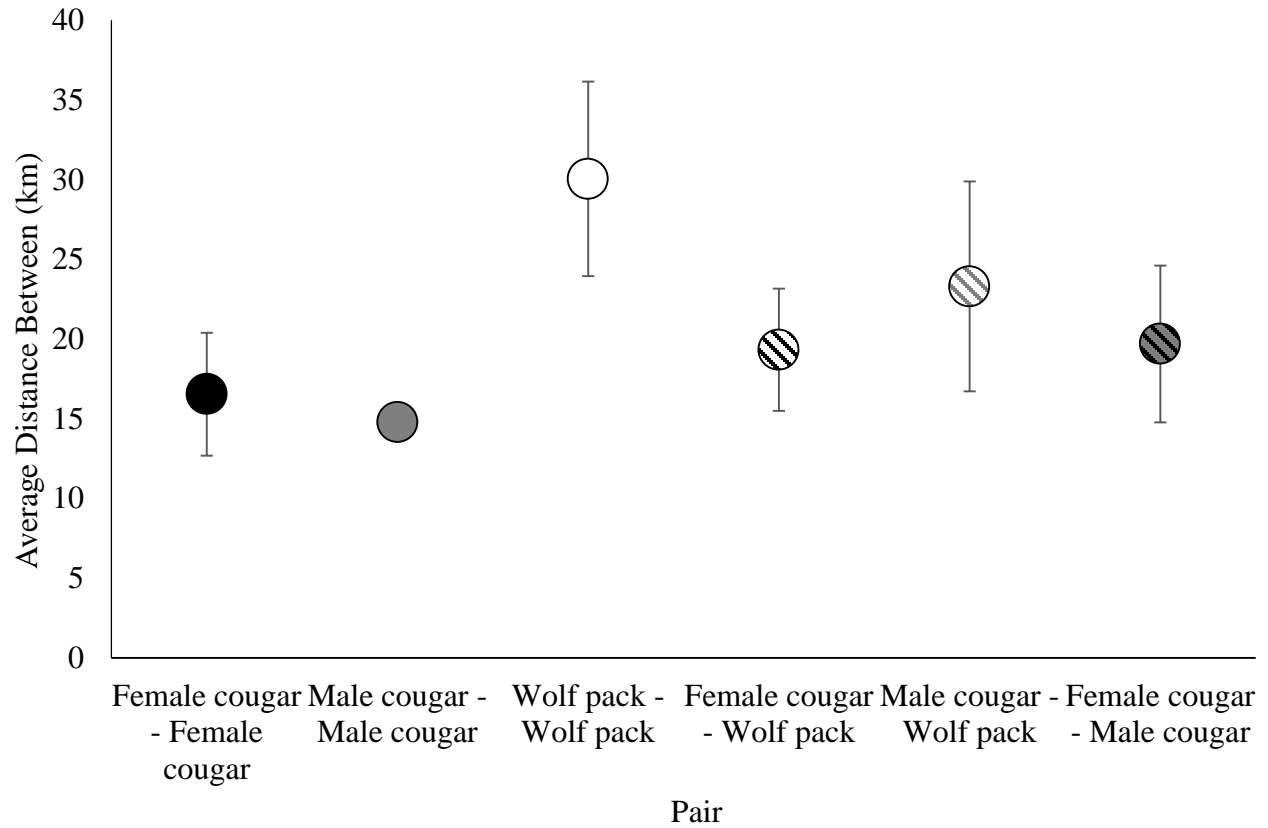


Figure 2.2. Mean spatio-temporal avoidance in winter 2006 of wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars with overlapping 100% MCP home ranges and temporally matching GPS fixes with error bars representing the 95% confidence interval in the central east slopes of the Alberta Rocky Mountains, Canada.

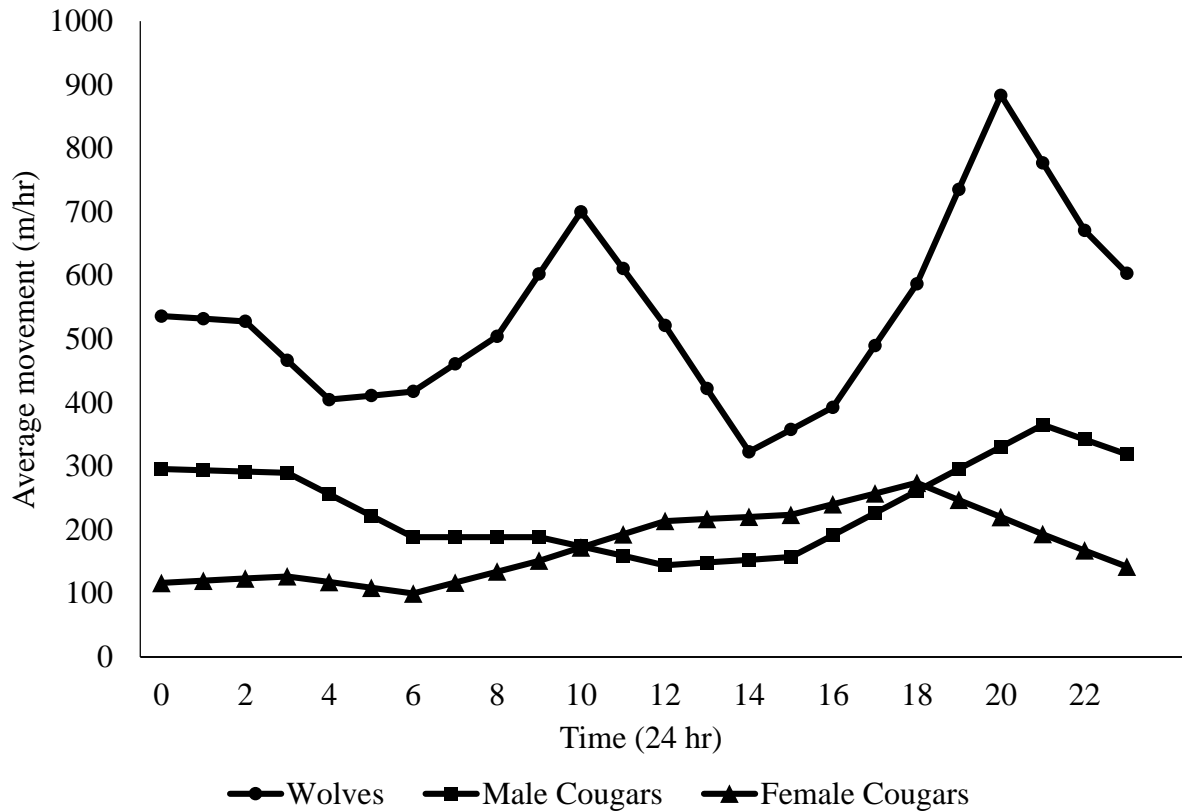


Figure 2.3. Daily movement patterns in winter 2006 measured with 2-hr fixes for wolf (*Canis lupus*) packs and 3-hr fixes for male cougars (*Puma concolor*) and female cougars with hourly averages interpolated based on a continuous linear trend in the central east slopes of the Alberta Rocky Mountains, Canada.

CHAPTER THREE

THESIS SUMMARY

In my thesis, I examined the potential interactions of wolves (*Canis lupus*) and cougars (*Puma concolor*) where their distributions currently overlap in the central east slopes of the Rocky Mountains of Alberta. I used radiotelemetry and kill site data collected on these species from past studies (Webb, Hebblewhite and Merrill 2008; Webb 2009; Knopff et al. 2009; Knopff et al. 2010). Cougars were found at higher densities than wolves during the time of the study, with approximately 0.97 – 2.2 wolves/100 km² (Webb 2009) and approximately 2.67 – 3.49 cougars/100 km² (Knopff et al. 2010). Wolves were hunted as predators for ~10 months/year with unlimited quotas and trapped on registered traplines between 1 October and 31 March (Webb, Allen and Merrill 2011); cougars were harvested as a big-game species with different harvests on males and females and subject to quota harvests of 10% from 1 December to 28 February or until quota filled. Wolves were never completely extirpated in this area but the populations were reduced with poisoning programs to reduce rabies in the 1950s and early 1960s, with localized wolf control until 1966, and have increased since the mid-1980s (Alberta Forestry, Lands, and Wildlife 1991; Webb 2009); cougar populations have increased and expanded from the southwestern part of Alberta further north and east over the last 2 decades (Knopff, Webb and Boyce 2014).

For my study, I focused on comparing the two species in terms of the composition of their kills, habitat selection, temporal movement patterns, and their pairwise spatio-temporal avoidance based on extensive GPS monitoring to understand the potential for resource partitioning. I focused on winter primarily because wolf pack cohesion is high (Metz et al. 2011)

and to prevent the complexity of having bears (*Ursus arctos*, *U. americanus*) as additional large predators in the area. I contrasted data from individual wolves as members of a wolf pack because of their cohesion in winter (Metz et al. 2011), but compared male and female cougars separately because they are solitary hunters with differing body sizes, and females may have kittens with them, leading to potentially different diets and habitat use (Holmes and Laundré 2006; Knopff et al. 2010). This is one of the first studies to have contrasted the behavior of the different cougar sexes to wolves.

In my study I found evidence for stronger avoidance by wolves of conspecifics than of cougars, whereas cougars appeared to avoid both wolves and conspecifics equally. The moderate spatial separation between cougars and wolves was reinforced by differences in their temporal movement patterns, with wolves having a distinct bimodal crepuscular pattern corresponding to that of their ungulate prey (Collins, Urness and Austin 1978; Lowe, Patterson and Schaefer 2010; Robinson, Hebblewhite and Merrill 2010), and cougars having a single peak differing between the sexes. Male cougar movement peaked in the late evening and was higher overnight than during the day, whereas female movement increased throughout the day and was highest in the evening.

Using latent selection difference functions (Czetwertynski 2008; Latham, Latham and Boyce 2011), I found some evidence that both male and female cougars selected for landscape features relative to wolves, whereas any greater selection by wolves was for prey densities, usually with the strength of the selection contingent upon habitat features. Differences in selection patterns between wolves and female cougars were consistent during the day and night whereas the differences in habitat selection between wolves and male cougars were more exaggerated during the night, concurrent with the time male cougars are most active. Male and

female cougars had many differences in habitat selection, possibly indicative of the threat of male cougar infanticide (Ross and Jalkotzy 1992; Logan and Sweanor 2001; Holmes and Laundré 2006). Most selection differences between wolves and cougars occurred for prey density contingent upon habitat features, specifically density of forest edge and proportion of forest, suggesting habitat differences for maximizing hunting efficiency.

Differences in the habitat selection between the species and cougar sexes may have reflected the hunting strategies for prey partitioning. I hypothesized prey selection and what each predator killed would reflect predator body size differences. Overlap in what male cougars and wolves killed was higher than the overlap for females with either other predator. A higher proportion of male cougar and wolf kills were large-bodied prey species, i.e., elk (*Cervus elaphus*), moose (*Alces alces*) and horse (*Equus caballus*), compared to female cougar kills, which were primarily deer (*Odocoileus virginianus*, *O. hemionus*), indicating the potential for competition between male cougars and wolves when prey are limited. Nevertheless, all predator groups appeared to kill elk equal to their availability, whereas female cougars selected for deer. Although not statistically significant, the magnitude of selection of moose and horse was higher for wolves than exhibited by male cougars, likely because only a few male cougars specialized on killing feral horses whereas more wolf packs killed some feral horses.

MANAGEMENT IMPLICATIONS

Conservation plans for wild lands often focus on large carnivores as umbrella or key species because they have large area requirements, they attract public attention, and they are considered ecologically important because of their top-down influence on ecosystems (Kellert et al. 1996; Noss et al. 1996; Ray 2005; Estes et al. 2011). A better understanding of how large

carnivores may compete or coexist within different ecological systems can help in selecting high priority areas for conservation, anticipate effects of landscapes, and manage populations.

Conservation strategies include conserving, maintaining or reintroducing large carnivores, using large carnivores as icons, noting large carnivore presence and habitat requirements, and evaluating the large carnivore's population status (Ray 2005). These strategies are used to conserve biodiversity, gain public support and determine the required size, configuration and location of priority conservation areas. For example, Kunkel et al. (2013) used two well-developed resource selection functions (RSFs) to assess the potential for using two carnivores, rather than one, to determine priority conservation areas in the basin of the North Fork of the Flathead River, Montana. They found suitable wolf habitat (RSF probability quantile > 66%) was 3x the size of the suitable area for cougars, but combining the habitat assessments for the two predators gave a 91% increase in the amount of rugged terrain required, and increased the extent of total priority area by 15%, from 1005 km² based on wolf alone to 1157 km² for both predator species considered together.

The results of my comparison of cougar and wolf habitat selection in the central east slopes of the Rocky Mountains indicate high topographic, vegetation and prey density diversity may be key for wolf and cougar coexistence. For example, when prey density was near its maximum, the three predator groups had the greatest differences in selection for proportion of forest and forest edge. This may be related to differences in hunting styles (Husseman et al. 2003; Atwood, Gese and Kunkel 2007). Supporting this, Kunkel et al. (1999) proposed that they did not find the differences they expected in prey selection between cougars and wolves because the dense vegetation and rugged terrain in northwestern Montana likely forced wolves to exhibit a stalking strategy comparable to cougars. In areas of low topographic and vegetation diversity,

differences in temporal movement patterns may be necessary to keep cougars and wolves apart. However, temporal movement patterns will keep these species separated only at certain times of the day, because both predators move in the evening, during a period of prey activity.

In the central east slopes of the Rocky Mountains, forest harvesting trends indicate that mature forests are being converted to young seral aged-stands, providing more deer preferred foraging habitat (Webb 2009; Latham et al. 2011b). Forest harvesting, as well as climate change, may have led to an increase in the population of white-tailed deer (Côté et al. 2004; Webb 2009; Latham et al. 2011b). In my study area, cougar and wolf populations will likely increase as white-tailed deer increase, because both are supported by deer as indicated by the proportion of deer in their kills, and past trends have shown cougar and wolf population fluctuations following that of their prey (Alberta Forestry, Lands, and Wildlife 1991; Alberta ESRD 2012).

Associated with the recent increase in deer has been a decline in number of elk (Alberta Sustainable Resource Development, unpublished data), which are a secondary prey whose recent decline may be related to apparent competition (Holt 1977; Schmitt 1987; DeCesare et al. 2010; Latham et al. 2013). Although increased early seral forest will provide more foraging habitat for elk (Boyce et al. 2003), the increase in predators due to the increase in deer may result in greater predation on elk. I found that elk were selected in proportion to their availability and therefore comprised a small portion of the kills relative to deer; nonetheless elk populations may not be able to sustain the same predation as deer because elk have lower reproductive rates than deer (DelGiudice, Lenarz and Powell 2007; Hebblewhite and Merrill 2011).

I found both wolves and cougars to select equally for elk. Knopff (2010) reported cougars were at higher densities in the area than wolves (Webb 2009; Knopff 2010) and I found male cougars and wolves killed similar proportions of elk. As a result, cougars may have as large or

larger influence on elk populations as wolves do. As well as selecting for high elk densities when in high forest edge habitat relative to wolves, male cougars also kill along forest edges (Holmes and Laundré 2006), suggesting that male cougars could decrease the elk population most in these areas. If forest management goals are to decrease areas on the landscape where elk are at a high risk of predation, then the density of forest edge should be decreased. Additionally, I suggest that large proportions of forest, at least > 80% (Appendix II), are maintained, and if possible, in high elk density areas because female cougars selected more for high density elk in forested areas relative to both male cougars and wolves. Due to female cougars' strong selection of deer, increasing their encounters with elk likely would not increase their predation on elk, as it may with male cougars and wolves who do not select for alternative prey species. Thus, the increase in the proportion of forest available may give elk a refuge. While I found that wolves select for high elk density in the forest relative to male cougars, wolves have low encounter rates with elk in the forest relative to grasslands (Hebblewhite, Merrill and McDonald 2005).

Although an approach to using multiple species of carnivores has been advocated for promoting biodiversity in the Rocky Mountains (Weaver, Paquet and Ruggiero 1996; Carroll, Noss and Paquet 2001; Kunkel et al. 2013), individual provincial management plans are species specific. Today, in Alberta, cougars are harvested as a big-game species with different quotas on males and females, varying depending on if the cougar management unit is considered source, sink or stable habitat (Alberta ESRD 2012). While the cougar management plan mentions the need for successful prey management for cougar conservation, it does not consider the relevance of other predators. Wolves, in contrast, are managed as a predator species with long hunting and trapping seasons (Alberta Forestry, Lands, and Wildlife 1991).

If the provincial harvest management goal is to slow elk population declines, for areas where cougar densities are approximately 1.2 – 3.6x higher than wolves, like wolves, cougars should be hunted as a predatory species. Cougar harvest is more likely to reduce the cougar population than wolf harvest on the wolf population, as recent studies show cougar harvest can be additive, rather than compensatory, as overall cougar survival declined and reproductive rates did not change with hunter harvest (Cooley et al. 2009; Robinson et al. 2014). Wolves in Alberta are primarily managed through traplines, though even with no quotas, human harvest rates are low and unlikely to lead to a decline in the wolf population (Robichaud and Boyce 2010; Webb, Allen and Merrill 2011). Cougars have longer biennial reproductive cycles and smaller litter sizes, relative to wolves' annual reproductive cycles and large litter sizes (Ross and Jalkotzy 1992; Weaver, Paquet and Ruggiero 1996; Webb, Allen and Merrill 2011). The cougar harvest must be focused heavily on male cougars rather than female cougars as male cougars kill a larger proportion of large-bodied ungulates while females selectively kill deer. However, even with different quotas, males and females can sometimes be difficult to distinguish in the field (Ross and Jalkotzy 1996). Increased cougar harvest must be done with caution, as it has potential to cause population declines and cougars are inherently hard to monitor (Knopff, Webb and Boyce 2014). Although controlling predators to keep prey populations stable is important, carnivore populations must also be maintained at healthy numbers to prevent too large of increase in ungulate populations, maintain recreational opportunities, and for ecotourism purposes (Leopold 1949; Kellert et al. 1996; Estes et al. 2011; Alberta Government 2013).

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APPENDIX I

SUPPLEMENTARY UNGULATE KILLS MATERIAL

Table I.1. Number of ungulate kills made by individual wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars from 2003-2008 in the central east slopes of the Alberta Rocky Mountains, Canada.

Predator	Prey				Total
	Deer	Elk	Moose	Horse	
<i>Wolf Packs</i>					
Blackstone	9	0	6	0	15
Brazeau	24	5	3	0	32
Colt Creek	12	2	5	1	20
Dam Pack	6	1	1	0	8
Jock Lake	10	0	3	1	14
McGregor Lake	9	5	5	0	19
Nordegg River	1	1	1	1	4
Prairie Creek	9	0	5	0	14
Radial Lake	8	0	4	1	13
Ranch	5	11	0	0	16
Trout Creek	1	1	0	4	6
Wildhorse	0	0	0	1	1
<i>Male Cougars</i>					
111	2	0	0	0	2
113	3	0	0	0	3
9827	4	0	0	7	11
9829	2	2	0	0	4
9872	1	0	1	0	2
9876	16	3	0	0	19
9877	3	1	0	0	4
9881	4	0	0	0	4
9887	8	3	2	0	13
9889	6	0	9	0	15
9895	5	0	0	0	5
9897	4	0	1	5	10

Table I.1. Continued

Predator	Prey				Total	
	Deer	Elk	Moose	Horse		
<i>Female Cougars</i>						
3	9	0	0	0	9	
108	2	0	0	0	2	
109	2	0	0	0	2	
112	5	0	0	0	5	
115	1	1	0	0	2	
9822	9	0	0	0	9	
9823	18	2	0	0	20	
9825	5	0	1	0	6	
9828	1	1	0	0	2	
9830	2	0	0	0	2	
9871	22	0	0	0	22	
9873	42	0	0	0	42	
9874	3	0	0	0	3	
9875	5	1	0	0	6	
9878	22	3	0	0	25	
9879	19	1	1	0	21	
9883	5	0	0	0	5	
9884	9	0	0	0	9	
9885	4	0	0	0	4	
9886	9	0	0	0	9	
9888	14	1	0	0	15	
9890	22	0	0	0	22	
9891	13	0	0	0	13	
9892	16	0	0	0	16	
9893	21	0	0	0	21	
9896	6	0	0	0	6	
9898	10	0	0	0	10	

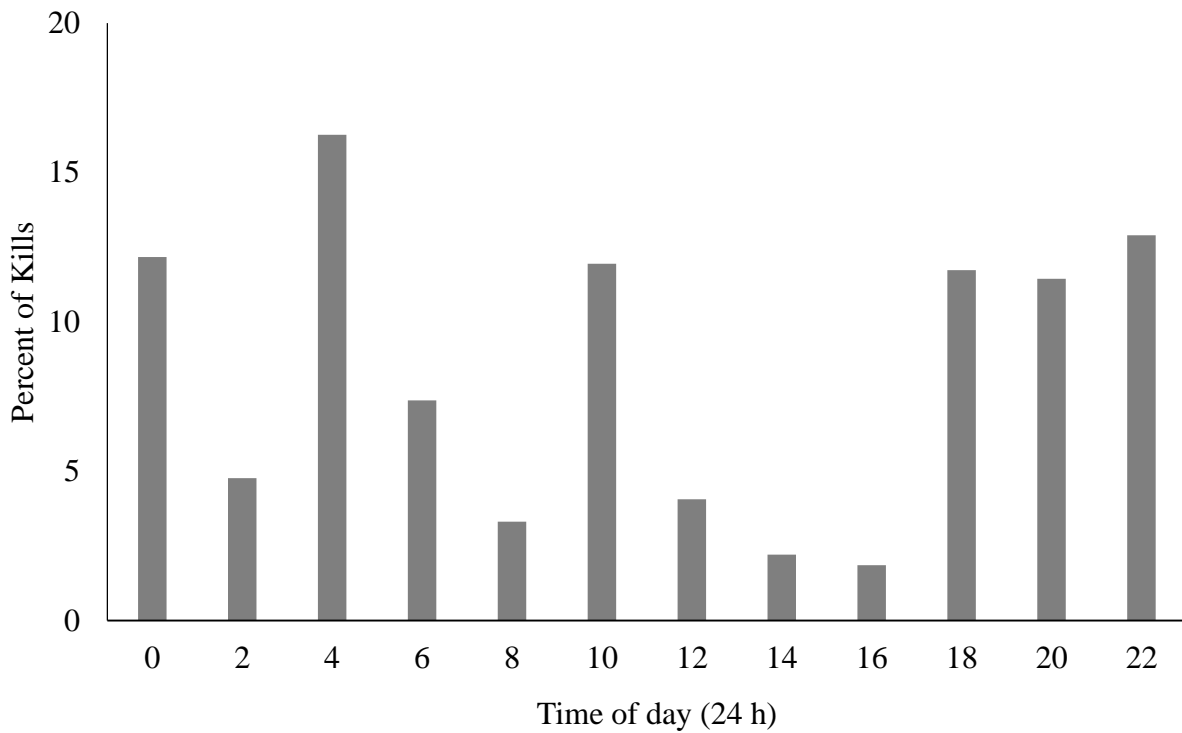


Figure I.1. Average percent of ungulate kills made by wolf (*Canis lupus*) packs in winter 2006 at each time of day in the central east slopes of the Alberta Rocky Mountains, Canada.

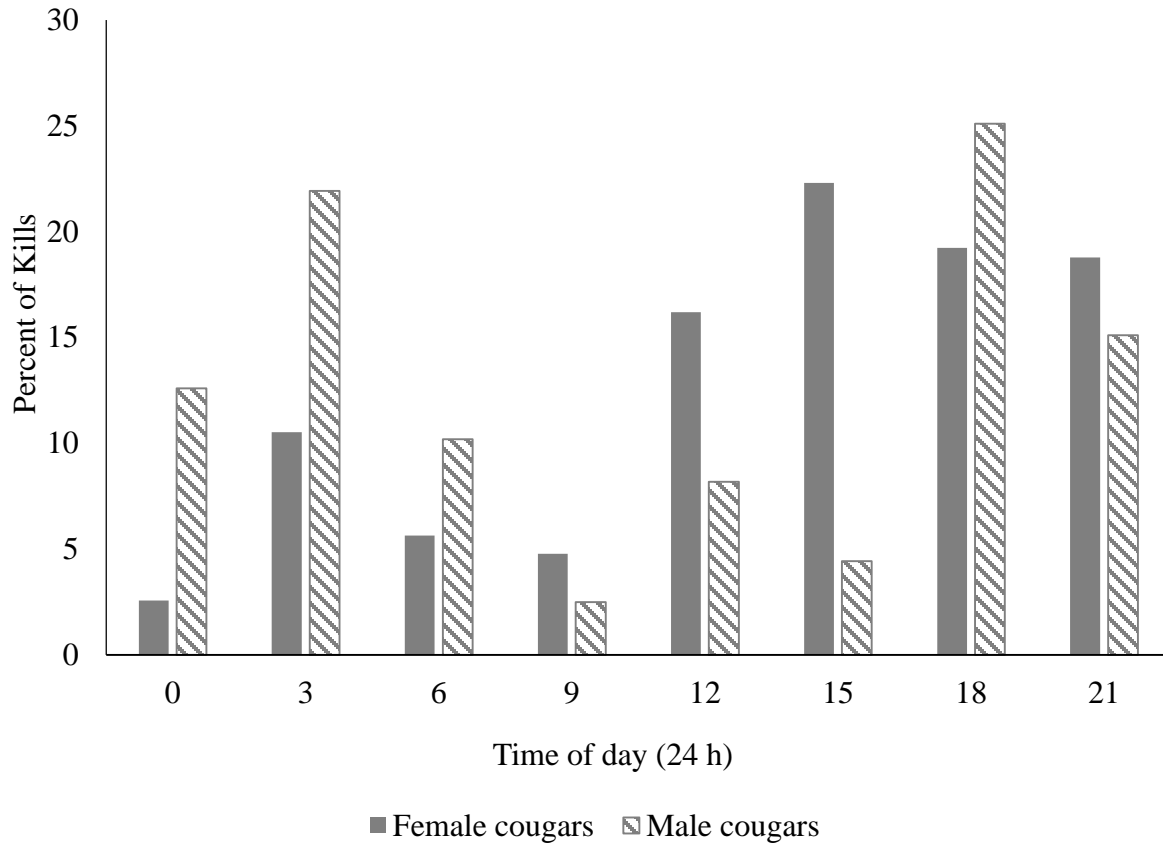


Figure I.2. Average percent of ungulate kills made by cougars (*Puma concolor*) in winter 2006 at each time of day in the central east slopes of the Alberta Rocky Mountains, Canada.

APPENDIX II

SUPPLEMENTARY SPACE USE MATERIAL

Table II.1. Number of GPS fixes and 100% MCP home range size (km²) of individual predators included in the latent selection difference function in winter 2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Predator	Home range	#GPS fixes
<i>Wolf packs</i>		
Blackstone	1064	223
Brazeau	1661	1129
Clearwater	1011	1144
Colt Creek	808	1497
Dam	1184	548
Jock Lake	1214	1511
Onion Lake	515	394
Prairie Creek	677	846
Radial Lake	1522	695
Ranch	568	1328
Trout Creek	287	500
<i>Male cougars</i>		
9824	336	137
9827	577	477
9829	563	278
9872	418	146
9876	550	534
<i>Female cougars</i>		
3	224	472
9822	174	218
9823	469	882
9825	123	718
9830	301	241
9871	294	699
9873	126	716
9874	95	254
9878	201	617
9879	229	546

Table II.2. Mean availabilities between individual wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars in winter 2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Variable	Female Cougars		Male Cougars		Wolf Packs	
	Mean	SD	Mean	SD	Mean	SD
Terrain ruggedness	12.5	10.1	17.1	9.08	15.1	8.0
Elevation (m)	1290	191.8	1277	180.8	1401	252.9
Aspect	54.0	31.9	49.5	16.9	56.6	18.8
Forest	151.7	25.8	145.1	17.3	137.1	22.9
Forest edge (km/km ²)	5.14	2.45	6.16	1.64	5.27	1.35
Road density (km/km ²)	0.66	0.37	0.62	0.75	0.48	0.36
Density of wells (# wells/km ²)	0.26	0.38	0.29	0.53	0.31	0.42
# Deer	0.12	0.04	0.14	0.04	0.12	0.03
# Elk	0.02	0.02	0.02	0.01	0.06	0.15
# Moose	0.07	0.03	0.06	0.02	0.06	0.02
# Horses	0.01	0.01	0.02	0.02	0.02	0.02

Table II.3. Number of predator pairs, minimum and maximum number of temporally matching GPS fixes between individual wolf (*Canis lupus*) pack, male cougar (*Puma concolor*) and female cougar pairs that had overlapping home ranges used in the spatial avoidance analyses for winter 2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Predator pair	# pairs	Minimum # fixes	Maximum # fixes
female cougar – female cougar	5	119	483
male cougar – male cougar	1	167	167
wolf pack – wolf pack	14	200	1220
female cougar – male cougar	11	6	341
female cougar – wolf pack	17	5	245
male cougar – wolf pack	12	42	202

Table II.4. Mean spatio-temporal avoidance of wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars with overlapping 100% MCP home ranges and temporally matching GPS fixes in winter 2006 in the central east slopes of the Alberta Rocky Mountains, Canada.

Pair	Avg. distance (km)	SD
Female cougars – Female cougars	16.5	3.11
Male cougars – Male cougars	14.8	N/A ¹
Wolf packs – Wolf packs	30.0	10.6
Female cougars – Wolf packs	19.3	7.44
Male cougars – Wolf packs	23.3	10.4
Female cougars – Male cougars	19.7	7.32

¹n = 1

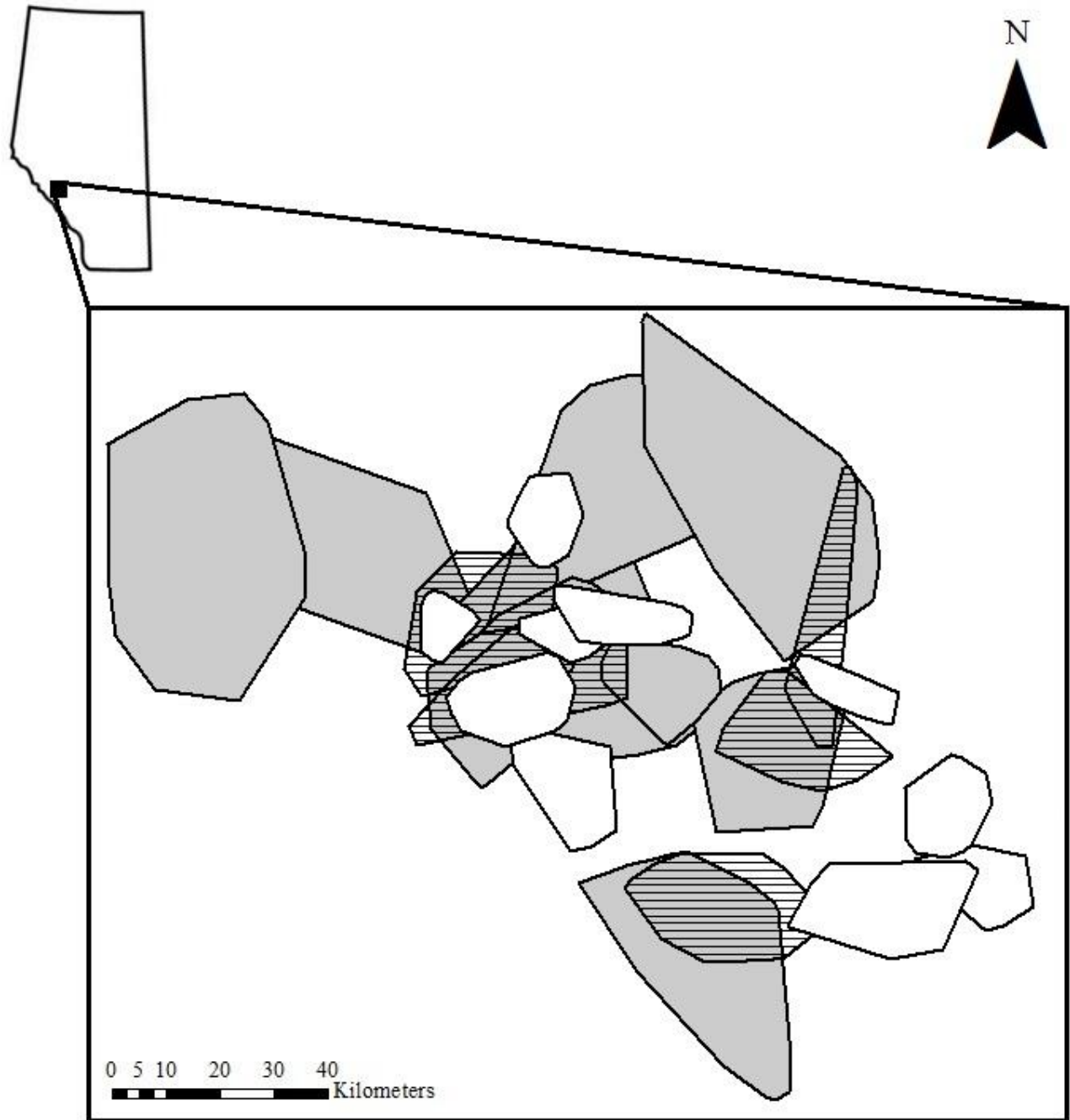


Figure II.1. Winter 2006 100% MCP home ranges of wolf (*Canis lupus*) packs (gray polygons), male cougars (lined polygons) and female cougars (white polygons) used in the latent selection difference function analysis in the central east slopes of the Alberta Rocky Mountains, Canada.

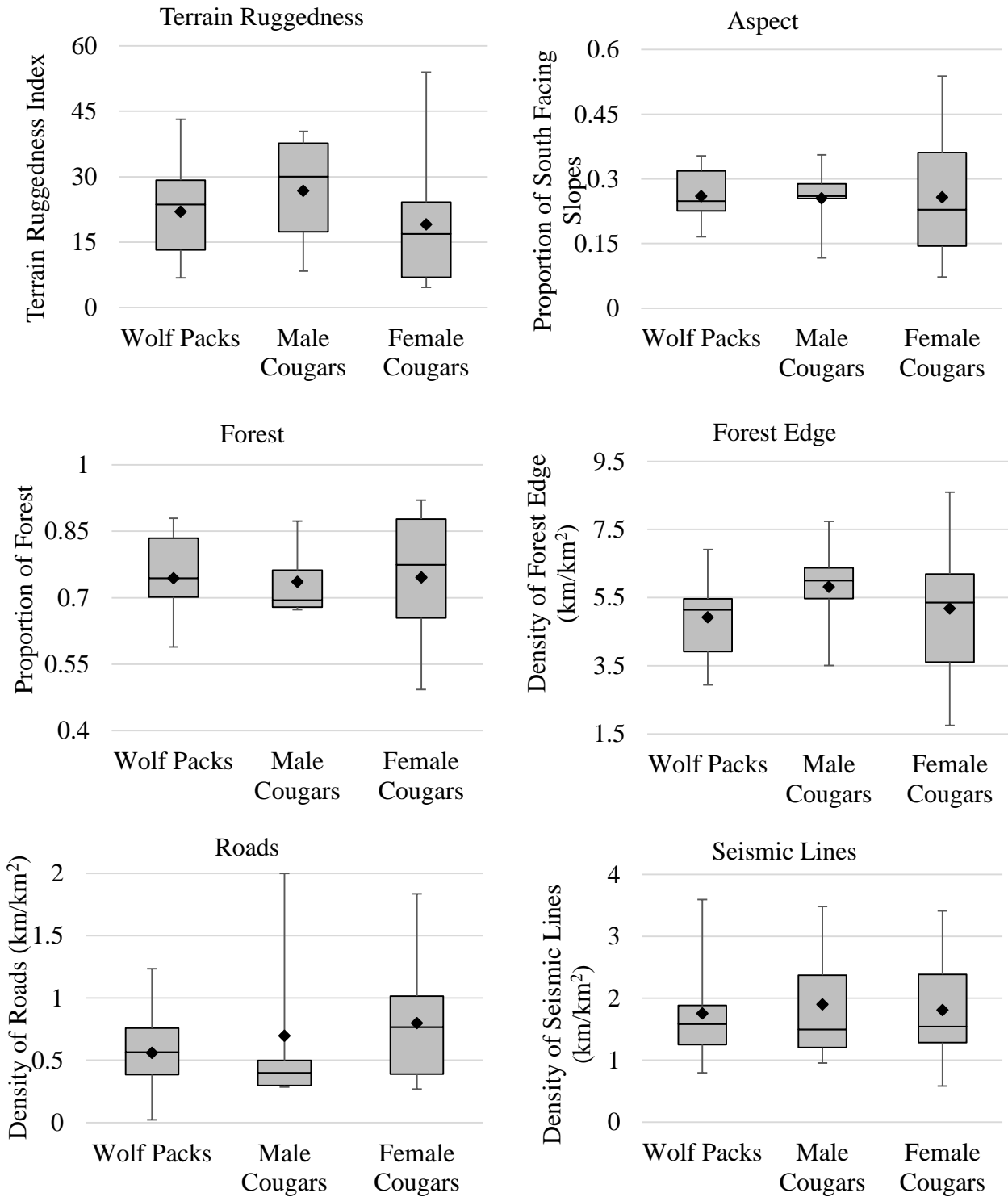


Figure II.2. Landscape feature use for wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars in winter 2006 the central east slopes of the Alberta Rocky Mountains, Canada.

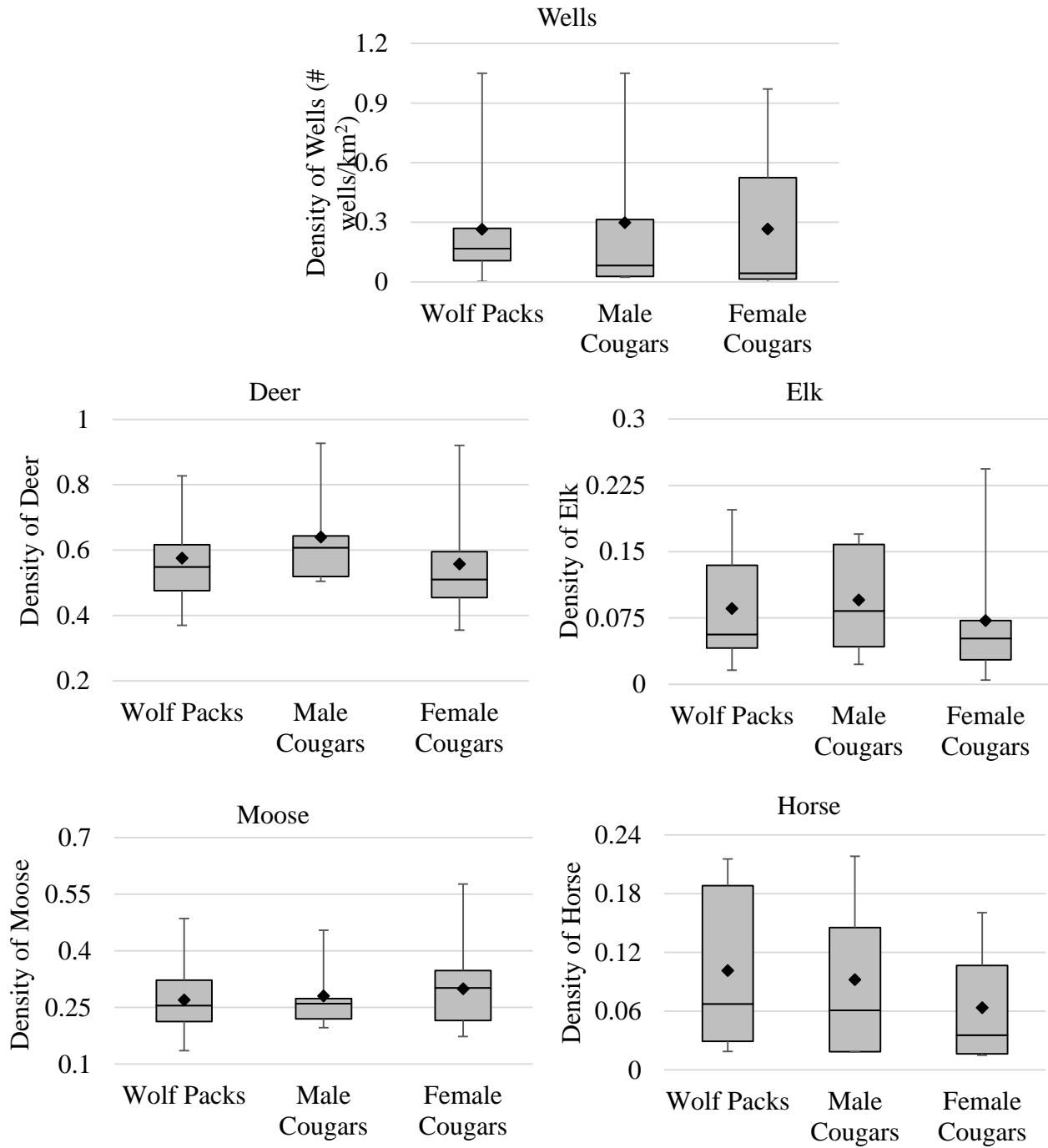


Figure II.2. Continued.

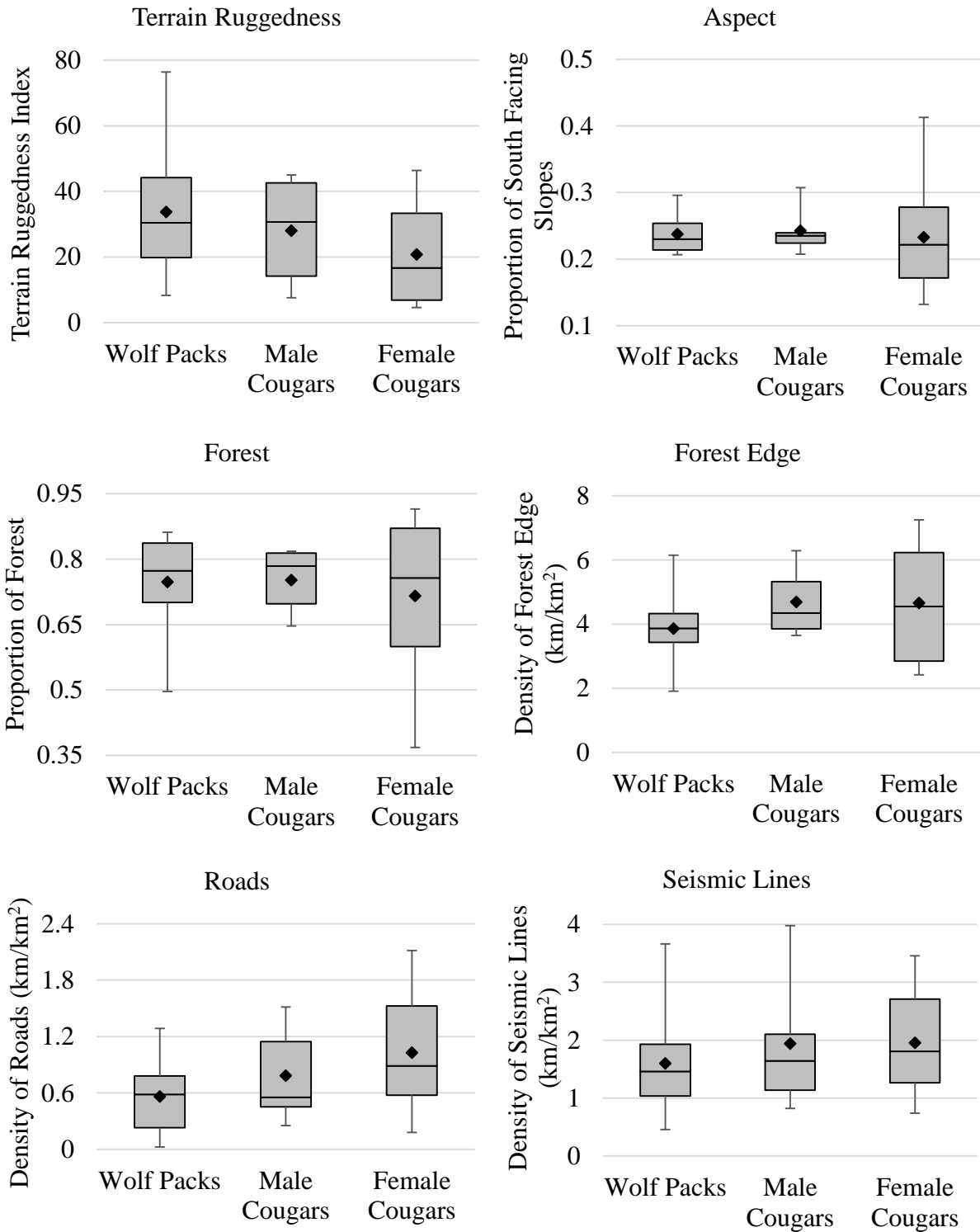


Figure II.3. Landscape feature availabilities for wolf (*Canis lupus*) packs, male cougars (*Puma concolor*) and female cougars in winter 2006 the central east slopes of the Alberta Rocky Mountains, Canada.

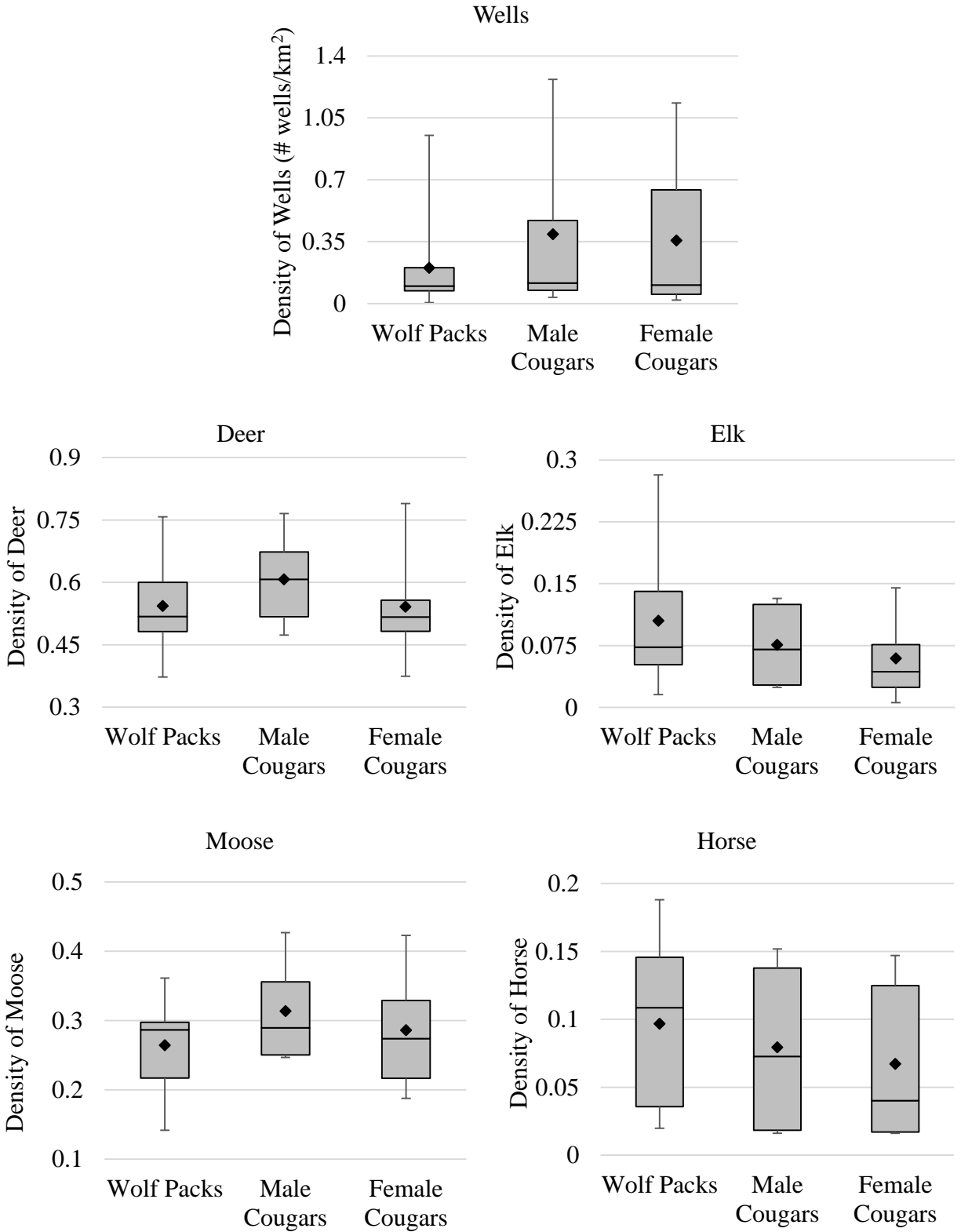


Figure II.3. Continued.

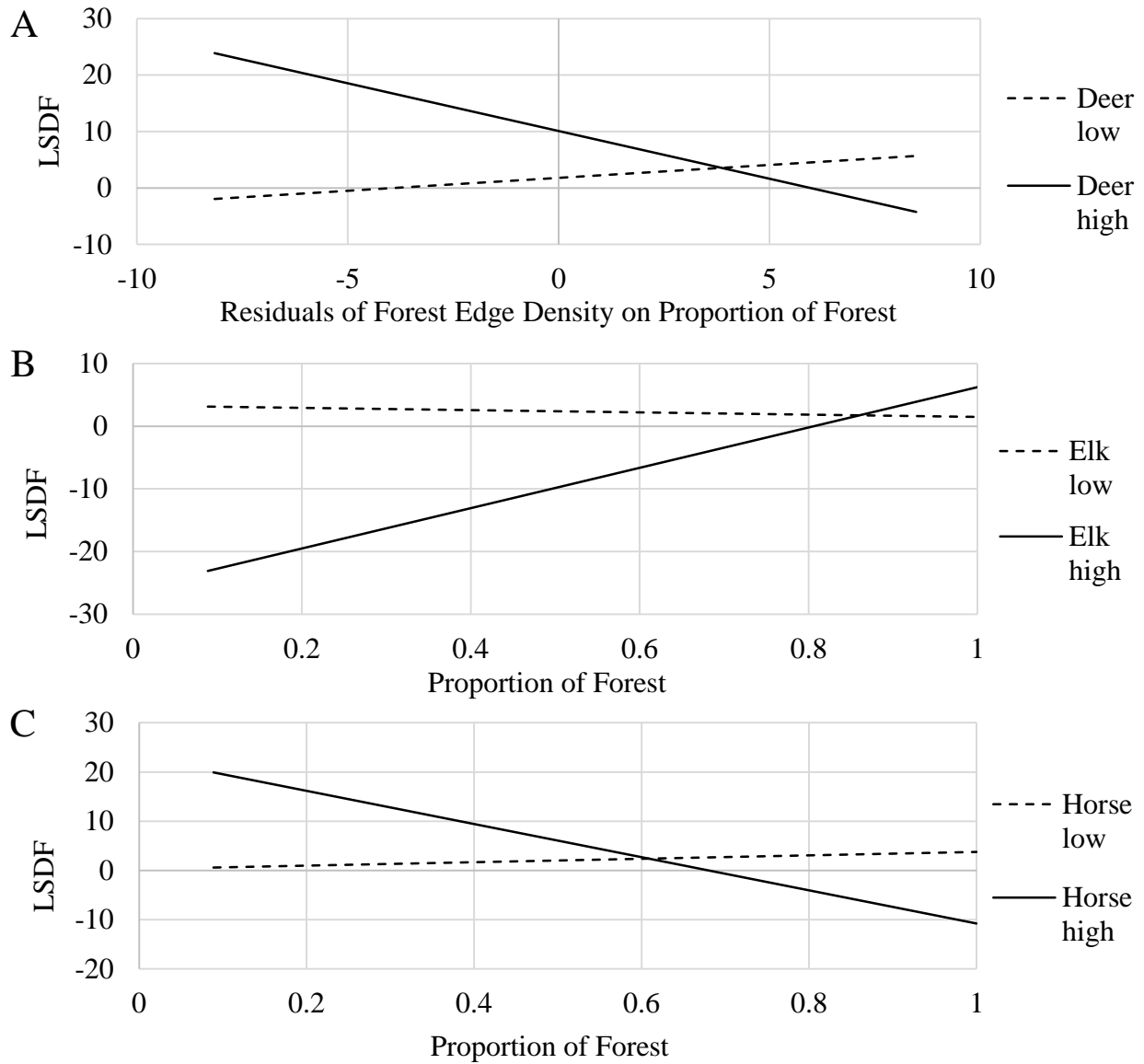


Figure II.4. Plot of logit latent selection difference function values (LSDF) for female cougars (*Puma concolor*) (1) relative to male cougars (0) in the daytime (0600 – 1700) in winter 2006 as a function of the residuals of density of forest edge on proportion forest (A) or proportion of forest in a buffer ($r = 500$ m) (B and C) showing the interactions with prey abundance in the central east slopes of the Alberta Rocky Mountains, Canada. Deer low = 0.15 deer/km²; deer high = 2.53 deer/km²; elk low = 0.001 elk/km²; elk high = 0.85 elk/km²; horse low = 0.001 horse/km²; horse high = 0.001 horse/km².

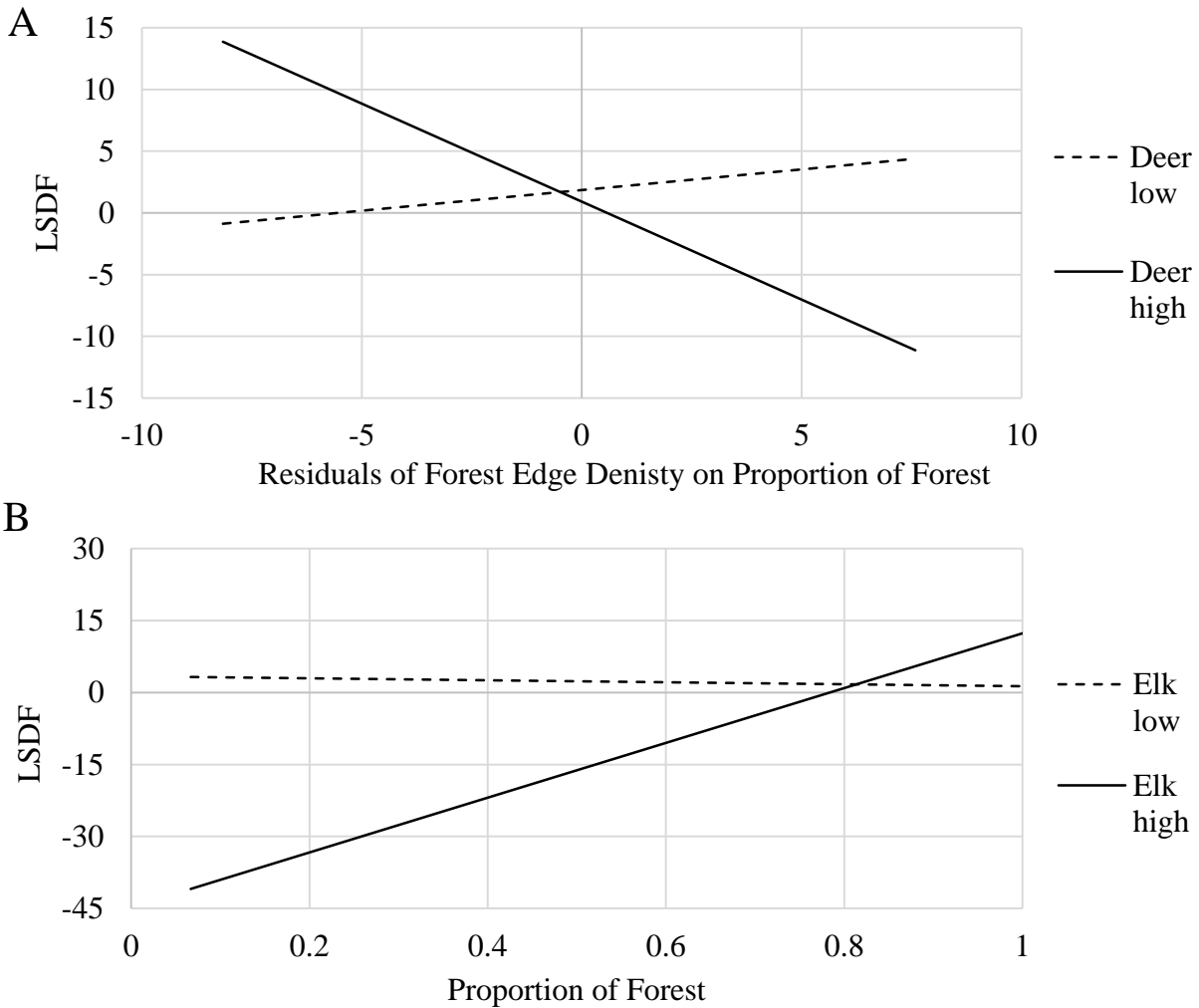


Figure II.5. Plot of logit latent selection difference function values (LSDF) for female cougars (*Puma concolor*) (1) relative to male cougars (0) at night (1800 – 0500) in winter 2006 as a function of the residuals of density of forest edge on proportion forest (A) or proportion of forest in a buffer ($r = 500$ m) (B) showing the interactions with prey abundance in the central east slopes of the Alberta Rocky Mountains, Canada. Deer low = 0.15 deer/km²; deer high = 2.55 deer/km²; elk low = 0.001 elk/km²; elk high = 1.66 elk/km².

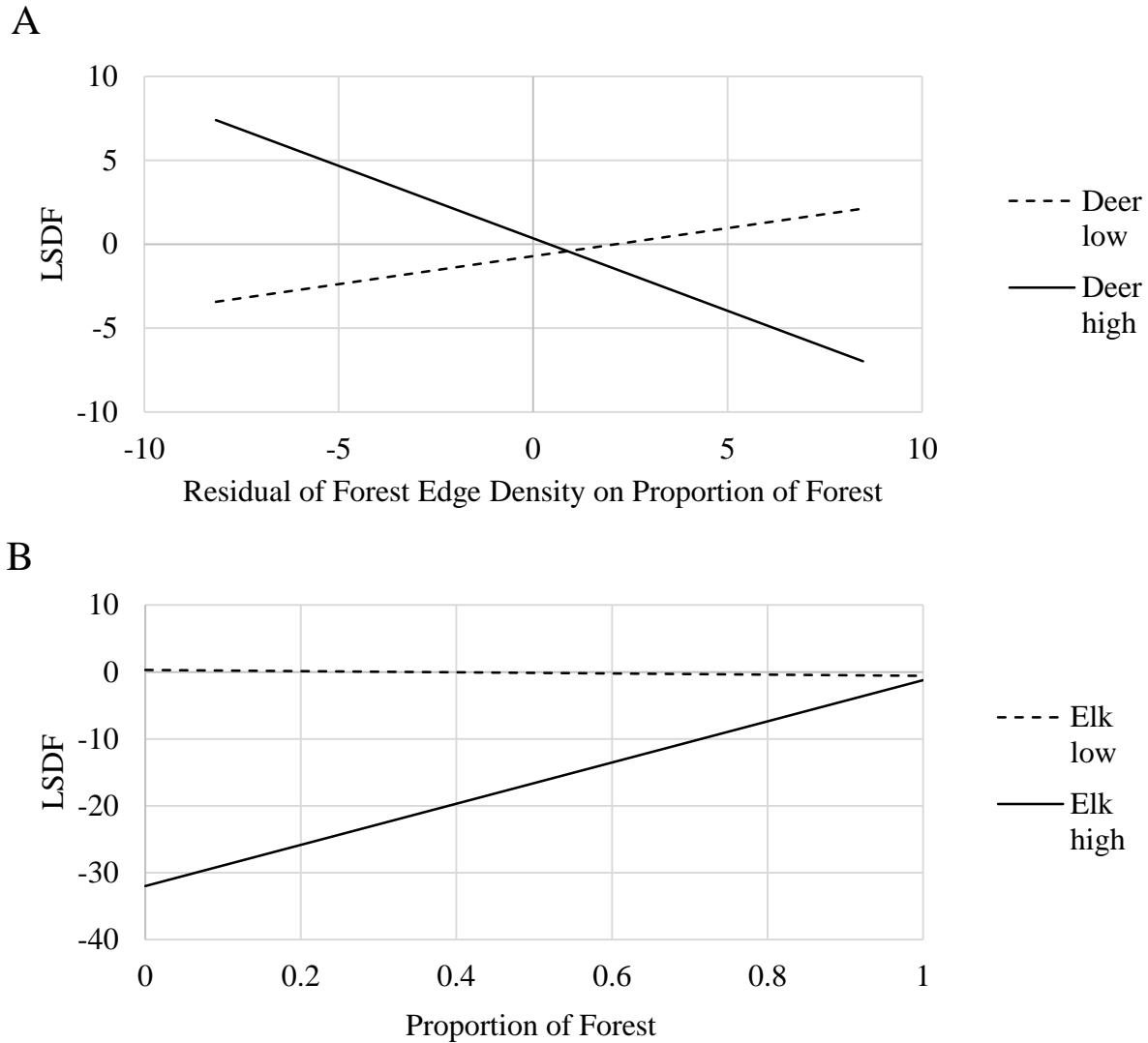


Figure II.6. Plot of logit latent selection difference function values (LSDF) for female cougars (*Puma concolor*) (1) relative to wolves (*Canis lupus*) (0) in the daytime (0600 – 1700) in winter 2006 as a function of the residuals of density of forest edge on proportion forest (A) or proportion of forest in a buffer ($r = 500$ m) (B) showing the interactions with prey abundance in the central east slopes of the Alberta Rocky Mountains, Canada. Deer low = 0.09 deer/km²; deer high = 3.10 deer/km²; elk low = 0.001 elk/km²; elk high = 3.31 elk/km².

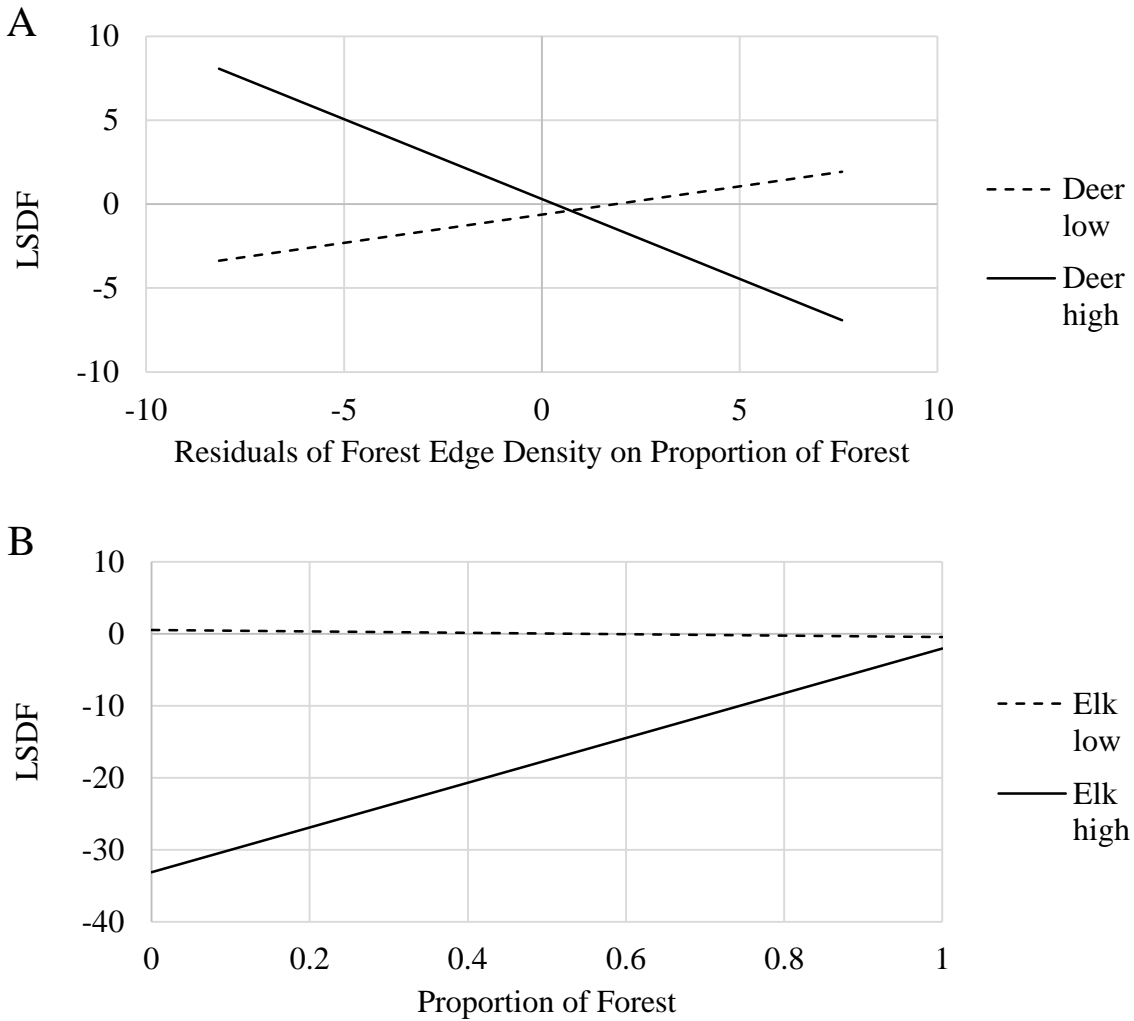


Figure II.7. Plot of logit latent selection difference function values (LSDF) for female cougars (*Puma concolor*) (1) relative to wolves (*Canis lupus*) (0) at night (1800 – 0500) in 2006 as a function of the residuals of density of forest edge on proportion forest (A) or proportion of forest in a buffer ($r = 500$ m) (B) showing the interactions with prey abundance in the central east slopes of the Alberta Rocky Mountains, Canada. Deer low = 0.09 deer/km²; deer high = 3.06 deer/km²; elk low = 0.001 elk/km²; elk high = 2.93 elk/km².

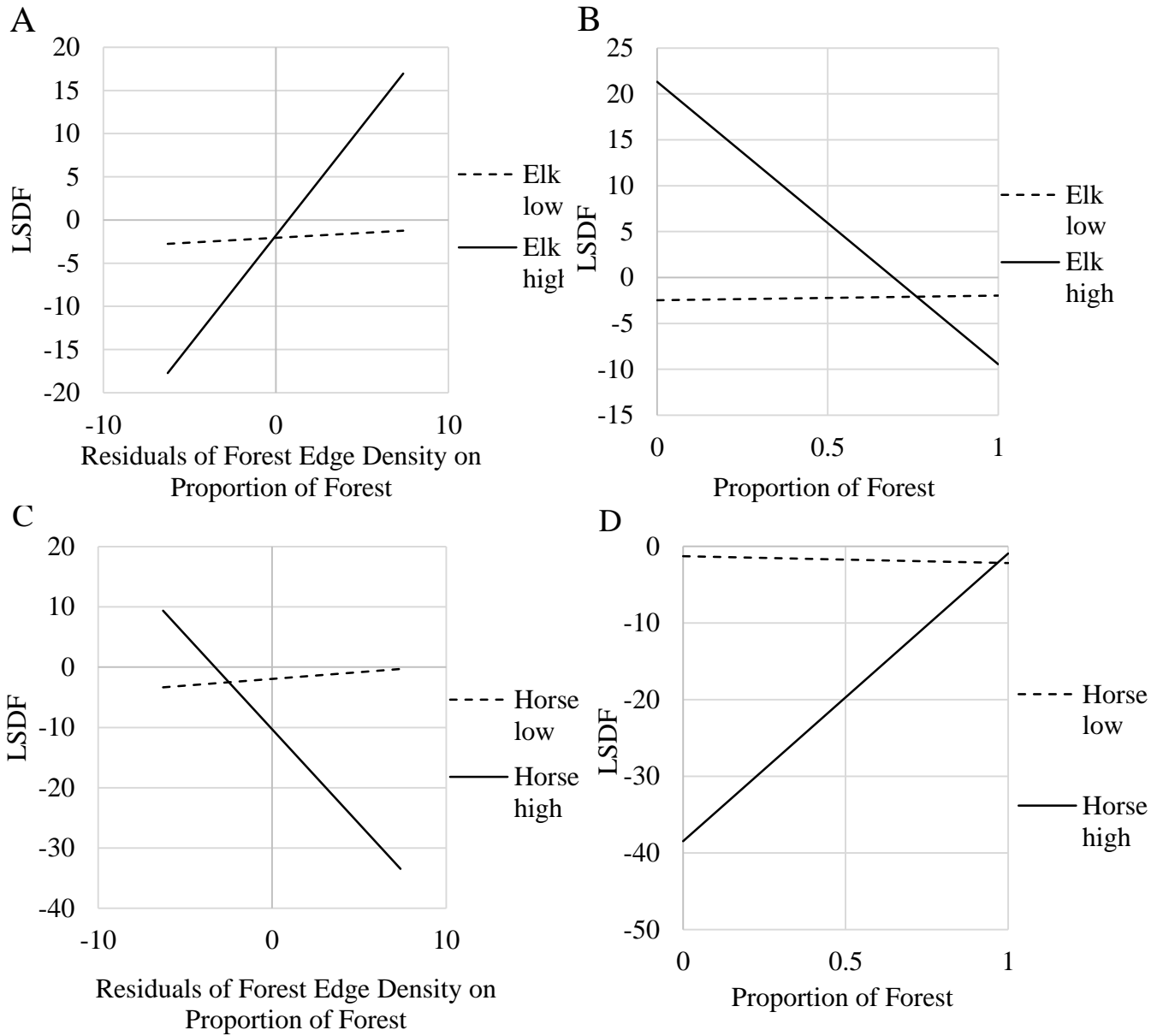


Figure II.8. Plot of logit latent selection difference function values (LSDF) for male cougars (*Puma concolor*) (1) relative to wolves (*Canis lupus*) (0) at night (1800 – 0500) in winter 2006 as a function of the residuals of density of forest edge on proportion forest (A, C) or proportion of forest in a buffer ($r = 500$ m) (B, D) showing the interactions with prey abundance in the central east slopes of the Alberta Rocky Mountains, Canada. Elk low = 0.001 elk/km²; elk high = 2.93 elk/km²; horse low = 0.001 horse/km²; horse high = 3.69 horse/km².

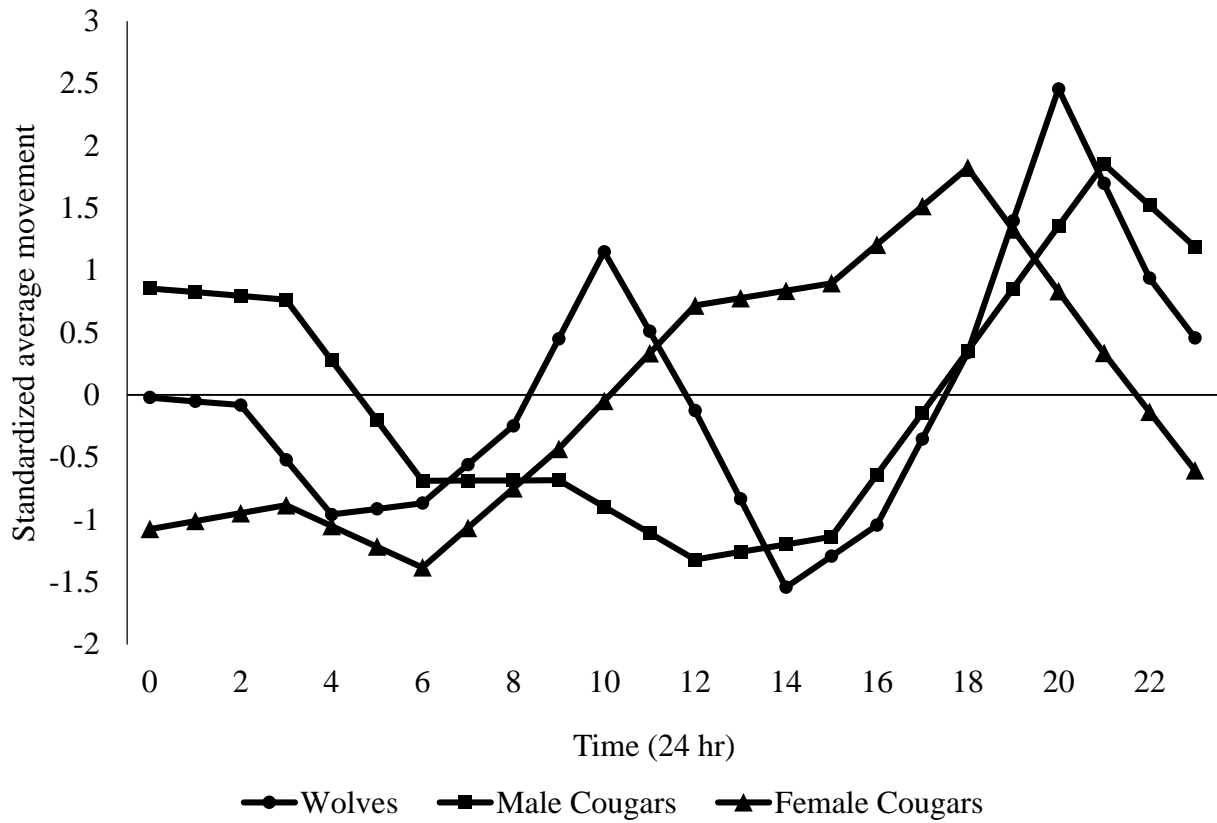


Figure II.9. Standardized daily movement patterns measured with 2-hr fixes for wolf (*Canis lupus*) packs and 3-hr fixes for male cougars (*Puma concolor*) and female cougars in winter 2006 with hourly averages interpolated based on a continuous linear trend in the central east slopes of the Alberta Rocky Mountains, Canada.