SPATIAL PREDATION RISK AND INTERACTIONS WITHIN A PREDATOR COMMUNITY ON THE ROCKY MOUNTAINS EAST SLOPES, ALBERTA

by

Eric Spilker

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Abstract

Understanding how large carnivores spatially partition the landscape is essential for understanding how they collectively pose risk to their prey. Most research on predation risk focuses on how prey respond to a single predator species, but prey respond to a community of predators. Additionally, simultaneously sampling multiple, wide-ranging species poses challenges. In this thesis I had two objectives related to quantifying elk and bighorn sheep predation risk. In Chapter 2, I first developed maps of predicted predation risk based on resource selection functions (RSF) using scat locations and intensity of use (IU) based on data from nearby remote cameras (n=54) and assess whether combining these two metrics at the fine-scale to predict relative use (RU) improves predictions of prey kill sites over each metric separately. Second, I investigated the occurrence of other predators on habitat selection of a focal predator. I used data for 4 predator groups (*Ursus arctos/U. americanus, Canis lupus, Canis latrans, Puma concolor*) and locations of adult and calf elk (*Cervus elaphus*) kill sites on the eastern slopes of the Rocky Mountains in southwest Alberta. Ursids and canids, but not cougars, selected against vehicle-permitted linear features, which created an increasing gradient in predation risk from the eastern portion of the study area to remote areas in the west. RSFs outperformed the camera-derived IU and RU for each predator in predicting elk kill sites. Calf elk kill sites were more likely than adult kill sites to occur in areas with low selection by their 2 main predators, bears and wolves, indicating risk-avoidance by maternal cow elk. In Chapter 2, I used predator RSFs to compare predation risk to bighorn sheep (*Ovis canadensis*) habitat to assess how predation risk differed between sheep ranges in Banff National Park and outside of the park on provincial lands, as well as between areas on sheep ranges and areas off ranges throughout the study area. Relative risk by all predators was highest in Banff National Park, but only cougar predation risk was higher on sheep ranges than areas off ranges. Multi-species predation risk quantified in this study can be used to assess forage-predation risk trade-offs of different migratory segments of the elk population and bighorn sheep in this region.

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TABLE OF CONTENTS

List of Tables

List of Figures

GENERAL INTRODUCTION

The understanding that large predators play a vital role in the structuring and function of ecosystems has resulted in increased focus on their conservation and management (Roberge and Angelstam 2004, Estes et al. 2011, Ripple et al. 2014). Research is increasingly demonstrating that investments made by prey in avoiding predation are substantial and widespread (Schmitz 1998, Laundré et al. 2001, Tolon et al. 2009). Specifically, risk of predation by large carnivores influences ungulate habitat selection, grouping dynamics, and anti-predator behaviours (Gustine et al. 2006, Robinson and Merrill 2013, Vanak et al. 2013, Creel et al. 2014).

Lima and Dill (1990) established a conceptual model of predation risk by isolating two critical components of Holling`s disk equation of the predator functional response (Holling 1959): the probability of encounter (α) and the probability of death given an encounter (*d*) during time (T):

$P(\text{death}) = 1 - \exp(-\alpha d T)$

Spatial analyses have applied the encounter (α) and death (d) components of predation risk to the landscape. For example, Hebblewhite et al. (2005) used track intersections of wolves (*Canis lupus*) and elk (*Cervus elaphus*) to represent the encounter stage, and locations of elk kills (death) by wolves to identify the spatial factors that influence these two components of predation. Their approach assumed track intersections reflected true temporal encounters, which is difficult to determine. As result, most studies have relied on utilization distribution (Robinson et al. 2010, Atwood et al. 2009, Kauffman et al. 2007) and resource selection functions (RSF) (McPhee et al. 2012, Theuerkauf and Rouys 2008) as a spatial surrogate for the risk of encountering a predator. For example, using GPS collared wolves and prey density data, McPhee et al. (2012) considered wolf locations preceding elk kill sites to be areas selected for hunting by wolves to represent encounter probability. This study found that wolves selected to hunt in open valleys and near habitat edges and in areas where there was higher prey density than the mean prey density for their territories.

The majority of research linking changes in ungulate behavior to predation risk has focused on single or pairs of predator species and as a result the mechanisms of how predation risk varies with the composition of predator communities is not as well understood**.** Theory predicts two alternative outcomes: (1) the additive model, where total predation risk is the sum of risk posed by each predator; or (2) a risk enhancement or risk reduction scenario where the combined risk is greater or less than what would be predicted by the additive risk model (Sih 1998). Reduction in predation risk may occur directly through interference competition, or indirectly (exploitation competition) when dominant competitors limit the distribution of subordinates, particularly when the subordinate predator is more efficient at killing the shared prey (Rosenheim et al. 1993). Risk enhancement may occur when one predator increases the success of another. Korpmaki et al. (2006) demonstrated risk enhancement between weasels (*Mustela nivalis*) and kestrels (*Falco tinnunculus*) as voles (*Microtus agrestis*) would become more susceptible to predation by kestrels when they left the dense underbrush to escape weasel predation. Temporal partitioning of daily activity allows predators to avoid negative interactions with other predators while allowing them to occupy the same areas and access similar, high-quality resources. Similar to spatial partitioning, there is a resulting decrease in refuge available to prey species. Bischof et al. (2014) have shown how the Altai Mountain weasel (*Mustela altaica*) is able to share prey (pika, *Ochotona* spp.) with larger carnivores (stone marten, *Martes foina,* and the red fox, *Vulpes vulpes*) without succumbing to predation itself by contrasting daily activity patterns.

On the east slopes of the Alberta Rocky Mountains, ungulates face the challenge of multiple-predator communities that can include combinations of wolves, coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and cougars (*Puma concolor*). Interactions among these predators are well documented. Interference competition has been seen with wolf packs killing and consuming black bears (Rogers and Mech 1981), and exhibiting aggression towards coyotes (Peterson 1996, Berger and Gese 2007). Bears have been shown to displace cougars from their kills to the extent that in some cases, scavenging of cougar kills can constitute a considerable part of the bear's diet (Murphy et al. 1998).

How these predators spatially partition the landscape as a result of these interactions is not as well understood. To date, studies of large carnivore spatial interactions have typically considered only pairs of large predators. For example, Kortello et al. (2007) demonstrated displacement of one predator by another using snow tracking to study cougar and wolf interactions in Banff National Park, Alberta. They found that cougars would wait longer to use areas recently occupied by wolves (66.5 ± 22.9 hrs.) than it would take wolves to use areas recently occupied by cougars (27.2 ± 4.1 hrs.). Wolves have also been shown to limit year-round distribution of coyotes (Berger and Gese 2007) and summer distribution of cougars (Murphy et al. 1998, Kunkel 1997). Upon reestablishment of the wolf population in Yellowstone National Park, cougar ranges shifted into more rugged terrain (Bartnick et al. 2013).

These spatial interactions within the predator community have implications for predation risk to prey. For example, with the reintroduction of wolves into Yellowstone National Park, elk changed their distribution by selecting for more rugged terrain to escape predation from wolves and as a result they were more exposed to cougar predation (Atwood et al. 2007). As well, Griffin et al. (2011) found that summer calf survival across 12 different elk populations differed depending on composition of the carnivore community, with elk populations exposed to more carnivore species experiencing higher calf mortality. Similarly, roe deer (*Caprelous capreolus*) density across Europe was over 5x higher in areas with both wolves and lynx (*Lynx lynx*) present compared to areas with only one predator (Melis et al. 2009). One of the difficulties in studying predation risk in multi-predator communities is simultaneously quantifying the spatial distribution of the different predator species due to the expense and the species-specific nature of sampling approaches. Two relatively recent methods, remote cameras and the use of detection dogs to aid in locating scat, have allowed for researchers to non-invasively collect large sample sizes from multiple carnivores over large study areas (Long et al. 2012).

In this thesis, I examine the spatial distributions of large carnivore species based on scat locations and remote camera data to develop species-specific and multi-predator risk maps for the upper Red Deer River watershed on the east slopes of the Rocky Mountains of Alberta. Specifically, in Chapter 2 I derived three metrics of predator distribution across this area: intensity of use based on number of events on remote cameras, scat-based resource selection function (RSF) and a combination of these metrics reflecting both predator use at the large-scale (camera data) and the small-scale by adjusting for selection based on the RSF. I evaluated which metric best predicted predation risk to elk in a model selection framework by modeling the location of kill sites of elk calves and adults as functions of each of these metrics. I also evaluated predator interactions at two stages. First, I assessed the effect of the presence of the number of scats of other predator species along a transect on the resource selection of the target predator species. Second, I evaluated the interactive effects among predator metrics on the location of kill sites to address the potential for additive, reduced, or increased predation risk in multiple predator communities. In Chapter 3, I refine locations of sheep ranges inside and outside Banff National Park and compare predation risk based on characteristics of predator habitat selection developed in Chapter 2 for each predator.

PREDATOR INTERACTIONS AND RISK TO ELK ON THE EAST SLOPES OF THE ALBERTA ROCKY MOUNTAINS

INTRODUCTION

Recognition that large predators play a key role in the trophic dynamics of ecosystems has led to a greater emphasis in their conservation and management across North America (Estes et al. 2011). Increasingly, research is showing that not only the direct killing, but also the *risk* of predation affects prey species as they navigate a 'landscape of fear' (Schmitz 1998, Laundré et al 2001, Tolon et al. 2009). In particular, predation risk from large carnivores can shape ungulate habitat selection, grouping dynamics, and anti-predator behaviours (Gustine et al. 2006, Vanak et al. 2013, Robinson and Merrill 2013).

A conceptual model of predation risk is provided by Lima and Dill (1990) that distinguishes two critical components of Holling`s disk equation of the predator functional response (Holling 1959) by including the probability of encounter and the probability of attack and success (i.e. prey mortality) given an encounter. In recent studies, these components of encounter and kill have been quantified. For example, studies have used telemetry data from collared predators to derive utilization distributions (Kauffman et al. 2007, Atwood et al. 2009, Robinson et al. 2010) and resource selection functions (RSF) (Theuerkauf and Rouys 2008) as proxies for potential predator encounters. Alternatively, others have used the spatial location of kill sites to reflect not only encounter, but the combined effect of encounter and the death of the prey (McPhee et al. 2012, Kauffman et al. 2007). Hebblewhite et al. (2005) decomposed the probability of encounter and the probability of death given an encounter by identifying the intersections of tracks of wolves and elk in snow (encounters) and locations of elk kills by wolves (mortality), and linked the two processes to environmental factors. They found that the probability of encounter between wolves and elk was higher in grasslands but the probability of death given an encounter was lower in grasslands than in pine forests. Kauffman et al. (2007) found wolf kills are not only a function of the distribution of wolves and elk on the landscape, but are also dependent on landscape attributes.

Most research addressing changes in ungulate behaviour in response to predation risk have focused on single or pairs predators, and as a result it is not well understood how predation risk changes with the composition of the predator community**.** Theory predicts two alternatives. The additive model of predation risk states that total predation risk is the sum of risk posed by each predator. This model has been demonstrated in experimental dragonfly communities (Wilbur et al. 2014, Van Buskirk 1988). Alternatively, Sih et al. (1998) illustrated how the combined predation risk may be either less (risk reduction) or more (risk enhancement) than would be predicted by the additive risk model. Reduction in predation risk may occur when one predator avoids another predator or otherwise directly interferes with another (Rosenheim et al. 1993). Risk enhancement may occur when one predator facilitates the hunting success of another, such as when response of a prey to one predator increases kill rates by another. For example, Korpimaki et al. (1996) found that voles became more susceptible to predation by kestrels when they leave dense underbrush to escape weasel predation. Thus, as the environment is saturated by predators there may be fewer spatial refuges available to prey species (Hayward and Slotow 2009).

Studies of the Ya Ha Tinda (YHT) elk herd in the southern Rocky Mountains of Alberta have shown that elk respond to predation risk (Hebblewhite and Merrill 2009, Robinson and Merrill 2009) and predators may be contributing to the ~70% decline in elk population and shifts in migratory behaviour (Hebblewhite and Merrill 2011, Eggeman et al. 2016). In the mid 1970s, the majority of elk that wintered on the YHT migrated into Banff National Park (BNP) during summers and few elk remained resident. Over the past four decades the migrant-to-resident (M:R) ratio has substantially decreased from 12:1 (1977-1987) to 3:1 (1988-2004) (Hebblewhite et al. 2006). Migrant elk in BNP access to higher-quality forage in Banff National Park in summer; however, higher predation-caused mortality for migrants resulted in an overall decreased fitness advantage (Hebblewhite and Merrill 2011). More recently, elk wintering at YHT have shifted their migration eastward onto forest industrial lands such that the western migrant to resident to eastern migrant ratio currently is about 25:50:25 (Berg et al. 2016). While wolves have been the major focus of predation studies at the YHT, elk face the challenge of multi-predator communities that also include coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and cougars (*Puma concolor*).

Spatial interactions among these predators are well documented but how this influences overall risk to elk is not well understood. For example, Mowat et al. (2005) found that black bear density differed from grizzly density, with black bear densities 3 times higher in eastern British Columbia. The same group suggested the presence of grizzly bears but not black bears at high-value, limited-availability resources was attributable to competitive exclusion. Bears can also displace cougars from their kills and to the extent that in some cases, usurping cougar kills can constitute a considerable part of the bear’s diet (Murphy et al. 1998). Kortello et al. (2007) found that cougars in Banff National Park would wait longer to occupy areas recently used by wolves than it would take wolves to use areas recently used by cougars, suggesting wolves are dominant in the relationship. Wolves also have been shown to limit distribution of coyotes, with coyote home range densities being negatively correlated with wolf densities (Berger and Gese 2007).

Despite a growing body of literature on predator co-occurrence in both space and time, few studies have translated co-occurrence into multi-species spatial predation risk to prey of the broader carnivore community. We attribute this, in part, to the economic and logistical difficulties in producing metrics of predation risk for multi-predator communities. Radio-collars can provide rich datasets but are expensive and can be invasive. Recent technological advances have allowed for two non-invasive techniques, remote cameras and scat or hair DNA analysis, to become widespread in predator research. However, because cameras are fixed to a location, if full landscape coverage is required for analysis (i.e., distribution mapping) and the data do not meet the assumptions of spatial interpolation, the single value from the point location is used to represent the area between cameras. Without a high camera density, this coarse-scale representation may include areas that do not reflect camera-site specific conditions. Additionally, camera site selection can hinder the ability to equally sample multiple species if the landscape variables associated with the site result in behavioural differences among study species.

The relatively recent use of detection dogs to aid in locating scat has offered researchers a method to collect large sample sizes from multiple carnivores over large study areas and diverse landcover types. Using scat detection dogs supported with DNA analyses, Vynne et al. (2011) surveyed an area 4600 km^2 for scats of five cryptic, wide-ranging mammals in the Brazilian Cerrado. With these data their group produced RSFs for each species, finding that giant armadillos (*Priodontes maximus*) and jaguars (*Panthera onca*) were highly selective of contiguous natural areas while giant anteaters (*Myrmecophaga tridactyla*), maned wolves (*Chrysocyon brachyurus*), and cougars did not select against landscapes fragmented by agricultural activity. Despite the insight gained from this study and the potential for application of these methods to multiple-species predation risk analyses, a critical limitation of RSFs is that they represent the likelihood that an animal would select a location based on available resources only if the animal actually went there, and do not reflect the specific areas that animals use (Lele et al. 2013). However, by representing resources rather than animal locations, the spatial resolution of a RSF is limited by the resolution of available mapping data. As such, combining point-source use metrics and selection offers the potential for the strengths of each approach to outweigh the other by representing the fine-scale probability of selection only within areas that are actually used by animals.

In this chapter, we assess whether metrics of predator distribution based on remote camera data, scat-based resource selection functions (RSFs) or their combination best predict where elk are killed in a portion of the upper Red Deer River watershed on the east slopes of the Rocky Mountains of Alberta. The goal was to use the best metric to produce a multi-predator map of predation risk for both adult and calf elk to incorporate into other portions of this long-term elk study. Our focus was on the summer because calf survival is hypothesized to be a major factor influencing trends in migratory segments of an elk population (Gaillard et al. 1998). Further, in developing these metrics we explore predator interactions and their influence first on habitat selection of other predators and then on potential predation risk to elk. We assessed whether: (1) the presence of another predator increased or decreased the selection of an area by the focal predator, and (2) whether the relative risk of mortality for elk at a location by a particular predator was increased (additive risk), decreased (risk reduction) or unaffected by the presence of other predators.

STUDY AREA

The study area is located on the eastern slopes of the Alberta Rocky Mountains (51º42´47.00´´ 115º38´22.00´´) approximately 60 km north of Banff, AB. It covers an area of

1425 km^2 that runs from east to west along the Red Deer River with an additional area in the Panther River valley and includes portions of Banff National Park and adjacent crown lands (Fig. 1). The area ranges in elevation from 1342-3018 m with an east to west increase in elevation and ruggedness, and a decreasing density of anthropogenic features including roads and off-road vehicle trails. High-elevation bare rock or ice (25%) and alpine areas (6%) of mixed shrub and herbaceous communities dominated areas >2100 m in the west. Conifer forests comprised of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) were the primary landcover (38%) at higher elevations with low-elevation forests consisting of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*). Early seral stands (<15-year stand age) consisted of logged areas (hereafter, "cutblocks"; 5%) and post-fire forest regeneration (13%). Most of the fire events were <10 km^2 with the exception of the 2001 Dogrib fire (7%) in the eastern portion of the study area. Mixed shrub (*Salix* spp., *Betula* spp., 4%), grassland (3%), and deciduous forest (*Populus tremuloides, P. balsamifera*, 5%) were scattered throughout the study area. Perennial waterbodies including lakes and streams covered the remaining 1% of the area. Summers from 2013-2016 (May-September) were warm (mean: 9°C, range: -4—25°C) with monthly precipitation averaging 254.8mm (Government of Alberta 2017). The previous winters (October – April) were cold with a mean daily temperature of -4°C, ranging between -10° and 3°C (Government of Canada 2017). At higher elevations, snow can begin accumulating as early as September and monthly averages (October – April) were between 113 and 213 mm.

The western portion of the study area is part of Banff National Park, under the federal jurisdiction of Parks Canada. Parks Canada also has jurisdiction on the Ya Ha Tinda (YHT), a 41-km^2 horse ranch at the centre of the study area, which is the winter and year-round range of the YHT elk herd (Fig. 2.1). The area east of the YHT is under provincial jurisdiction where considerable recreation, and resource-extraction including forestry, and oil and gas activities occur. Gravel roads built for resource-extraction are open to public traffic and have connected various regulated campgrounds and unregulated campsites. Gas pipelines and recreational trails have created a high density of linear features that are primarily used by people in/on Off-Highway Vehicles (OHVs) or on horseback (Fig. 2.1).

Major ungulate prey species include elk, moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and wild horses (*Equus caballus*). Deer, and in particular white-tailed deer, have increased in the area over the past 10 years whereas elk have declined from a high in the 1980s of over 2000 individuals to a current wintering population at the YHT of under 400 (Berg et al. 2016). Bull elk hunting is permitted within the study area east of Banff National Park in Wildlife Management Units (WMU) 416, 417, 418, 420, 316, and 318, whereas antlerless special licenses and general archery-only seasons occur in WMU 318. The area offers white-tailed deer and bighorn sheep hunting through a general season, and mule deer and moose through a special license draw. The local population of feral horses are present year-round and grazing leases permit free-ranging cattle (*Bos taurus*) during the summer and fall in the eastern portion of the study area.

Carnivores that occur in the study area include wolves, coyotes, red fox (*Vulpes vulpes*), cougars, grizzly and black bears, lynx (*Lynx canadensis*), and mustelids (Steenweg et al. 2015). Wolves in the area have increased since the 1970 and numbers likely remained stable between the mid 1980s and the early 2000s (Hebblewhite 2006). Although local cougar population numbers are not well documented, in the last two decades provincial cougar numbers have increased (Knopff et al. 2014). Wolves, coyotes, and black bears are hunted during the spring and fall the eastern portion of the study area with no bag-limit, and cougar hunting is permitted with the use of dogs and licenses are available through a quota system. Several trapping leases also cover this area and all carnivores except for cougars and bears are included as trappable furbearers. Estimates of number of grizzly bears in this general area was 4.79-5.25 bears/1000 km^2 from 2004 to 2014 (Alberta Grizzly Bear Recovery Plan 2016). There are an uncertain number of black bears in the area but estimates suggest there are approximately 49 bears/1000 km^2 in the 6 wildlife management units that cover the study area (Alberta Black Bear Management Plan 1993).

METHODS

We derived a fine-scale map of relative predation risk to elk in two steps. First, we derived metrics of relative intensity-of-use (*IU*) based on data from remote cameras, resource selection functions (RSF) based on where scats were found compared to random locations along transects, and then combined these to derive a RSF-adjusted metric of predator relative use (*RU*) for each predator. Second, to assess which of these metrics had the potential to best reflect elk predation risk at a location, we modeled the relative probability of a location being a kill site of either an adult female or calf elk compared to available sites as a function of the three predator distribution metrics using model selection approach (Burnham and Anderson 2002). In modeling predation risk, we assessed the effect of other predators on a focal predator's habitat selection and on kill site locations.

Intensity-of-use

We used the frequency of photographic events from remote cameras (n=54) placed within separate cells of a 5x5-km grid across the study area from 1 May – 30 September in 2013 and 2014 (Steenweg et al. 2015) as a broad-scale metric of intensity-of-use (*IU*) of predators. Cameras were set to operate 24-hr per day and were located on trails in areas that were expected to receive the greatest use by wildlife in the 25-km^2 cell. We assumed the bias associated with trails was consistent throughout the study area within a species. Additionally, a comparison between cameras located on trails and cameras baited with a scent lure located off-trails (deployed in years 2011 and 2012) showed no significant difference between mean number of camera events (Steenweg et al. 2012).

Camera events were defined by the number of predators captured within the field of view of the camera and cameras were set with an image delay of 5 minutes. However, because cameras were not operating simultaneously due to battery loss or camera malfunction, we used number events/active trap days to standardize the index for sampling effort over the 1 May – 30 September sampling period (O'Brien et al. 2003). We compared the mean IU values (events/day) for all pair-wise combinations of the 4 predator groups using a Kruskal-Wallis test pairing species by camera site. We used a contagion index (Li and Reynolds 1993) to assess the clustering of camera sites that recorded at least one event of each species.

Instead of extrapolating the *IU* homogeneously within 5 x 5-km cell in which a camera was located, we assumed that topography would most influence predator movement. Therefore, we created Thiessen polygons using least-cost distance based on terrain ruggedness (Riley et al. 1999) rather than Euclidean geometry around each camera site and assumed *IU* reflected the resistance to predator use. Terrain ruggedness was calculated for each 30 x 30-m cell as difference in elevation from every cell and the mean elevation of the 8 adjacent cells.

Resource Selection Functions

Scat Sampling

We used scat-detection dogs to sample predator scats along sampling transects allocated to 57 5 x 5-km grid cells from 18 July to 22 September 2013, 2 July to 12 September 2014, 7 July to 15 September 2015 and 1 August to 30 August 2016. Data collected from 2014-2016 were used in model development and data collected in 2013 were used for model validation because collection methods and study design were being developed in 2013. We established 1 July as the start date, which allowed us to sample scats deposited during the elk calving season (May-June). An end date of 30 September allowed us to finish the sampling season before snow accumulated at high elevations, which may have altered animal distributions and hindered our ability to detect scats. Transects were plotted and then adjusted to ensure they covered a variety of habitat conditions based on land cover classification maps (ABMI 2010) and followed different routes among years and in individual cells; however, due to the difficult topography the actual survey routes differed from the mapped survey routes. Still, final coverage of the main land cover types generally did not differ from the study area by more than ~6% (percentage points) for landscape variables other than bare rock/ice at elevation >2000m, which differed in the transect from the overall study area by 18% (Appendix 2.1). Due to the difficult logistics in sampling these areas, and because we rarely found radio-collared elk in this habitat (<0.01% of 634,004 locations of over 300 collared elk, summers 2002—2016), we omitted these areas from our predation risk analysis and restricted the available area in producing our predator RSF (see next section). Approximately one third of the final transect length was located on major human use trails, one third on animal trails, and one third off-trail.

Four dog and handler teams were used for scat surveys. Three teams were trained at Conservation Canines at the University of Washington. The fourth team was trained under the guidance of Conservation Canines. During 2015, detection abilities of two of the teams were subject to blind-trails to assess scat detection across habitats using scats sourced from the study area and under typical field conditions; both teams detected >90% of the scats in the trial (see Appendix 2.4 for details). Surveys were not conducted under hot conditions (>25°C), high winds, or heavy precipitation because these conditions significantly reduce a dog's scenting ability (Reed et al. 2011). Handlers rested dogs frequently to avoid over-exerting the dog and compromising the dog's scenting ability.

When a scat was detected along a transect, a GPS location was recorded and the age of the scat was visibly classed in one of 4 categories from fresh to very old following Wasser et al. (2004, Appendix 2.5). We used age classes (i.e., number of days since deposition) to remove scats found during the survey that were thought to be deposited before to our timeframe of interest. We discarded scats when subtracting the mid-point of the age class (Appendix 2.4) from the date of collection indicated the scat was deposited prior to 1 July. We recorded scat diameter and physical description to identify the scats to species (Weaver and Fritt 1979; Rezendes 1992; Elbroch 2003) and supplementary natural sign such as tracks. We also collected DNA on scats to assess and improve the accuracy of our species identification procedures, and used these data to modify the criteria for distinguishing species identification in the field between species (see Appendix 2.5 for details).

We used a minimum-distance criterion of 10 m for coyotes and wolves to consider scats independent samples because canids are known to use scats for intraspecific communication (Peters and Mech 1975) and scats may be from multiple individuals within a pack marking the same location at the same time. We did not use a minimum-distance criterion between locations of bear and cougar scats because of the solitary nature of these predators and due to the processing time between digesting and excreting a scat, we assumed that scats of an individual in close proximity would retain some temporal independence.

Modeling Resource Selection

We developed RSFs for wolves, coyotes, cougars, and bears following Johnson et al. (2006), where ‘used’ samples were the locations of scats along transects and ‘available’ samples were random locations in a ratio of 10 random points to every scat location placed within a 50-m buffer on each side of the survey transects to reduce any discrepancies between what was surveyed and what was considered available. Fifty meters was also the approximate effective detection distance of dogs working along a transect (Appendix 2.7). We did not develop RSFs for black bears and grizzly bears separately because of low field-identification accuracy to species for bears (grizzly bear = 65%, black bear = 0%; Appendix 2.6.2). Overall, random locations were generally representative of the range of environment covariates with the exception of bare rock/ice. We assumed used and random points were normally distributed along environment covariates (Appendix 2.8). We used an exponential RSF fitted using logistic regression:

$$w(x) = exp\left(\beta_i x_i + \beta_j x_j + \cdots \beta_z x_z\right)$$

where $w(x)$ is the relative selection of a 30 x 30-m pixel based on scat location and β_i are selection coefficients based on variables x_i. Prior to modeling, we tested for collinearity among variables ($r > 0.6$, Appendix 2.9) and correlated variables were not entered into the same model. We then applied the full set of candidate environment variables and interactions to each species and used a model selection framework based on $\mathrm{AIC_c}$ calculated as:

$$\mathrm{AIC_C} = \mathrm{AIC} + \frac{2\mathrm{k}(\mathrm{k}+1)}{\mathrm{n}-\mathrm{k}-1}.$$

to arrive at best supported RSFs (Burnham & Anderson 2002). We used a conservative criterion of 4 ΔAIC points in distinguishing competing models to increase confidence that potential explanatory variables would not be excluded during model selection (Burnham & Anderson 2004). In the case of competing models, we selected models comprised of variables with confidence intervals that did not overlap 0.

Landscape Covariates

We related selection to variables associated with terrain, land cover, and anthropogenic features (Table 2.1) that were hypothesized to influence selection by predators (Appendix 2.10). We measured landcover variables (vegetation type, greenness, forest fires, cutblocks) as mean proportion of 30 x 30-m (900 m^2) pixels within a 1.3-km radius (5.3 km^2) buffer around a scat or random location. This buffer size reflected the movement of black bears in a 24-hr time period (Amstrup and Beecham 1976, Garshelis 1978, Garshelis et al. 1983), and was chosen because it represents the shortest 24-hr movement distance among the predator species included in the study based on a literature review of their movements. Use of vehicle-restricted trails by a predator was input as a categorical variable where scats or random points within 30 m of a trail were considered on-trail and those further than 30m were off-trail. The remaining variables (proximity to roads, off-highway vehicle trails, waterways) were measured as shortest distance (m) to the nearest feature.

Evaluation of RSFs

We evaluated the scat-based RSF in three ways. To assess the relationship between selection and intensity of use, we first assessed the ability of the scat-based RSF to predict events detected at remote cameras. For this, we correlated the number of events of a predator species to mean 30 x 30-m RSF values at 4 scales: the terrain based-polygons, and the mean within a 50, 250, and 500-m radius around the camera. Second, we evaluated the scat-based RSFs for being proportional to the occurrence of both within-sample and out-of-sample scats on the landscape following the general approach of Johnson et al. (2006). However, we did not use the iterative k-fold approach of withholding a testing data set and redeveloping the RSF. Instead, for in-sample scats, we plotted the proportion of observed scats relative to expected proportion of the species specific scats in the entire data in 10 equal area bins. We used the mean RSF value for each bin to assess the overall relationship between selection and scat occurrence. Our out-of-sample scats were collected during the 2013 sampling session and were not used in producing our RSFs. The fit of a straight line between the observed and expected proportion of scat indicates that the scat-based RSF makes a prediction that is proportional to the occurrence of a predator scat.

Third, we compared the predicted scat-based RSF value for a 30 x 30-m pixel for the same pixel from RSFs derived from locations of GPS-collared wolves and grizzly bears at a random set of points (n=1000) distributed across the study area except for high elevation (>2000m) bare rock or ice. For wolves, we used the RSFs for night and day derived by Hebblewhite et al. (2005) that were based on 15 GPS-collared wolves (representing 5 packs) from data pooled for summers 2002 to 2004 because there was no more recent RSF for wolves in this area. We averaged the RSF predictions for night and day applied to landscape conditions in summers 2013 to 2016. The telemetry-based RSFs did not have the exact same metrics of variables as those in the scat-based RSF. Nevertheless, each model included similar components of topography, landcover classes, and proximity to main waterways and linear features. Both wolf RSFs were scaled linearly to provide values between 0-1.

We also compared scat-based RSF predictions for bear selection to that of a RSF derived from GPS-collared grizzly bears (n=9: 6 females, 3 males; Nielsen et al. 2002) and applied to landscape conditions for 2013 to 2015. Telemetry-based grizzly bear RSF values were scaled from 0-1, then aggregated into 10 classes based on approximately equal area representation

(Nielsen et al. 2002). We evaluated predictions for the seasons of hypophagia (~15 April - 14 June), early hyperphagia (15 June - 07 August), and late hyperphagia (08 August to denning) by using the average prediction value across seasons. We justified this comparison because there was no other RSF for bears in this region and we estimated about 85% of bear scats used for developing the scat-based RSF were from grizzly, even with the uncertainty in correct classification (Appendix 2.6.2). Further, although black bears may avoid grizzly bears in some areas (Mowat et al. 2005) they tend to select similar landscape features (Appendix 2.10). We conducted Spearman rank correlations for telemetry-based vs. scat-based RSF for the 1000 sample points, but present smoothed graphs based on the means of 10 equal-area bins of RSF values. Using 10 bins allowed for sufficient characterization of the nature of the relationship between increasing RSF values between models.

Predator interactions: Habitat selection

To investigate whether habitat selection of a target predator species was influenced by the presence of other species, we compared the top RSF model for each predator (landscape model) to models incorporating the presence of other predators in a model selection framework using AIC_c to compare the weight of evidence for competing models. The presence of other predators was measured as number of scats from other predators within a 1300-m radius of the target scat. Because our transects did not follow straight paths, we then adjusted the number of scats from each species by transect length within each 2600-m diameter circle around each scat (represented as #scats/transect meters).

Relative Use

We estimated the relative use (RU_{ij}) for each 30 x 30-m cell (i) within each polygon (j) using the scat-based, species-specific RSF predictions for the cell following Boyce and McDonald (1999).

This was based on the simplifying assumption that intensity-of-use (IUj) among polygons was independent. RU_{ij}, which is the estimated relative use of a cell i in polygon j was derived as:

$$\mathrm{RU}_{(\mathrm{ij})} = \mathrm{IU}_{\mathrm{j}} * \frac{w_{ij}}{\sum_{i}^{n} w_{ij}}$$

where IU_j is the intensity-of-use for polygon (j) based on events data from the camera data, and $w_{(ij)}$ is the scat-based selection value of cell i in polygon j. Because all cells are of equal size (30x30 m) and we sum w_i across all cells in a polygon, we have explicitly incorporated the weights of availability (A_{ij}) as noted by Boyce and McDonald (1999). This assumes that relative use in one polygon is independent of the others.

Spatial Predation Risk

To determine whether intensity of predator use (*IU*), resource selection (RSF), or relative use (*RU*) most closely reflected predation risk, we modeled kill sites of adult and calf elk in 2 sets. Our first predation risk model (hereafter, PR_1) compared calf and elk kill sites to random locations as a function of each metric either alone and with additional landscape covariates. We also evaluated the presence of other predators or landscape variables for calf or elk kill sites known to be caused by either bears ($\mathrm{PR}_{2\mathrm{Bears}}$) or wolves ($\mathrm{PR}_{2\mathrm{Wolves}}$) to differentiate age-specific risk by the primary predators of the YHT elk herd.

Elk kill sites

Elk kill sites were locations of dead collared and uncollared (n = 44 adult females, n=36 calves) elk killed by predators between 1 May and 30 September 2002-2016. Uncollared elk were found opportunistically or by tracking radio-collared wolves (Hebblewhite et al. 2005) and adult elk with VHF/GPS collars were found when on mortality mode. Dead elk calves were located following mortality signals emitted from GPS collars of adults, tracking VHF-ear tags on calves, or were opportunistic finds. Once dead elk were located, investigators searched the area around the kill sites for evidence (scats, tracks, hair) of the predator to identify predator-specific mortality. Kill sites without identifiable sign or sites with sign from >1 predator were classified as unknown predator kill sites.

Modeling locations of elk kill sites

We produced 2 sets of models based on subsets of elk kill-sites to predict predator mortality risk at a site (30x30-m cell). In our first risk model (PR_1), we used all predator-caused mortality sites (n= 138), including elk kill sites of unidentified predators (n=136). This model represented the predation risk to an elk from any predator. We used a multinomial logistic regression that compared locations of random sites (0) with mortality sites of calf (1) and adult elk (2) with our 3 metrics of predation risk based on predator distribution (RSF, *IU*, *RU*) as well as landscape features that we hypothesized would influence prey vulnerability at a site (Appendix 2.9). Landscape variables that were already in the predator RSF as a predictive variable were not used in the same model as the RSF. We used only the variables with parameter coefficients (βs) whose confidence limits did not overlap 0 to assess whether distributions of other predators influence the effect of a variable on selection (i.e., interactions terms within the model). We used AIC_c to guide our model selection. We considered inclusion of an interaction between predators as evidence of spatial interactions between predators during the mortality stage of predation risk. The top model was used to map age-specific predation risk to elk, assuming that our sample of elk mortalities reflect the relative predator-specific kill rates.

For our second set of mortality risk models, we used logistic regression to compare mortality sites of elk calves (0) and adults (1) only, in 2 separate models where kill sites were known to be caused by either bears (PR_{2Bears} n=54) or wolves ($PR_{2Wolves}$ n=26). Kill sites by each predator were modelled as a function of predator search metrics (RSF, *IU, RU*) with or without additional environmental covariates. The intent of this analysis was to contrast factors influencing locations of calf and adult female elk mortality from their primary predators: bears and wolves. Due to low sample size by age class, we used a maximum of 2 variables per candidate model. Again, landscape covariates occurring in predator RSFs were not used in the same candidate model as the RSF.

RESULTS

Intensity-of-use

Of the 153 sampling days between 1 May and 30 September, the remote cameras functioned on average for 93.3 ± 34.4 days (±SD) in 2013 and 97.6 ± 29.5 days in 2014, recording a total of 1991 predator events. Wolf events/day at camera sites averaged almost 4x that of bears, 5x more than coyotes, and 10x more than cougars across the 2 years. Based on pair-wise comparisons, these differences in events/day were significant (Kruskal-Wallis, $P > 0.01$) except between cougars and coyotes (Appendix 2.11). Bears and wolves were detected at least once at about twice as many cameras as coyotes and cougars, and cameras with at least one event of coyotes and cougars were more clumped than camera sites detecting wolves and bears (Table 2.2). Terrain-based least cost polygons sizes around cameras (n=54) averaged 26.4±12.7 km^2 (Fig. 2.2).

Resource Selection Functions

Scat Sampling

We surveyed 183 km of scat transects (10.8±6.6 km/cell, n=17) in 2013, 652 km (13.6±4.4, n=48) in 2014, 405 km (9.2±5.3, n=44) in 2015 for all predator groups, and 82 km (5.1±5.0 km, n=16) only for cougar scats in 2016. We detected 470 wolf, 373 bear, 223 coyote, and 42 cougar scats that were within our scat-age classification.

Resource Selection Analyses

In all species, our chosen top selection models were better supported than both their respective null models and the full candidate model with 13 variables (Appendix 2.12). For bears, there was equal support (ΔAIC < 4) for 2 models that differed by the inclusion of percent of area in cutblocks. We chose the model including cutblocks as the top model because the confidence limit of the coefficient for cutblocks did not encompass zero (Table 2.3). Bears selected against conifer forest areas, for areas with cutblocks and of high NDVI, steeper slopes, further from vehicle-permitted trails and roads, and for categorical use of vehicle-restricted trails, particularly with increased distance from vehicle-permitted trails. (Table 2.3). There was equal support for 4 models describing resource selection for wolves, which differed based on the inclusion of either edge, grassland or both (Appendix 2.12). Wolves selected to be near waterways, in areas with less slope, further from vehicle-permitted trails and on vehicle-restricted trails (Table 2.3). For coyotes, there were 5 models that had equal support, all of which included areas with decreased slope, areas further from vehicle-permitted trails and selection for the use of vehicle-restricted trails. (Appendix 2.12). Areas with a higher percent shrub cover were also included in our chosen model because it was the only additional variable in the candidate set with confidence limits that did not overlap 0 (Table 2.3). For cougars, 3 models had equal support for predicting resource selection (Appendix 2.12). We chose the model predicting selection for areas with less conifer forest cover and higher edge density because the confidence limits of only these 2 variables did not overlap zero. Maps of predicted selection values standardized within species for each predator are given in Fig. 2.3.

Evaluation of RSFs

Mean scat-based RSF values were not significantly correlated with camera events based (IU) within the terrain-based polygons or local buffers with the exception of wolves at the scale of 500 m (r = 0.32 P=0.01). The observed and expected proportion of scats within the 10 equal-area RSF bins were not proportionally related, but it was clear that scats were found primarily in areas of high scat-based RSF values not only for the within-sample but also out-of-sample (2013) observations (Fig. 2.4 and Fig. 2.5). Summer scat-based and radio-collar based RSFs values were correlated for wolves (r= 0.18, P <0.0001, n=1000), and bears depending on season (r = 0.17-0.25, P <0.001, Fig. 2.6). Although the respective RSF values were not linearly related, if aggregated to into 10 bins, rank correlations of the mean RSF bin values indicated much higher correspondence (wolf: r_s =0.92, P <0.0001; grizzly bear: (r_s =0.68, P <0.0001).

Predator Interactions: Habitat selection

The wolf RSF showed positive selection for areas with a greater number of bear scats but the relationship was not reciprocal (Table 2.4). The coyote RSF model was improved by 4 candidate models, of which contained areas with more bear scats (Model 10, Table 2.4), wolf scats (Model 11), and areas with either bear or wolf scats (Model 13). An interaction effect showed negative selection by coyotes for areas with higher numbers of both bear and wolf scats, although confidence intervals for the interaction overlapped 0 (Model 14). The cougar RSF and bear RSF were not improved by the presence of other species' scats.

Relative Use

The effect of very low or zero *IU* values (Fig. 2.2) was apparent with large sections of the study area receiving very low *RU* values, particularly for coyotes and cougars (Fig. 2.7). *RU* polygons that had intermediate *IU* values were more heterogeneous and visually displayed differences in selection seen in RSF maps (Fig. 2.3). A single polygon in the south-east portion of the study area had very high *IU* values for both bears and coyotes, which translated into very high *RU* values despite mid-range RSF values for the same area. Two polygons in the western portion of the study area received homogeneously high *RU* values, although both RSF and *IU* values were very high for the same area.

Spatial Predation Risk

Elk Kill sites

Of known-predator kill sites, the large majority of calf kills were caused by bears (74%) and the majority of adult elk sites were caused by wolves (67%; Appendix 2.13). Only 1 bear-caused and 1 unknown-predator kill site were within Banff National Park, both located in close proximity to the Red Deer River. Nearly 90% of all calf kills were within the boundary of the Ya Ha Tinda ranch, with the highest clustering of kills in the eastern portion of the ranch and concentrated between the confluence the Red Deer River and 2 important tributaries, Scalp Creek and Bighorn Creek. A smaller group of calf kills were located east of the ranch, near the confluence of the Red Deer and Panther Rivers. The remainder of the calf kills were in close proximity to the north border of the YHT along Scalp and Bighorn Creeks, with two bear kills and one unknown-predator kill in locations not fitting the above general descriptions. Adult elk kill sites followed a similar distribution pattern as calf kills, except with 9 more kill sites located in Banff National Park.

Models of elk kill sites

In both sets of predation risk modelling and among all 4 predator groups, resource selection was found to be a stronger predictor of the location of an elk kill than either the intensity-of-use or relative use models, although *IU* and/or *RU* of each predator did show improvement in AIC_c

scores over the null model (Appendix 2.12). Wolf and coyote RSF values were correlated (r^2 =0.72; Appendix 2.14). Because the wolf RSF values had stronger predictive strength than coyote RSF values in both sets of PR models, we developed our models without coyote RSF as a variable.

For our multinomial (PR_1) model, two candidate models had equal support ($\Delta AIC_c < 4$; Table 2.5) with the difference between models being the inclusion of wolf *IU* as a variable. Because wolf *IU* had beta coefficients overlapping 0 for calves and we found that wolf *IU* values was related to mean wolf RSF values 500-m scale, we chose the more parsimonious model based only on RSFs. The RSF of bears, wolves, cougars, and an interaction between wolf and cougar RSFs were in the remaining top model as predictor variables (Table 2.6). Beta coefficients indicated both adult and calf kill sites were more likely to occur in areas of lower bear RSF values and higher wolf RSF values. In contrast, calves were more likely to be killed in areas of higher cougar RSF while adults were less likely. An interaction effect between areas of high wolf and high cougar selection shows that these areas increase likelihood of a calf elk kill site beyond the individual RSF effects; however, for adult kill sites confidence intervals did not overlap 0 so we do not consider the interaction to be well supported for adult elk.

The set of models depicting the difference in predation risk to calves and adults by either bears or wolves both had a range of variables in their respective candidate models, although each species own RSF was the only candidate model without component variables that had confidence intervals not overlapping zero (Table 2.7). Both RSF variables had positive coefficients indicating a higher likelihood of adult elk being killed in areas selected for by bears or wolves than calf elk.

Predictive maps of predation risk

The resulting predictive maps showed predation risk to adults was concentrated to the west, on vehicle restricted trails, and in valley bottoms along important waterways (Fig. 2.8). Risk to calves was similarly higher in closer proximity to important waterways but values increased in a west-to-east gradient and risk on vehicle-restricted trails was lower for calves than surrounding areas (Fig. 2.8). Risk to calves was also higher in closer proximity to vehicle-permitted trails/roads than was risk to adults, creating risk hotspots for calves in areas with both roads and waterway confluences. Specifically, these areas are within the YHT ranch boundary and at the confluence of the Red Deer River and Panther River.

DISCUSSION

Contrary to our expectation, we found scat-based RSFs consistently better predicted kill locations than camera-derived *IU* across the broad-scale or adjusting use with small-scale selection (*RU*). Intensity of use may not reflect predator use because the cameras were originally deployed for an occupancy survey based on the 5 x 5-km grid cell design, which is likely too coarse of a scale to extrapolate across the entire polygon. As well, cameras were placed on trails, which cougars tend not to use (Steenweg et al. 2015). Limited trail use by cougars is also supported by the RSF results in this study. Further, selection for trails by top predators can reduce the detection probability at a camera location of sub-dominant predators (Wang et al. 2015, Ramesh et al. 2017) increasing variability. Combining observations of both species of bears may also have added variability that did not represent species-specific use. Nevertheless, IU maps did reflect high use by wolves on the east side of the study area and on the YHT ranch, which are areas where wolf use was expected to be because 2 active den sites were reported (Hebblewhite 2006). Whether these den sites were active during the study is unknown, but whereas site-fidelity for specific denning sites are reported for only several years they tend to remain associated with high densities of prey (Fuller 1989, Capitani et al. 2006). Less is known about coyotes in the area to assess the reliability of camera data to measure patterns of relative intensity of use.

We found that RSF values alone best predicted kill site locations among predators with little influence of other variables that might also reflect additional factors influencing attack success. The most consistent factors influencing predator selection was the effect of human-used roads and trails, which has been reported elsewhere in montane systems (Brodeur et al. 2008, Nielsen et al. 2009, Musiani et al. 2010, Wasser et al. 2011). In comparison to RSFs created for radio-collared wolves (Hebblewhite et al. 2008) and for grizzly bears (Nielsen et al. 2002) that used distance to trails as a candidate variable, the RSF we developed here reflected high selection for use of trails as a categorical variable which may have contributed to the non-linearity between the predictions of these different RSFs. Hebblewhite (2006) also found positive selection for cutblocks by wolves whereas our models showed selection against areas with cutblocks, which may be because of a considerable increase in logging activity within the decade between scat collection and the wolf GPS data collection (Hebblewhite 2008). Similarly, Boisjoly (2010) found that coyotes in eastern Quebec also selected for cutblocks where we did not see any influence. The authors attributed coyote selection for cutblocks to be a result of higher fruiting groundcover and greater likelihood of containing ungulate carrion. In our study area, grasslands and burned areas provide canopy openings for fruiting groundcover and we would expect that carrion availability would be associated with the distribution of the primary predator of adult ungulates, which would be wolves that select against areas with cutblocks. Cougar selection was similar to Knopff et al. (2014) but a higher proportion of very rugged terrain and lower density of anthropogenic development in our study area likely resulted in these landscape characteristics not occurring in our models.

We found some evidence that predator selection was influenced by other predators as reported in the literature (Bartnick et al. 2013, Lendrum et al. 2014, Elbroch et al. 2015, Droge et al. 2016). As a meso-predator, it is likely that coyotes benefit from scavenging from larger predators as ungulate carrion represents an important resource in this system. The negative selection by coyotes for areas with both high wolf and bear scats suggests that they may avoid areas that require mitigating threat from more than one dominant predator. Wolf selection for areas with more bear scats indicates that spatial avoidance between these predators is not occurring. These results could be the result of being restricted to certain areas due to topography but if this were the case we would not have expected to see strictly one-way relationships. We suspect that where wolf and bear scats co-occur are highly productive areas for both predators, such as calving grounds, rather than wolves selecting areas based on the presence of bears.

Wolf and bear-specific kill site models both showed calf elk kill sites are more likely than adult kill sites to occur in areas with lower RSF values of the respective predators. A possible explanation for this is that cow elk mitigate risk from wolves and bears by selecting calving areas that these predators are not as likely to use. Bears, in particular, are effective predators of neonatal ungulates on calving grounds (Zager and Beecham 2006, Barber-Meyer et al. 2008) and kill a greater proportion of calves than adults in comparison with other predators at the YHT (Berg et al. 2016). However, they tend to be major predators on elk calves shortly after calving (~1 month; Rauset et al. 2012, Zager and Beecham 2006, unpublished data, J. Berg). Therefore, kill sites of calves are less likely to occur in areas with higher bear RSF because the RSFs are derived from scats collected over 5 months when bears are primarily herbivorous (unpublished data, MacAulay). Bear behaviour over this time period is more likely to be influenced by vegetation dynamics (i.e. berry production and green-up) than elk behaviour. In contrast, wolves are responsible for the majority of adult elk kill sites and have been considered the primary predator of the YHT elk herd (Hebblewhite and Merrill 2007, Berg et al. 2016). Foraging—predation risk trade-offs are amplified in habitat selection for birth sites and during the first few months post-parturition because of increased energy requirements during lactation (Cook et al. 2004) and vulnerability of calves (Barber-Meyer and Mech 2008, Rearden et al. 2011). Studies have found that site-selection for parturition and rearing are more influenced by forage availability than predation risk, although each has taken place in systems with less diverse predator communities (grizzly bears, wolves: Bowyer et al. 1999; cougars, black bears, coyotes: Rearden et al. 2011) or used simple cover and visibility metrics as proxies for predation (Bowyer et al. 1999). Interactions among wolves and cougars resulted in increased risk to calf elk beyond the distribution metrics of the individual predators alone. We suspect that this is because calves are generally more vulnerable than adults. Even if cows reduce encounter rates through selecting birth sites and rearing habitat in less-risky areas, as the pair moves across the landscape and enters areas with higher risk calves will be more susceptible to a successful attack.

Selection by bears and wolves for areas in the west and cougars in the east provides preliminary evidence supporting that differential predation may play a role in the observed shifts from elk migrating in summer into Banff National Park to migrating east onto industrial forest lands. Bears and wolves appear to be the primary predators on both adult elk and calves (Eggeman et al. 2016, Berg, unpublished data). Adult elk that migrate west into BNP have a higher incidence of being killed by bears (Berg et al. 2016), and while this may be true of elk calves, documenting calf mortalities in BNP have been limited by its remoteness. Alternatively, bears may use low elevations during calving and shift their distribution to high elevation in summer (McLellan and Hovey 2001). Cougars, which select areas east of YHT likely present lower risk to adult elk than bears and wolves because although male cougars will specialize on elk, deer are the major component of cougar diets in this in this region (Krawchuk 2014). Results of this study also provide evidence that most predators avoid human infrastructure, indicating that predator refuges may exist east of YHT because of the higher density of roads, recreational trails, and buildings in this area. On-going studies of cow elk habitat selection and survival of their calves (J. Berg) may provide a direct link between predator distribution documented in this study and the consequence to elk populations.

Table 2.1. Landscape covariates used in developing resource selection functions or predation risk models for 4 predator groups on the eastern slopes of the Alberta Rocky Mountains. All variables were sourced from the Alberta Biomonitoring Institute.

Variable	Code	Description	Units	Resolution (m)	Analysis scale	Year of Data
Elevation	Elev	Digital elevation model (DEM)	m.	30 x 30	900m^2	2010
Slope	Slope	Elevation difference between 8 neighboring cells	m.	30 x 30	900m^2	2010
Ruggedness	Rug	SD of elevation among each cell and 8 neighbouring cells, linearly transformed 0-1	0 - 1	30 x 30	8100m^2	2010
Conifer forests	Conifer	Treed areas with >10% canopy cover and species composition >75% coniferous	%[a]	30 x 30	5.3km^2	2010
Mixed & deciduous forests	Mixed	Treed areas with >10% canopy cover and species composition <75% coniferous	%	30 x 30	5.3km^2	2010
Shrub	Shrub	Areas with >10% ground cover, <10% canopy cover and >33% shrub species	%	30 x 30	5.3km^2	2010
Grassland	Grass	Areas with >75% grass species	%	30 x 30	5.3km^2	2010
Alpine vegetation	Alpine	Shrub and herbaceous cover above treeline	%	30 x 30	5.3km^2	2010
Forest edge	Edge	Areas within a 30-m buffer of a conifer or mixed & deciduous forest interface with any other landcover typef	%	30 x 30	5.3km^2	2010

Forest fire regeneration	Fire	Year of fire 2000-2016	%	30 x 30	5.3km^2	2010

Table 2.1. (continued)

Cutblock density	Cut	Year of timber harvest, 1984-2015	%	30 x 30	5.3km^2	2014
Greenness	NDVI	Normalized Differentiated Vegetation Index derived from a TM Landsat image taken on 28 July	-1 to 1	30 x 30	5.3km^2	2014
Distance to water	DisWat	Water includes perennial streams, rivers, and lakes	m.	30m	--	2010
Distance to OHV trail/road	VP_rd	Off-Highway Vehicle (OHV) permitted trails and roads	m.	30m	--	2014
Distance to road	Dist_rd	Public-use gravel roads	m.	30m	--	2014
Trail use	Trail	Categorical variable: ≤30m straight line distance of a trail (1, on trail) or >30m from trails (0, off trail)	0/1	30m	Distance of 30 m	2014

Table 2.2. Mean, standard error (SE), maximum (Max.) intensity of use (*IU*), number and percent of cameras within at least one event, contagion of index reflecting aggregation of cameras sites with at least one event by predator groups, east slopes of Rocky Mountains, Alberta, Canada. *IU* is based events on remote camera (n=54) from 1 May – 30 June combining data across 2013 and 2014. Different superscripts indicate significant differences between species (Appendix 2.11).

	Mean IU			Cameras with ≥1 event		
	$\bar{x}$	SE	Max.	No	(%)	Contagion index
Bear	0.033^{b}	0.04	0.19	48	89	73.12
Wolf	0.112^{a}	0.23	1.52	46	85	71.68
Coyote	0.020^{c}	0.04	0.25	28	52	48.94
Cougar	0.009^{c}	0.02	0.12	22	41	49.74

Table 2.3. Beta coefficients (β), upper and lower 95% confidence interval (CI), based on AIC$_c$ for the top resource selection functions for 4 carnivores, east slopes of the Rocky Mountains, Alberta, Canada.

			95% CI	
Species	Variable	β	Lower	Upper
Bears	Conifer forests	-0.71	-0.19	-1.23
	Cutblocks	0.84	0.23	1.45
	NDVI	0.0002	0.00007	0.00033
	Slope	0.02	0.2	0.4
	VR trail use[a]	0.86	0.41	1.31
	Distance to VP trail/road[b]	0.00005	0.00003	0.00007
	VR trail use*Distance to VP trail/road	0.00005	0.00001	0.00009
Wolf	Distance to water	-0.0001	-0.00005	-0.00015
	Cutblocks	-2.47	-0.46	-4.48
	Slope	-0.04	-0.02	-0.06
	VR trail use[a]	1.29	0.99	1.59
	Distance to VP trail/road	0.00005	0.00004	0.00006
Coyote	Shrub	2.63	0.21	5.05
	Slope	-0.05	-0.02	-0.08
	VR trail use[a]	1.62	1.27	1.97
	Distance to VP trail/road	0.00006	0.00004	0.00008
Cougar	Conifer	-1.92	-0.46	-3.38
	Edge	8.39	1.12	-15.66

[a] Vehicle-restricted trails, a categorical variable where on-trail=1, off-trail=0.

[b] Vehicle-permitted trails and roads.

Table 2.4. Predator interaction models produced for 4 carnivores. Resource selection functions (RSF) were developed for each predator using scat locations and landscape characteristics. Scats from other predators detected within a 1300 m radius of each scat were counted and corrected by survey transect density. These values were added to the RSF as an additional variable for a new candidate model. Models with < -4.0 ΔAIC were considered improvements over the RSF alone.

Model		ß	+/- 95% CI	AIC	ΔAIC
	Bear RSF[a]			1464.7	
1	Nr_[b]wolves	0.03	0.06	1465.4	0.7
2	Nr_cougars	-0.03	0.10	1465.0	0.3
3	Nr_coyotes	-0.03	0.10	1466.2	1.5
	Wolf RSF			1635.9	
4	**Nr_bears**	**0.08**	**0.05**	**1626.4**	**-9.5**
5	Nr_cougars	0.21	0.37	1635.6	-0.3
6	Nr_coyotes	0.05	0.06	1634.4	-1.5
	Cougar RSF			355.3	
7	Nr_bears	-0.05	0.18	356.6	1.2
8	Nr_wolves	-0.06	0.15	356.3	1.0
9	Nr_coyotes	-0.28	0.34	353.6	-1.8
	Coyote RSF			1041.3	
10	Nr_bears	0.09	0.07	1037.2	-4.1
11	Nr_wolves	0.10	0.06	1033.3	-8.0
12	Nr_cougars	0.07	0.52	1042.7	1.4
13	**Nr_bears**	**0.08**	**0.07**	**1031.1**	**-10.2**
	Nr_wolves	**0.09**	**0.06**		
14	Nr_bears	0.10	0.09	1032.6	-8.7
	Nr_wolves	0.11	0.08		
	Nr_bears*Nr_wolves	-0.01	0.02		

[a] See Table 2.3 for selection models.

[b] “Nr_$pred_i$” refers to scats of another predator ($pred_i$) near to each target predator scat, corrected for transect distance.

Table 2.5. Summary of model selection results based on AIC$_c$ for predation risk derived for predicting relative probability of elk kills from any predator including unknown source of predation being present at a site in the east slopes of the Rocky Mountains, Alberta, Canada. Relative selection is based on beta coefficients derived from on multinomial logistic models comparing the predictive ability of the intensity of use (*IU*), selection (RSF) or relative use of (*RU*) at random locations (0), calf (1) and adult female elk (2) kill sites. Indicated are the signs of the beta coefficient of each variable. See Appendix 2.12 for full model selection.

Model	Elk age class	Model variables	*k*	AIC$_c$	ΔAIC$_c$
1	**Calf**	**-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$+Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$**	**5**	**904.4**	**0.0**
	Adult	**-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$-Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$**			
2	Calf	-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$+Wolf $_{\text{IU}}$+Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$	6	905.3	0.9
	Adult	-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$+Wolf $_{\text{IU}}$-Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$			
3	Calf	-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$+Cougar$_{\text{RSF}}$	4	911.2	6.8
	Adult	-Bear$_{\text{RSF}}$+Wolf$_{\text{RSF}}$+Cougar$_{\text{RSF}}$			
4	Calf	-Wolf$_{\text{RSF}}$-Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$	4	963.6	59.2
	Adult	Wolf$_{\text{RSF}}$-Cougar$_{\text{RSF}}$+Wolf$_{\text{RSF}}$*Cougar$_{\text{RSF}}$			
13	Calf	Null	2	1144.9	240.5
	Adult	Null			

Table 2.6. Beta coefficients (β), upper and lower 95% confidence intervals (CI) for the top model (PR_1) parameters based on AIC_c for a multinomial model distinguishing between calf (0) and adult (1) cow kill sites from random locations based on resource selection (*RSF*) of predators on the east slopes of the Rocky Mountains, Alberta, Canada.

			95% CI	
	Variable	β	Lower	Upper
Calf elk	Intercept	-5.52	-7.19	-3.85
	$Bear_{RSF}$	-10.08	-13.02	-7.14
	$Wolf_{RSF}$	1.43	-5.54	5.11
	$Cougar_{RSF}$	0.56	-2.78	3.90
	$Wolf_{RSF}$*$Cougar_{RSF}$	13.09	6.13	20.05
Adult female elk				
	Intercept	-8.2	-13.44	-2.96
	$Bear_{RSF}$	-3.15	-8.26	-0.56
	$Wolf_{RSF}$	4.94	-3.36	13.24
	$Cougar_{RSF}$	-0.47	-8.66	7.72
	$Wolf_{RSF}$*$Cougar_{RSF}$	9.63	-3.54	22.8

Table 2.7. Summary of model selection results based on AIC$_c$ for predation risk (PR$_2$) derived for predicting relative probability of elk kills from either bears or wolves being present at a site in the east slopes of the Rocky Mountains, Alberta, Canada. Relative selection is based on beta coefficients derived from logistic models comparing the predictive ability of the intensity of use (*IU*), selection (RSF) or relative use of (*RU*) and landscape features at calf (0) and adult female elk (1) kill sites. Indicated are the signs of the beta coefficient of each variable. Variables in bold indicate confidence intervals that do not overlap 0.

Model			AIC$_c$	ΔAIC$_c$
Bears	**-Bear$_{RSF}$**	+Bear$_{IU}$	36.5	0.0
	-Bear$_{RSF}$	+Shrub	36.7	0.2
	-Bear$_{RSF}$	+Dist Wat	37.0	0.5
	Bear$_{RSF}$		37.2	0.7
	-Bear$_{RSF}$	+Grass	37.7	1.2
	-Bear$_{RSF}$	+Dist_Ranch	38.6	2.1
	Bear$_{RSF}$	+ Edge	38.8	2.3
	Bear$_{RSF}$	+Wolf$_{RU}$	38.9	2.4
	-Bear$_{IU}$		41.8	5.3
	Null		*42.5*	6.1
Wolves	**Wolf$_{RSF}$**		34.0	0.0
	-Wolf$_{RSF}$	+Edge	34.7	0.6
	-Wolf$_{RSF}$	+Grass	34.8	0.8
	Wolf$_{RSF}$	+Bear$_{RSF}$	34.9	0.8
	-Wolf$_{RSF}$	+Cougar$_{RSF}$	35.1	1.0
	Wolf$_{RU}$		35.2	1.2
	-Wolf$_{RSF}$	+Dist_Ranch	35.9	1.9
	WolfI$_{U}$		36.1	2.1
	Null		40.0	6.0

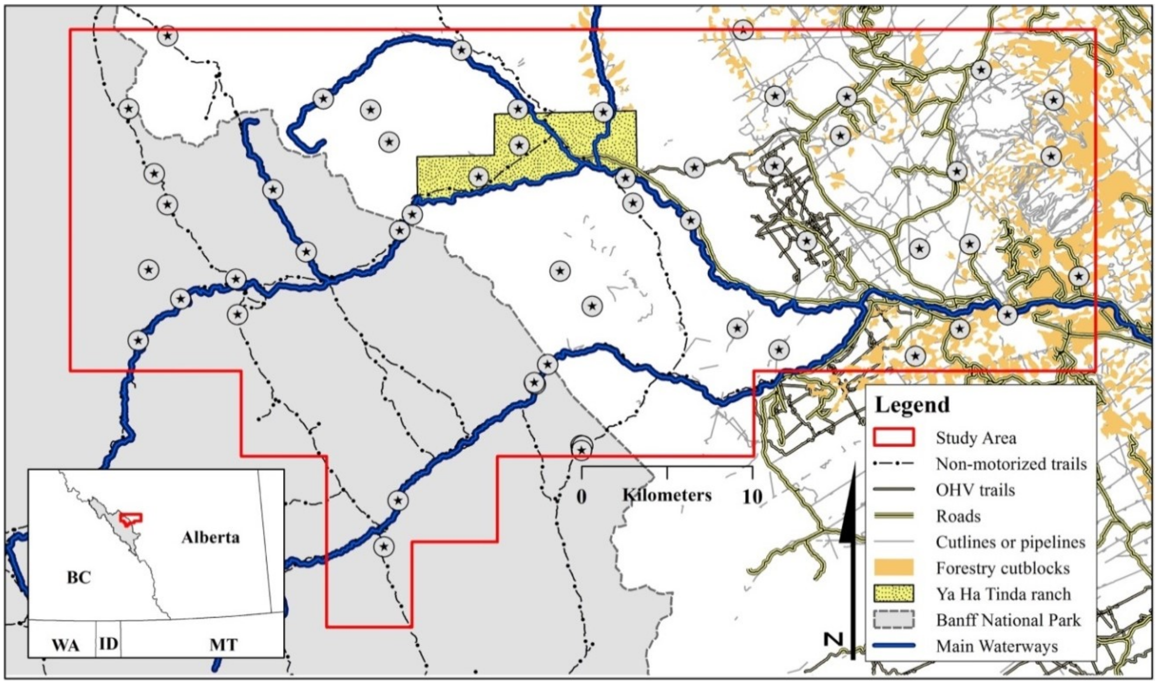

Fig. 2.1. Study area within the Red Deer River and Panther River drainages along the east slopes of the Rocky Mountains of Alberta where carnivore scats were collected from 2013-2016. Circles with stars represent remote camera sites used in 2013-2014 (Steenweg 2013).

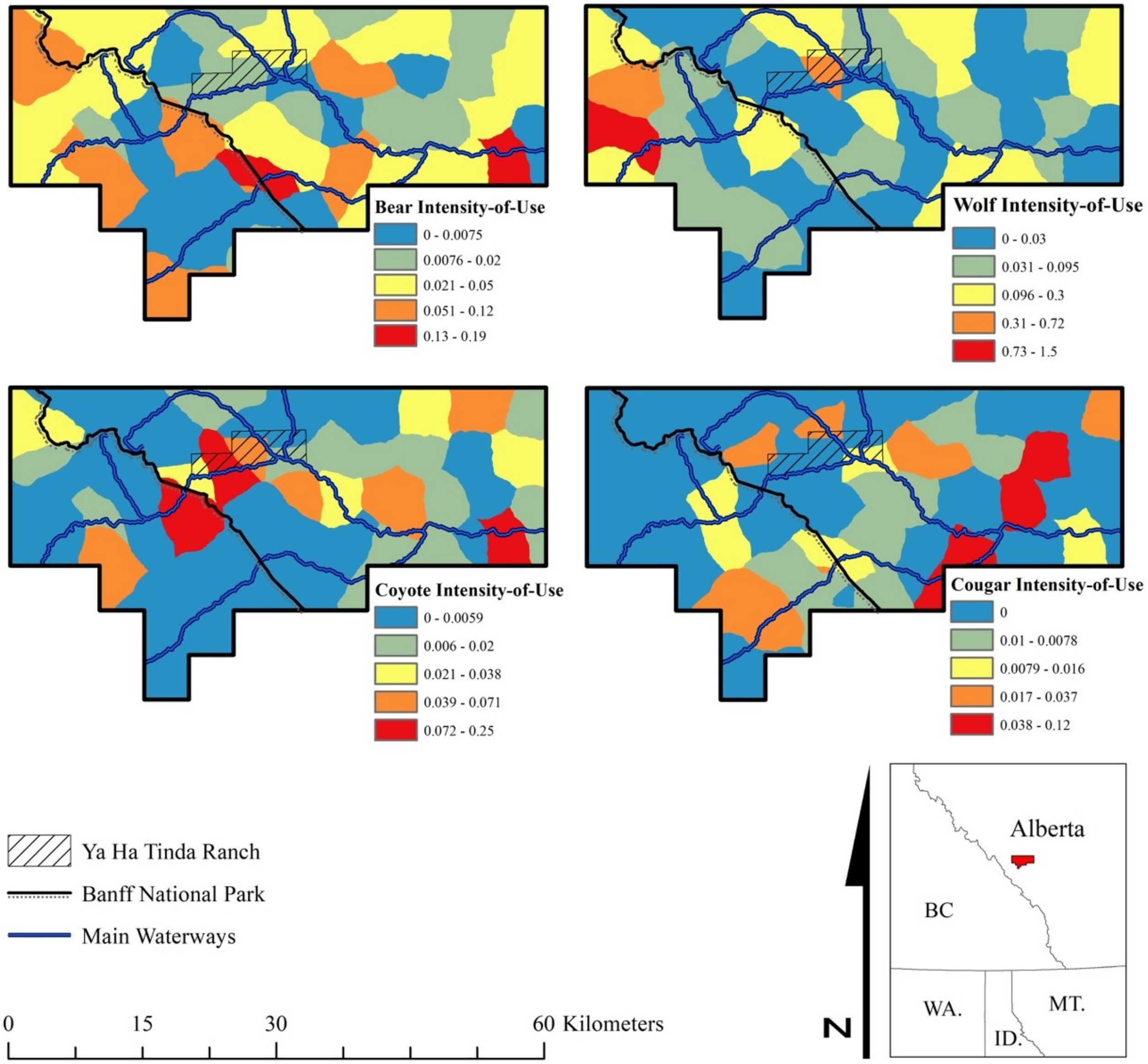

Fig. 2.2 Intensity of use (*IU*) derived from camera events (detections /active camera days) of 4 species of carnivores with terrain-based least cost polygons, east slopes of the Rocky Mountains, Alberta. For display, colors of use classes across species were based on natural breaks (Jenks) in the range of *IU* values specific to each predator.

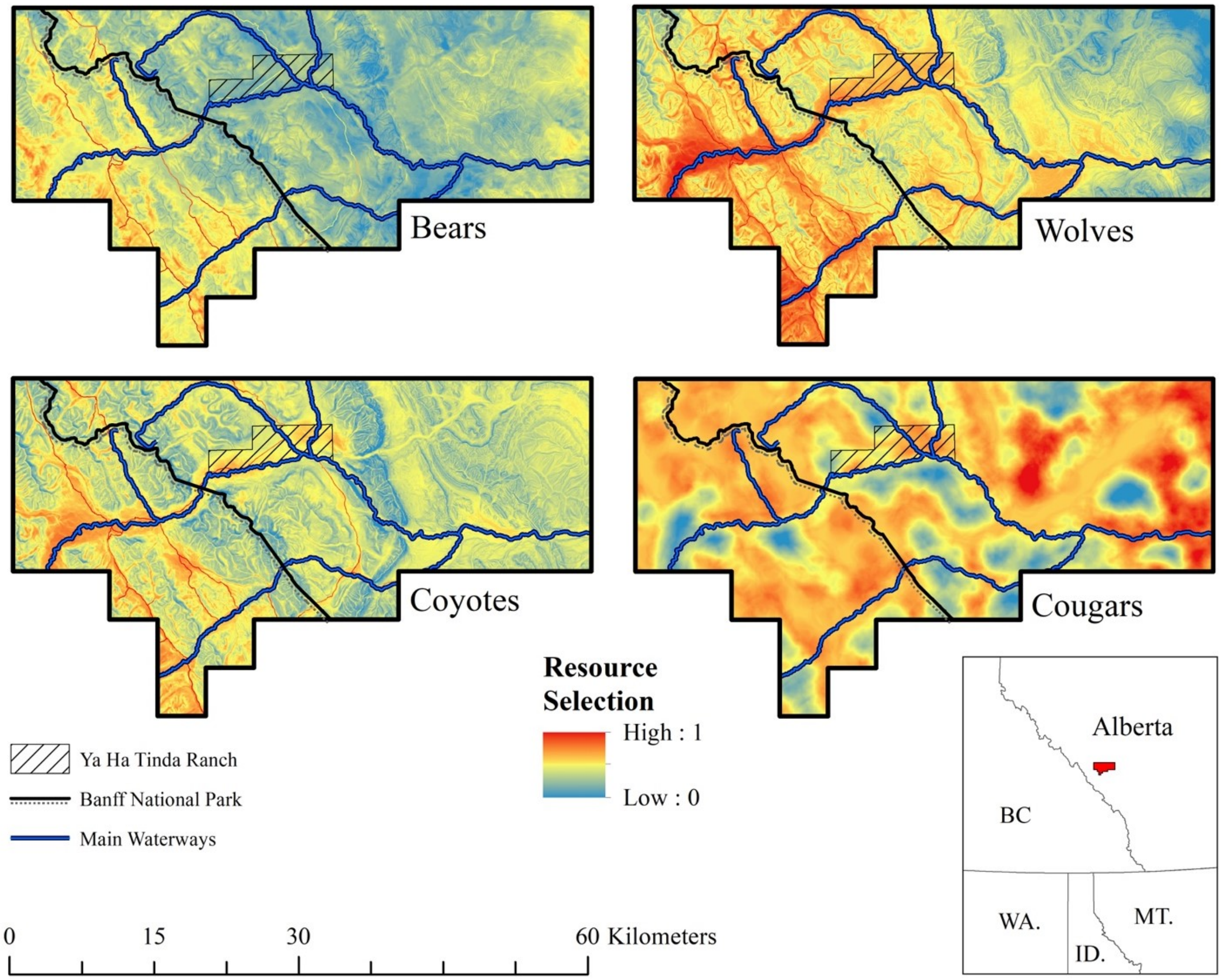

Fig. 2.3. Scat-based predictions of Resource Selection Function values from data collected from 1 May - 30 September, 2014 – 2016 with values being standardized between 0-1 for 4 predator groups, east slopes of the Rocky Mountains, Alberta, Canada.

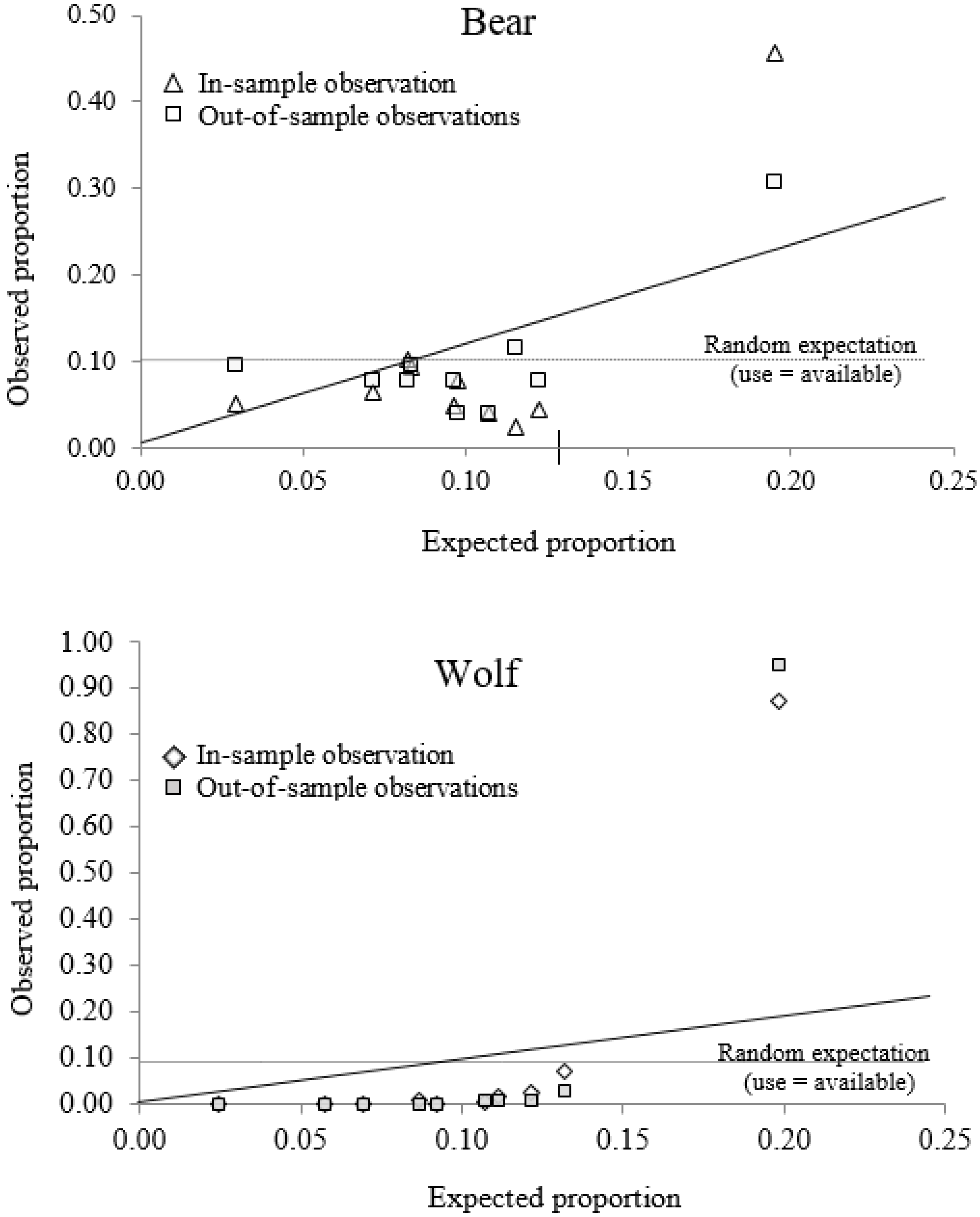

Fig. 2.4 Relationship between the expected proportion and the observed proportion of in-sample (n=373) and out-of-sample (n=52) observations of bear scat (a) and in-sample (n=470) and out-of-sample (n=132) observations of wolf scats (b) in 10-equal area bins. Dotted line at 0.10 represents where use is equal to available (random use). Solid line indicates whether scat-based RSF values are proportional to the occurrence of scats on the landscape.

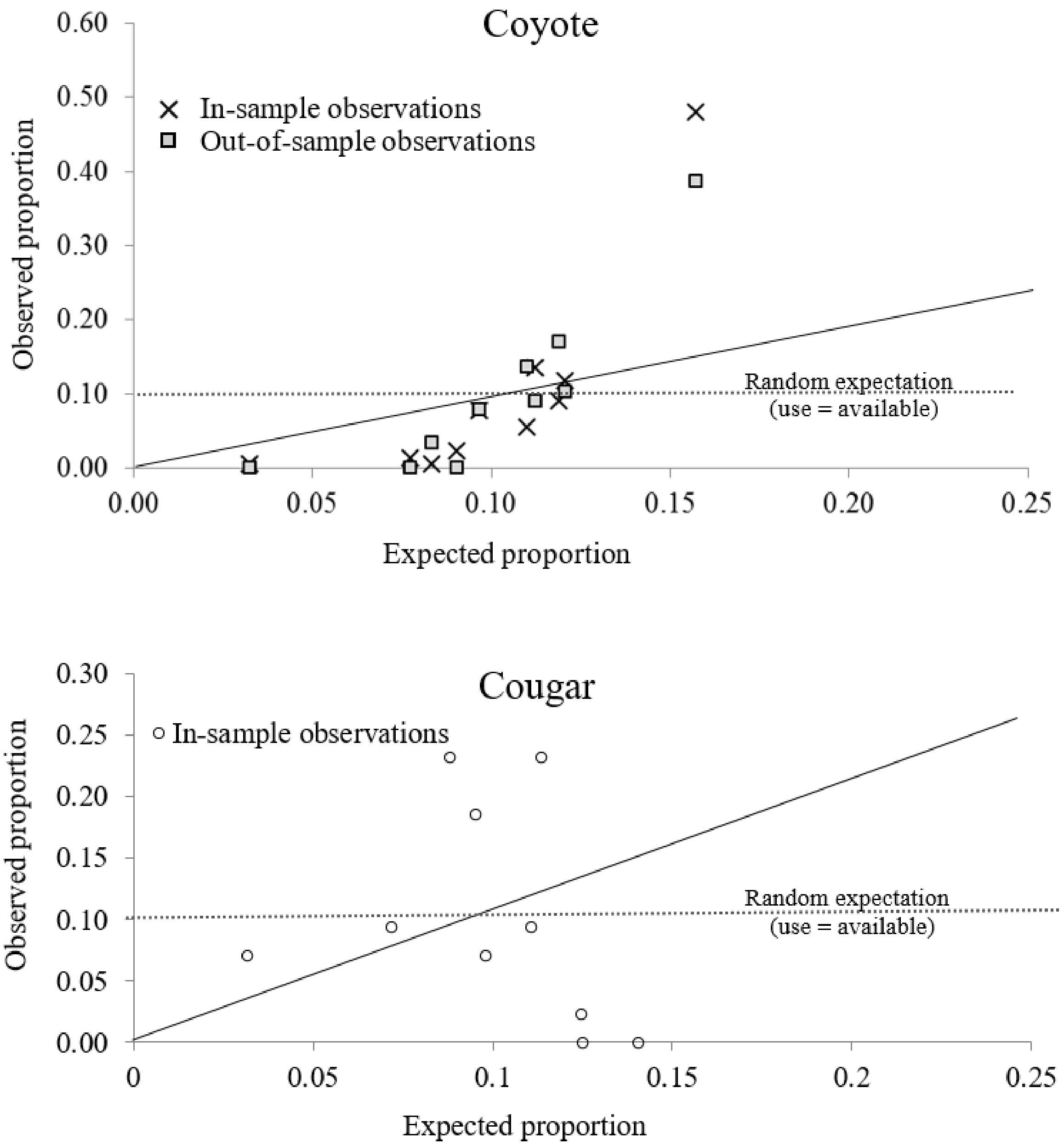

Fig. 2.5. Relationship between the expected proportion and the observed proportion of in-sample (n=221) and out-of-sample (n=88) observations of coyote scat (a) and in-sample (n=43) observations of cougar scats (b) in 10-equal area bins. Dotted line at 0.10 represents where use is equal to available (random use). Solid line indicates whether scat-based RSF values are proportional to the occurrence of scats on the landscape.

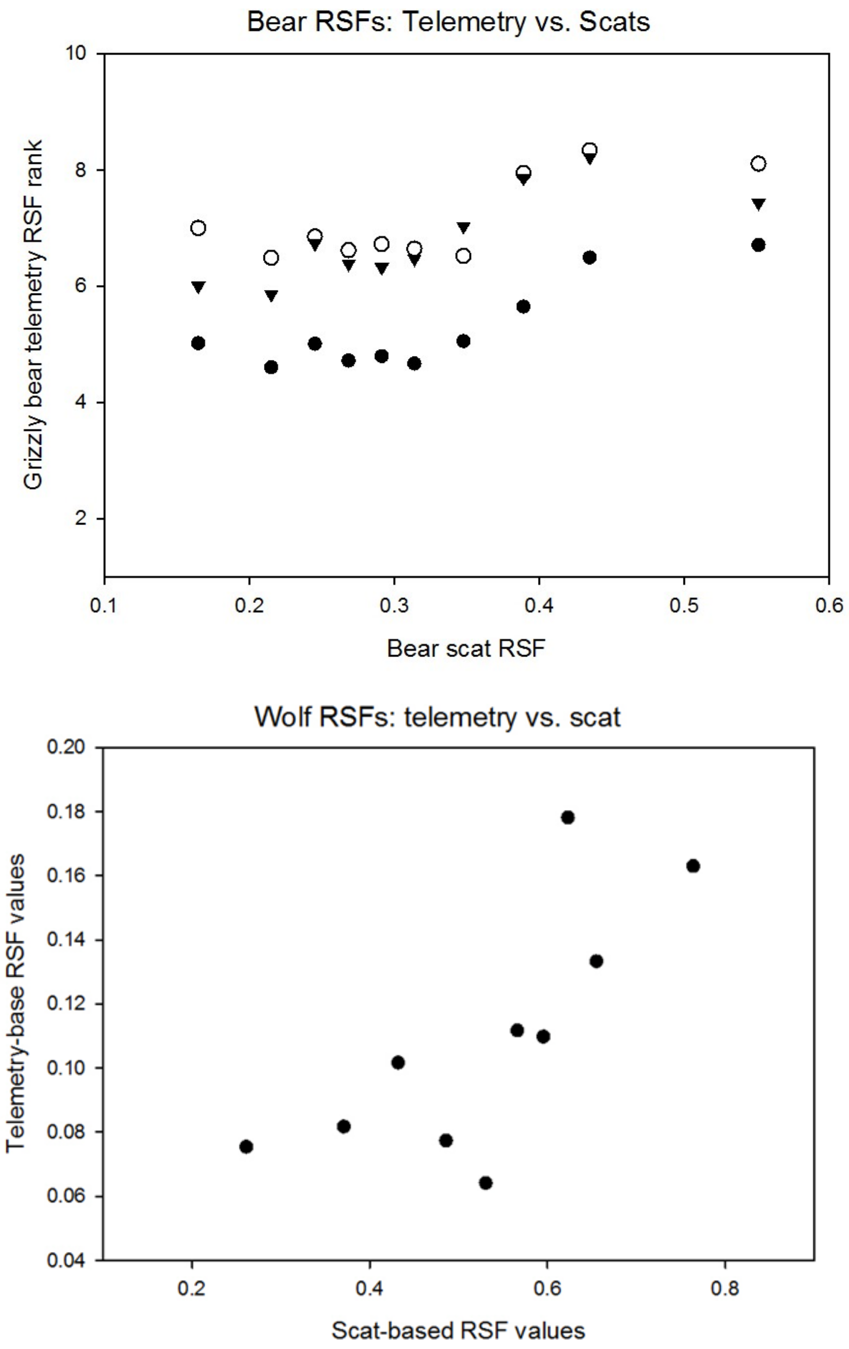

Fig. 2.6. Relationships between (a) mean predicted scat-based on the average of a day-time and a night-time wolf RSF values compared to mean predicted telemetry-based selection values for wolves and (b) mean rank of grizzly bear selection from a telemetry-based on RSF compared to mean RSF value from a scat-based RSF. Binning has smoothed the data so the nature of the relationships can be seen more clearly.

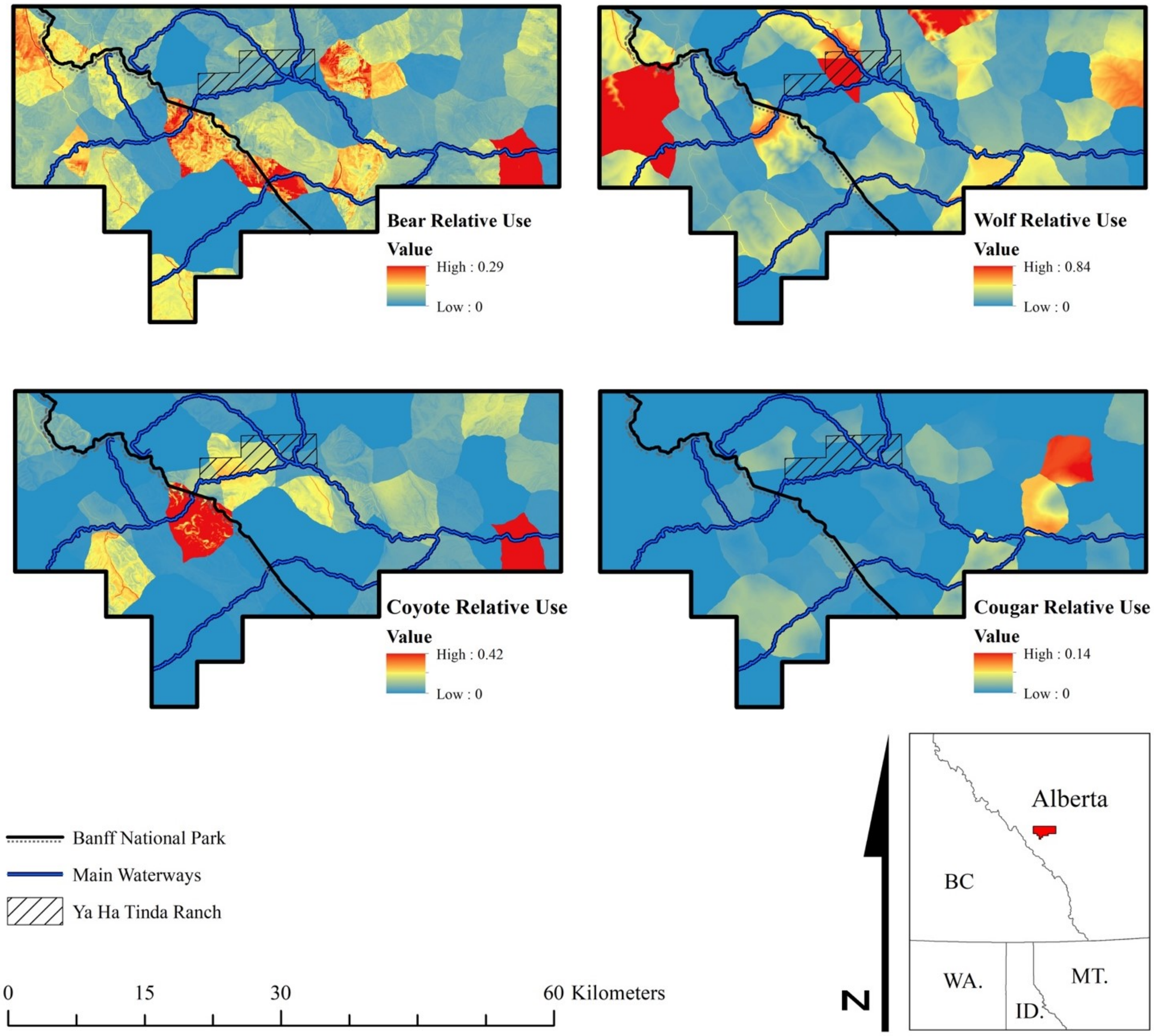

Fig. 2.7. Spatially adjusted relative use across the study area for 1 May - 30 September for 4 predator groups, east slopes of the Rocky Mountains, Alberta, Canada. Predictions were derived from intensity of use (Fig. 2.2) and landscape predictions of selection (Fig. 2.3) by the respective predators. See text for details.

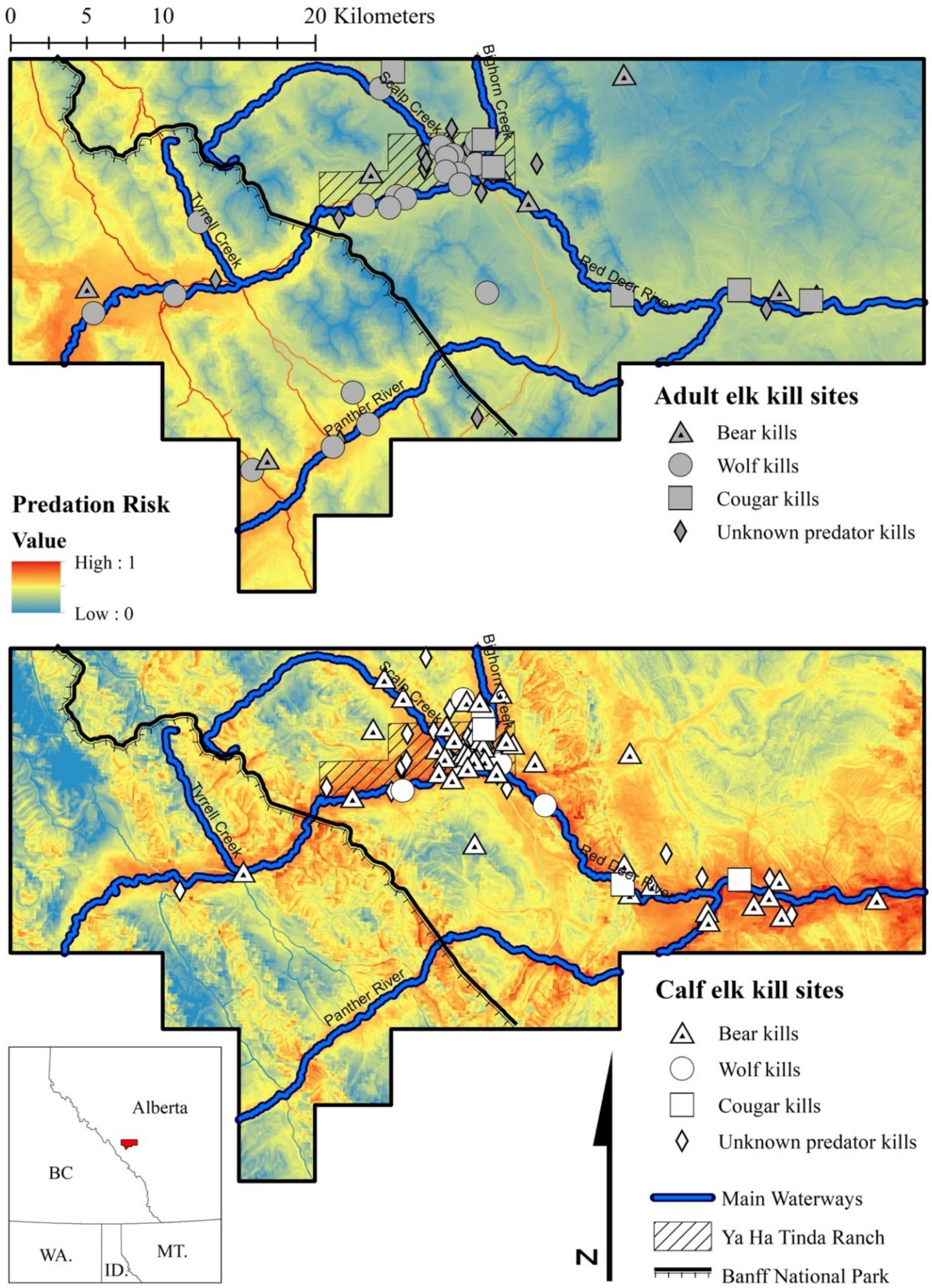

Fig. 2.8. Maps of predicted predation risk to elk calves (top) and adult female elk (bottom) based on a multinomial logistic regression comparing random locations to kill sites by any predator, including unknowns.

SPATIAL PREDATION RISK POSED TO BIGHORN SHEEP BY A PREDATOR COMMUNITY

INTRODUCTION

Bighorn sheep (*Ovis canadensis*) are designated as Alberta's official provincial wildlife species due to their economic and recreational importance. Provincial population estimates of bighorn sheep have remained relatively stable for the past 40 years, although considerable fluctuations have been seen in certain populations (Alberta Environment and Parks 2015). Despite specializing in the use of rugged terrain which presumably acts as a refuge from predators, predation remains a threat to bighorn populations, particularly in cases where populations are isolated or when other factors such as disease can compromise a herd (Alberta Environment and Parks 2015). Bighorn sheep leave escape terrain for dispersal, seasonal range migrations, and to access off-range resources where they may be exposed to a greater risk of encountering the wider predator community (Nichols and Bunnell 1999). Along the Alberta Rocky Mountains, bighorn share the landscape with wolves (*Canis lupus*), cougars (*Puma concolor*), coyotes (*Canis latrans*) and bears (*Ursus arctos, U. americanus*), all of which are known to kill sheep (Sawyer and Lindzey 2002).

Predation on bighorn sheep populations in multi-predator systems is highly variable across time and space and likely depends on a number of factors. These include the overlap of predator ranges with bighorn sheep distribution, alternative prey availability (Johnson et al. 2013), and the propensity of a predator species or individual to kill sheep (Festa-Bianchet et al. 2006,). For example, studies on wolf predation near Nordegg, AB in winter (Webb 2009) and in summer (Knamiller 2011), found kill sites were primarily comprised of deer and elk with no records of sheep being killed. In the same area, Knopff (2012) reported bighorn sheep comprised

~ 4% of cougar kills, but primarily by one individual. In Banff National Park bighorn sheep comprised 3% of wolf diet overall whereas they were up to 20% of the diet in areas where wolves overlapped sheep ranges in central west Alberta and eastern British Columbia (DeCesare 2012). With recent increases in cougars and wolves along the Alberta Rocky Mountains (Alberta Environment & Sustainable Resource Development 2012) there may be increasing overlap of predators with bighorn sheep populations that could pose direct threats when individual predators have a propensity to kill sheep (Ross et al. 1997). Indirect effects whereby sheep alter range selection may also occur (Festa-Bianchet et al. 1998). Although wolves and cougars are likely the main predators on bighorn sheep in Alberta, coyotes have been shown to affect lamb/ewe ratios in British Columbia (Herbert and Harrison 1988) and Montana (Hass 1989). Bears have also been reported to kill sheep (Frid 1997); however, predation is most likely to occur during lambing periods based on their predation of other ungulate species (Zager and Beecham 2006).

Approximately 40% of the over 11,000 bighorn sheep currently estimated to inhabit Alberta occur in Parks and Protected Areas (Alberta Environment and Parks 2015). National parks represent the majority of protected land in Alberta occupied by bighorns and are highly regulated relative to other protected area classifications. Widely considered important in bighorn conservation, national parks offer the absence of domestic livestock, reducing exposure to pathogens (Lawrence et al. 2010, Wolfe et al. 2010, Besser et al. 2012), and full restrictions on hunting may buffer against potential exploitation that can result in demographic or evolutionary effects if harvesting is selective (Coltman et al. 2003, Festa-Bianchet et al. 2014). Even small-scale developments can influence bighorn sheep: upon construction of a recreation trail in western North Dakota, sheep were seen to have lower fidelity to lambing areas and lower recruitment rates (Wiedmann and Bleich 2014). However, national parks also protect predators that kill sheep, potentially increasing predation risk and offsetting advantages of beneficial regulations for bighorns.

Predator distribution inside and outside national parks will depend on prey availability and ecological conditions. In particular, recent evidence suggests that predators will respond to the degree of human activity in their use of anthropogenic features such as roads and other linear features. For example, in southwestern Alberta, the use of areas with roads by grizzly bears is dependent on vehicle traffic intensity rather than road density (Northrup et al. 2012). Comparably, Whittington et al. (2005) found that wolves strongly selected for human-used recreational trails in remote areas of Banff National Park but selection was negatively related with human activity. Knopff et al. (2014) found the opposite effect for cougars with use of anthropogenic features positively correlated with the prevalence of those features on the landscape. Of the 4 predators, coyotes are the most adaptable to anthropogenic landscapes, with healthy populations common in urban areas (Gehrt and Riley 2010). Murray and St. Clair (2017) found that coyotes will even select residential properties based on specific features related to movement, food accessibility, and visual cover.

As a result of predators' response to habitat conditions and human disturbance, risk to bighorn sheep from predators may differ between sheep ranges inside and outside National Parks. Further, where there is a spatial gradient in human use and infrastructure from outside to inside National Parks, one might expect a "reserve edge effect" (Woodroffe and Ginsberg 1998). In most cases, the reserve edge effect has been attributed to human poaching where people are willing to cross borders to illegally kill animals, potentially resulting in a population sink along reserve edges (Woodroffe and Ginsberg 1998). In terms of predators, a similar reserve edge effect may develop due to contrasting land uses, in particular habitat changes, human activity, and infrastructure from managed lands outside National Parks to inside National Parks. If spatial patterns in the human footprint promote a reserve edge effect in predation risk that is not offset by other habitat conditions, bighorn populations along this predation risk gradient could be influenced differentially, either directly through predation (Sawyer and Lindzey 2002) or indirectly by trading-off site selection and fidelity to avoid predation (Smith et al. 2015, Festa-Bianchet et al. 1998, Bleich et al. 1997).

In this chapter, we delineate sheep ranges based on aerial sheep surveys and compare predation risk on (1) sheep ranges inside Banff National Park (hereafter, BNP) to sheep ranges on adjacent lands outside BNP, and (2) along a distance gradient from inside to outside BNP, both on and off sheep ranges. For this comparison, we characterize predation risk to sheep based on scat-based RSFs of 4 predator groups derived in Chapter 2. Inside BNP, we predicted predation risk from bears and wolves to be higher on sheep ranges primarily because we expected lower human activity compared to sheep ranges outside BNP, and that other habitat conditions would not offset this effect. We also expected to see a decreasing gradient in predation risk of these species from inside to outside BNP because we expect the influence of landscape features associated with human activity to decrease with distance rather than create a distinct change in risk at the border. In contrast, we did not expect differences in cougar and coyote predation risk on sheep ranges inside and outside BNP or along a spatial gradient because of flexibility in habitat use. Further, we compared predation risk in sheep ranges to areas across the study area and expected predation risk to be higher for bears and cougars on sheep ranges due to similar habitat use in the summer with sheep in high elevations and rugged terrain. We expected risk from wolves and coyotes to be lower than bears and cougars on ranges because of their affinity to waterways and valley bottoms.

STUDY AREA

The study area covered 1025 km^2 and was located on the eastern slopes of the Alberta Rocky Mountains in the upper Red Deer watershed (Fig. 3.1). Conifer forests consisting of spruce (*Picea* spp.) and lodgepole pine (*Pinus contorta*), and bare rock/ice were the dominant landcover types with mixed/aspen (*Populus tremuloides*) forests, grasslands, and shrub cover types in lower abundance. Rivers are small and would not act as a barrier to sheep movement. Other ungulate species commonly occurring in the study area included elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and wild horses (*Equus caballus*).

The study area was divided into approximately equal parts, with the western portion in BNP and the eastern portion being Crown land and falling under Sheep Management Area 4b – Clearwater/Ram (hereafter, "SMA"). The BNP portion of the study area is in a remote section of the Park and there is minimal development except for vehicle-restricted trails for approximately 45 km perpendicular to the BNP/SMA boundary. The SMA portion is subject to forestry, oil and gas extraction, and rangeland grazing, all of which increase in intensity east of the study area boundary. Hunting is also permitted in the SMA portion and Wildlife Management Units falling within the study area include 416, 417, 418, and 420. In these Wildlife Management Units general seasons are available for residents hunting trophy rams and special licenses are available for non-trophy sheep hunting and non-resident trophy sheep hunting. Despite populations remaining relatively stable since provincial surveys began in 1980, hunter success records show a greater decline in numbers of rams harvested per year for SMA 4b—which is thought to be driven by sheep moving out of BNP—than other SMAs, with ~60 rams/year taken during the mid-1980s thru the mid-1990s and ~30 rams/year harvested from the mid-2000s to 2014 (Alberta Environment and Parks 2015). Hunting of carnivores also occurs in the SMA except for grizzly bears, which are protected. Several trapping leases cover this area and all carnivores except for cougars and bears are included as trappable furbearers. Additionally, landowners are permitted, without a hunting license, to kill a wolf, coyote, cougar or black bear on private land any time of year.

METHODS

Delineating sheep ranges

Because winter range is typically considered the seasonal range of highest priority for bighorns in the northern parts of their range, available survey data are typically limited to the winter season. To determine sheep summer ranges, we assumed seasonal range overlap with winter ranges of sheep and refined the areas based on a published bighorn sheep resource selection function for spring through autumn (DeCesare and Pletscher 2006). In the provincial Sheep Management Area outside of BNP, we obtained boundaries of 6 separate winter ranges from Alberta Environment and Parks that were derived from aerial surveys conducted in 2002 (Appendix 3.1A). Boundaries of sheep ranges within BNP were determined from locations of individual sheep observed by Parks Canada on aerial surveys from winters 1988 to 2012. To obtain a polygon boundary of the range including the locations, we placed a 1-km buffer around each point location and aggregated buffer polygons using a 1 km threshold (Appendix. 3.1B). Observation data from Parks Canada included 12 point locations outside of BNP and not within SMA ranges that we also buffered and aggregated then included to the SMA ranges.

We delineated spring-fall range within winter range polygons for bighorn sheep (Appendix. 3.1C), based on resource selection functions (RSF, DeCesare and Pletscher 2006). produced for 16 ewes representing 3 populations (n=2,7,7) of bighorn sheep in Montana during 2 seasons: lambing (May-July) and autumn (August-November). We used variables that were common to at least 2 populations and averaged beta coefficients between populations. The resulting RSF indicated selection by bighorns increased in areas with higher elevations (β=0.007), steeper slopes (β=0.057), closer proximity to escape terrain (β=-0.007), and further from water sources (β=0.002). We used the same variable for escape terrain described by DeCesare and Pletscher (2006) as areas with slopes >27° and a minimum patch size of 0.007 km^2. The remaining model inputs were based on variables described in Chapter 2. To define areas considered high-quality habitat, we removed areas with RSF values not falling within the top 40% of the RSF values in the sheep ranges. The 40% threshold value represented a natural break (ESRI 2014, Jenks and Caspall 1971) in the RSF values.

Scat-based Resource Selection Functions

We used the scat-based RSFs for 4 predator groups developed in Chapter 2 to define predation risk within sheep ranges and across the landscape within and adjacent to BNP. Scat surveys were conducted from mid-July to mid-September in 2013-2015 and 1 August to 30 August 2016, along routes within 54 5 x 5-km grid cells. Surveys started in July to allow scats to accumulate on the landscape, and ended in September because snow began to restrict surveys at higher elevations. Scats were identified by predator species in the field and a subset were DNA-verified. DNA verification was used to apply a correction factor based on diameter to canid scats (see Chapter 2). We developed RSFs based on a use-availability design where attributes of sites where scats were collected during the 2014-2016 survey years were compared to those of random points located with a 50-m buffer of the survey transect using an exponential RSF fitted using logistic regression. Top models were selected using AIC$_c$ and models were evaluated with independently created telemetry-based RSFs for grizzly bears and wolves, and with scats collected during the 2013 survey season (Chapter 2).

Predation Risk Analyses

We predicted RSF values at a resolution of 30 x 30m across the study area for the 4 predator groups using their respective RSFs. To assess predation risk at the scale of a sheep range, we first delineated individual sheep ranges using a distance criterion of 1-km aggregation between ranges (Fig. 3.2). We then determined average predator RSF values for predators for each range. We tested mean RSF values between ranges inside and outside BNP (BNP n=7, SMA=6) using a Wilcoxon rank-sum test.

Second, to investigate whether land use patterns created gradients in predator RSF values (i.e. reserve edge effects) across BNP's boundary, we plotted 4000 points located randomly across the study area and recorded the distance of each point to the boundary of BNP as outside BNP (positive distance value) or inside BNP (negative distance value). We took the average RSF value for each set of sequential 100 points along this distance gradient from inside BNP to outside BNP both on sheep ranges and off ranges (Appendix 3.2) and plotted the mean RSF value for each predator species reflecting a spatial trend in predation risk. We used linear regression to test for a linear trend across space and compared slopes of regression between areas on sheep ranges and areas off ranges using the t-distribution (Zar 2010). Finally, we used a Wilcoxon rank-sum test to compare mean RSF values of each 100-point subsample in sheep ranges with subsamples from areas outside of sheep ranges.

RESULTS

Sheep ranges ranged from 3 to 51 km^2 and mean range sizes were not different inside and outside BNP (Table 3.1, Fig. 3.2). RSF values of sheep ranges averaged higher within BNP areas for wolves, coyotes, and bears (Fig. 3.2, Table 3.1). Differences in mean RSF values of sheep ranges inside and outside BNP was greatest in bears (30% lower outside) and least in cougars

(10% lower). We found negative relationships between distance to BNP's border and predator RSF values on ranges and across the landscape in general for all predators, although the relationship was considerably weaker for cougars (Fig. 3.3, Table 3.2). Only RSF values of cougars averaged higher within sheep ranges than in the landscape (W=376, $P < 0.001$) but the rate of change in RSF values along the gradient did not differ between inside sheep ranges and in the landscape (Table 3.2). In contrast, RSF values on sheep ranges were lower for wolves and coyotes than in the landscape, but similar in bears (Table 3.2). Regression coefficients for wolves, coyotes and bears were similar and at least double that of cougars, although we did not find selection differed significantly between areas on or off sheep ranges (Table 3.2).

DISCUSSION

We hypothesized that sheep ranges in BNP would be exposed to greater risk than sheep ranges in the SMA by only wolves and bears; however, all predator groups, including coyotes and cougars, showed higher selection for areas within BNP. The sheep ranges in BNP were nearly 3 times further from road access and had 8 times the vehicle-restricted trails, on average, than SMA ranges (Appendix 3.2) and is likely why RSF values averaged higher in BNP for bears, coyotes, and wolves. Because proportion edge cover on ranges was similar in BNP compared with the SMA (Appendix 3.2), the lower proportion conifer forest in BNP would have provided the higher selection values in the park for cougars.

In comparing sheep ranges with areas off-ranges across the study area, cougar selection was, as predicted, higher on sheep ranges. Again, average conifer forest was lower on ranges (mean=0.22, SD=0.39) than off-ranges (0.40, SD=0.49) and may have been accountable for the higher cougar selection on ranges. Vehicle access distance was similar between on-ranges and off-ranges, and so it is not likely to have impacted the on range/off range comparison for bears, wolves and coyotes. However, the availability of vehicle-restricted trails was 4 times greater off-range than on range and increased selection values off ranges for bears, wolves, and coyotes. Slope, the third variable common to canids and ursids also differed between on-ranges (mean=28°, SD=7) and off-ranges (mean=17°, SD=12), although this would have only contributed to stronger selection for off-ranges than on ranges by wolves and coyotes but not bears because of bear selection for steeper slopes. Further reducing the difference in bear selection created by more vehicle restricted trails off ranges, proportion conifer forest off-range (mean=0.22, SD=0.39) was nearly double that of on-range (mean=0.40, SD=0.49). Areas with a greater proportion of cutblocks and higher NDVI values were similar off and on ranges and probably had minimal impact on bear selection. It appears that higher availability of vehicle restricted trails off-ranges was sufficient to offset the greater availability of bear-selected natural landscape variables on sheep ranges. Wolf and coyote selection favored areas off ranges due to higher availability of trails and natural landscape features. Consistent with the reserve edge effect hypothesis, we found relationships between distance to border and RSF values that were consistent across predators except cougars. Selection by bears, wolves, and coyotes for areas further from vehicle-permitted roads is likely driving this effect.

Low selection for areas associated on bighorn sheep range by bears, wolves, and coyotes suggests that off-range resources may play a role in risk to sheep by these predators. Natural mineral licks are a strong single-point attractant that are often located off-sheep range in low-lying areas (Jokinen et al. 2014) and can influence range use (Festa-Bianchet 1988), in some cases drawing sheep 10s of kilometers out of their range (Dibb 2006). Nichols and Bunnell (1999) found that off-range forays would be the only time thinhorn sheep (*O. dalli*) would experience predation from wolves, and because ewes have greater mineral requirements and are driven to lick sites during lactation (Ayotte et al. 2008) their lambs may face a greater threat of predation from bears and coyotes. Bighorn sheep will also readily use artificial mineral sources. Within our study area, Morgantini and Bruns (1988) found oil and gas wellsites were often used as artificial mineral licks, with 2 of the 5 wellsites located 3 and 6 km away from the nearest sheep range. Strategic placement of mineral supplements is effective in managing distribution of free ranging cattle (Bailey 2004, Probo et al. 2013) and adding artificial mineral blocks in close proximity to escape terrain may offer a simple measure that could alleviate predation pressure from ursids or canids, if considered necessary.

Management of human used and maintained trails also appears to influence wolves, bears, and coyotes. Human activity and vehicle-permitted trails are generally considered to have negative effects on wildlife populations although this could be an overgeneralization because of the opportunity for refuge for prey species. Land use guidelines for industrial activity on provincial land (Alberta Environment and Parks 2015) and conservation objectives for BNP restrict development of additional access into areas wildlife-sensitive areas. In remote areas, decommissioning maintained, low-use trails may be effective in reducing carnivores access to bighorn sheep.

Table 3.1. Mean resource selection function (RSF) values within bighorn sheep ranges inside Banff National Parks (BNP) for 4 predator groups found in southern Alberta's Rocky Mountains. *P* values are given for a test of differences in mean RSF values between 7 sheep ranges in BNP and 6 ranges in the Sheep Management Area using a Wilcoxon signed-rank test.

		BNP (143km^2)	Sheep Management Area (102 km^2)	*W*	*P*
Cougar	Mean	0.58	0.53	35	0.05
	SD	0.06	0.08		
Wolf	Mean	0.53	0.46	36	0.04
	SD	0.06	0.05		
Coyote	Mean	0.44	0.37	38	0.01
	SD	0.07	0.06		
Bears	Mean	0.41	0.29	41	<0.01
	SD	0.10	0.06		

Table 3.2. Summary statistics for linear regressions for predicting RSF values along a distance-to-border gradient of 4 predators. Mean RSF values were for random points grouped by the 100 sequential distances to the border of Banff National Park on each side of the border. Results are given for random points on delineated sheep ranges and off sheep ranges. *P* values reflect differences mean RSF values based on Wilcoxon rank-sum comparing 2000 points on and off sheep ranges, and differences in the slope of the regression *(β)* between sheep ranges and areas off sheep ranges.

	Distance to border											
	Sheep ranges				Off sheep ranges				Wilcoxon rank-sum		Slope difference	
	β	SE	r^2	p	β	SE	r^2	p	W	P	t	P
Cougar	-0.0020	0.001	0.15	0.090	-0.0015	0.000	0.40	0.003	376	<0.001	0.85	0.39
Wolf	-0.0052	0.001	0.81	<0.001	-0.0032	0.001	0.61	<0.001	392	<0.001	1.19	0.24
Coyote	-0.0046	0.001	0.83	<0.001	-0.0030	0.001	0.57	<0.001	398	<0.001	1.10	0.28
Bear	-0.0054	<0.001	0.87	<0.001	-0.0065	0.001	0.65	<0.001	203	0.946	0.49	0.62

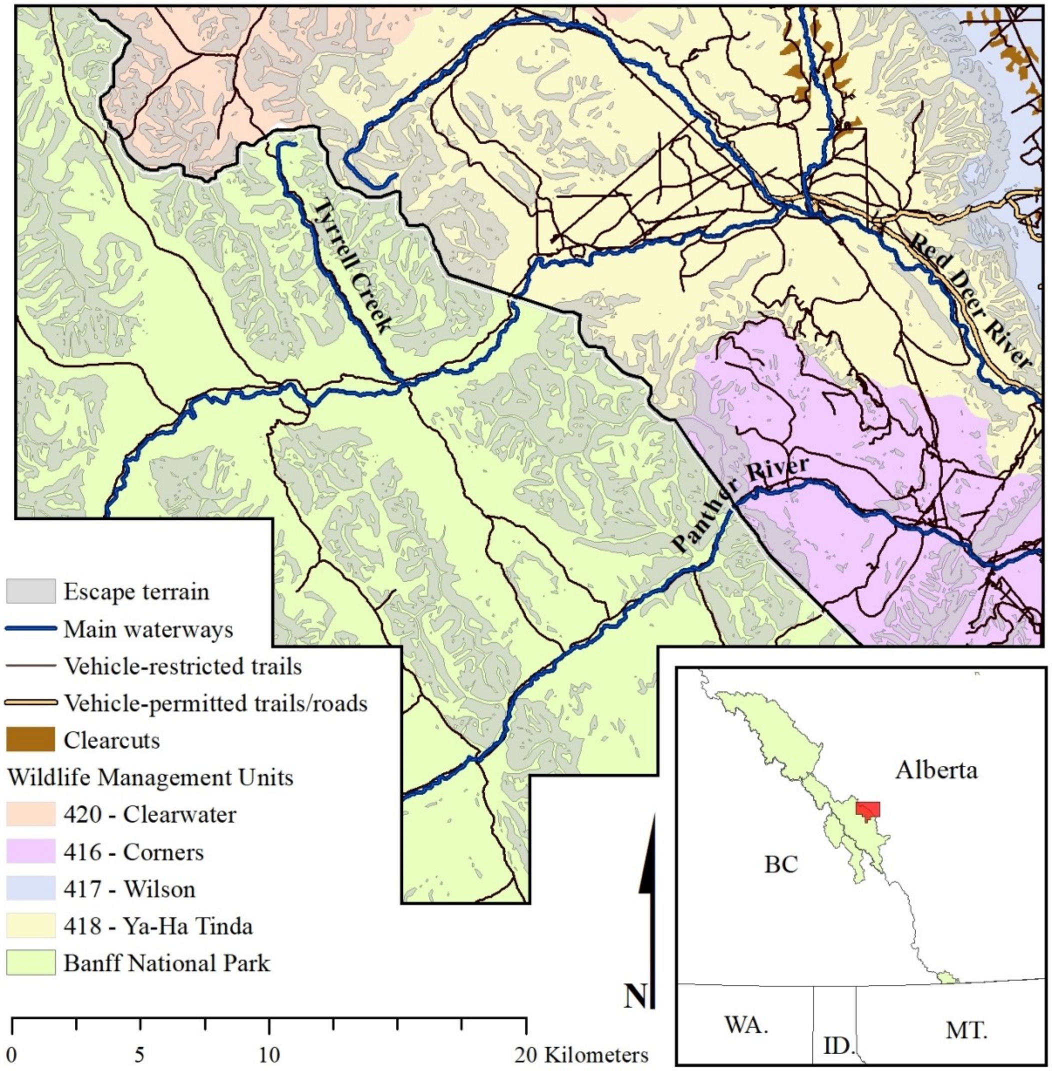

Fig. 3.1. Study area used for predation risk analyses for bighorn sheep. Escape terrain, a landscape characteristic strongly-associated with bighorn habitat, is defined as areas with slopes >27° (Smith et al. 1991; Johnson and Swift 2000; DeCesare and Pletscher 2006).

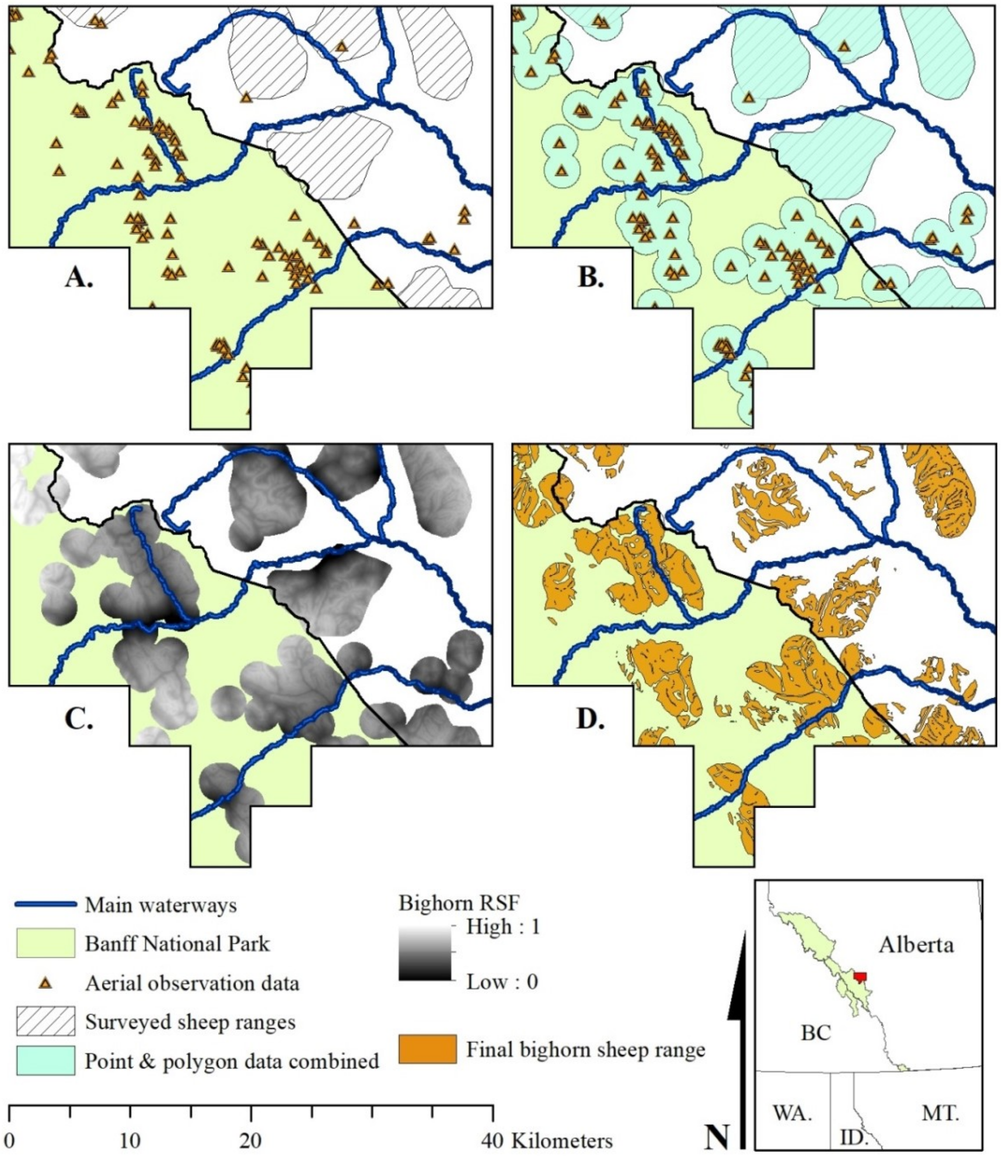

Fig. 3.2. Graphical delineation of how bighorn sheep ranges used in spatial predation risk analyses were derived. Panels include: polygons of sheep ranges used for surveys since 1972 within Sheep Management Area (SMA 4b) provided by Alberta Environment and Parks, and point locations of sheep observations during aerial surveys (1988-2012) provided by Parks Canada (A); unrestricted polygons derived from buffers of sheep point observations overlaid with sheep ranges (B); predictions of bighorn resource selection values using the RSF of DeCesare and Pletscher (2006) within unrestricted polygons of sheep ranges (C); final sheep ranges derived by removing areas not falling within the top 40% of the bighorn RSF values (D).

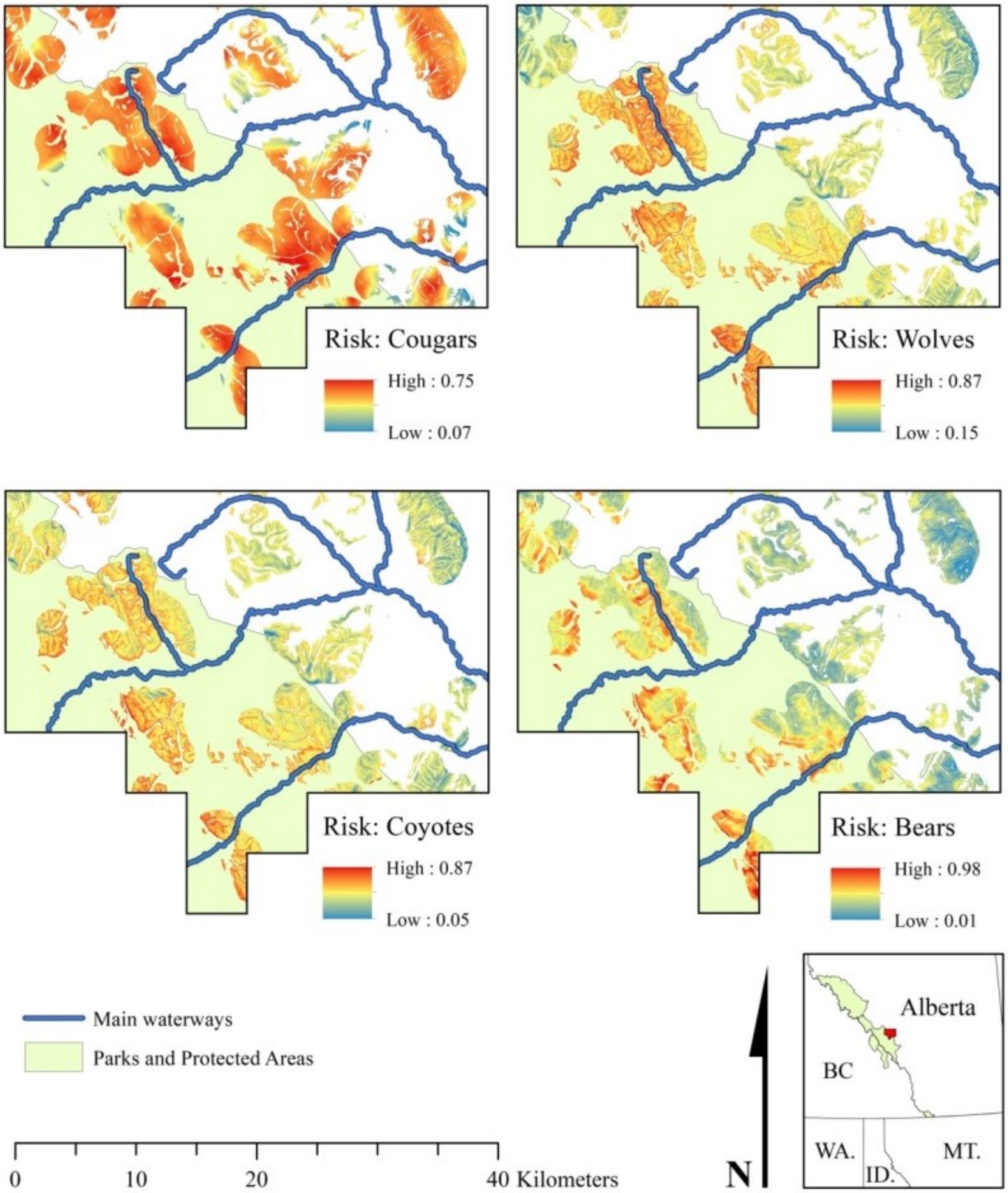

Fig. 3.3. Scat-based RSF values standardized between 0 and 1 mapped for 4 predator groups in bighorn sheep ranges inside (green area) and outside (white area) of Banff National Park along the east slopes of the Alberta Rocky Mountains, Alberta.

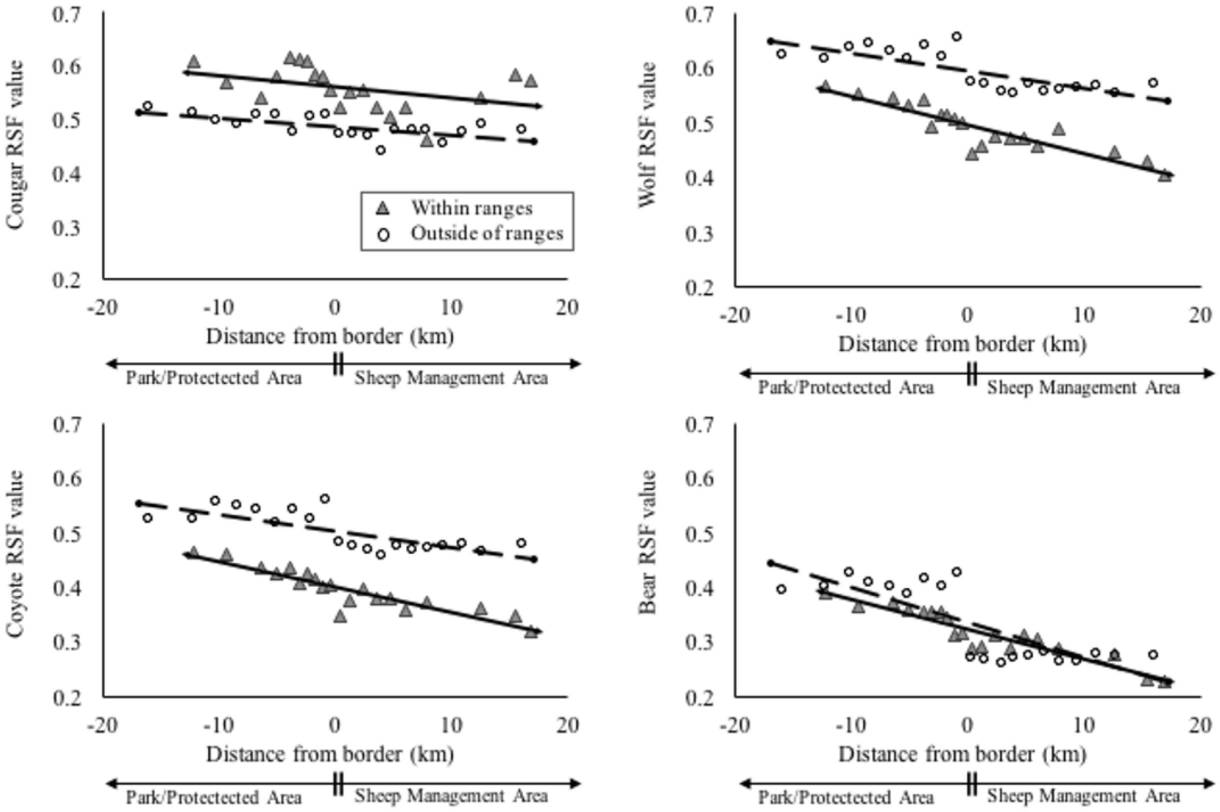

Fig. 3.4. Plots of mean RSF values for 100 sequential points along a distance gradient from inside Banff National Park (protected area) into the provincial Sheep Management Unit.

CONCLUSION

In this thesis I examined predation risk to elk and bighorn sheep during summer posed by a carnivore community on the east slopes of the Alberta Rocky Mountains. As species of considerable economic and social importance to Alberta, elk (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*) are a high priority for wildlife managers. The Ya Ha Tinda (YHT) elk herd has declined in numbers and is experiencing shifts in migratory behavior. One possibility for these changes could be predation. Predation by wolves on the YHT elk herd has received recent research attention (Hebblewhite et al. 2005, Hebblewhite and Merrill 2008); however, the YHT elk share a landscape with a community of large predators also including bears (*Ursus americanus, U. arctos*), coyotes (*Canis latrans*), and cougars (*Puma concolor*), all of which are known to predate on elk. Provincial population estimates of bighorn sheep have remained relatively stable for the previous several decades, but there have been localized population fluctuations that likely have been contributable to predation (Alberta Environment and Parks 2015).

We used cost-efficient, non-invasive approaches to assess the spatial distribution of four predator taxa as an index to predator risk because prey must first encounter a predator before it is killed. We combined data from remote cameras (*IU*), which we expected to reflect relative abundance or intensity of use, with resource selection modeling (RSF), based on scats detected by dogs along transects, to derive a fine-scale map (30 x 30m) of relative predator use (*RU*) as an index to predation risk over the summer. However, because predator distribution is related to the first component of predation, i.e., the search phase (Lima and Dill 1990), it may not reflect attack success (Holling 1959). In an attempt to improve the quantification of the actual risk to ungulate prey, as a second step we related metrics of predator distribution and other landscape variables at a site to the relative risk of the site being the location of an elk kill.

Unexpectedly, we found that the scat-based RSF better predicted elk kill locations than RU, the metric that extrapolated intensity of use at a camera site and combined it with RSF modeling at the fine scale. We attributed this to the fact that predator use indexed by photographic events at the camera site did not represent use across the broader area to which it was extrapolated, and may have induced variation in the local predation risk metric. A higher density of camera sites may improve this because camera data has the potential to reflect animal densities (Royle et al. 2013, Minin et al. 2014, Steenweg et al. 2017). Additionally, we found that selection values predicted from scat-based RSF were related to where an independent set of scats were found, even if the relationship was nonlinear. This correspondence was especially strong at high RSF values, indicating that selection was a good index of actual use across the landscape, at least as indicated by scats. Because scat-based RSF values also corresponded to telemetry-based RSF, using scats to reflect predator use is at least similar to that based on telemetry locations of collared animals.

In devising the scat-based RSFs for individual predators, our results were comparable to other studies in that ursids and canids showed selection for low-use, vehicle-restricted trails particularly when further distance from vehicle-permitted trails (Chruszcz et al. 2003, Whittington et al. 2005). Bears selected for areas with greater slopes (Apps et al. 2004) whereas wolves and coyotes selected areas for lower slopes (Koehler and Hornocker 1991, Hebblewhite and Merrill 2008), and cougars selected for areas with a lower proportion of conifer forest and higher proportion of edge habitat (Knopff et al. 2014). We did not find much evidence that a predator's selection was influenced by other predators as reported in the literature (Bartnick et al.

2013, Lendrum et al. 2014, Elbroch et al. 2015, Krawchuk 2015, Droge et al. 2016), with perhaps the exception being coyotes avoiding areas used by bears and wolves. RSFs based on scats indicate spatial avoidance over long periods and in this study area due to topography predators may use generally the same types of areas but avoid each other in time rather than space. Spatial refuges due to predator interactions may not exist at least over long time intervals, suggesting that risk from multiple predators may be additive for elk calves, which is indicated by an increase in the likelihood of a calf being killed at a site based on the inclusion of multiple individual predator RSFs.

An end goal of the work in this thesis was to map risk of predation by multiple predators for use in other on-going studies in the region. In particular, these predation risk maps are to provide a basis for comparing potential predator risk on cow and calf elk in resource selection and survival analyses among migratory elk segments to help explain shifts in population in migratory herd segments over time (J. Berg, PhD ongoing). In examining predation risk based on kill sites caused by any predator, we found elk of both age classes were more likely to occur in areas with higher wolf and lower bear RSF values, and calves but not adults had a higher probability of occurring in areas of both higher cougar and wolf selection. Bear and wolf-specific kill site models showed that calf elk had a lower probability of being killed in areas with high selection values of the predator's respective RSFs.

Bighorn sheep inhabiting the region appear to be exposed to the greatest risk by cougars across our study area and are able to avoid high risk areas for bears, wolves, and coyotes by occupying areas with greater slopes and with a lower proportion of maintained, vehicle restricted trails. Sheep outside of Banff National Park may be further protected from predation risk posed by ursids and canids by being in close proximity to roads and human activity. However, sheep do leave refuge areas for migration or to access off-range resources (Dibb 2006, Ayotte et al. 2008, Jokinen et al. 2014), which may increase their risk to the wider predator community at certain times of the year (Nichols and Bunnell 1999).

MANAGEMENT CONSIDERATIONS

Large carnivores and their ungulate prey are charismatic species that are highly valued by the public. Cost-efficient, non-invasive methods are evolving to provide information on the distribution of these sympatric species and their interactions (Steenweg et al. 2017) that may improve their management. However, each method and analyses approach has drawbacks and thorough consideration of how the data will be applied is crucial before undertaking a study. We have demonstrated how an apparent best-approach did not perform as well as expected. Management of human-used and maintained trails appears to have a large influence on the predators of elk and bighorn sheep. In very remote areas, decommissioning maintained, low-use trails may be effective in reducing the use of trails by carnivores to access prey. Multi-species predation risk quantified from this study can be used to assess forage-predation risk trade-offs of different migratory segments of the elk population and bighorn sheep in this region.

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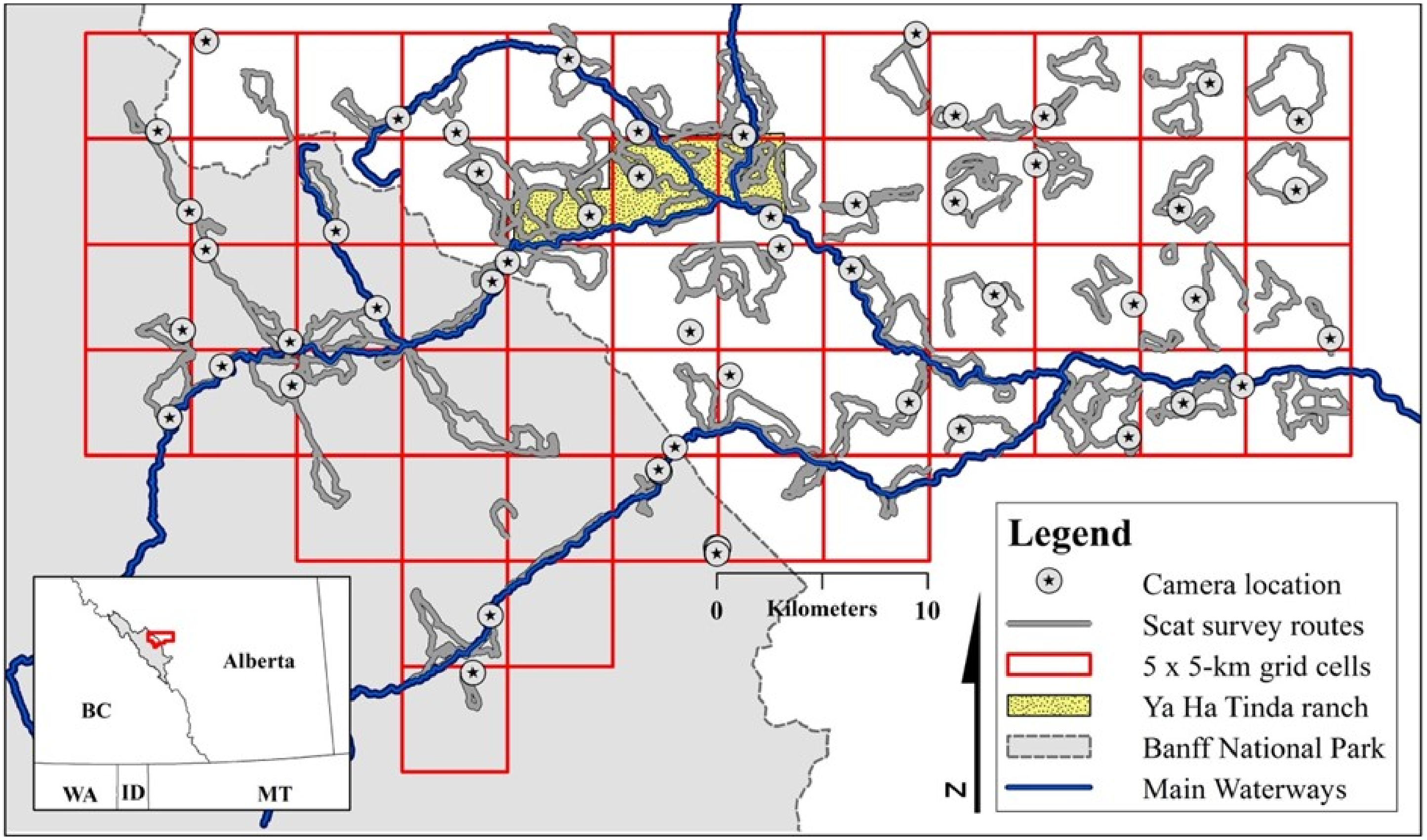
APPENDICES

CHAPTER 2 SUPPLEMENTARY MATERIAL

APPENDIX 2.1. Percent land cover type within the 1425 km^2-study area boundary and percent coverage of land cover types along actual transects surveyed for carnivore scats in 5 x 5-km cells conducted in of 2014 and 2015 on the eastern slopes of the Alberta Rocky Mountains.

Land cover type	Study area (%)	Sampled transects	Transect-study area difference
Forest	42.7	50.4	5.7
Grassland	3.1	4.7	1.7
Shrub	4.0	7.5	3.5
Alpine vegetation	5.7	3.3	-2.4
Perennial waterbodies/wetlands	0.9	2.0	1.1
Bare rock/ice	25.3	7.3	-18.0
Forestry cutblocks 1990-2014	5.1	8.0	2.9
Forest fires 2000-2014	13.3	16.9	3.5



APPENDIX 2.2. Camera locations and survey routes used for predator scat sampling during summers 2013-2016 on the eastern slopes of the Alberta Rocky Mountains, Canada.

APPENDIX 2.3. Description of scat dog/handler background and scat detection trials.

Four dog handlers and 4 dogs (2013: Jodi Berg/Shrek; 2014: Eric Spilker/Shrek; Caleb Stanek/Chester; 2015: Eric Spilker/Rounder; Julie Ubigau/Simpson, 2016: Eric Spilker/Rounder) were used for scat surveys. Three of the dogs (Shrek, Chester, Sampson) were trained at Conservation Canines, an established detection dog training facility at the Center for Conservation Biology at the University of Washington, and the other (Rounder) was trained by Eric Spilker under guidance by Conservation Canines. The detection dogs were trained following similar procedures used to train drug and explosive detection dogs (Appendix 2.3.1). Three of the dogs were handled only by their individual handlers and one dog (Shrek) was handled by 2 different handlers in different years.

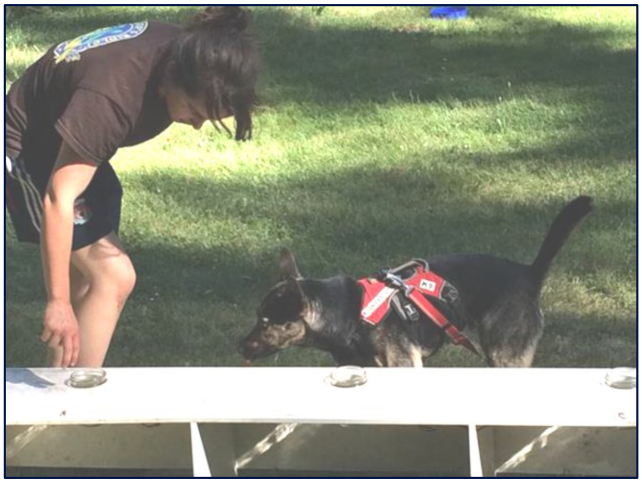


Fig. 2.3.1. Detection dog training at Conservation Canines, University of Washington. One of the six jars on the apparatus contains a coyote scat. The dog must correctly indicate which jar it is in. *Photo credit: Eric Spilker*.

In 2015 we evaluated two dog-handler teams' ability to find scats. Each dog/hander team completed 24-26 blind trials. In each trial, 5 scats including a mix from the 4 carnivore species were used that were collected either opportunistically and during scat surveys. Scats were placed scats at least 10 m apart within a 10-m buffer along a 100 to 200-m route. The route changed direction at least once to account for favourable wind direction. Scats were placed on or within 1 m of roads and human-use trails, and off-trail in the 5 dominant land cover classes (conifer, mixed forest, open grassland, shrub, and riverbed) in the study area. At the beginning of each trial, wind speed (none/light/moderate), precipitation (none, light, moderate), and time since last precipitation event (0 – 24-hrs, 24-hrs – 1 week, > 1 week. Before trials, dogs were exercised for a minimum of 15 minutes to increase their heart and breathing rate to a level similar to what they would be experiencing on surveys. During trials, handlers made an effort to work the dog at the same intensity level they would work during surveys. If the handler suspected the dog passed a scat without alerting to it, the dog would not be directed back to search the area again. Each placed scat was recorded as either being detected (1) or not (0).

Average detection rate for both handler/dog team was above 90% (Eric/Rounder=91%, Julie/Sampson=92%). Based on logistic regression and using a model selection approach based on AIC_c, only the model including Shrub had a $\Delta\text{AIC}_c > 4$ improvement over the null model. Four other models containing combinations of shrub, mixed forest, and dog team with $\Delta\text{AIC}_c < 4$ were equally supported as the null model; however, only the confidence limit for coefficient for shrub (β= -1.43, CL= -0.43 – -2.42) did not overlap zero. As a result, we may have missed some scats in shrub sites and attempted to compensate for this by travelling slower in these regions.

APPENDIX 2.4. Scat detection trial data for 2 handler/dog teams conducted in situ in August 2015 by dog/handler team Sampson/J. Ubigau (Team 1) and Rounder/E. Spilker (Team 2) and environmental conditions during trials.

						Dog/handler	
Trial	Date	Land cover	Rain	Time since last precipitation	Wind speed	Team 1	Team 2
1	14-Aug	Grass	None	<24 hours	Light	3	5
3	25-Aug	Shrub	None	24 hrs-1 week	Light	4	4
4	25-Aug	Road[1]	None	24 hrs-1 week	Light	4	4
5	25-Aug	Conifer	None	24 hrs-1 week	Light	5	5
6	26-Aug	Conifer	None	24 hrs-1 week	Light	5	4
7	26-Aug	Trail	None	24 hrs-1 week	Variable	5	5
8	26-Aug	Mixed	None	24 hrs-1 week	Variable	5	5
9	27-Aug	Grass	None	24 hrs-1 week	Light	5	5
10	27-Aug	Grass	None	24 hrs-1 week	Light	5	4
11	30-Aug	Conifer	None	24 hrs-1 week	Light	5	--
12	30-Aug	Mixed	None	24 hrs-1 week	Variable	5	--
13	14-Sep	Grass	None	24 hrs-1 week	Moderate	5	3
14	14-Sep	Riverbed[2]	None	24 hrs-1 week	Moderate	5	5
15	14-Sep	Trail	None	24 hrs-1 week	Light	5	4
16	14-Sep	Shrub	Light	24 hrs-1 week	Light	3	3

APPENDIX 2.4 continued

17	20-Sep	Grass	Light	<24 hours	Moderate	5	5
18	20-Sep	Mixed	None	<24 hours	Light	5	--
19	20-Sep	Mixed	Light	<24 hours	Light	3	--
20	21-Sep	Conifer	None	<24 hours	Moderate	5	5
21	21-Sep	Mixed	None	<24 hours	Light	4	5
22	21-Sep	Road	None	<24 hours	Light	5	5
23	22-Sep	Mixed	None	24 hrs-1 week	Strong	5	5
24	22-Sep	Conifer	None	24 hrs-1 week	Light	5	4
25	09-Oct	Shrub	None	24 hrs-1 week	Light	4	5
26	09-Oct	Conifer	None	24 hrs-1 week	Light	5	5
27	09-Oct	Road	None	24 hrs-1 week	Light	5	5
Mean						4.6	4.5
SD						0.7	0.7

[1] Trial conducted along dirt road

[2] Trial conducted along river bank or dry riverbed consisting of river-rocks with sand patches.

APPENDIX 2.4.1. Candidate models and Akaike's Information Criterion (AIC) scores used to select a predictive model for factors determining detection of a scat by a dog. Models were derived from scat-detection trial based-data used in a logistic regression. The handler did not know where scats were placed prior to trials and did not look for scats themselves.

Candidate models	β	SE	k	AIC	ΔAIC
Shrub	-1.43	0.51	1	146.1	0.0
Conifer	1.11	0.76	1	150.2	4.0
NULL[a]	--	--	0	150.9	4.8
Temp. (°C)	0.05	0.04	1	151.1	5.0
HNDLRDOG[b]	0.29	0.45	1	152.5	6.4
Road	0.34	0.77	1	152.7	6.6
Mixed[c]	-0.18	0.54	1	152.8	6.7
Grass	-0.05	0.53	1	152.9	6.8

[a] Null model, no covariates.

[b] One of 2 detection dog and handler teams composed of 1 handler and 1 dog.

[c] Mixed deciduous and coniferous forest, understory woody vegetation often present.

APPENDIX 2.5. Scat age classes adapted from Wasser et al. (2004) used for assessing deposition date of scats collected during carnivore scat surveys in the upper Red Deer River watershed, Alberta, 2013-2016. Scats were aged based on moisture level, colour, weathering of fecal material, and presence of mold. Age is range in days (mid-point); mid-point was used to determine if scat was deposited after the beginning of the sample period.

Type	Characteristics	Age in days (mid-point)	Photo # (Appendix 2.4.1.)
Fresh	Mucous covering the scat was still visible. Minimal signs of insect activity on scat surface. Surface was dry and discoloured in direct sunlit areas.	≤ 2 days (1)	1a. – 1d.
Semi-old	Mucous traces visible in seams of scat or underside. Dry, depending on shade and precipitation, and showed signs of weathering including a cracked surface and/or up to ~10% loss of soft fecal material. More than 90% of solid material remained intact. In shaded/moist areas, scats appeared fresh but vegetation may have begun to regrow around scat.	3 – 14 (8)	2a. – 2d.
Old	Up to 50% of the fecal material was gone and often signs of insect activity were present throughout the scat. Solid material at the surface can be degraded but solid material inside the scat remains intact.	14 – 60 (37)	3a. – 3d.
Very-old	Up to 75% fecal material is gone and the remaining solid material is considerably degraded.	60 – 120 (90)	4a. – 4c.

APPENDIX 2.5.1: Photos of predator scats at different age classes. Row 1 are examples of fresh scats, row 2 were semi-old scats, row 3 were old scats and row 4 were considered to be very old scats (see Appendix 2.4 for further descriptions).

APPENDIX 2 .6. Modification of scat criteria for species-specific identification of scats. In the field we measured scat diameter, shape, examined contents, as well as observed other sign in the area to identify the species-specific scat with the intent to use characteristics from the published literature to distinguish among predator species (Appendix 2.5.1).

APPENDIX 2.6.1. Scat characteristics used for field identification of scats during carnivore scat surveys in the upper Red Deer River watershed, Alberta, 2013-2016.

Species	Diameter (cm)	Shape	Contents	Reference
Grizzly Bears	> 5	Highly varied, often tubular and unsegmented, or in piles of loose, unformed pellets	Often contains vegetation	Rezendes 1992
Black Bears	3.2 – 7.0			
Wolves	1.4 – 4.8	Cord-like, well tapered at one end	Often contain large bone fragments and high hair content. Berries and other vegetation sometimes present in coyote scats	Thompson 1952, Weaver and Fritts 1979, Rezendes 1992
Coyotes	1.4 – 3.3			
Cougars	2.5 – 3.8	Well segmented, not tapered	Rarely contains bones	Elbroch 2003, Rezendes 1992

We also collected DNA samples on a subset of scats (n=218) to assess identification accuracy. We did not collect DNA of very-old scats for DNA analyses because Piggott (2004) showed amplification success decreased from 100 to 0% over a 90-day period in red fox (*Vulpes vulpes*) scat in summer. DNA was collected with unfinished toothpicks by gently scraping the clear mucous off the scats. Toothpicks were placed in breathable coin envelopes and stored at room temperature (Waits and Paetkau 2005). DNA was extracted by Wildlife Genetics International (Nelson, B.C.) using the Qlagen QlaAmp Mini Stool Kit (Qiagen Inc., Valencia, CA). Once extracted, the 16S ribosomal ribonucleic acid (rRNA) mitochondrial gene (Johnson & O'Brien 1997) was analyzed and compared with existing known samples for species identification. DNA results showed the field identification based on the published criteria did not meet a (≥75%) correct classification at the species level except for cougars (Appendix 2.5.2).

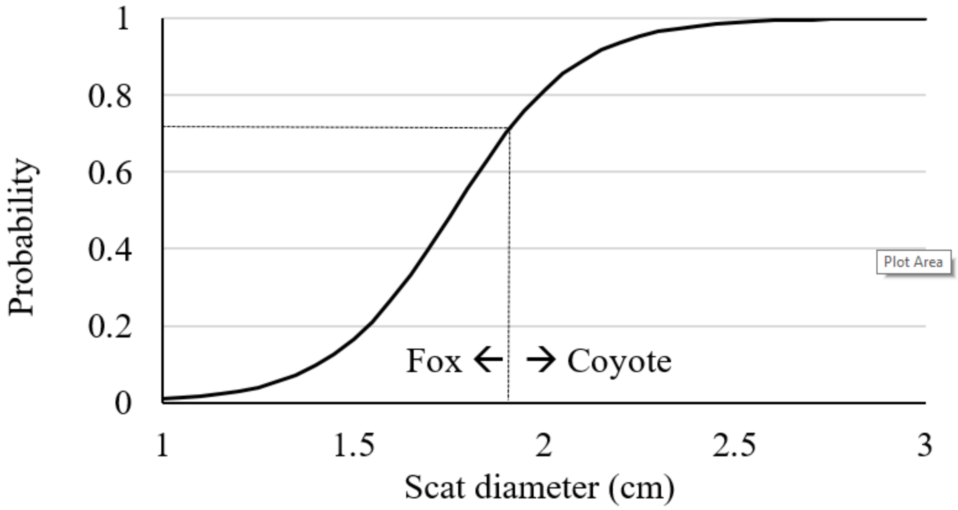
Due to the small sample of cougar scats, we retained all scats identified in the field based on published criteria as cougars for our analyses. In the case of ursids, low accuracy in identifying scats between the two ursid species forced us to use one ursid category for modeling. For canids, we redeveloped the diameter criterion after the 2015 collection season to distinguish foxes from coyotes because the accuracy was below 75% correct classification threshold. We regressed the diameter of the scat against the species (1=coyote, 0=fox, Appendix 2.5.3). We then selected the diameter size of 1.78 cm because the model predicted it had a 0.75 probability of being a coyote. Coyote scats collected in 2016 were identified using this criterion. This improved the accuracy level to meet our accepted identification level of 75% (Appendix 2.5.2).

APPENDIX 2.6.2. Amplification success for identifying species from scat DNA on scats collected during the summer and fall, 2014, 2015 and 2016, Alberta, Canada and analyzed by Wildlife Genetics International, Nelson BC. Of the successfully amplified scats, the percent correctly classified to either family or species in the field based on published and modified scat criteria.

	Number submitted and successfully amplified	Field identification accuracy[a] (%)	Modified identification accuracy[b] (%)
Bear	63	95	95
Black Bear	10	0	--
Grizzly Bear	23	65	--
Wolf	56	84	84
Coyote	55	56	78
Cougar	15	80	80

[a] Classification of amplified scats based on published criteria, see Appendix 2.5.1.

[b] Reclassification of canid scats to species based on modified criterion of 1.78 mm diameter to distinguish between fox (smaller) and coyotes (larger).

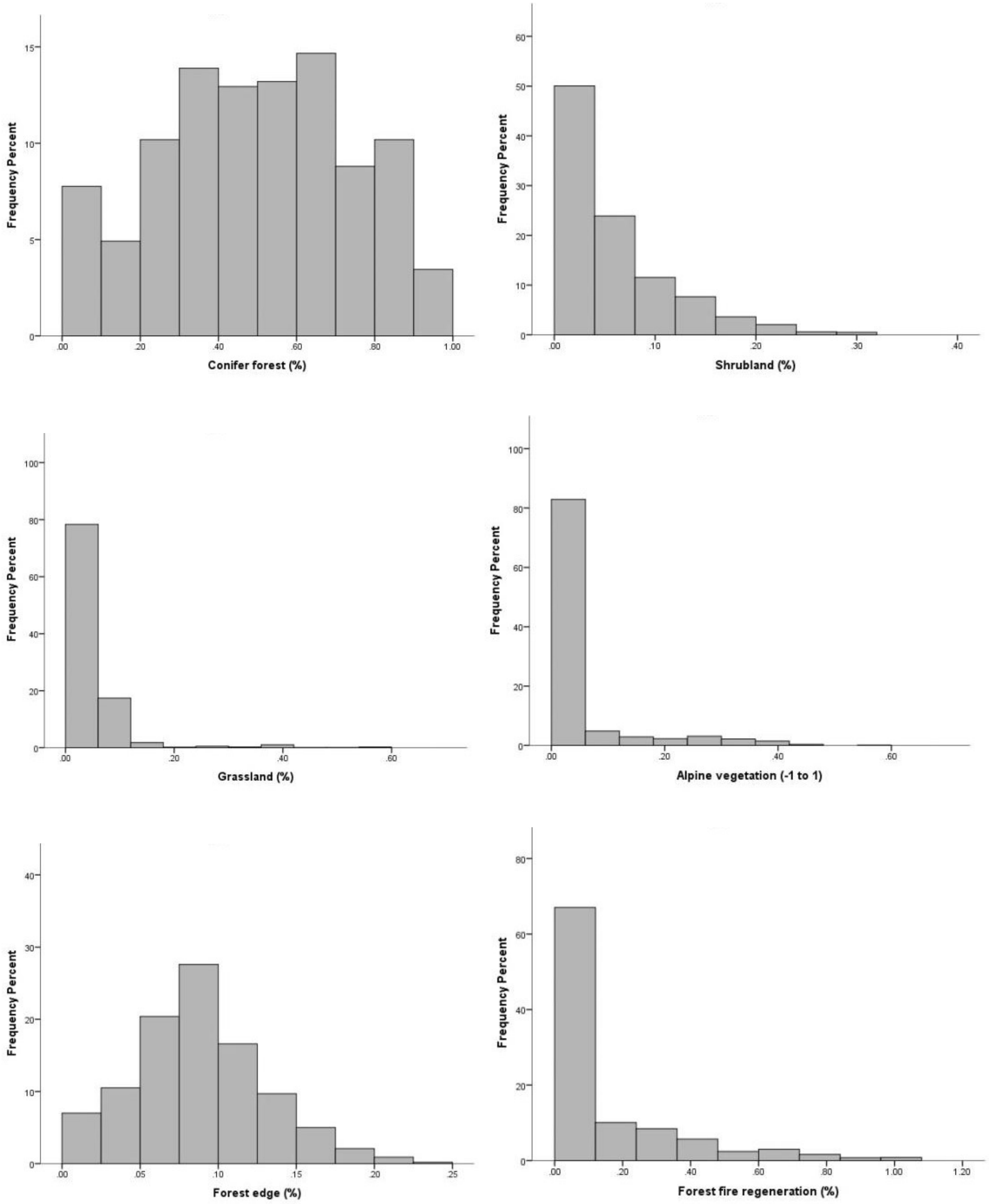


APPENDIX 2.6.3. Logistic regression showing probability that a canid scat has a probability of 0.75 of being from a coyote if its diameter is $\geq$1.78 cm. Logistic regression based on known species of coyotes (n=22) and red foxes (n=16) based on DNA from the Red Deer River valley, Alberta, in 2014 and 2015. Coyote scats collected in 2016 were identified using this criterion.

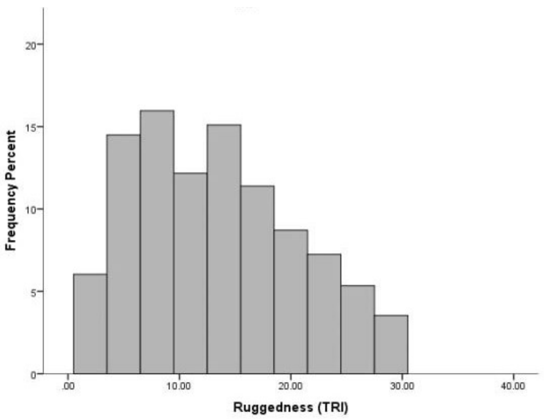
APPENDIX 2.7. Distances that dogs can detect scats of targeted species reported in conservation detection dog studies. Distances were used to guide survey transect buffer distance selection.

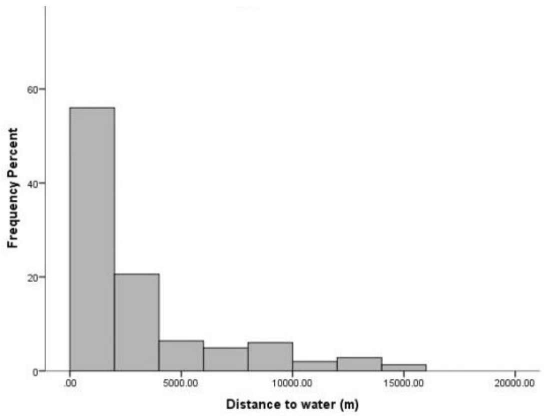
Detection distance	Study species	Habitat type, Location	Citation
100-m buffer on transect	Black bears (*Ursus americanus*), bobcats *(Lynx rufus),* fishers (*Martes pennanti*),	Temperate forest, Vermont (state-wide), USA	Long et al. 2007a
63 m max	Tortoises (*Gopherus agassizii*)	Mohave desert, California, USA	Cablk et al. 2008
7 m max	Brocket deer (*Mazama americana, M. bororo, M. gouazoubira*)	Atlantic forest, São Paulo, Brazil	Oliveira et al. 2012
>75% detection at 10m	Bobcat, cougar (*Puma concolor*), domestic cat (*Felis catus*), fox (*Vulpes* spp.*)*	California oak woodlands, San Francisco Bay, California, USA	Reed et al. 2011

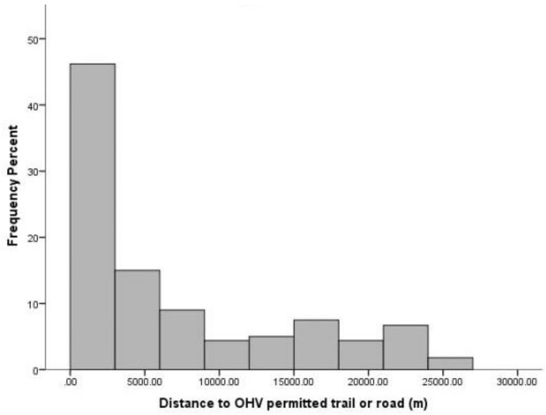
APPENDIX 2.8. Histograms representing frequency distributions of continuous variables used in developing Resource Selection Functions for 4 predators in the Alberta Rocky Mountains.

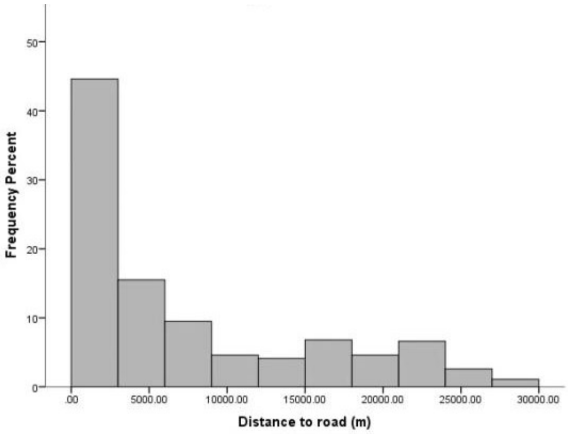


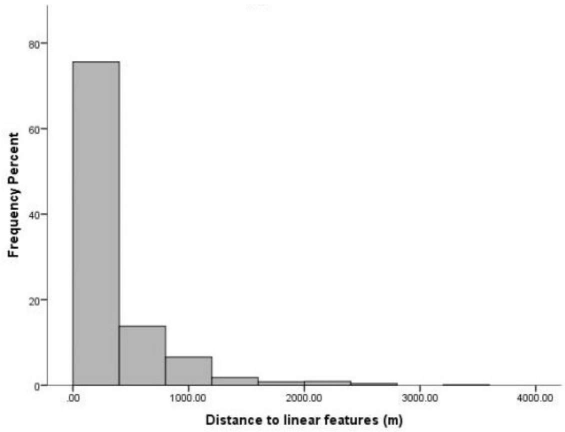
APPENDIX 2.8 continued

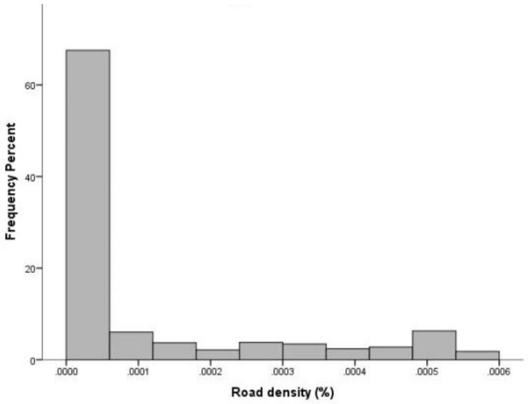












APPENDIX 2.9. Correlation matrix of continuous variables in used in resource selection analyses for 4 predators in the Alberta Rocky Mountains. Values in bold font are considered correlated.

	Alpine	Conifer	Cut	DisWat	DisLF	DisOHV	DisRd	Edge	Elev	Fire	Grass	NDVI	Rug	Shrub	Slope
Alpine	--	-0.04	-0.03	-0.08	0.12	0.04	0.10	0.02	0.33	-0.04	0.03	-0.19	0.00	-0.07	0.30
Conifer		--	0.05	0.00	-0.12	0.05	0.03	0.31	-0.17	**-0.65**	-0.31	-0.01	0.10	-0.19	0.07
Cut			--	-0.13	-0.12	-0.08	-0.20	0.28	-0.24	-0.15	-0.06	-0.17	-0.04	0.07	-0.01
DisWat				--	-0.15	0.16	-0.12	0.29	0.04	0.03	-0.30	0.28	-0.01	-0.19	0.23
DisLF					--	-0.03	0.17	-0.14	0.23	0.08	-0.03	-0.14	0.03	-0.03	0.07
DisOHV						--	**0.57**	-0.03	0.07	-0.09	0.08	0.08	0.08	0.03	0.07
DisRd							--	-0.14	0.30	-0.05	0.10	0.01	0.11	0.07	0.03
Edge								--	-0.07	-0.58	-0.10	0.14	0.01	0.14	0.08
Elev									--	0.06	0.12	0.14	0.12	-0.19	0.40
Fire										--	-0.17	-0.12	-0.10	-0.30	-0.01
Grass											--	0.10	-0.02	**0.61**	-0.23
NDVI												--	-0.01	0.22	0.05
Rug													--	0.03	0.03
Shrub														--	-0.26
Slope															--

APPENDIX 2.10. Habitat variables reported to be associated with predator summer selection in North America.

Variables	**Location**	**Citation**
Wolves		
Alpine vegetation + burned areas + cutblocks + hard edges + low elevation + open conifer – steep slopes	Rocky Mountains, AB, Canada	Hebblewhite & Merrill 2008
Conifer forest + density of cutblocks + density of natural openings – density of well sites + distance to roads – distance to water + mixed forest – moose pellet group density – ruggedness	Rocky Mountains, AB, Canada	Webb et al. 2009
Areas within 25-m of roads, trails, and railways + low elevation + shallow slopes + southwest aspects + low-use roads and trails selected for over high-use roads and trails	Rocky Mountains, AB, Canada	Whittington et al. 2005
Coyotes		
All forest habitat types – alpine areas + aspect (S-SW) + low elevation ($\bar{x}$ =1503 m) + open areas	Idaho, USA	Koheler and Hornocker 1991
Cutblocks 5-20 years of age – coniferous forest	Quebec, Canada	Boisjoly et al. 2010
Grizzly bears		
Alpine vegetation + avalanche chutes + barren surfaces + burned forests + high elevation - young and logged forests + low human access + low linear disturbance density + steep slopes + rugged terrain	Southeast B.C., Canada	Apps et al. 2004

APPENDIX 2.10. continued.

Alpine and subalpine vegetation (versus montane forest) + herb and shrub cover (versus upland forest) + high greenness + intermediate soil wetness + lower and intermediate road densities + proximity to water + quadratic slope (spring) + ≤ 40% crown closure	Rocky Mountains, AB, Canada	Chetkiewicz & Boyce 2009
Alpine vegetation – cut blocks 22-44 years of age + greenness – high and high-impact density - low impact density + moderate impact density + open forest + perennial streams + recent burns + shrub-wetlands	Rocky Mountains, AB, Canada	Nielsen et al. 2002
Black bears		
High vegetation greenness index (Landsat) + valley bottom terrain	Southeast B.C., Canada	Apps et al. 2006
Riparian + deciduous forest + meadows + shrub cover	Central Washington, USA	Lyons et al. 2003
Cougars		
– Anthropogenic features + edge habitat– core forest + ruggedness + south-facing aspect + shrub cover	Rocky Mountains, AB, Canada	Knopff et al. 2014
Elevation ($\bar{x}$ = 2001m) + timbered areas with non-rocky terrain (summer)	Idaho, USA	Koehler & Hornocker 1991

APPENDIX 2.11. Results of Krukal-Wallis test (H) for pair-wise comparisons among intensity of use derived for 4 predator groups from events (events/ active day) at remote cameras (n=54).

	k	H	*df*	*P*-value
Bears, wolves	2	4.52	1	0.034
Bears, coyotes	2	15.58	1	<0.001
Bears, cougars	2	31.30	1	<0.001
Wolves, coyotes	2	22.42	1	<0.001
Wolves, cougars	2	35.60	1	<0.001
Coyotes, cougars	2	2.40	1	0.121

APPENDIX 2.12. Summary of model selection for scat-based resource selection functions, east slopes of the Rocky Mountains, Alberta, Canada. Model chosen as top model in bold.

Model variables[a]	k	AIC_c	ΔAIC_c
Bear			
-Conifer+NDVI+Slope+Trail+DisOHV+Trail*DisOHV	6	1462	0
-Conifer+NDVI+Slope+Trail+DisOHV+Cut+Trail*DisOHV	7	1465	3
-Conifer+Cut+NDVI+Slope+Trail+DisOHV	5	1466	4
-Conifer+NDVI+Trail+DisOHV+Trail*DisOHV	5	1467	5
Full model[b]	13	1483	21
Null model	0	1608	146
Wolf			
-DisWat-Slope-Cut+Trail+DisOHV	5	**1637**	**0**
-DisWat-Slope-Cut+Trail+DisOHV+Edge	6	1639	2
-DisWat-Slope-Cut+Trail+DisOHV-Grass	6	1639	2
-DisWat-Slope-Cut+Trail+DisOHV+Edge-Grass	**7**	1642	4
-DisWat-Slope+Trail+DisOHV	4	1647	10
Full model[c]	13	1653	16
Null model	0	1844	207
Coyote			
Shrub-Slope+Trail+DisOHV	**4**	**1041**	**0**
Shrub, Edge, -Slope+Trail+DisOHV	5	1041	0
Shrub, -Slope+Trail+DisOHV-Grass	5	1041	0
Shrub, Edge, -Slope+Trail+DisOHV-Grass	6	1042	1
Edge, -Slope+Trail+DisOHV-Grass	5	1043	2
-Slope+Trail+DisOHV	3	1044	3
-Slope+Trail+DisOHV-Trail*DisOHV	4	1046	5
Full model	13	1053	12
Trail, DisOHV	2	1061	20
Null model	0	1163	122

APPENDIX 2.12. Continued

Cougar			
-Conifer+Edge	**2**	**355**	**0**
-Conifer	1	358	3
-Conifer+Edge+Shrub-Rug	4	359	4
Null model	0	360	5
Edge	1	361	6
Edge+Rug	2	362	7
Full model[d]	13	375	20

[a] Variable codes are defined in Table 2.1.

el : ± Elev ± Slope ± Conifer ± Mixed ± Shrub ± Grass ± Alpine ± Edge ± Fire ± Cut ± NDVI ± DisWat ± DisOHV ± DisRd ± Trail ± DisLF

APPENDIX 2.13. Number of elk kill sites used in predation risk modeling determined from cows and calves killed by unknown and suspected predators during 2002 to 2016, east slopes of Rocky Mountains, Alberta.

Year	Unknown			Bear			Wolf			Cougar			**Year total**
	yoy	adult	total	yoy	adult	total	yoy	adult	total	yoy	adult	total	
2002	1	3	4	0	2	2	0	4	4	0	2	2	**12**
2003	0	2	2	0	0	0	0	2	2	0	0	0	**4**
2004	0	1	1	0	3	3	0	4	4	0	0	0	**8**
2005	0	1	1	0	1	1	0	0	0	0	0	0	**2**
2006	0	2	2	0	0	0	0	0	0	0	0	0	**2**
2007	0	2	2	0	0	0	0	2	2	0	0	0	**4**
2008	0	2	2	0	0	0	0	0	0	0	0	0	**2**
2009	1	0	1	0	0	0	0	0	0	0	0	0	**1**
2010	0	0	0	0	2	2	0	7	7	0	0	0	**9**
2011	0	2	2	0	0	0	0	1	1	0	0	0	**3**
2012	0	0	0	0	0	0	0	2	2	0	0	0	**2**
2013	4	1	5	5	0	5	1	0	1	1	0	1	**12**
2014	7	0	7	10	0	10	3	0	3	2	0	2	**22**
2015	5	3	8	11	1	12	2	0	2	0	1	1	**23**
2016	13	0	13	13	0	13	4	1	5	1	0	1	**32**
Sp. Total	**31**	**19**	**50**	**39**	**9**	**48**	**10**	**23**	**33**	**4**	**3**	**7**	**138**

APPENDIX 2.14. Correlation matrix for variables representing predator intensity of use (*IU*), resource selection (RSF) or relative use (*RU*) used in modelling predation risk to elk in the Alberta Rocky Mountains.

	Bear$_{\text{IU}}$	Bear$_{\text{RSF}}$	Bear$_{\text{RU}}$	Cougar$_{\text{IU}}$	Cougar$_{\text{RSF}}$	Cougar$_{\text{RU}}$	Coyote$_{\text{RU}}$	Coyote$_{\text{IU}}$	Coyote$_{\text{RSF}}$	Wolf$_{\text{IU}}$	Wolf$_{\text{RSF}}$	Wolf$_{\text{RU}}$
Bear$_{\text{IU}}$	--	0.01	**0.95**	0.03	-0.02	0.01	0.48	0.46	0.09	0.29	-0.12	0.29
Bear$_{\text{RSF}}$		--	0.14	0.20	0.18	0.18	-0.12	-0.13	0.44	0.10	0.44	0.14
Bear$_{\text{RU}}$			--	0.04	0.00	0.03	0.41	0.39	0.09	0.25	-0.11	0.25
Cougar$_{\text{IU}}$				--	0.21	**0.99**	-0.07	-0.08	0.05	-0.14	0.02	-0.14
Cougar$_{\text{RSF}}$					--	0.25	0.16	0.17	0.31	-0.24	0.25	-0.24
Cougar$_{\text{RU}}$						--	-0.06	-0.07	0.03	-0.13	0.01	-0.13
Coyote$_{\text{RU}}$							--	**0.99**	0.19	0.00	-0.01	0.01
Coyote$_{\text{IU}}$								--	0.15	0.01	-0.03	0.01
Coyote$_{\text{RSF}}$									--	0.17	**0.74**	0.21
Wolf$_{\text{IU}}$										--	0.32	--
Wolf$_{\text{RSF}}$											--	0.35
Wolf$_{\text{RU}}$												--

APPENDIX 2.15. Summary of model selection results based on AIC_c for predation risk (PR) derived for predicting relative probability of elk kills from any non-human predator including unknown sources of predation being present at a site in the east slopes of the Rocky Mountains, Alberta, Canada. Relative selection is based on beta coefficients derived from on multinomial logistic models comparing the predictive ability of the intensity of use (*IU*), selection (*RSF*) or relative use of (*RU*) and landscape features at random locations (0), calf (1) and adult female elk (2) kill sites. Indicated are the signs of the beta coefficient of each variable.

Model	Elk age class	Model variables	*k*	AIC_c	ΔAIC_c
1	Calf	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}+\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$	5	904.4	0.0
	Adult	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}-\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$			
2	Calf	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}+\text{Wolf}_{IU}+\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$	6	905.3	0.9
	Adult	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}+\text{Wolf}_{IU}-\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$			
3	Calf	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}+\text{Cougar}_{RSF}$	4	911.2	6.8
	Adult	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}+\text{Cougar}_{RSF}$			
4	Calf	$-\text{Wolf}_{RSF}-\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$	4	963.6	59.2
	Adult	$\text{Wolf}_{RSF}-\text{Cougar}_{RSF}+\text{Wolf}_{RSF}*\text{Cougar}_{RSF}$			
5	Calf	$\text{Wolf}_{RSF}+\text{Cougar}_{RSF}$	3	971.2	66.8
	Adult	$\text{Wolf}_{RSF}+\text{Cougar}_{RSF}$			
6	Calf	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}$	3	982.0	77.6
	Adult	$-\text{Bear}_{RSF}+\text{Wolf}_{RSF}$			
7	Calf	Wolf_{RSF}	2	1021.7	117.3
	Adult	Wolf_{RSF}			
8	Calf	Coyote_{RSF}	2	1061.2	156.8
	Adult	Coyote_{RSF}			
9	Calf	Cougar_{RSF}	2	1066.5	162.1
	Adult	Cougar_{RSF}			
10	Calf	Bear_{RSF}	2	1128.5	224.1
	Adult	Bear_{RSF}			
11	Calf	Wolf_{RU}	2	1135.9	231.5
	Adult	Wolf_{RU}			
12	Calf	Wolf_{IU}	2	1138.2	233.8
	Adult	Wolf_{IU}			
13	Calf	Null	2	1144.9	240.5
	Adult	Null			
14	Calf	$-\text{Bear}_{RU}$	2	1145.6	241.3
	Adult	$-\text{Bear}_{RU}$			
15	Calf	$-\text{Coyote}_{IU}$	2	1145.9	241.5
	Adult	$-\text{Coyote}_{IU}$			

16	Calf	-Bear$_{\text{IU}}$	2	1146.0	241.7
	Adult	-Bear$_{\text{IU}}$			

APPENDIX 2.15. Continued

17	Calf	-Coyote$_{\text{RU}}$	2	1147.5	243.1
	Adult	-Coyote$_{\text{RU}}$			
18	Calf	-Cougar$_{\text{IU}}$	2	1148.6	244.2
	Adult	-Cougar$_{\text{IU}}$			
19	Calf	-Cougar$_{\text{RU}}$	2	1148.8	244.4
	Adult	Cougar$_{\text{RU}}$			

CHAPTER 3 SUPPLEMENTARY MATERIAL

APPENDIX 3.1. Summary spatial statistics used in predation risk analyses for individual and combined sheep ranges, both inside and outside Banff National Park.

	Range polygon centroid (UTM)					
	Easting	Northing	Distance from border (km)	Area (km^2)	Raster cell count	Perimeter (km)
Banff National Park						
Sheep Ranges						
BNP1	571675	5736240	-1.63	14	15390	86
BNP2	579651	5729840	-3.95	51	56113	227
BNP3	593552	5720220	-3.81	36	39536	224
BNP4	582743	5720770	-9.68	23	25159	104
BNP5	581801	5715610	-14.81	3	3229	20
BNP6	599464	5716270	-1.55	5	6052	35
BNP7	588866	5710630	-13.17	12	13639	63
Mean			**-6.94**	**20**	**22731**	**108**
SD			**5.54**	**17**	**19139**	**85**
On range total				**143**	**159118**	**758**
Outside of sheep ranges				**357**	**396322**	
Sheep Management Area						
Sheep Ranges						
SMA1	576327	5738050	1.98	9	9704	56
SMA2	591076	5735210	6.34	20	21705	137
SMA3	597886	5737830	11.52	3	3738	36
SMA4	605604	5736470	15.68	27	29544	149
SMA5	596573	5726190	2.11	26	28960	178
SMA6	605309	5717790	3.62	18	20023	153
Mean			**6.88**	**17**	**18946**	**118**
SD			**5.11**	**9**	**9470**	**53**
On range total				**102**	**113674**	**708**
Outside of sheep ranges				**419**	**465769**	

APPENDIX 3.2. Predator Resource Selection Function (RSF) values and landscape variables averaged for delineated sheep ranges and areas off sheep ranges on the east slopes of the Alberta Rocky Mountains. inside and outside Banff National Park.

	Cougar RSF		Wolf RSF		Coyote RSF		Bear RSF	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Banff National Park								
Sheep Ranges								
BNP1	0.59	0.05	0.42	0.06	0.40	0.06	0.39	0.09
BNP2	0.58	0.06	0.57	0.06	0.45	0.06	0.40	0.09
BNP3	0.60	0.05	0.52	0.06	0.42	0.07	0.36	0.10
BNP4	0.55	0.09	0.56	0.06	0.47	0.07	0.44	0.09
BNP5	0.61	0.03	0.55	0.05	0.49	0.06	0.50	0.09
BNP6	0.51	0.11	0.47	0.06	0.38	0.07	0.32	0.08
BNP7	0.60	0.06	0.60	0.05	0.48	0.07	0.50	0.10
Ranges combined	**0.58**	**0.06**	**0.53**	**0.06**	**0.44**	**0.07**	**0.41**	**0.09**
Off sheep range	**0.50**	**0.14**	**0.64**	**0.12**	**0.54**	**0.13**	**0.41**	**0.11**
Sheep Management Area								
Sheep Ranges								
SMA1	0.59	0.03	0.47	0.05	0.42	0.07	0.35	0.08
SMA2	0.50	0.08	0.49	0.04	0.38	0.05	0.30	0.05
SMA3	0.48	0.07	0.47	0.03	0.38	0.04	0.29	0.04
SMA4	0.57	0.05	0.41	0.06	0.33	0.07	0.23	0.06
SMA5	0.53	0.10	0.46	0.06	0.37	0.07	0.29	0.07
SMA6	0.49	0.13	0.46	0.05	0.36	0.07	0.27	0.07
Ranges combined	**0.53**	**0.08**	**0.46**	**0.05**	**0.37**	**0.06**	**0.29**	**0.06**
Off sheep range	**0.47**	**0.13**	**0.56**	**0.08**	**0.47**	**0.10**	**0.27**	**0.08**
Total area on sheep ranges	**0.56**	**0.07**	**0.50**	**0.05**	**0.41**	**0.06**	**0.36**	**0.08**
Total area off ranges	**0.48**	**0.13**	**0.60**	**0.10**	**0.51**	**0.11**	**0.34**	**0.10**

APPENDIX 3.2. continued

	Elevation		Slope		Distance to VPtrails		VRtrail_use		Conifer forest	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Banff National Park										
Sheep Ranges										
BNP1	2373	172	28	7	12600	1897	0.008	0.088	0.16	0.37
BNP2	2358	202	28	7	17949	2118	0.005	0.070	0.12	0.33
BNP3	2247	226	28	7	13642	2130	0.005	0.073	0.13	0.33
BNP4	2294	196	29	7	20383	1130	0.011	0.104	0.19	0.39
BNP5	2475	157	28	7	24090	362	0.000	0.000	0.09	0.28
BNP6	2131	201	30	7	10746	1227	0.013	0.115	0.24	0.43
BNP7	2185	174	29	7	22131	873	0.013	0.111	0.18	0.38
Ranges combined	**2295**	**190**	**29**	**7**	**17363**	**1391**	**0.008**	**0.080**	**0.16**	**0.36**
Off sheep range	**2183**	**281**	**18**	**12**	**18496**	**4474**	**0.033**	**0.179**	**0.34**	**0.47**
Sheep Management Area										
Sheep Ranges										
SMA1	2390	187	28	7	13024	1013	0.000	0.000	0.11	0.31
SMA2	2188	150	25	5	7081	1531	0.000	0.000	0.21	0.41
SMA3	2023	72	24	4	3410	1495	0.000	0.000	0.55	0.50
SMA4	2119	158	29	7	4388	1996	0.000	0.000	0.15	0.36
SMA5	2221	201	28	8	7209	2067	0.000	0.000	0.22	0.41
SMA6	1951	186	27	7	5021	1854	0.003	0.053	0.40	0.49
Ranges combined	**2149**	**159**	**27**	**6**	**6689**	**1659**	**0.001**	**0.009**	**0.27**	**0.41**
Off sheep range	**1973**	**311**	**15**	**11**	**6207**	**4773**	**0.015**	**0.123**	**0.46**	**0.50**
Total area on sheep ranges	**2227**	**176**	**28**	**7**	**12436**	**1515**	**0.004**	**0.047**	**0.21**	**0.38**
Total area off ranges	**2078**	**296**	**16**	**11**	**12352**	**4624**	**0.024**	**0.151**	**0.40**	**0.49**

	Shrub		Edge		NDVI		DisWat		Cutblocks	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Banff National Park										
Sheep Ranges										
BNP1	0.01	0.08	0.07	0.26	5280	2011	8.9	1.2	0.00	0.00
BNP2	0.01	0.12	0.05	0.21	4261	1993	2.2	1.6	0.00	0.00
BNP3	0.05	0.22	0.06	0.23	4451	2089	3.0	1.7	0.00	0.00
BNP4	0.03	0.18	0.06	0.24	4634	2076	3.8	1.7	0.00	0.00
BNP5	0.00	0.00	0.07	0.26	4729	2089	6.8	0.4	0.00	0.00
BNP6	0.03	0.17	0.07	0.26	4043	2131	3.2	0.6	0.00	0.00
BNP7	0.04	0.19	0.08	0.27	4996	1889	1.7	1.1	0.00	0.00
Ranges combined	**0.02**	**0.14**	**0.06**	**0.24**	**4628**	**2040**	**4.2**	**1.2**	**0.00**	**0.00**
Off sheep range	**0.03**	**0.17**	**0.06**	**0.24**	**5486**	**2393**	**3.0**	**2.4**	**0.00**	**0.00**
Sheep Management Area										
Sheep Ranges										
SMA1	0.01	0.09	0.05	0.22	3611	2091	5.7	1.0	0.00	0.00
SMA2	0.03	0.18	0.07	0.25	4878	1599	2.7	1.0	0.00	0.00
SMA3	0.07	0.26	0.16	0.37	6368	769	1.6	0.5	0.00	0.00
SMA4	0.05	0.22	0.06	0.23	3603	1695	3.9	1.2	0.00	0.00
SMA5	0.05	0.21	0.07	0.25	4756	2276	3.2	1.3	0.00	0.00
SMA6	0.07	0.26	0.09	0.29	5652	2067	2.3	1.1	0.00	0.00
Ranges combined	**0.05**	**0.21**	**0.08**	**0.27**	**4811**	**1750**	**3.2**	**1.0**	**0.00**	**0.00**
Off sheep range	**0.06**	**0.24**	**0.07**	**0.25**	**5869**	**2040**	**2.0**	**1.7**	**0.01**	**0.10**
Total area on sheep ranges	**0.04**	**0.17**	**0.07**	**0.26**	**4712**	**1906**	**3.8**	**1.1**	**0.00**	**0.00**
Total area off ranges	**0.05**	**0.21**	**0.06**	**0.25**	**5678**	**2217**	**2.5**	**2.1**	**0.01**	**0.05**