Complex Effects of Human-Impacted Landscapes on the Spatial Patterns of Mammalian Carnivores

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by

Nicole Alexis Heim
B.Sc., Thompson Rivers University, 2011

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of the Requirements for the Degree of

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in the School of Environmental Studies

Supervisory Committee

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Abstract

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In the face of an expanding global human footprint, mammalian carnivores have become vulnerable to the effects of large-scale landscape change. Throughout North America, wide-ranging terrestrial carnivores have experienced significant species declines and range retractions. Understanding the complex and interacting effects of human-caused habitat disturbance on highly mobile species remains an ongoing challenge for ecologists. To address these challenges, studies commonly select a focal species to examine the adverse effects of human disturbance. Due to the paucity of multi-species study, little is yet known about the relative role interspecific interactions play within communities of carnivores in human-altered systems. In an effort to address this knowledge gap, I examined occurrence patterns of one species known to be sensitive to human disturbance – the wolverine – and compared occurrence patterns among multiple carnivores across a gradient of increasing human land use within a rugged and heterogeneous landscape in the Canadian Rocky Mountains of Alberta.

I surveyed carnivore occurrence by combining remote camera trapping and non-invasive genetic tagging. Using a systematic grid based design, medium to large sized carnivores were detected over an area approximately 15,000km^2. Consistent with the literature, I found wolverines to be less likely to occur outside of protected areas boundaries and with increasing human-caused landscape disturbance. Contrary to recent climate-focused hypotheses, the spatial pattern of wolverine occurrence was best explained by cumulative effects. When modeling multiple carnivore occurrence across this spatial gradient of human land use, no generality in response was observed. However, a consistent and distinct dissimilarity in response to natural and anthropogenic landscape features was found between wolverine and coyote.

The patterns of occurrence led me to infer that habitat condition in the more human-altered systems found along eastern slopes of the Canadian Rocky Mountains is less suitable for some more sensitive species and benefits more human-adapted species. I further hypothesized that an indirect and additive effect of human disturbance is increased interspecific competition between co-occurring carnivores that differentially respond to changes in habitat condition. My results emphasize that by broadening our scope to investigate both single and multiple species, ecologists and managers may better understand the full suite of factors influencing current and future distribution patterns.

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And many many more…

Dedication

This work is dedicated to my parents, who showed their children all the beautiful things in the natural world worth fighting for. And to my brother, who shared all the precious years that made me who I am today.

And most of all, this thesis would be a blank page without the two men in my life -

My loyal black lab Harley
&
My loving husband and best friend Mike Davidson!

Chapter 1: An Introduction to the Ecological Implications of Landscape Disturbance on Mammalian Carnivores.

The natural world is experiencing significant and widespread landscape alteration due to increasing human demands and the resulting human footprint (Wilson 1999). In the last two centuries, extirpations and range retractions of North American mammals have been widespread (Laliberte and Ripple 2004) and most often attributed to the degree of human footprint, a measure of anthropogenic influences such as population density and land transformation (Sanderson *et al.* 2002). Diamond (1975) highlighted two main effects of human expansion: first, the shrinking of total area occupied by natural habitat and species; and second, the fragmentation of formerly continuous natural habitats (Diamond 1975). Since the definition of habitat depends on required resources to permit long-term survival for the species or communities under consideration, the degree to which habitat is altered, lost, and or fragmented will also depend on the species and scale at which the disturbance is occurring (Franklin *et al.* 2002).

A high degree of habitat loss can directly relegate species to less suitable habitat, or result in the extirpation of a species from a particular region (Weins and Moss 2005). Fragmentation is typically defined as the breaking apart of habitat (Fahrig 2003), which can alter habitats across larger landscapes and disrupt connectivity between habitat patches – a measure of the extent animals can move, or disperse between habitat patches within fragmented landscapes (Beckman *et al*. 2010), restricting or significantly reducing the availability of habitat to species even if it is of otherwise high quality. Today, landscape disturbance resulting in adverse effects from habitat loss and fragmentation are the predominant correlates of species declines across North America (Farhig 2003, Hilty *et al.* 2006).

Correlations between species declines and human-caused habitat disturbance are most notable throughout the literature for large-ranging mammalian carnivores (Gittleman 2001). Mammalian carnivores often exhibit high dispersal rates, low population density, low fecundity, and require expansive intact home ranges – all characteristics that make them particularly vulnerable to landscape alteration occurring across large spatial scales (Gittleman 2001, Crooks 2002, Watts and Handley 2010). Since individuals within these wide-ranging populations integrate habitats over large spatial scales, populations are supported through exchange of individuals over vast areas by means of dispersal. Alterations to the landscape can disrupt such movement and may thereby threaten persistence by limiting resource acquisition and preventing species dispersal and mixing among individuals. This leads to reduced resiliency and gene flow, lower genetic complexity, and thereby populations that are more vulnerable to stochastic events or disease outbreak (Landa *et al.* 1997, Gittleman 2001).

The effective magnitude of human disturbance on a species' ability to disperse, find necessary resources, and locate mates depends upon the species behaviour, habitat requirements, and the degree and pattern of the habitat change (Bowne and Bowers 2004). Each species is uniquely adapted to make decisions about how they navigate their environment (Krebs *et al*. 1985). Following an economic budget optimization theory, species-specific behaviour includes search strategies that maximize the amount of energy gained relative to the amount of energy expended while accessing resources (MacArthur and Pianka 1966, Real and Levin 1991). Search strategies are described under Optimal Foraging theory as a function of "trade-off" decisions that balance resource acquisition and competition, or mortality risk (Deon 2002, Mittlebach 2012). Anthropogenic activities that influence how a species moves across the landscape may affect their ability to optimize trade-offs, thereby incurring an energetic cost that could ultimately affect survival.

However, survivorship for more generalist species of carnivores has been found to benefit from human-caused changes to habitat. Linear features such as packed roads and trails, often attributed to fragmenting high quality habitat for wide-ranging mobile species, instead act as travel corridors for wolves into areas otherwise difficult to exploit or are inaccessible (Paquet and Callahan 1996, Whittington *et al.* 2005, Latham *et al.* 2011). Behaviourally mediated shifts to spatial and temporal habitat use and variable resource requirements have enabled populations of some medium-sized carnivores to exploit landscapes altered and dominated by human disturbance (Virgós *et al.* 2002, Tigas *et al.* 2002, Markovchick-Nicholls *et al.* 2008). It is therefore important to consider the various ecological processes that may drive individual species response to landscape features within their community or guild.

Dunning *et al.* (1992) outlined four ecological processes that drive species composition and spatial arrangement as a function of their ability to move to access critical resources distributed across the landscape (Dunning *et al.* 1992, Taylor *et al.* 1993). First, landscape complementation and second, landscape supplementation, occurring when individuals disperse to access critical non-substitutable and substitutable resources respectively across different habitat types. Third, source-sink dynamics, when different individuals occupy habitat with varied quality. And lastly, neighbourhood effects occur when critical resources are in the landscape immediately surrounding a species preferred habitat (Dunning *et al.* 1992). These ecological processes can be impacted by anthropogenic impacts that alter habitat quality and reduce areas of suitable habitat. The importance of landscape connectedness and the implications of habitat change on key ecological processes described by Dunning *et al.* (1992) are implicit in the development of logical hypotheses that predict the spatial patterns of large ranging carnivores.

Since implications of habitat change can be more severe for some carnivore species than others (Weaver *et al.* 1996), it is therefore necessary to also consider the ecological role that these individual species play within their community and local environment. “Apex”, or top, carnivores – species that occupy the top trophic position in a community – are more susceptible to extirpation and extinction than any other taxa (Ritchie and Johnson 2009). Some evidence suggests that these charismatic mega-fauna may play a significant ecological role driving top-down trophic cascades (Estes *et al.* 1998, 2011, Duffy 2003). Top carnivore species are termed keystone species; defined as one whose effect, if removed from an ecological community, is disproportionate relative to its abundance (Power *et al.* 1996). For example, top dominant predators are shown to the limit abundance and distribution of co-occurring subdominant carnivores (Caro and Stoner 2003, Beschta and Ripple 2009) and local prey species, indirectly mediating patterns of resource exploitation and over-grazing in both terrestrial and aquatic ecosystems (Pace *et al.* 1999, Springer *et al.* 2003, Fortin *et al.* 2005, Wirsing *et al.* 2007). Evidence of top-down trophic cascades highlights the ecological importance of maintaining single and multiple carnivores in a system as key players in maintaining ecological stability. With increasing anthropogenic pressures, threats for carnivores are imminent and ecological repercussions of these species loss may be detrimental. But remarkably, little is yet known about species-habitat relationships in naturally complex and human-impacted environments (Morrison 2009) or the role that species interactions may play in these altered systems (Godsoe and Harmon 2012, Betts *et al.* 2014).

Investigating spatial patterns of carnivore occurrence in relation to biophysical and anthropogenic factors are an important first step in understanding the complex effects of human land-use and habitat alteration, and in examining potential mechanisms of species declines and range contractions. To infer potential mechanisms driving single- and multi-species carnivore occurrence across large spatial scales and along a gradient of anthropogenic influences, I formulated two research objectives. In Chapter 2, I focus on wolverine (*Gulo gulo*) to explicitly examine how biophysical and anthropogenic landscape-scale factors influence the spatial distribution patterns of one vagile, wide-ranging carnivore. The wolverine operates at broad spatial scales, across a wide range of habitat types, and has been shown to be sensitive to human disturbance (Aubry *et al.* 2007, Krebs *et al.* 2007, Fisher *et al.* 2013). I model species-specific occurrence of wolverine in relation to landcover and climate factors, human land-use activities and landscape alteration. In addition, I incorporated the presence, or absence, of co-occurring carnivores from multi-species detection data to evaluate the relative role of interspecific competition on wolverine occurrence. In Chapter 3, I broaden my lens to examine how a community of medium- to large-sized carnivores may be responding to spatially widespread habitat disturbance in a naturally complex and heterogeneous mountain landscape. I begin with a multivariate approach to examine for community composition in relation to the same biophysical and anthropogenic landscape-scale factors that were incorporated into single-species distribution models described in Chapter 2. I then examined species-specific distribution models for individual carnivores detected in an effort to detect for generalities in response among intra-guild members of the carnivore community to the landscape factors as well as to detect for the additive effects of interspecific interactions.

It is difficult to test mechanisms that drive population processes at large spatial scales but we can measure patterns from empirical data and test logical arguments hypothesized to explain these patterns (Burnham and Anderson 2002). During this study, I tested multiple competing hypotheses about broad-scale correlations in order to make strong inferences (Platt 1964) about the underlying mechanisms driving dynamic population processes that predict current and future spatial distribution patterns. Previous research has examined obvious disturbance features for some wildlife such as roads, but this is one of the first to examine species occurrence and distribution patterns across a marked gradient of spatially extensive human land-use activity and habitat fragmentation.

In addition, past research on the east slopes of Alberta has focused on a single species – usually grizzly bear (Nielsen *et al.* 2002, 2004, 2006) or wolves (Hebblewhite *et al.* 2005, Hebblewhite and Merrill 2007) – or has addressed only a very limited landscape with a specific land-use, such as human activity on roads and trails, and a specific predator-prey behavioural response (Muhly *et al.* 2011, Ciuti *et al.* 2012). My research extends beyond a single-species focus to examine multiple mammalian carnivore species at once, across a spatially extensive, highly heterogeneous landscape (approximately 15,000km^2) with multiple human land-use activities including recreation (non-motorized and motorized), transportation, and industrial and resource extraction – the necessary design to attempt to disentangle the relative effects of biophysical and anthropogenic factors on carnivores communities at landscape scales (Fisher *et al.* 2011).

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CHAPTER 2: Spatial Patterns of Wolverine (*Gulo gulo L.*) Occurrence at the Canadian Rocky Mountain Range Margin.

2.0 Introduction

Habitat loss and fragmentation remain two prominent and adverse effects of human expansion and are primary correlates of decline for an exhaustive list of terrestrial species (Fischer and Lindenmayer 2007). Most notably these processes alter species distributions across landscapes (Wiens 1995). Understanding how a species relates to its environment and responds to landscape-scale habitat change can help ecologists elucidate ecological mechanisms driving distribution shifts (Wiens *et al.* 1993, Wiens 1995). Habitat changes can affect species distribution directly via human-caused mortality and habitat loss, or indirectly due to factors such as altered competition for resources, predation, or mutualistic interactions (Dunning *et al.* 1992). Examining response to multiple direct and indirect effects across large landscapes is particularly important for those species with low population density, low fecundity, large home range sizes and high dispersal requirements (Weaver *et al.* 1996), all characteristics that amplify sensitivity to habitat change (Gittleman 2001). The wolverine (*Gulo gulo luscus*, 1758) is a low-density, medium-sized carnivore occupying expansive home ranges (Rowland *et al.* 2003, Copeland *et al.* 2007, Inman *et al.* 2012b). Wolverines occur across many eco-regions with different ecological characteristics and disturbance regimes (Pasitschniak-Arts and Larivière 1995).

I examined how wolverine distribution is associated with a suite of biophysical and anthropogenic land-use factors at the edge of their North American range. I selected wolverine as a focal species because evidence suggests this wide-ranging species to be one of the most vulnerable to human impacted landscapes among the North American mammalian carnivores (Gittleman 2001). Due to their sensitivity, wolverines are extirpated from most of their range in the contiguous United States and much of eastern Canada (Laliberte and Ripple 2004, Aubry *et al.* 2007). Wolverines are also suspected to be declining in western Canada, where they are federally listed as a species of Special Concern (COSEWIC 2003). In southwestern Canada, the eastern boundary of their current geographic range occurs along the Rocky Mountains of Alberta (Figure 2.1) where this species is provincially listed as “data deficient” (Alberta Fish and Wildlife Division 2008), signifying a paucity of information for legal assessment and protection.

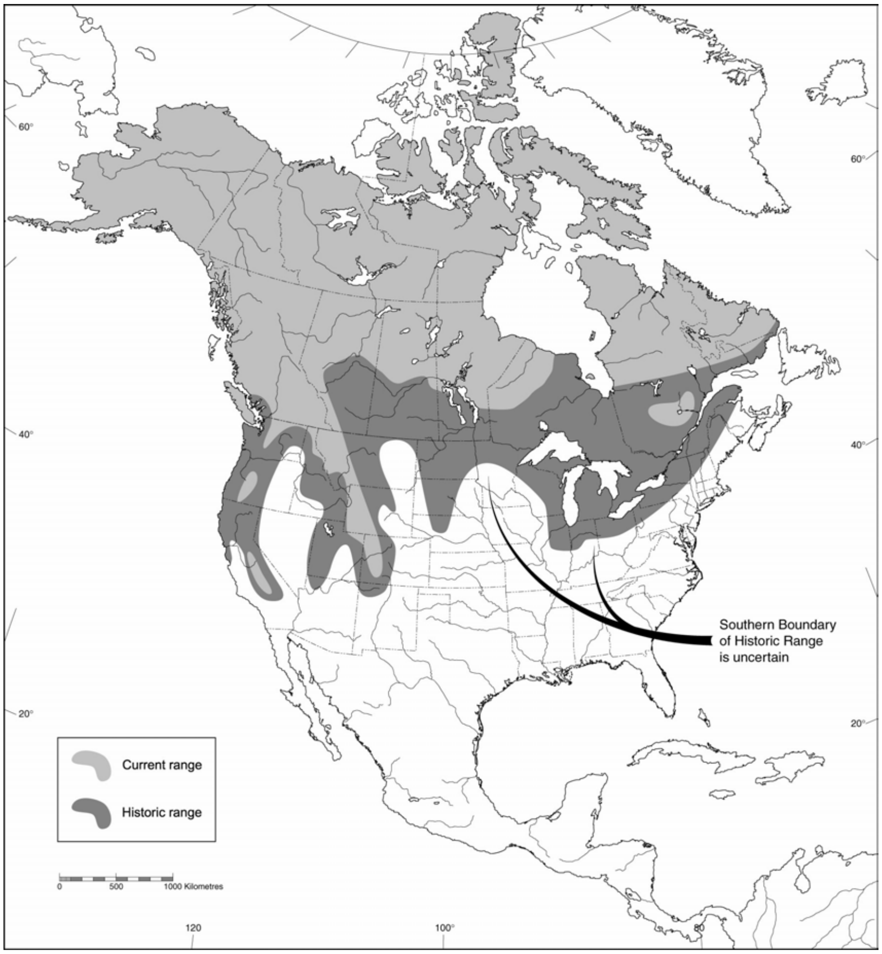


Figure 2.1 Current and historic distribution map of wolverine (Gulo gulo L.) throughout North America (COSEWIC 2003)

This map is the most recent available, however outdated and inaccurate. Extirpations exist within the current distribution boundary, including Colorado and California, and no data exists for much of coastal western Canada inlcuding Vancouver Island.

Wolverine abundance is negatively correlated to anthropogenic landscape alteration in the northwest United States, British Columbia, and west-central Alberta (Rowland *et al.* 2003, Krebs *et al.* 2007, Fisher *et al.* 2013). In Alberta, habitat within the current wolverine range is increasingly fragmented by activities driven by resource extraction and urban expansion, especially in the southern part of its range outside national parks and protected areas. For example, the density of linear features (roads and cut lines used for oil and gas exploration, or seismic lines) increase eastward outside of the nationally protected areas. West of Alberta in the North Columbia Mountains, Krebs and Lewis (1999) suspected that protected areas within Mount Revelstoke and Glacier National Parks were acting as refugia for wolverines, particularly for breeding females. Modern accounts of wolverines describe this species as a high-alpine mountain dweller (Chadwick 2010). However, historical records indicate that wolverines once occupied a greater variety of habitat types and elevations, throughout Eurasia (Landa *et al.* 1997) and North America, including arctic tundra and prairie plains (Slough 2007). For example, Alberta's harvest records dated back to 1985 report trapped wolverine to the east of their current distribution boundary beyond the alpine habitats of the Rocky Mountain range (Webb *et al.* 2013).

Recent research in the mountainous regions of North America, stretching from northern regions of the United States through western Canada and into Alaska, found wolverine positively associated with rugged, high-elevation alpine and avalanche terrain that contained areas of persistent spring snow cover (Copeland *et al.* 2007, Lofroth and Ott 2007, Schwartz *et al.* 2009). Wolverine are believed to select for rugged topographic features for cold food storage and to avoid areas of high human disturbance and negative inter-specific interactions – interference interactions among species within their guild, such predation or competition (Copeland *et al.* 2010, Inman *et al.* 2012a, Fisher *et al.* 2013). Described as a facultative scavenger, wolverine select for various habitat types that balance maximizing resources gained and minimizing risk associated with interference interactions (Lofroth *et al.* 2007, Krebs *et al.* 2007, van Dijk *et al.* 2008, Mattisson *et al.* 2011). In Norway, wolverines selected for more remote high elevation areas of alpine tundra and display local differentiation in habitat preference and distribution from co-occurring carnivores (brown bear (*Ursus arctos*), grey wolf (*Canus lupus*), and European lynx (*Lynx lynx*) (May *et al.* 2006, May *et al.* 2008). Though competitive exclusion may be occurring in some regions, researchers in southern Norway and Sweden found wolverine to greatly benefit from enhanced scavenging opportunities provided by co-occurring top predators (van Dijk *et al.* 2008, Mattisson *et al.* 2011), suggesting wolverine habitat selection may be context-dependent. In other words, wolverine space use may vary where scavenging opportunities outweigh inter-specific risk. Along the Canadian Rocky Mountain range, wolverines appear to be highly susceptible to fluctuations in scavenging opportunities (Weaver *et al.* 1996). Therefore, I predict habitat features as well as interspecific interactions significantly shape wolverine occurrence on the landscape.

Although broad-scale correlations suggest that climate-related habitat features and anthropogenic activities are the major drivers of wolverine occurrence (Schwartz *et al.* 2009, Copeland *et al.* 2010, Brodie and Post 2010), these conclusions are often formed in isolation from other competing mechanisms. There has been no investigation of complex interacting and cumulative effects of habitat and topography, climate, human activity and landscape alteration, and the intra-guild carnivore occurrence on wolverine occurrence across large spatial scales. The objective of this study was to investigate the relative effects of multiple species-habitat and species-species relationships explaining the spatial distribution patterns of wolverine across a gradient of both biophysical and anthropogenic landscape alteration along the Rocky Mountain Range margin in Alberta, Canada.

I hypothesized that the cumulative effects of human footprint, landcover, climate and interspecific interactions within the carnivore community influence wolverine occurrence patterns. Wolverine occurrence and genetic data were collected to model the current distribution pattern across the central region of the Rocky Mountain range to determine: (i) the biophysical and anthropogenic (human footprint) variables that best explain wolverine occurrence; and (ii) if intra-guild species occurrence influence wolverine occurrence.

2.1 Methods and Materials

2.1.1 Background

Sampling methods for surveying and monitoring wide-ranging carnivore species such as wolverine include snow tracking, aerial surveys, telemetry, and traditional mark-recapture techniques (Gittleman 2001). These techniques are often financially and logistically unfeasible to effectively survey wolverine across the large spatial scales at which this species operates. Non-invasive genetic tagging (NGT) has been used as an alternate and effective approach to obtain population estimates of some wide-ranging terrestrial carnivores, including grizzly bears (Kendall *et al*. 2009, Mowat *et al*. 2005) and wolverine (Copeland *et al.* 2010, Magoun *et al.* 2011), but can be subject to detection underestimation bias (Dreher *et al.* 2009). Camera trapping is an increasingly popular technique used to sample and monitor low density species (Thompson 2004, O'Connell *et al.* 2011) and provides an independent way of validating underestimation bias from NGT (Fisher and Bradbury 2014), therefore improving our ability to collect robust abundant data on single and multiple species at a reasonable cost and across large areas (Thompson 2004, Long *et al.* 2008, O'Connell *et al.* 2011).

A multi-method approach combining camera traps and NGT can effectively survey a spectrum of mammalian carnivores, including wolverine, in mountain environments (Fisher and Bradbury 2014). Fisher and Bradbury (2014) demonstrated that NGT provides information on unique individuals but is, by itself, not a wholly reliable measure of occurrence and abundance. The combination of NGT with camera trap detection provides occurrence data that can be used to model occupancy estimates and allows for calculation of the probability of detecting a species if it is in the area (MacKenzie 2006, Royle 2006, Fisher and Bradbury 2014). During the winter seasons of 2010-2013, wolverine and other co-occurring carnivore species were surveyed using the multi-method approach (Fisher *et al.* 2009). These data were used to test hypotheses about natural and anthropogenic landscape factors and inter-specific co-occurrence patterns that may explain wolverine occurrence in the central region of the Rocky Mountains.

2.1.2 Study Area

In collaboration with national park-based research efforts focused on wolverine population demographics and genetics (Clevenger and Barrueto 2014; Clevenger *et al.* 2011, *unpubl. data*), wolverine occurrence and individual identification were surveyed throughout the central Canadian Rocky Mountains within a complex of National Parks and eastward into the provincially managed region of Kananaskis Country (Figure 2). The National Parks complex included Banff, Yoho and Kootenay National Parks; as well as areas outside of the parks boundaries west to Golden, BC. Wolverines were also surveyed within the Ghost River Wilderness area located to the east of Banff National Park and to the north of the Kananaskis Country region. Since the Ghost River Wilderness Area is a provincially managed land-use area situated adjacent to the eastern boundary of Banff National Park, survey results for this area were summarized as part of the Kananaskis Country region. Therefore, the regional study area was comprised of two contiguous study areas - the National Parks complex and the Kananaskis Country region – represented a mosaic of mountain topography with varying degrees of landscape protection and density of human landscape alteration.

National Parks are federally protected and can provide refuge from increasing human land-use practices, such as resource extraction and motorized recreation. Within the Parks complex, the Trans-Canada Highway and Canadian Pacific Railway bisect Banff and Yoho National Parks through the main river valley bottom. Human impacts in the Banff-Bow Valley are spatially restricted to existing recreational trails, lease areas, and two town sites. Activities within the National Parks complex include non-motorized recreational hiking, biking, and camping, human impacts. In contrast, land management units designated as protected areas, wildland parks, and public land use zones partition land use activities in the Kananaskis Country region. The various management units encourage conservation of natural and cultural heritage while providing for economic land use practices. Furthermore, human impacts in the Kananaskis Country region are subject to expansion and include non-motorized (e.g. hiking, biking, skiing, equestrian) and motorized (e.g. off-road vehicles, snowmobile, and motorbike) recreation, trapping, and various types of resource extraction (e.g. oil and gas exploration, mining, timber harvest, and agriculture).

Ecological characteristics of both the National Parks complex and the Kananaskis Country region (Figure 2.2) are described by Rocky Mountain Natural Region (Natural Regions Committee 2006). The Rocky Mountain Natural Region is home to a native suite of large mammalian carnivore and ungulate species that include: wolverine (*Gulo gulo*), grizzly and black bear (*Ursus arctos and americanus*), cougar (*Puma concolor*), wolf (*Canus lupus*), mountain goat (*Oreamnos americanus*), moose (*Alces alces*), elk (*Cervus canadensis*) and deer (*Cervidae sp*.). This natural region is classified by three subregions: alpine, subalpine, and montane. The alpine natural region occurs above treeline and is dominated by low growing vegetation adapted to harsh climatic conditions. Occurring at mid-elevation, the forested slopes of the subalpine subregion vary in condition depending on aspect but are generally sheltered from the extreme conditions experienced at higher elevations. The subalpine subregion is dominated by Engelmann spruce (*Picea englemannii*), Subalpine fur (*Abies lasiocarpa*), and Subalpine larch (*Laryx lyallii*). On the lower front ranges of the Rocky Mountains, the montane natural subregion is dominated by mixed forests of Douglas-fir (*Pseudotsuga menziesii*), Trembling aspen (*Populus tremuloides*), and Lodgepole pine (*Pinus contorta*).

While alpine and Subalpine dominate the Parks complex with areas of Montane found in the main valley bottom corridors, Kananaskis Country transitions from Alpine and Subalpine into Montane and is bordered to the east by Foothills Parkland. The convergence of natural subregions in the Kananaskis Country region provides for increased biodiversity compared with the central regions of the Rocky Mountains to the west. Topography across both regions is rugged, with high peaks and steep-sloped ridges trending to low elevation foothills in the east, spanning an elevation gradient from a low point of 825m to above 3600m. The west-east gradient of varied landscape protection and increasing anthropogenic activity overlaying this topographically rugged and naturally complex study area provides a unique opportunity to investigate the relative effects of biophysical and anthropogenic landscape-scale factors that may explain patterns of wolverine occurrence.

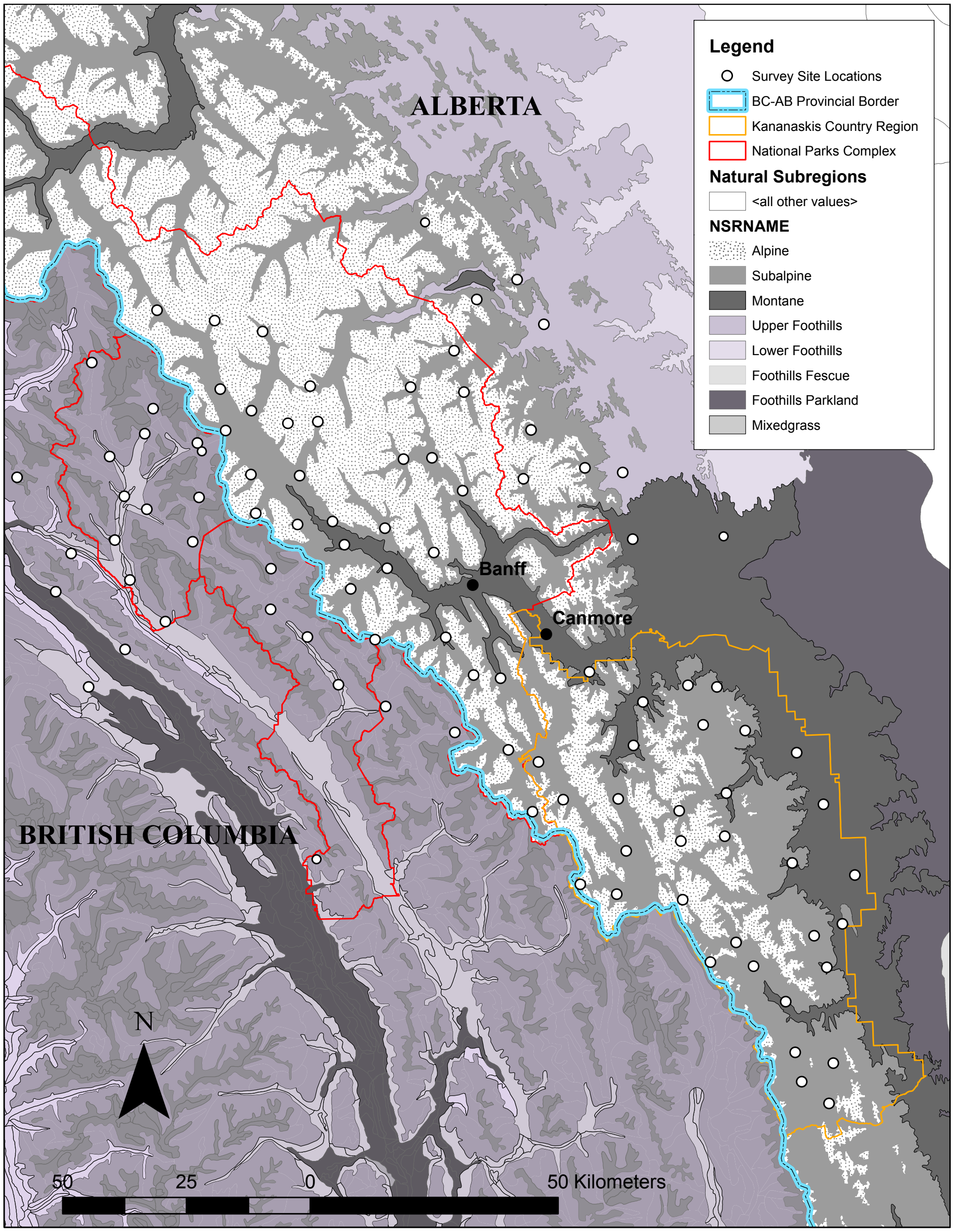


Figure 2.2 Map of natural subregions and park boundaries

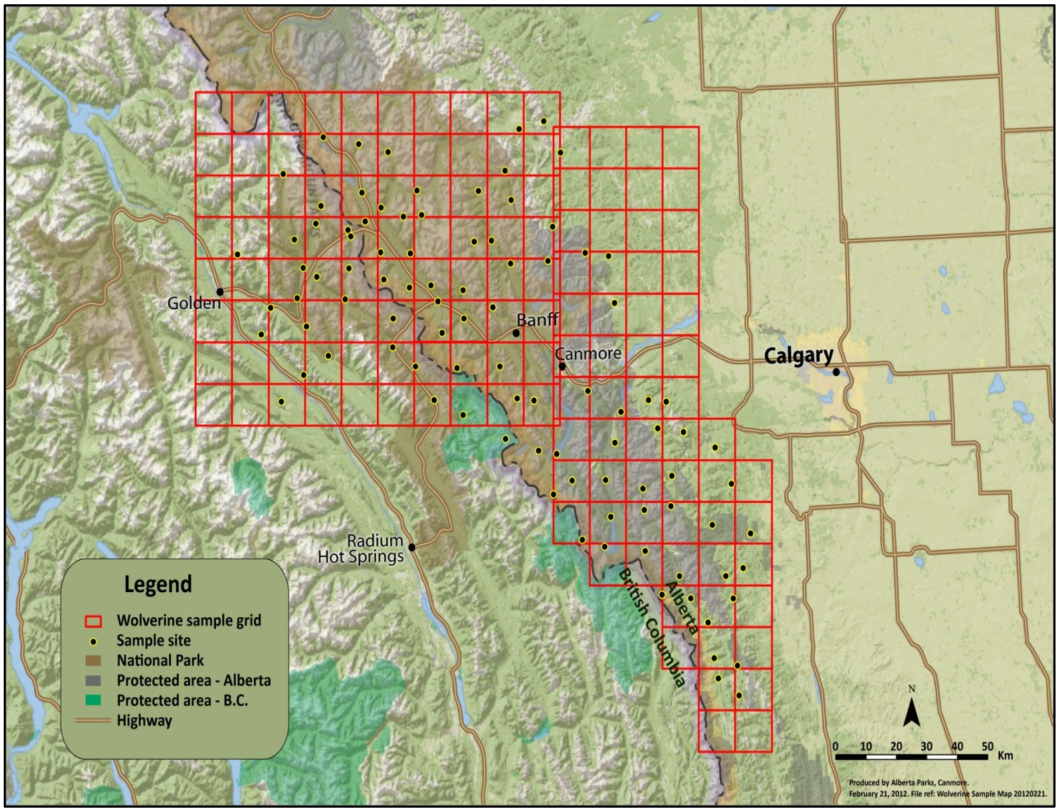
Maps point locations used to survey species occurrence (white dots) throughout the regional study area and across various Natural Subregions. The regional study area is situated along the Canadian Rocky Range, crossing a provincial boundary between British Columbia and Alberta and falls within National and Provincial Park boundaries.

2.1.3 Sampling Design

Carnivore occurrence was surveyed using a systematic grid-based sampling design (Figure 2.3), generated in ESRI ArcGIS 9.3 (Environmental Systems Research Institute 2009). Our systematic study design is a probabilistic approach that minimizes bias by spreading survey efforts uniformly across a large spatial area and allows for generalizations to be made from our analysis of random surveys to the broader population in the region (MacKenzie and Royle 2005).

To effectively study wide-ranging species such as wolverines the survey design must encompass several thousand square kilometers (Magoun *et al.* 2005) and include repeat survey periods that reflect average individual movements across these scales (MacKenzie 2006). Sampling unit (grid cell) size can influence estimates of species occurrence and occupancy and is recommended to be no smaller than the minimum home-range size but large enough to have a reasonable probability of detecting that species if it is present within a single survey (Gompper *et al.* 2006). Given that the minimum home range size of female wolverines is estimated between 100-150km^2 (Banci 1994), a 10x10km^2 (100km^2) grid cell size matches the spatial scale of the ecological process under investigation (Wiens 1989) and is consequently the suggested scale to survey wolverine populations (Koen *et al.* 2008). Since the National Park complex is covered by a substantial proportion rock and ice, a slightly larger cell size of 12x12km^2 (144km^2) was plotted over the study area and assumed unlikely to reduce sampling success (Clevenger and Barrueto 2014). For consistent and comparable study design the same grid cell size was plotted over the regional study area.

Grid cells were plotted across the regional study area of approximately 15,000km^2 (Figure 2.3). Of these grid cells surveyed, a total of 104 grid cells were included for purposes of this study, 43 were situated in the Kananaskis Country region and 61 in the National Parks complex. Each grid cell is considered one sampling unit. One survey site was located within each sampling unit. All sites were separated by a minimum distance of 6000m to facilitate sampling independence among sampling units and consistent with previous study by Fisher *et al.* (2013). Site locations were determined largely by logistics and accessibility, but generally were at mid-elevation drainages, travel corridors, and in areas with escape cover and evidence of animal movement in order to optimize animal detection. Subjectivity at the site level serves to maximize probability of detection, but does not affect our probabilistic design, since statistical inference will occur at the scale of the grid-cell (MacKenzie *et al.* 2006). All sampling sites were accessed by ground (ski, snowmobile, 4x4 vehicle) or helicopter.



Produced by Alberta Parks, Canmore.
February 21, 2012. File ref: Wolverine Sample Map 20120221.

Figure 2.3 Map of systematic grid-based study design and survey site locations

This map shows the grid overlay used to survey species occurrence throughout the regional study area. Individual sample, or survey, sites (black dots) are nested within the grid cells, or survey units, outlined in red. The sample grid of 12km x 12km cells stretches across the Rocky Mountain Range from Golden, BC to the eastern slopes of Alberta, representing a west-east gradient of variable land use practices within and adjacent to protected areas boundaries.

2.1.4 Field Collection

At each site infrared camera traps (IRC's) and NGT were simultaneously deployed (Figure 2.4). The IRC's deployed were Reconyx RM30 or PM30 infrared-triggered digital cameras (Reconyx, Holmen, Wisconsin, USA) and were positioned facing the hair trap. Digital photographs were used to identify species detected at each site. Animals were lured to hair traps by both bait, one beaver carcass secured 2m above ground on a limbed tree trunk, and scent lure. The tree trunk below the bait was wrapped loosely with Gaucho® barbed wire (Bekaert, Brussels, Belgium; Fisher and Bradbury 2014). Approximately one tablespoon of O'Gorman's LDC Extra scent lure (O'Gorman's Co., Montana, USA) was smeared onto a rag and hung on an adjacent tree, increasing scent dispersal. Once lured to the sampling site, the bait encouraged an animal to move into view of the camera trap, and for wolverines to climb the baited tree leaving hair samples on the barbed wire (Figure 2.4).

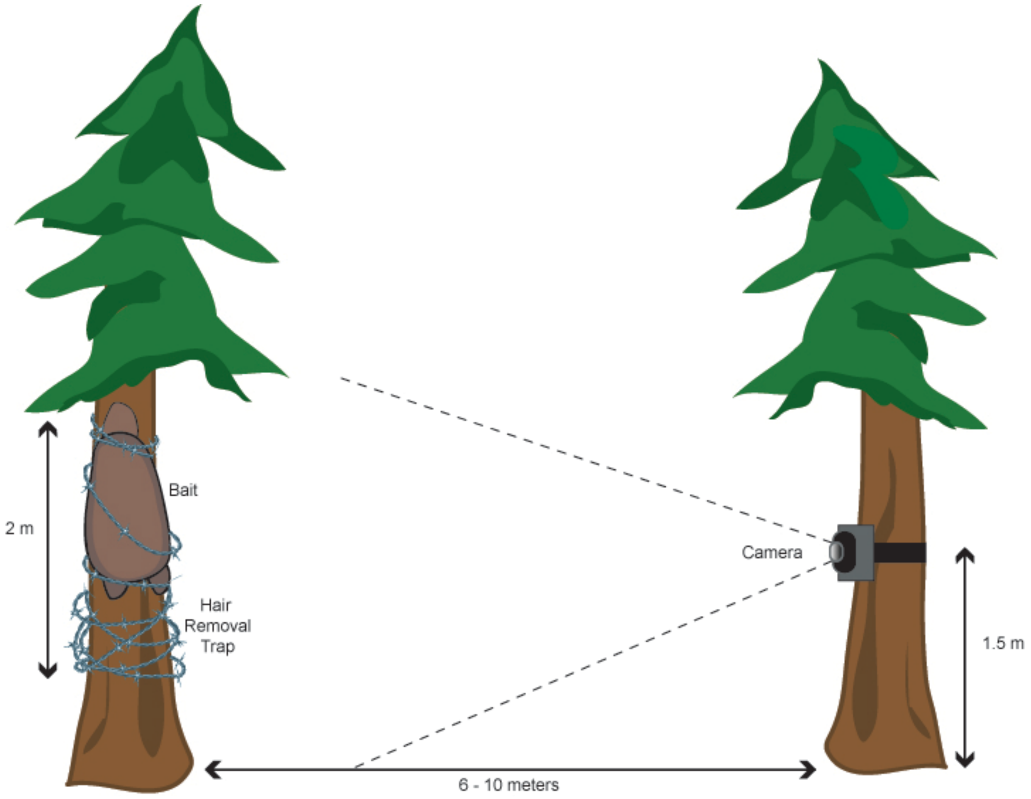


Figure 1.4 Illustraion of a multi-method survey approach

We surveyed wolverine occurrence using a multi-method approach that combines remote camera trapping and non-invasive genetic tagging, or hair trap. The hair trap (located on the tree on the left) consisted of barbed wire loosely wrapped around a baited tree. The digital camera (located on the right) was positioned on a tree 6-10m away to photograph the hair trap and the area around it.

Through collaborative efforts, wolverines were surveyed for three years within the National Parks complex (2010-11 and 2012-13) and for two consecutive years within the Kananaskis Country region (2010-11 and 2011-12) during mid-December to mid-April. The number of sites surveyed increased in the second year within the Kananaskis Country region and extending north into the Ghost Wilderness area, broadening the spatial extent of the regional study area. For this reason, species occurrence data from the second more spatially extensive survey season for each of the two areas (2012-13 and 2011-12, respectively) were used to answer questions about wolverine distribution patterns for this study. All sites across the regional study area were sampled at monthly intervals across 3 survey periods each season. Due to logistic constraints, approximately 25% of the total survey sites were restricted to only two monthly survey periods. The month-long survey duration satisfies random sampling assumptions – a member of a population having an equal and independent chance of being detected. As wolverines can travel a home range within a two week period (Inman et al. 2012b), a monthly survey duration gives ample time for this assumption to be met (Koen 2008). During each monthly survey, hair traps were re-baited and new scent lure was applied, camera images were uploaded, and hair samples were collected from barbed wire for genetic analysis. Hair samples were individually collected in envelopes using sterilized forceps to avoid cross-contamination between follicles as per Depue and Ben-David (2007).

2.1.5 Genetic Analysis

We used the genotyped individuals to estimate the minimum number of individuals detected and examine the pattern of spatial occurrence and distribution of wolverines; however, were not used to test competing hypotheses about relationships between wolverine occurrence and landscape variables because camera data provided more reliable occurrence estimates (Fisher and Bradbury 2014).

We used standard genotyping techniques were used to extract DNA from hair samples using the QIAGEN DNeasy Blood and Tissue kit with modifications for hair sampling (Mills *et al.* 2000) and assayed with a 16 locus mtDNA microsatellite panel (Schwartz *et al.* 2009) at the USFS Rocky Mountain Research Station, Missoula, Montana, USA. Sex was established using a wolverine sex test (Hedmark *et al.* 2004). Mitochondrial DNA haplotype, individual, and sex were analyzed at the 344bp region of the genome that has been examined in multiple studies to assess wolverine haplotype diversity (Tomasik and Cook 2005, Cegelski *et al.* 2006, Schwartz *et al.* 2007).

2.1.6 Image-based Identification and Occurrence

Preliminary analysis of remote camera imagery suggested wolverines detected were less likely to climb a baited tree in the Kananaskis Country region compared to wolverine detected in the National Parks complex, thus having a lower chance of leaving hair for genetic analysis. To more reliably estimate the number of individuals in the Kananaskis Country region, I was assisted by A. Magoun in the analysis of camera images to identify individuals using match points, or visual markings, based on the relative position and configuration of lightly-coloured pelage on the ventral surface of individual wolverines that could be later linked to the genetic results (Magoun *et al.* 2011).

Camera imagery (Figure 2.5) also provided species presence-absence data to model as the response variable against a number of explanatory variables related to biophysical landscape factors and human disturbance. I classified all images as a count of species detection (1) or non-detection (0) across each monthly survey, yielding a 0-3 index of wolverine presence-absence use for each sampling unit. Counts of species detection data were modeled against UTM (Universal Transverse Mercator) east coordinates to evaluate probability of wolverine occurrence across the study area. Similarly, the number of unique wolverine individuals genetically identified was plotted across UTM East (UTMx) coordinates to examine spatial patterns of relative abundance, though did not account for slight variation in the number of grid cells surveyed across space.

Figure 2.5 Remote camera image of wolverine at a survey site

Photograph from a camera trap in Kananaskis Country captures the sampling technique that combines non-invasive genetic tagging as part of a standardized multi-method approach to surveying wolverine throughout the Rocky Mountains regions of Alberta, Canada. The top right-hand inset figure shows an example of one hair sample collected from barbed wire that is wrapped around the tree trunk below the bait.

2.1.7 Occupancy Estimation

We used presence-absence data to estimate the probability of species occupancy (ψ) and to model relationships with proposed explanatory variables. Occupancy is an estimate of the probability of species occurrence that adjusts for imperfect detection, when the detection probability (p), the probability a species is detected given it is present, is less than 1 (MacKenzie 2006, Royle 2006, Nichols *et al.* 2008). Occupancy models are analogous to simultaneous generalized linear models on serial detection data to estimate both p and occupancy. For wide- ranging and elusive species, imperfect detection is often a concern and has led to the increased use of occupancy modeling to understand spatial distribution patterns (MacKenzie *et al.* 2002, MacKenzie 2006). When p is low ($p < 0.5$) or varies across time or space in relation to measured explanatory variables, the variance in species occurrence may be attributed to imperfect detection, increasing the chance of spurious results induced by detection error. If p does not vary in relation to explanatory variables, unadjusted occurrence counts can be used in a traditional regression approach, such as generalized linear modeling.

We estimated occupancy to evaluate: (1) the probability of wolverine occurrence across survey periods, along the west-east (UTMx) axis, and (2) to estimate and assess variation in p in relation to landscape covariates across the two study areas. To estimate occupancy, we used custom single-season hierarchical models that assume (i) all parameters are constant across sites and that any change in site occupancy within the duration of the survey period is random; and (ii) sites were closed to changes in occupancy at the species level (PRESENCE v.4.4 software, Hines 2006, MacKenzie *et al.* 2006). To account for variation across covariates, we grouped alternative models into model sets according to the landcover, human footprint, climate, topographic, and interspecific species variables predicted to differentially influence wolverine occurrence. We compared models within and across models sets using an Information-Theoretic Approach (Akaike Information Criterion, AIC). This approach uses maximum likelihood estimation and the principle of parsimony to evaluate the relative support for alternative hypotheses by estimating the model that best explains wolverine occurrence while balancing bias and variance (Burnham and Anderson 1998). Lower AIC scores indicate a more parsimonious and better-fit model relative to alternative models tested (Anderson 2008). We ranked alternative models using AIC weights (AIC_w) and calculated evidence ratios (ER) to weigh support for each covariate modeled against the probability of detecting wolverine (p).

2.1.8 Quantifying Landscape Covariates

We used ESRI ArcGIS 9.3.1 software and digital map inventories (ABMI Human Footprint Map 2010, and National and Alberta Provincial Parks' geo-databases) to acquire spatial data to measure natural and anthropogenic covariates, or landscape features, around each sampling point. Measured landscape features included those hypothesized to be important for wolverine and having spatial data available with continuous coverage across the regional study area. We quantified the proportion of each landscape feature was quantified by creating circular buffers around each sampling point, across 20 spatial scales ranging from 500m up to 10,000m (q.v. 1.1.10).

We obtained a 16 class landcover raster dataset (McDermid *et al.* 2009) to quantify the average percent area of natural landcover classes within each spatial buffer around each sampling point. We quantified topographic ruggedness, measured as the mean elevation difference over an area, using a topographic ruggedness index created from a 30m cell resolution digital elevation model (Riley *et al.* 1999). We calculated persistent spring snow as the number of years over a 12-year period an area was covered by snow during the spring (defined between the 14th of April and the 15th of May) using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data (Copeland *et al.* 2010, Hall and Riggs 2007). We separated anthropogenic or "human footprint" features (ABMI Human Footprint Map 2010) into 12 composite classes (Appendix A, highlighted in blue). We used spatial layers from a Parks Canada database (Parks Canada 2014) to summarize the human footprint features found within the National Parks Complex, features described by the ABMI Human Footprint Map (2010). To accurately model human footprint features across the regional study area, we buffered spatial layers from the Parks Canada database to meet the same spatial extent of layers described by the ABMI Human Footprint Map (2010).

We then grouped the 12 human footprint classes into two main categories: block or linear features. Block features were further broken down as areas altered by either urban or industrial human footprint. Urban block features are spatially broad areas disturbed for human-use such as town sites and recreational lease areas; whereas, industrial block features are areas disturbed for resource development that include oil well and mining sites, timber harvest cut blocks, and cleared or cultivated areas. Urban and industrial block features were measured as the percent area of each footprint type. Linear features are disturbed areas arranged in or extending along a straight line. We summarized these features by classes that included roads, cutlines, pipelines, seismic lines, and recreational trails. Using the ABMI (2010) database, all road types were grouped together (e.g. paved, unpaved, single and double lanes). Linear features were calculated as the mean density (km/km^2) of each linear feature class within the spatial buffers. Recreational trails were also broken into two classes by non-motorized, or quiet, recreational features and off-road motorized, or loud, recreational features. Since off-road motorized recreation is not permitted in the National Parks, the linear loud recreational features were only quantified from areas within the Kananaskis Country region.

Monthly presence-absence of carnivore species (listed in Table 2.1) was summed across the study period (0-3) to test for effects of intra-guild carnivore occurrence on wolverine distribution.

2.1.9 Parameter Simplification

I estimated multicollinearity to remove collinear variables, therefore reducing imprecise parameter estimation and type II errors (Zuur *et al.* 2013). I used Pearson correlation coefficient (r^2) matrices and multi-panel scatterplots to evaluate collinearity among proposed landscape covariates. I chose variance inflation factor (VIF) estimation to evaluate the degree of collinearity among covariates (Belsey *et al.* 1980, Craney and Surles 2002). A stepwise approach to VIF estimation reduced the number of variables to those with VIF < 5. A tolerance level of VIF < 3 is preferred (Craney and Surles 2002), however a VIF < 5 enabled retention of variables hypothesized to be ecologically meaningful into a saturated global model (described in Table 2.1). Using this stepwise approach, I excluded four collinear variables from model specification (Table 2.2).

Following the principle of parsimony, two wetland cover types (treed and open wetlands) were also excluded from the saturated global model having no a priori hypotheses to suggest these landscape variables to be important factors explaining wolverine occurrence. However, I retained two collinear snow-related measures in the global model as unique factors hypothesized to influence wolverine habitat selection (Schwartz *et al.* 2009b, Copeland *et al.* 2010, Inman *et al.* 2012a). The snow/ice landcover class was generated from a single satellite image taken during the fall of 2008 and represents the presence of perennial, or semi-permanent, snow and ice (McDermid 2013, personal communication). In contrast, persistent spring snow is an annual average measure of snow cover during the spring presumed to be important for denning females (Magoun and Copeland 1998, Aubry *et al.* 2007).

Table 2.1 List of landscape variables

Landscape variables hypothesized to explain wolverine occurrence and their predicted direction of association across the greater study area of National Parks complex and the Kananaskis Country region, Alberta.

Category	**Landscape Variable**	**Description**	**Hypothesized Association (+, -, neutral)**
Landcover	DENSECON	>70% crown closure; >80% coniferous	+
	MIXED	21-79% coniferous	-
	OPENCON	<30% crown closure; >80% coniferous	-
	SHRUB	shrub cover, represents avalanche path cover.	+
	HERB	herb cover	neutral
	REGEN	regenerating portions of the landscape	-
	SNOW.ICE	perennial, or permanent, snow and ice cover	+
Human Footprint	BLOCKURB	Blocks of urban footprint (eg. towns, developed recreational lease areas)	- , neutral
	LINROAD	Linear road features including paved and unpaved transportation	-
	LININD	Linear industrial cutlines (eg. seismic lines, powerlines)	-
	LINREC_Q	quiet linear recreational features (designated hiking trails)	- , neutral
	LINREC_L	loud linear recreational features (designated atv and snowmobile trails)	-
Abiotic	TRI	topographic ruggedness index, average elevational difference in a given area	+
	SP.SNOW	number of years (out of 12) an area was snow covered during spring months	+

Biotic	WOLF	wolf occurrence	+ , -
	COUG	cougar occurrence	+ , -
	COYO	coyote occurrence	-
	LYNX	lynx occurrence	+
	BOBC	bobcat occurrence	neutral
	FOX	red fox occurrence	- , neutral
	MART	*American* marten occurrence	- , neutral
	SCAVENGER	sum of lynx, bobcat, coyote and fox occurrences	- , +, neutral
	PREDATOR	sum of cougar and wolf occurrence	-

Note: DENSECON, dense conifer cover
MIXED, Mixed forest Cover
OPENCON, Open conifer cover
SNOW.ICE, Perennial snow and ice over
BLOCKURB, Urban block shaped features
LINROAD, Linear roads
LININD, Linear industrial cutlines
LINREQ_Q, Quiet linear recreational trails
LINREQ_L, Loud linear recreational trails
TRI, Topographic ruggedness index
SP.SNOW, Annual spring snow cover

Table 2.2 List of collinear landscape variables

Collinear landscape variables excluded from model specification using a stepwise approach of variance inflation factor (VIF) estimation and a tolerance level of VIF < 5.

Category	Excluded Landscape Variables	Description	Collinear Landscape Variable
Landcover	BROAD	>60% crown closure, >75% broadleaf	Mixed Forest Cover (MIXED)
	BARREN	<6% vegetation cover	Persistent Spring Snow (SP. SNOW) and Topographic Ruggedness (TRI)
Human Disturbance	BLOCKIND	Blocks of industrial footprint (eg. well and mine sites, cutblocks, disturbed vegetation)	Linear Industrial Features (LININD)
Abiotic	ELEV	Elevation (m) of survey site location	Persistent Spring Snow (SP. SNOW) and Topographic Ruggedness (TRI)

Note: BROAD, broad leaf forest cover
BARREN, barren ground
BLOCKIND, industrial block shaped features
ELEV, Elevation (m)

2.1.10 Characteristic Scale of Habitat Selection

Determining the appropriate scale of species habitat selection is of fundamental importance when trying to understand observed patterns and the ecological mechanisms driving species distributions (Levin 1992); however, there remains no single known scale at which ecological distribution patterns should be studied. The scale a species may be responding can be estimated by considering research questions, organism studied, and time periods of study (Wiens 1989, Wiens et al. 1993); or, scale may be considered at a species point of view based on habitat selection from microsites, home range, to geographic range (Elith and Leathwick 2009). In British Columbia, a multi-scale analysis by Krebs et al. (2007) defined wolverine habitat selection across three spatial scales (circular radii), ranging from a fine scale of 700m to a landscape scale of 7,600m. In west-central Alberta, Fisher et al. 2011 found wolverine habitat selection to be best explained at the 5000m scale, the largest scale under examination. Given the expansive home range size of some wolverine occupying rugged mountain landscapes, I predicted wolverine habitat selection in this region of the Canadian Rocky Mountains to be best explained by a larger scale than previously identified. With no a priori knowledge of a single scale at which wolverines select the biophysical or anthropogenic landscape features being tested, I applied a cross-scale analysis using generalized linear modeling and a stepwise AIC selection approach to examine for the scale that best predicts wolverine occurrence appropriate for multi-model inference. I modeled wolverine occurrence against landscape covariates across 20 spatial scales that spanned those found by Krebs et al. (2007) and Fisher et al. (2011), starting at circular radius of 500m up to a radius of 10,000m.

2.1.11 Modeling Wolverine Occurrence and Landscape Features

I further used generalized linear models (GLM) (R version 3.0.2, R Core Team 2014) to test hypotheses about the relative importance of biophysical and anthropogenic landscape, or explanatory, variables in explaining wolverine occurrence. I could confidently use these more flexible models to test species-habitat and species-species relationships since occupancy models suggested weak evidence relating detection error with landscape covariates (q.v. 1.2.2). GLMs are a family of models that deal with non-normal distributions by transforming, or generalizing, constrained response data using a log-link function specified by an error distribution (Matthiopoulos 2011). I used the number, or count, of wolverine detections summed across three survey periods (0-3) for each of the 104 sampling locations to index residency, or frequency of use, and modeled as the response variable in these analyses. I modeled the count of wolverine detections during the fixed sampling periods using a Poisson error distribution that assumes detection events are independent and infinite. Violation of assumptions were investigated by extracting model residuals using three diagnostic plots: (1) simple residuals against predicted values, (2) Q-Q plot using standardized deviance residuals, (3) and an approximate Cook's distance; as well as, examining for over- and under-dispersion by calculating the deviation of a dispersion statistic from 1 to determine if the Poisson distribution is appropriate for the data (Matthiopoulos 2011, Zuur *et al.* 2013). I examined for outliers in the data for both the response and explanatory variables using Cleveland plots Zuur *et al.* 2010). I standardized all measured explanatory variables by subtracting the mean from the individual values and then dividing by the standard deviation for accurate comparison of parameter effect size. I then grouped the standardized explanatory variables within candidate model sets according by the type of influence, or single-factor, hypothesized to explain wolverine distribution (Table 2.3). Landscape variables, or model parameters, retained in the best model from each model set were then included in a cumulative effects model (Table 3.0) to evaluate the relative support of a combination of landscape factors in explaining wolverine occurrence.

To reduce parameters within each model set to those that best explained wolverine occurrence, I used GLM's in a stepwise progression of model simplification to select the best-fit, or minimum adequate, model (Crawley 2007). This approach uses maximum likelihood estimation and the principle of parsimony to evaluate the relative support for alternative hypotheses by estimating the model that best explains wolverine occurrence while balancing bias and variance (Burnham and Anderson 2002). Lower AIC scores indicate a more parsimonious and best-fit model relative to alternative models tested (Anderson 2008). Models were ranked using differences in AIC values (ΔAIC) and weight of evidence (AIC_w). ΔAIC calculates the difference between the minimum AIC value of the best-fit model from the AIC value of each alternative model (Burnham and Anderson 2002). The further deviation from the minimum AIC value, the less plausible the alternative model best-fits the data among the candidate set. AIC_w approximates the probable likelihood of a model by weighting the strength of evidence in favor of alternative models within a candidate model set (Anderson *et al.* 2000). I calculated evidence ratios (ER's) to weigh the relative support for each covariate by comparing the relative strength of support for the inclusion of a variable (or set of variables) in the cumulative effects model (Burnham and Anderson 2002). Finally, we report the magnitude and direction of parameter estimates for each individual landscape covariate retained in the overall top ranked model, or minimum adequate model, to assess the relative strength of these variables in explaining wolverine occurrence.

Table 2.3 Wolverine species-habitat models

Wolverine species-habitat models for the south-central Rocky Mountain region of Alberta. Explanatory, or model, variables were grouped into model sets according to the type of influence hypothesized to explain wolverine occurrence.

Model set	Model	Model variables	Hypothesis: wolverine occurrence is predicted by:
Saturated Global Model		DENSE + MIXED + OPEN + SHRUB + HERB + REGEN + SNOWICE + BLOCKURB + LINROAD + LININD + LINREC_Q + LINREC_L + TRI + SP.SNOW + WOLF + COUG + COYO + LYNX + BOBC + FOX + MART	All landcover types, human footprint features, abiotic, and biotic factors equally.
Landcover	1	DENSE + MIXED + OPEN + SHRUB + HERB + REGEN + SNOWICE	All landcover types equally.
	2	DENSE + OPEN	Conifer forest cover.
	3	DENSE	Dense conifer cover only.
	4	MIXED	Mixed forest only.
	5	SHRUB + HERB	Herb and shrub cover.
	6	SHRUB	Shrub cover only.
	7	REGEN	Regenerating cover only.
	8	SNOWICE	Snow/ice cover only (annual).
Human Footprint	9	BLOCKURB + LINROAD + LININD + LINREC_Q + LINREC_L	All human footprint features equally.
	10	BLOCKURB	Urban town sites and permanent resort areas.
	11	LINROAD + LININD + LINREC_Q + LINREC_L	Linear features only.
	12	LINROAD	Density of linear road features.
	13	LININD	Density of industrial cutline features.
	14	LINREC_Q + LINREC_L	Density of quiet and loud recreation Trails.
Abiotic	15	TRI + SP.SNOW	Topographic ruggedness and persistent spring snow cover equally.
Topography	16	TRI	Topographic ruggedness only.
Climate	17	SP.SNOW	Persistent spring snow cover only (perennial).
Biotic	18	WOLF + COUG + COYO + LYNX + BOBC + FOX + MART	All species equally.
Mega-carnivore	19	WOLF + COUG	Wolf and cougar.
Food	20	WOLF + COUG + COYO	Wolf, cougar, and coyote.

Meso-carnivore	21	LYNX + BOBC + COYO + FOX + MART	Lynx, bobcat, coyote, red fox, and marten.
Meso-canid	22	FOX + COYOTE	Coyote and red fox.
food	23	LYNX	Lynx only.
Cumulative Effects Model	**24**	**DENSE+ MIXED+ OPEN+ SHRUB + HERB + REGEN + SNOWICE + LININD + SP.SNOW + COYOTE + FOX**	**The combined effect of the best supported landcover variables, persistent spring snow (the best supported abiotic variable), and linear industrial features (the best supported human footprint variable), and meso-canid detections across sites.**

2.2 Results

2.2.1 Spatial Patterns of Individual Occurrence

We genetically identified 68 wolverine individuals across the regional study area. This represents the minimum number known alive wolverine during the 3+ year period, and does not adjust for imperfect detection or missed animals, so is a conservative estimate. There were 64 wolverines identified the National Parks complex over 3 survey seasons, including incidentals (39 males, 25 females) (Clevenger and Barrueto 2014). In contrast, only 4 unique individuals (2 male, 2 female) were identified in the Kananaskis Country region over 2 survey seasons. Using remote camera images displaying wolverine chest, throat, or gular patches (Magoun *et al.* 2011), we were able to supplement the low genetic identification success in the Kananaskis Country region to identify an additional 3 individuals, adjusting the total number of individuals detected in that region to 7 unique individuals (Figure 2.6).

Figure 2.6 Remote camera images displaying wolverine unique ventral patterns

Infrared remote camera images showing seven individual wolverines detected in the Kananaskis Country region, Alberta. Individual identification was achieved by comparing unique light-coloured pelage markings found on their ventral surface.

The number of wolverine individuals uniquely identified by genetic analyses per site location ranged from 0 to 6 (Appendix B). The number of wolverine individual identifications across the west-east spatial gradient declined in a parabolic function, with low abundance to the west outside the boundary of the National Parks complex, peaking within the central areas of the National Parks complex (within Banff National Park), and gradually declining eastward outside of the National Parks complex and into the multi-use region of Kananaskis Country (Figure 2.7).

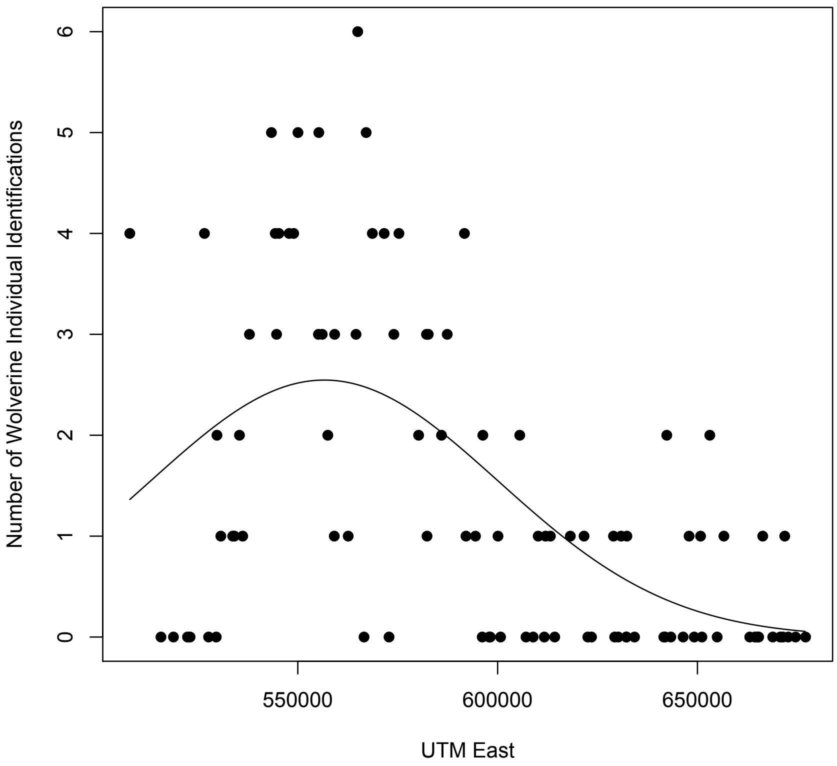


Figure 2.7 Spatial pattern of the number of wolverine individuals

Shows spatial pattern of the number of wolverine individuals uniquely identified by genetic analyses per site location modeled across sampling sites along a west-east gradient from National Parks complex to the Kananaskis Country region. Wolverine individual identification, based on the number of different genetically unique individuals identified per site (0-6) declined in a parabolic function across sampling sites located along UTM East coordinates (Map Datum: Nad 83, Zone 11).

2.2.2 Spatial Patterns of Occupancy

Custom single-season occupancy models suggested that detection probability (p) varied across sampling sessions and trended differently across the two study areas (Table 2.4, Figure 2.8). Estimated (p) increased over time in National Parks complex and decreased over time in the more developed areas of the Kananaskis Country region (Figure 2.8).

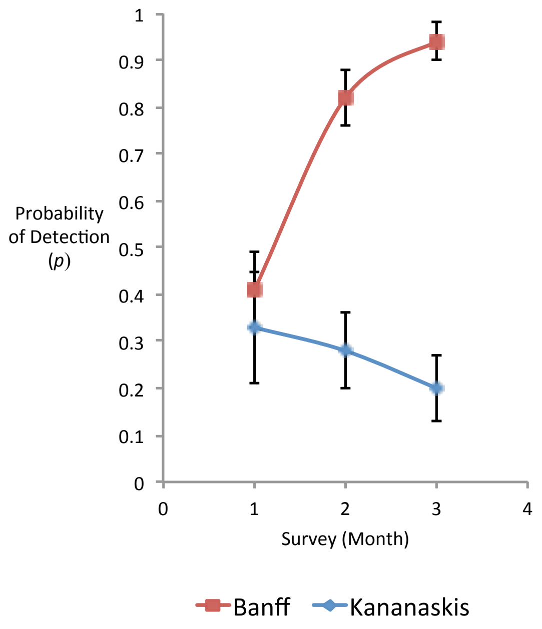


Figure 2.8 Comparing probability of detecting wolverine over time and study area

Shows the probability of detecting a wolverine (given it is present) differs through time and study area. The trend in detection probability increases over time in the National Parks complex (represented by Banff) and decreases over time in the more developed study area of Kananaskis Country region (represented by Kananaskis).

When modeling the probability of wolverine occurrence over space (UTM East), wolverine occupancy declined in a parabolic function across sites located along the west to east gradient (Figure 2.9). The spatial pattern of wolverine occurrence mirrors the spatial pattern of individual identifications, showing a more obvious peak in the central region of the Parks complex within Banff National Park and steeply declining to the east in the Kananaskis Country region (Figure 2.10).

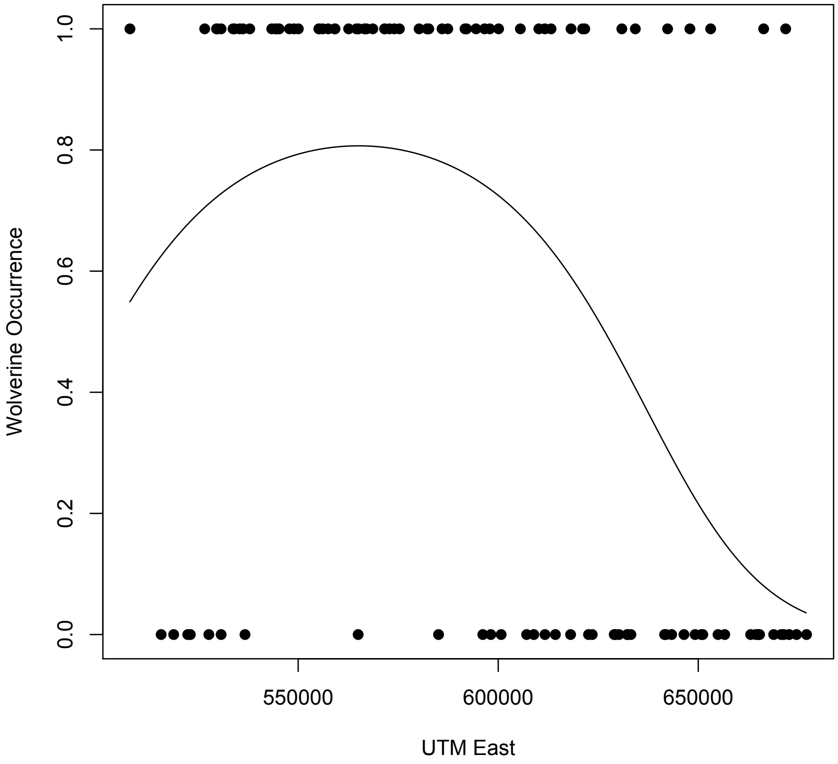
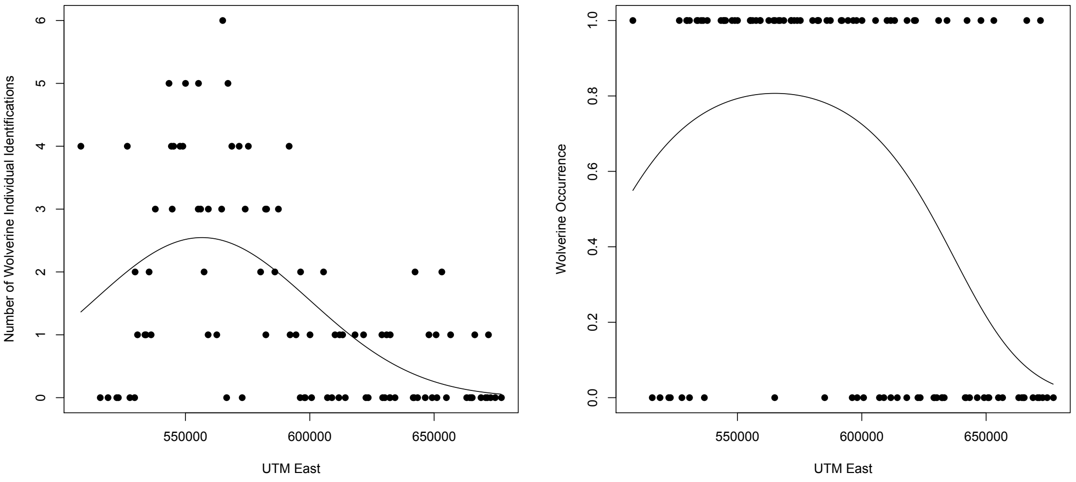


Figure 2.9 Spatial pattern of wolverine occurrence probability

Shows spatial pattern of wolverine occurrence probability modeled across sampling sites along a west-east gradient from the National Parks complex to the Kananaskis Country region. Wolverine occurrence, based on species detection (1) and non-detection data (0), declined in a parabolic function across sampling sites located along UTM East coordinates (Map Datum: Nad 83, Zone 11).



a. b.

Figure 2.10 Spatial pattern of wolverine individuals vs. occurrence probability

Compares the spatial pattern of the number of wolverine individuals uniquely identified by genetic analyses per site location (a) to the spatial pattern of wolverine occurrence probability (b) modeled across sampling sites along a west-east gradient from the National Parks complex to Kananaskis Country region. Both wolverine individual identification and wolverine occurrence probability is described by a parabolic spatial pattern, increasing into the nationally protected areas and declining outside of the nationally protected areas, across sampling sites located along UTM East coordinates (Map Datum: Nad 83, Zone 11).

Wolverine occupancy (ψ) in the National Parks complex was over double that estimated in the Kananaskis Country region (ψ = 0.88, SE = 0.05, CI = 0.72 – 0.95; vs. (ψ = 0.36, SE = 0.11, CI = 0.12 – 0.56) (Figure 2.11). Standard error was 2.2 times higher in the Kananaskis Country region compared to the National Parks complex, suggesting the significant difference in wolverine occupancy across study areas may be influenced by better detection rates in the National Parks complex. However, estimated wolverine occupancy remained 36% higher in the National Parks complex than estimated occupancy in the Kananaskis Country region, even after adjusting occupancy estimates according to their respective error margins.

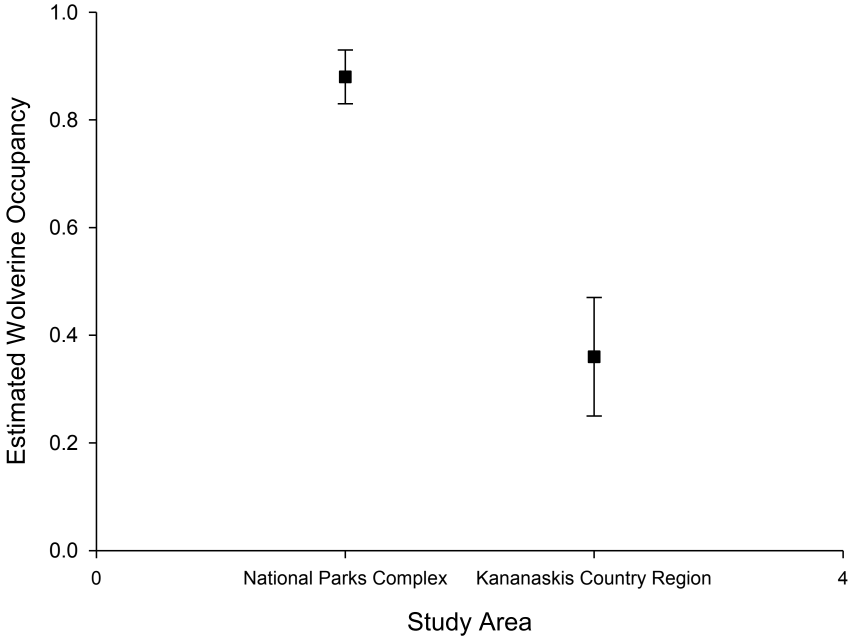


Figure 2.11 Plots of estimated wolverine occupancy

Estimated average and standard error of wolverine occupancy, the probability a wolverine occupies an area, if it is in fact present, compared across two study areas (National Parks complex and Kananaskis Country region) located in the central Rocky Mountain region of Alberta.

Though detection probability was low ($p = 0.4$) and varied across study areas and survey month (Σ AICw = 0.825, ER = 412.55), there was no evidence that p varied with any of the abiotic landscape covariates tested (Table 2.4).

Table 2.4 Wolverine detection probability modeling results

Wolverine detection probability (p) modeled by study AREA (National Parks complex and Kananaskis Country region), time (monthly SURVEY period), and landscape covariates (Topographic Ruggedness Index, Persistent Spring SNOW cover, CUMULative Human Footprint, and all LINEAR features) using a fully crossed design.

Evidence for	Covariate	ΣAICw	ER
p(SURVEY)	Survey period	0.002	0.750
p(AREA)	Study area	0.165	82.450
p(AREA+SURVEY)	Study area + survey period	0.825	412.550
p(TRI)	Topographic ruggedness	0.000	0.100
p(SP. SNOW)	Persistent spring snow cover	0.003	1.300
p(CUMUL HF)	Cumulative human footprint	0.005	2.400
p(LINEAR)	Cumulative linear features	0.000	0.150

2.2.3 Spatial Scale of Selection

The weight of evidence explaining wolverine occurrence was best supported at the 10,000m scale for sets of biophysical and anthropogenic landscape covariates tested (AICw Landcover = 0.45, AICw Sp. Snow = 0.99, AICw TRI = 0.73, and AICw Human Footprint = 0.78), highlighted by persistent spring snow modelled with wolverine occurrence across spatial scales (Figure 12.0). Since recent research by Fisher et al. (2011) modeled a clear peak in wolverine habitat selection at the 5,000m scale, I tested alternative models at both the 5,000m and 10,000m scales to compare model fit at both spatial scales while examining for spatial autocorrelation at the larger spatial scale. A cross-scale analysis estimated wolverine occurrence to be best explained at the 10,000m scale compared with the 5,000m scale. In addition, variables that best explained wolverine occurrence patterns did not change greatly when the scale was increased 5,000m to 10,000m. These results suggest no loss of independence occurred when increasing the spatial scale of selection and therefore has not inflated the chance of a Type 1 error due to spatial autocorrelation.

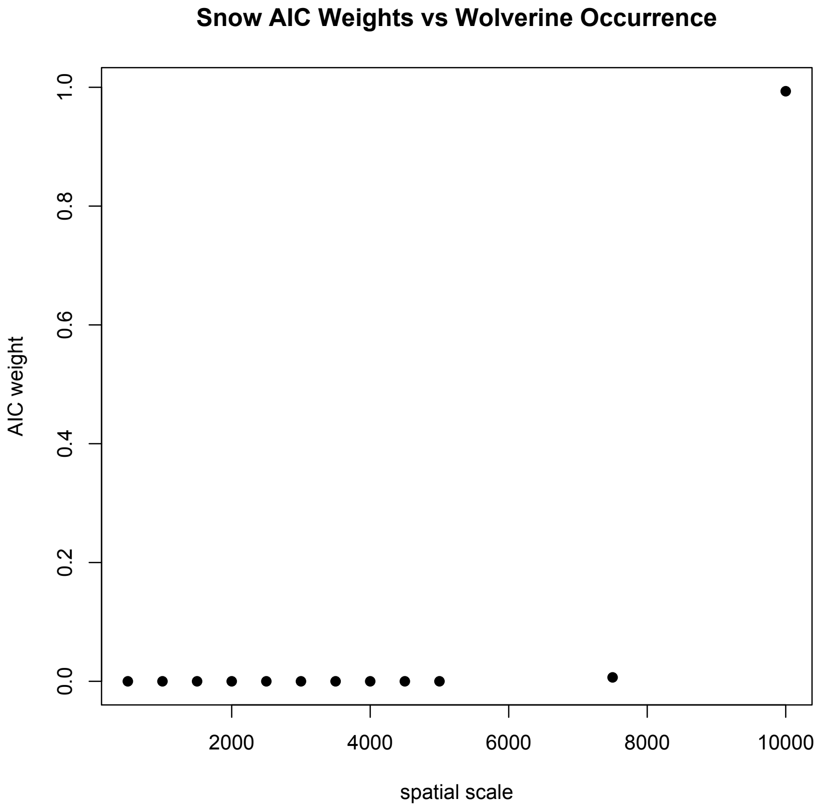


Figure 2.12 Model support for persistent spring snow across spatial scales

Modeling AIC weight of persistent spring snow (□) across 20 spatial scales (range: 500m – 10,000m) shows wolverine occurrence to be best predicted by this landscape variable at a spatial scale of 10,000m (AICw = 0.99).

2.2.4 Drivers of Wolverine Occurrence

Species-habitat models - Six landcover types best described the probability of wolverine occurrence, including: dense conifer cover, mixed forest, shrub and herb cover, regeneration forest, and snow and ice cover. While wolverines were most positively associated with dense conifer cover and annual snow/ice cover; there was a strong negative association with mixed forest cover (Table 2.5). Among abiotic models, persistent spring snow cover is positively associated with wolverine occurrence, and better supported than topographic ruggedness (AICw = 0.66, AICw = 0.34; relatively, Table 2.6). Among footprint models, linear industrial features alone are the best human footprint type describing wolverine occurrence (Table 2.7) with a negative association.

Species-species models – Among biotic models, wolverine occurrence was best described by a negative association with coyote and fox, or meso-canid, occurrence relative to the effects of other spatially co-occurring carnivore species (Table 2.8).

Table 2.5 Wolverine-landcover model selection

Model selection within the wolverine-landcover class model set. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00.

Model	**Variables**	**residual deviance**	**residual d.f.**	**AIC**	**ΔAIC**	**AIC weight**	**-2LL**
1	**DENSECON+ MIXED + OPENCON + SHRUB + HERB + REGEN + SNOWICE**	**65.01**	**83**	**213.78**	**0.00**	**1.00**	**199.78**
2	DENSECON + OPENCON	125.70	88	264.48	50.7	0.00	260.48
3	DENSECON	147.73	89	284.51	70.73	0.00	282.51
4	MIXED	126.12	89	262.90	49.12	0.00	260.90
5	SHRUB + HERB	144.46	88	283.23	69.45	0.00	279.23
6	SHRUB	151.90	89	288.67	74.89	0.00	286.67
7	REGEN	134.76	89	271.53	57.75	0.00	269.53
8	SNOW.ICE	105.03	89	241.80	28.02	0.00	239.80

Table 2.6 Wolverine-abiotic model selection

Model selection within the wolverine-abiotic model set. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00.

Model	Variables	residual deviance	residual d.f.	AIC	ΔAIC	AIC weight	-2LL
15	TRI + SP.SNOW	93.71	88	232.49	1.32	0.34	228.49
16	TRI	137.10	89	273.88	42.71	0.00	271.88
17	**SP.SNOW**	**94.39**	**89**	**231.17**	**0.00**	**0.66**	**229.17**

Table 2.7 Wolverine-human footprint model selection

Model selection within the wolverine-human footprint model set. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00.

Model	Variables	residual deviance	residual d.f.	AIC	ΔAIC	AIC weight	-2LL
9	BLOCKURB + LINROAD + LININD + LINRECQ + LINRECL	79.30	85	224.08	2.12	0.23	214.08
10	BLOCKURB	150.92	89	287.69	65.73	0.00	285.69
11	LINROAD + LININD + LINRECQ + LINRECL	82.86	86	225.63	3.67	0.11	217.63
12	LINROAD	145.53	89	282.31	60.35	0.00	280.31
13	**LININD**	**85.18**	**89**	**221.96**	**0.00**	**0.66**	**219.96**
14	LINRECQ + LINRECL	116.38	88	255.16	33.2	0.00	251.16

Table 2.8 Wolverine-abiotic model selection

Model selection of within the wolverine-biotic model set. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00.

Model	**Variables**	**residual deviance**	**residual d.f.**	**AIC**	**ΔAIC**	**AICw weight**	**-2LL**
18	WOLF + COUG + COYO + LYNX + BOBC + FOX + MART	104.56	83	253.33	7.02	0.03	239.33
19	WOLF + COUG	141.98	88	280.76	34.45	0.00	276.76
20	WOLF + COUG + COYO	110.21	87	250.98	4.67	0.08	244.98
21	LYNX + BOBC + COYO + FOX + MART	138.42	86	281.20	34.89	0.00	271.20
22	**FOX + COYOTE**	**107.53**	**88**	**246.31**	**0.00**	**0.89**	**242.31**
23	LYNX	150.58	89	287.35	41.04	0.00	285.35

Cumulative Effects - The cumulative effects model (24) better explained wolverine occurrence than any other single-factor model that was best-supported across the landcover, abiotic, anthropogenic, or interspecific model sets (AIC = 207.74, AICw = 0.95, Table 2.9). Within the cumulative effects model, landcover variables are the variables most likely to be included in a best-fit model (ER = 19) with dense conifer cover showing a strong positive effect and mixed forest cover showing a comparatively strong negative effect. Linear industrial features are the second best-supported (ER = 6.33) and showed the strongest negative effect. Persistent spring snow and meso-canid occurrence were less supported (ER = 0.86, ER= 0.35; respectively) and showed weak effect size in opposing directions, though still selected as key parameters in the best-fit cumulative effects model. Though the relative likelihood and strength of variables within the cumulative effects model describing wolverine occurrence vary, the 95% weight of evidence supporting the cumulative effects model suggests no single factor is driving wolverine occurrence.

Table 2.9 Wolverine best-fit model selection

Selection of best-fit wolverine-distribution models in the central Rocky Mountain region, Alberta. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00.

Best Model, Model Set	**Variable(s)**	**residual deviance***	**residual d.f.**	**AIC score**	**ΔAIC**	**AIC weight**
1, Landcover	DENSECON + MIXED + SHRUB + HERB + REGEN + SNOW.ICE	65.01	83	213.78	6.04	0.05
13, Human Footprint	LININD	85.18	89	221.96	14.22	0
17, Abiotic	SP.SNOW	94.392	89	231.17	23.43	0
22, Biotic	FOX + COYOTE	107.53	88	246.31	38.57	0
24, Cumulative Effects	**DENSECON + MIXED + SHRUB + HERB+ REGEN + SNOW.ICE + BLOCKURB + LININD + LINRECL + SP.SNOW + COYOTE + FOX**	**48.631**	**78**	**207.74**	**0**	**0.95**

Note: AIC, Akaike information criterion. Wolverine occurrence counts modeled against measured landscape variables at the 10,000m scale using generalized linear modeling. Comparing across the best-fit, or minimum adequate, models (1, 13, 17, 22) suggests that a combination of the natural and anthropogenic variables included in the cumulative effects model (24) best explain patterns of wolverine occurrence.

*Null model deviance is 48.631 on 78 degrees of freedom (d.f.)

Table 2.10 Lists estimated parameters across best-fit model variables

Estimated β parameters from wolverine from the cumulative effects species distribution model.

Parameter	Estimate	SE	z-value	Pr(>IzI)	ER
intercept	-1.218	0.381	-3.201	0.001	
DENSE	0.605	0.200	3.023	0.002	
MIXED	-0.929	0.450	-2.062	0.039	
SHRUB	0.338	0.120	2.811	0.005	
HERB	0.363	0.230	1.579	0.114	
REGEN	-0.003	0.507	-0.005	0.996	
SNOWICE	0.048	0.026	1.842	0.065	19.00
BLOCKURB	0.002	0.112	0.022	0.983	
LINRECL	1.056	0.653	1.617	0.106	
LININD	-1.243	0.648	-1.919	0.055	6.33
SP.SNOW	0.409	0.320	1.279	0.201	0.86
RED FOX	-0.170	0.162	-1.051	0.293	
COYOTE	-0.306	0.297	-1.030	0.303	0.35

*ER, Evidence Ratio = AICw with variable of interest / AICw without variable of interest. Evidence ratios describes the relative likelihood of support for inclusion of one variable (or a group of variables) compared to the exclusion of the variable(s) in a global model (Burham and Anderson 1998). *Example:* the ER for the set of landcover variables shows 19 times more weight to be included into the best-fit model relative to other set(s) of variables.

2.3 Discussion

2.3.1 Spatial patterns of wolverine detection and occupancy

Wolverine occupancy and abundance based on camera detections and number of genotyped individuals all declined with along the west to east gradient, along a gradient of increasing human-altered habitat. Occupancy was 9 times higher the National Parks complex than within the multi-use areas of the Kananasksis Country region. The abrupt decline in occurrence towards the west-central areas of Kananaskis Country was unexpected when considering wolverine population abundance historically supported trapping here (Poole and Mowat 2001), and this region is composed of predicted suitable habitat and prey for wolverines (Banci and Harestad 1990, Copeland 1996, Lofroth 2001, Krebs *et al.* 2007, Copeland *et al.* 2007). These results mirror studies in Scandinavia that have demonstrated a strong negative relationship between wolverine density and increasing proximity to human landscape disturbance relative to preferred habitat characteristics (Petersen 1997, May *et al.* 2006).

Patterns of wolverine detectability, abundance, and occupancy are similar to those observed between the undeveloped Willmore Wilderness area and the more developed Foothills Natural region of Alberta (Fisher *et al.* 2013; *unpubl. data*). In both studies, detection probability varied over time (Figure 2.13), with detection probability increasing over time in the undeveloped landscapes and decreasing over time in more developed landscapes. Detectability as we have quantified it is a function of repeated visitation. Hence, lower detectability in the Kananaskis Country suggests less frequent visits compared to the National Parks complex, possibly due to increased sensitivity to landscape features or perceived risk associated living in more disturbed landscapes. Accounting for detection error across both studies, the probability of wolverine occupancy within the undeveloped areas was approximately twice that of developed areas in Alberta's eastern slopes.

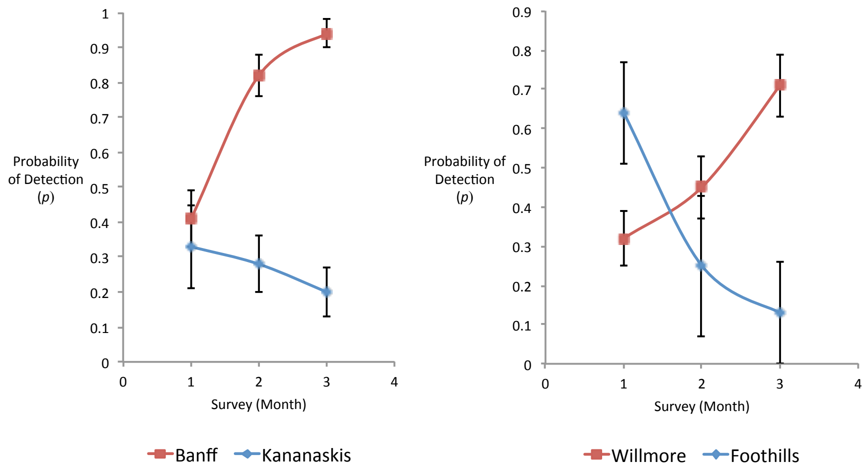


Figure 2.13 Comparing probability of detecting wolverine over time

Probability of detecting a wolverine (given it is present) differs through time in (a) Banff-Kananaskis and (b) Willmore-Foothills (from Fisher et al. 2013; unpubl. data). The trend in detection probability increases over time in the National Parks complex (represented by Banff) and decreases over time in the more developed study area of Kananaskis Country region (a). Trends in (a) are mirrored by the increasing trend in detection probability in the Willmore Wilderness area and the decreasing trend in the developed landscape along Alberta's Foothills Natural region (b).

These results, derived from two vast areas within the south-central Canadian Rocky Mountains, contrast the provincial wolverine status report for Alberta which concluded wolverine population instability was restricted to further southern-most regions of Alberta (Slough 2007). Instead, the decreased spatial pattern of occurrence found here along with those reported by Fisher *et al.* (2013) suggest wolverines may also be sensitive along the greater areas of Alberta's eastern slopes in the Canadian Rocky Mountains.

2.3.2 Wolverine land use described by cumulative effects

Unlike more recent climate-focused predictions (Aubry *et al.* 2007, Copeland *et al.* 2010, Brodie and Post 2010, Inman *et al.* 2012a), I found multiple factors to best describe wolverine occurrence across the central region of the Rocky Mountains in

Alberta. Here, wolverine distribution was best explained by a combination of landcover types, linear industrial features, persistent spring snow cover, and meso-canids over a large spatial scale. My findings showed wolverine to be more likely to occur in areas with dense conifer cover, shrub and herb, and perennial snow and ice cover (Figure 2.14). These landcover types also describe subalpine and alpine habitat selected by wolverine in other mountainous regions, which provide high-elevation small mammal and avalanche-killed prey items (Banci and Harestad 1990, Krebs *et al.* 2007, Lewis *et al.* 2012). In the boreal regions of northwest Alberta and into British Columbia wolverines preferred dense conifer upland, thought to provide for easier routes of travel compared with deep powder snow found in lowland landscapes (Wright and Ernst 2004). Evidence of wolverine spending time in dense canopy cover adjacent to more open areas with actively feeding wolves suggests this habitat may provide for better cover when accessing some scavenging opportunities (Krebs 2014, personal communication). In Idaho, Copeland (1996) also found wolverine to prefer closed forest types while avoiding more open cover types.

A recent study within the Flathead region of south-western British Columbia also reported moderate avoidance of relatively open stands, represented by parkland forest cover, from GPS telemetry data (McLellan and Servheen 2013). In the more northern regions of Alberta's Rocky Mountains Fisher *et al.* (2013) found that open forest types, represented by mixed forest cover, were negatively associated with wolverine occurrence. Similarly, wolverines in the central Rocky Mountains are less likely to select areas dominated by mixed forest cover (Figure 2.14).

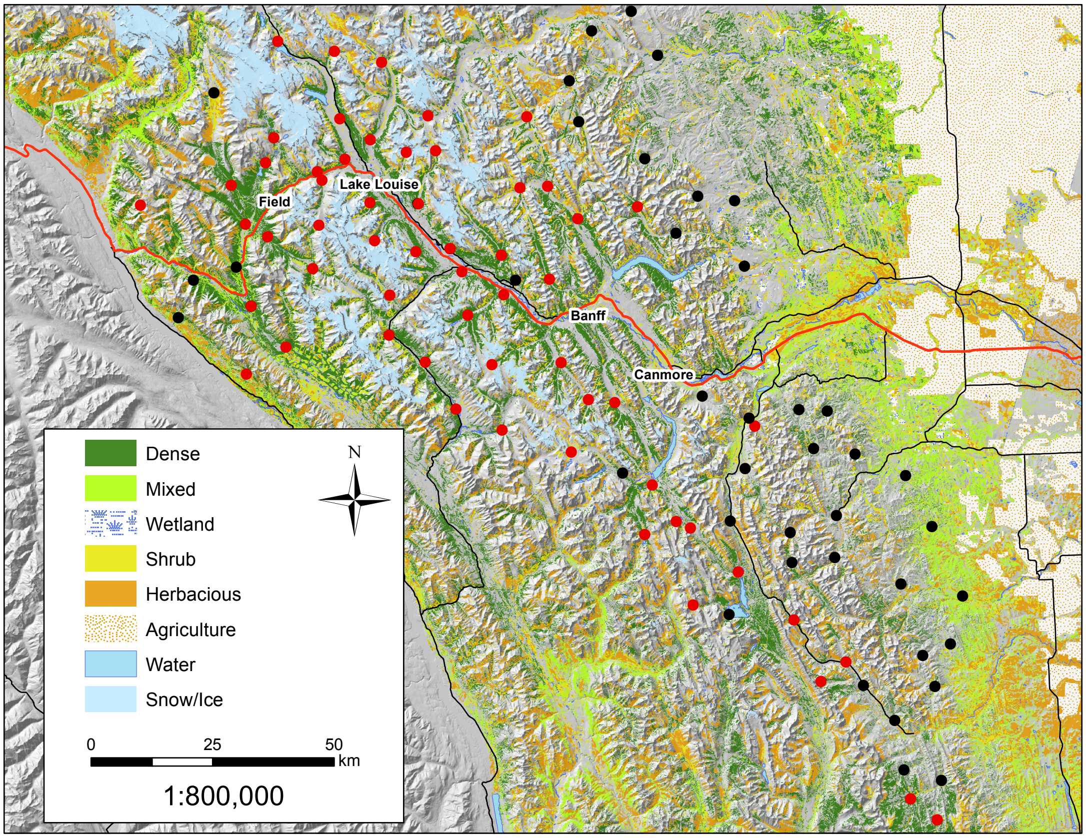


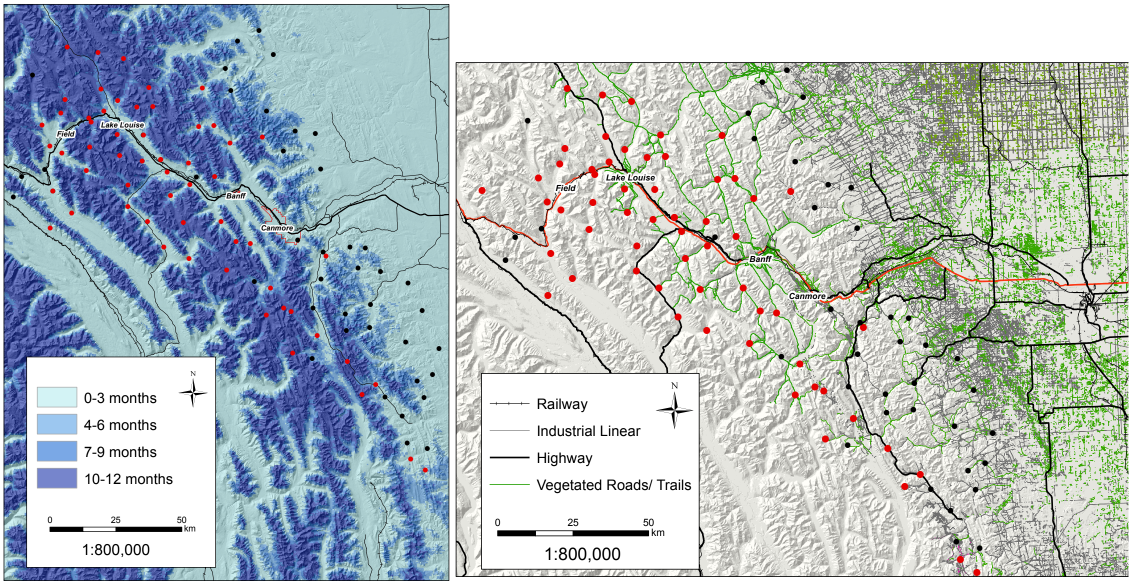
Figure 2.14 Maps wolverine detections in relation to landcover

Wolverine occurrence (presence/detection highlighted by red points and absence/non-detection highlighted by black points) in relation to landcover types hypothesized to explain the spatial distribution pattern of wolverine distribution found along a west-east gradient from National Parks complex to the Kananaskis Country region, AB.

These mixed forest cover stand types dominated by a deciduous stand structure may represent a more open habitat with limited escape cover, increasing the level of risk relative to the reward gained by scavenging. Therefore, the negative relationship between wolverine occurrence and low-density landcover types could be explained by asymmetric trade-off effects of risk-related foraging opportunities in areas exposed to increased inter-specific competition. This type of behaviourally-mediated space use and habitat selection associated with risk has been known to influence distribution of prey species (Lotka 1925, Lima and Dill 1990, Sih 2005). However, these same principles may be applied to predators. Durant (1998) found cheeaths avoided competitively high-risk areas and preferentially used competitive refugia where lions were present.

For wolverine, high elevation and topographically rugged areas are hypothesized to act as spatial refuges from competition (Copeland *et al*. 2007, Inman *et al.* 2012a). While topographic ruggedness explained wolverine habitat selection in the Willmore Foothills regions of Alberta (Fisher *et al.* 2013), the average topographic ruggedness varied only modestly across my study area and not surprisingly played no significant role in explaining the pattern of wolverine occurrence. In addition, persistent spring snow cover, a climatic condition typically found at higher elevation and is suggested to be a factor limiting wolverine distribution (Aubry *et al.* 2007, Copeland *et al.* 2010, Inman *et al.* 2012a), was not identified as a single factor best explaining wolverine occurrence in this region.

In the central Rocky Mountains, where climate-related and anthropogenic factors overlap, linear industrial features better explained the probability of wolverine occurrence relative to persistent spring snow cover. This is demonstrated by several survey sites within the eastern region of Kananaskis Country that did not detect wolverine within the boundary of persistent spring snow cover, but are heavily impacted by linear features (Figure 2.15a). Similar to findings by Fisher *et al.* (2013), anthropogenic linear features are one of the most important factors influencing the probability of wolverine occurrence throughout this regional-scale study area (Figure 2.15b).



a. b.

Figure 2.15 Maps Wolverine detections in relation to spring snow and linear features

Wolverine occurrence (presence/detection highlighted by red points and absence/non-detection highlighted by black points) in relation to (a) linear industrial features, and (b) persistent spring snow cover hypothesized to explain the spatial distribution pattern of wolverine distribution found along a west-east gradient from the National Parks Complex to the Kananaskis Country region, AB.

Though wolverine movement does not seem to be impeded by linear features (Hornocker and Hash 1981, Fisher *et al.* 2013 *unpublished snow tracking data*), wolverines negatively respond to spatially extensive and increasing density of linear features, such as road networks (May *et al.* 2006, Krebs *et al.* 2007) and seismic lines (Fisher *et al.* 2013). The mechanism for this negative relationship to linear features remains unknown; however, linear infrastructure and associated disturbance are known to intensify the effects of landscape fragmentation and habitat degradation by further disconnecting continuous habitat (Primack 2006). Expanding habitat disturbance along the eastern regions of Alberta has resulted in significant forest cover loss (Global Forest Watch Canada 2014) and increased access into previously remote areas by both humans and competitively dominant carnivores, such as wolves (Latham *et al.* 2011, Ciuti *et al.* 2012). Linear features may therefore be changing habitat condition through direct removal of resources as well as reducing availability of refuge habitat, increasing the probability of risk-related interactions for some species.

A population's resilience to changes in habitat condition depends on home range size, dispersal capabilities, recruitment rates, and plasticity in foraging behavior (Weaver *et al.* 1996). While wolverine and other wide-ranging carnivore species occurring in areas of high human disturbance are more likely to experience range contraction and population reduction, some species such as coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) are experiencing range expansion and population growth (Laliberte and Ripple 2004). In the case of coyote, this species apparent success in human developed landscapes is attributed to their high rates of survival and fecundity, ability to travel across disjunct habitat patches, and generalist exploitation of both natural and anthropogenic food items (Riley *et al.* 2003, Atwood *et al.* 2004, Gehrt 2007, Gehrt *et al.* 2009).

Species exhibiting more generalist niche requirements is favoured in human-altered habitat compared with species more constrained by specialized niche requirements, in some cases resulting in increased relative abundance of the more generalist species (Cove *et al.* 2012, Šálek *et al.* 2014). Such differential niche space requirements can promote spatial co-existence among intra-guild carnivores where intra-specific competition within species is greater than interspecific competition between species (Murrell *et al.* 2002), a process referred to as heteromyopia (Murrell and Law 2003, Amarasekare 2003). Alternatively, changes to habitat condition resulting in increased relative density of the more common anthropogenic-adapted species might negatively influence heteromyopia (Amarasekare 2003), tipping the balance of spatial co-existence whereby inter-specific competition now outweighs intra-specific competition. Reduced or extirpated wolf populations decreases interference competition for coyotes, thus increasing coyote density (Arjo and Pletscher 1999, Hebblewhite et al. 2005, Berger and Gese 2007). Wolves are actively harvested on registered traplines outside of the National Parks complex (URL: http://www.albertaregulations.ca); however, no robust data exists to accurately evaluate if the level of harvest constitutes a reduction in wolf abundance that translates to meso-predator release in the more human-altered regions of this study area.

Following the classic competition-colonization trade-off model (Levins and Culver 1971), increased in relative abundance of one or more common species within a particular guild – irrespective of the mechanism – can influence interspecific interactions, limiting niche space for rarer species (Murrell and Law 2002, Amarasekare 2003, Ordeñana *et al.* 2010). Regardless of environmental variables and resource supply, the presence of a competitor can shift species distribution models by reducing the probability a habitat is suitable for species within the same guild (Godsoe and Harmon 2012, Fisher *et al.* 2013, Lindenmayer *et al.* 2014). For wolverine, ecological theory might therefore lead us to infer that the negative association between the occurrence patterns of wolverine and two meso-canid species (coyote and fox) is driven by a human-caused change in habitat condition along Alberta's eastern slopes. Furthermore, strong inference may then lead us to hypothesize that wolverines are experiencing an additive effect of habitat change, resulting in increased inter-specific interactions occurring among the medium-sized carnivore guild within more human-developed landscapes.

Current understanding of wolverine ecology supports my findings associating wolverine occurrence with natural landcover types, human footprint, and persistent spring snow pack. Lastly, this study suggests biotic interactions may also play a significant role in shaping wolverine distribution patterns and warrants the consideration and inclusion of intra-guild co-occurrence into future species distribution models.

2.4.0 Caveats and Data Limitations

Levels of recreational activities – The intensity and frequency of anthropogenic stressors on wildlife populations vary spatially and temporally across landscapes. While our data was limited to spatial proportions of landscape features; no regionally comprehensive data on human activity levels exist, such as the intensity and frequency of off-road vehicle or foot traffic on trails. As levels of human activity increase, avoidance by a range of wildlife species occurring in the Canadian Rocky Mountain Parks has been observed (Rogala *et al.* 2011). In Idaho, some evidence of den abandonment was observed where motorized winter recreational activities are prevalent (Heinemeyer *et al.*

2010, Heinemeyer and Squires 2014). Avoidance of winter recreational activities was also found to influence den selection location for individual wolverines in Norway (May *et al.* 2012). Currently, a high degree of spatial overlap of recreational activities and wolverine occurrence is evident in many regions of western Canada. However, large-scale distribution shifts may arise if local recruitment rates are and continue to be negatively influenced in high recreational areas. Evaluating how localized effects associated with varying degrees and types of human activity influence wolverine distribution over time may be an informative next step. Efforts to procure these data were not possible given the scope and time constraints.

Effect size of interspecific occurrence – Carnivore occurrence patterns overlapped for several species surveyed at the distribution scale. The sympatric co-occurrence patterns observed at the large spatial scale may have weakened our ability to detect a strong effect of heterospecific species occurrence on wolverine occurrence. A better test of association between intra-guild carnivore and wolverine occurrence may require monitoring of finer spatial and temporal scale to examine activity patterns of co-occurring carnivores. Though investigations of space at a finer spatial and temporal scale may provide for further information on interspecific interactions between wolverine and co-occurring carnivores, wolverine occurrence was negatively associated with meso-canid occurrence in my study area at a large spatial scale, the scale best explaining wolverine occurrence patterns.

Prey availability – Empirical and anecdotal evidence suggests this regional study area supports a variety of prey species important for wolverine. For example, our remote camera imagery detected moose and other large ungulate prey known to be a seasonal prey item for wolverines (Persson *et al.* 2006, Krebs *et al.* 2007). Anecdotal observations indicate an abundance mountain goat and hoary marmot (*Marmota caligata*), high elevation ungulate and small mammal prey items selected by wolverine (Hornocker and Hash 1981, Landa *et al.* 1997, Lofroth *et al.* 2007, Van Dijk *et al.* 2008), particularly for denning females found in mountain environments (Magoun and Copeland 1998). As site locations and seasonal timing of surveys were targeted for carnivore occurrence and movement through winter travel corridors, reliable estimates of prey occurrence were not available to include as model covariates. However, the broad compliment of prey species detected throughout this regional study led me to expect the inclusion of prey would not enhance our ability to evaluate factors influencing wolverine occurrence.

Human-related mortality and management – As a low-density furbearer, wolverines are sensitive to harvest pressure (Krebs *et al.* 2004, Aubry 2006) and have been positively associated with protected areas that provide for refugia from trap-related mortality (Lofroth 2001, Squires *et al.* 2006, Lofroth and Ott 2007). Though wolverine are designated as "data deficient" in Alberta, meaning there is insufficient data to determine whether the population is at risk, legislation specifies a harvest quota of one wolverine per trapline per season (Alberta Fish and Wildlife 2008). This quota, albeit seemingly small, may have a disproportionate effect on already reduced populations persisting on the edge of their distribution. There are currently 35 Registered Fur Management Areas (RFMA) along Alberta's eastern slopes. Out of these, only 10 RFMA's have reported harvested wolverine since 1985, reporting a total of 18 individuals harvested (Webb *et al.* 2013). It is unknown whether the low harvest records represent a genuine lack of wolverine occurrence, lack of harvest effort, or inaccurate reporting (Webb *et al.* 2008). Since no robust measure of trap effort currently exists, harvest data was not included as a model covariate for this study. Nevertheless, the declining spatial trend of occurrence observed in actively trapped areas along Alberta's east slopes indicates a conservative approach to harvest for wolverine should be recommended for this region.

2.5.0 Wolverine persistence along the Rocky Mountain range margin

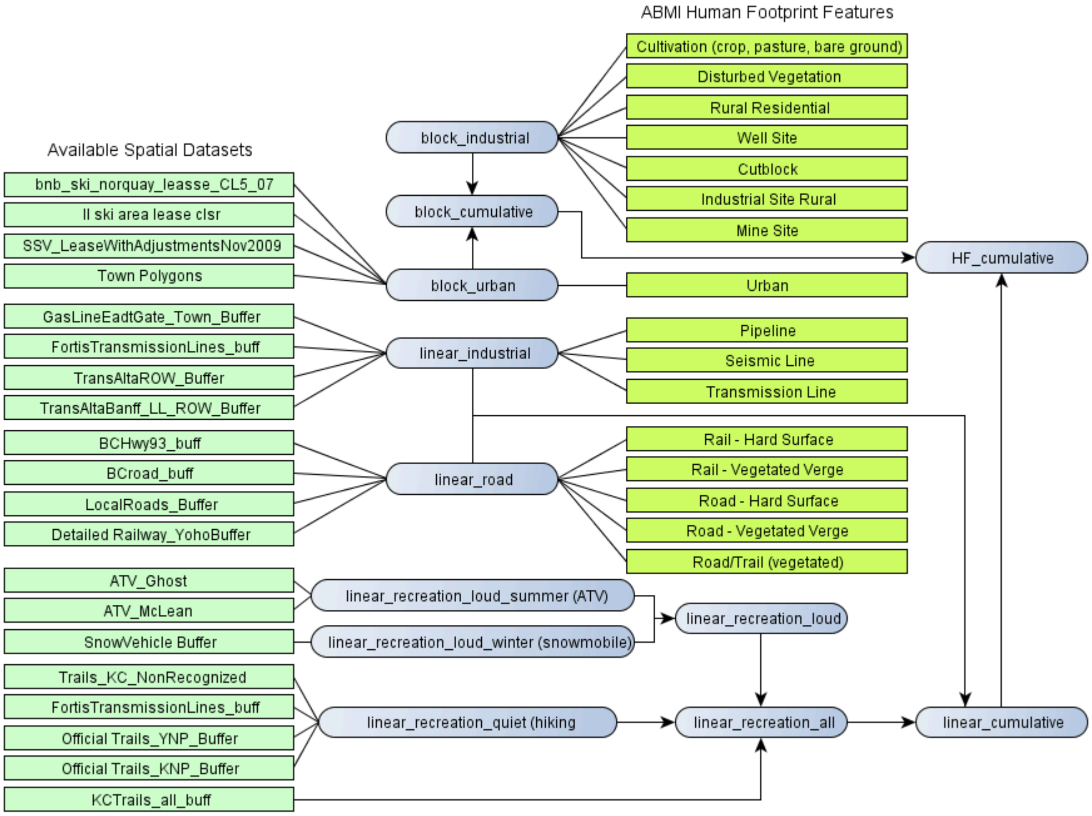
Building upon Fisher *et al*. (2013), this decrease in occupancy along the west to east spatial gradient suggests wolverine populations may be undergoing spatial range contraction along the east slopes of the Canadian Rocky Mountains. The negative association between wolverine and human disturbance (May *et al.* 2006, Krebs *et al.* 2007, Fisher *et al.* 2013), and future climate change scenarios that reduce spring snow (Copeland *et al.* 2010, Brodie and Post 2010, Inman *et al.* 2012a), could be used to forecast continued wolverine range contractions in regions such as the one studied here. If so, the eastern region of their distribution range in Alberta – even within provincially protected areas – might be perceived as lower quality habitat neighbouring higher quality, or source, habitat in the National Parks complex. Access to both refuge habitat and scavenging opportunities with limited human disturbance, as well as minimal predator- and anthropogenic- mortality in remaining areas of lower quality habitat will be important for long-term population persistence. Successful dispersal and colonization into unoccupied habitats by immigrants and excess offspring from neighbouring or distant source populations can promote gene flow and supplement total population size (Dunning *et al.* 1992).

With naturally low recruitment rates in areas of source habitat (Banci 1994), wolverine populations may be particularly vulnerable to such edge effects, stressing the importance of large, intact and naturally heterogeneous landscapes that provide for refugia and population connectivity (Weaver *et al.* 1996, Squires *et al.* 2006). Large landscapes are inherently influenced by a multitude of biophysical and anthropogenic factors. Therefore, evaluation of which and how these complex and interacting factors translate to suitable habitat condition for wide-ranging species, such as the wolverine, is essential to answering questions in ecology and conservation. In a comprehensive synthesis, Crain *et al.* (2008) highlighted that the overall effects of multiple interacting stressors was synergistic, meaning that multiple factors taken together were greater than the sum of their separate effects at the same levels. Similarly, our study revealed cumulative effects of multiple factors help explain wolverine occurrence along the central region of Alberta's Rocky Mountains.

Changing mountain landscapes are likely to influence not only wolverine but with them multiple carnivore species. Simultaneous evaluation of interacting abiotic, biotic, and anthropogenic factors will be integral to better understanding the broad suite of ecological mechanisms driving wolverine populations at the distribution scale. While single-factor hypotheses may reveal important factors influencing wolverine occurrence, the exclusion of cumulative effects may result in poor conservation outcomes. Effective conservation and management of wolverine should incorporate a multi-faceted framework to protect large, connected, and minimally disturbed tracts of land that support a diverse carnivore community.

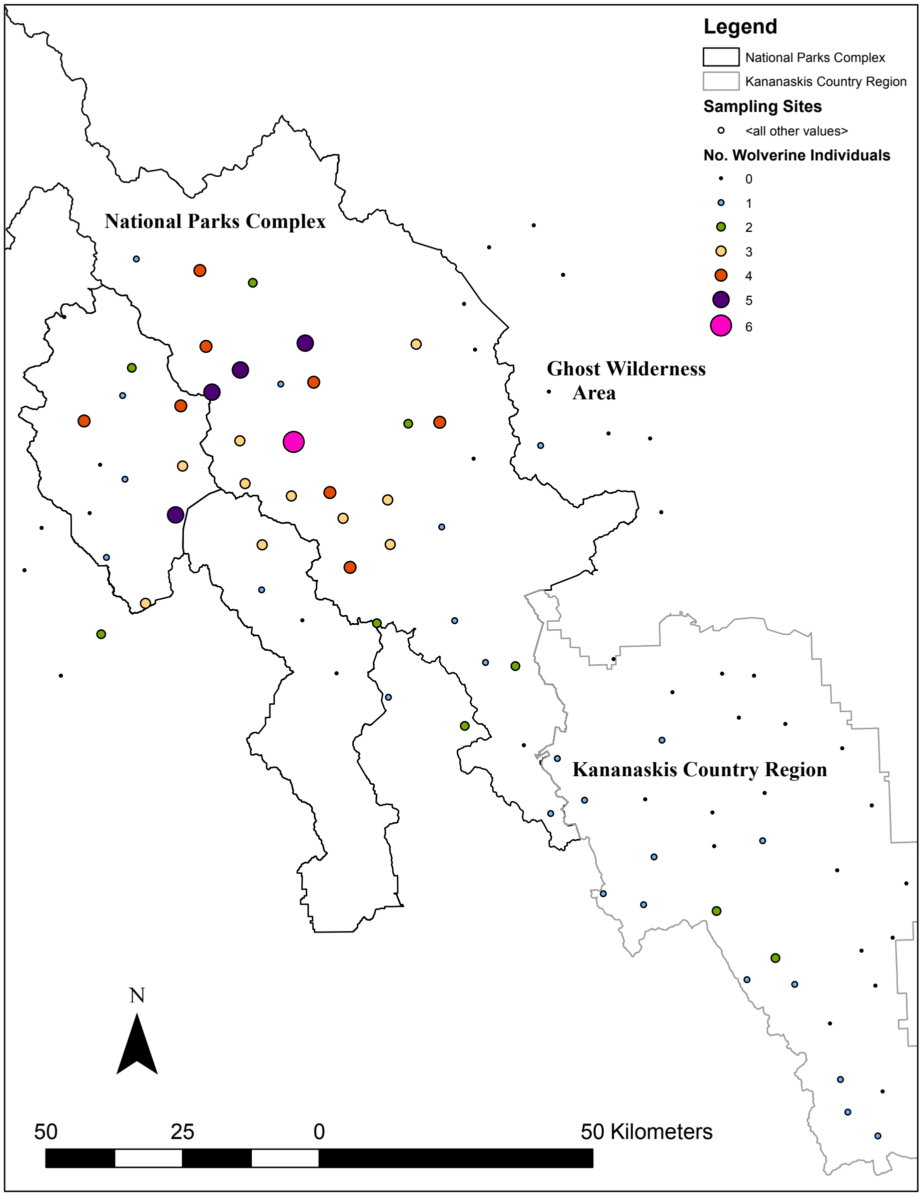
APPENDIX A

Flow chart (Kent Richardson, Alberta Innovates – Technology Futures) shows the data input used to create 12 human footprint categories hypothesized to influence wolverine occurrence by merging available spatial datasets and ABMI human footprint Features dataset in ESRI ArcGIS 9.3.



APPENDIX B

Maps the number of individual wolverine genetically identified at each sampling site within the national parks complex (including Banff, Yoho, and Kootenay National Parks), just west towards Golden, BC, and extending east into the Kananaskis Country region, AB. The highest number of individuals identified at a single sampling site (6) was found at the heart of Banff National Park (sampling site 21a).



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CHAPTER 3: Evaluating Carnivore Community Occurrence Across a Gradient of Biophysical Factors and Human Footprint.

3.0 Introduction

Mammalian carnivores are wide-ranging species with low population densities and slow recruitment rates, making them particularly sensitive to imminent and ongoing threats from expanding human land-use practices and the associated effects of a global human footprint (Gittleman 2001). Over the past two decades, increasing evidence supports the important role a diverse community of carnivores can play in maintaining ecosystem stability by weakening the negative effects of top-down trophic cascades (Duffy 2003, Estes *et al.* 1998, Estes *et al*. 2011). Human-mediated changes to habitat condition, such as habitat loss and fragmentation, can adversely effect ecosystem stability by shifting the spatial distribution of available resources (prey species) and thereby influence intra-guild dynamics of carnivore communities (Amarasekare 2003, Weins 1993, Putman 1994), when species share prey resources and are therefore potential competitors (Polis *et al.* 1989). Research and monitoring efforts commonly focus on the direct effects of habitat loss and fragmentation on carnivore occurrence (Farhig 2003, Hilty *et al.* 2006); however, indirect effects of human landscape alteration may also be a significant factor influencing where carnivores occur through changes to interspecific competitive interactions (e.g. Crooks and Soulé 1999, Hebblewhite *et al.* 2005).

As demonstrated in a review by Glen and Dickman (2005), carnivores do not operate in isolation of each other and their interspecific interactions are broadly documented to show profound effects on community composition by influencing species relative abundance and distribution patterns (Linnell and Strand 2000, Glen and Dickman 2005). While the spatial and temporal effects of interactions between predators and their prey have long been understood (Lotka 1925), recent attention has shifted to better understanding predator-predator interactions (Durant 1998, Palomares and Caro 1999, Linnell and Strand 2000) and accounting for the functional role of interspecific interactions within these communities (Soulé *et al*. 2003). Unlike predator-prey interactions which are a function of direct or anticipatory consumption of one species by another, predator-predator interactions can result from a complex combination of predation and competition between dominant and subordinate species within their guild (Polis *et al.* 1989). Therefore, consequences of altered interspecific interactions might include: (1) increased interference interactions, such as competition and predation, (2) heightened avoidance of 'risk' by co-occurring carnivores in space and time, and (3) the partial exclusion of subordinate species from their preferred habitat (Palomares and Caro 1999, Linnell and Strand 2000). If interference interactions change the relationship between resource acquisition and the probability that the habitat is suitable for another given (subordinate) species, selection of suboptimal habitat for the subordinate species can be observed by patterns of space use across the scale at which an animal is distributed, or the distribution scale (Godsoe and Harmon 2012).

The strength of these interactions among community members may be context dependent. For example, the use of suboptimal habitat by subordinate carnivores may depend upon the density and distribution of the dominant competitor, as in the case of coyote-wolf interactions (Peterson 1995). However, the strength of the interaction effects may also relate to the ability of the subordinate carnivore to compensate for lost predation opportunities (i.e. through scavenging), or to balance the fundamental need to access prey resources with the risk of competitive interactions or direct predation (Gittleman *et al.* 2001). Large areas covered by diverse habitat types, or heterogeneous landscapes, may also dampen the adverse effects of interference interactions on communities by allowing for spatial refugia from competition or predation (Amarasekare 2003). In addition, species with more generalized characteristics that allow for the use of varying home range sizes and plasticity in foraging behaviour can better adapt to large-scale environmental and human-caused changes to habitat condition (Weaver *et al.* 1996). Understanding the complex conditions that influence carnivore community dynamics is a prerequisite to asking questions and making predictions about how carnivores may respond to natural and anthropogenic features in a landscape.

Using infrared remote camera imagery, I examined the spatial patterns of multiple medium- to large-sized carnivore species occurrence in a naturally heterogeneous and rugged landscape located in the central region of Alberta's Rocky Mountains. The central Rocky Mountain region is home to a biologically diverse suite of carnivore and prey species and is subject to a west-east gradient of high-low landscape and wildlife protection, and low-high anthropogenic activity, providing a unique opportunity to investigate the relative effects of biophysical and anthropogenic factors affecting patterns of multi-carnivore occurrence. Throughout this region we surveyed multiple carnivore species to ask: (i) How does carnivore occurrence vary across a gradient of increasing anthropogenic landscape disturbance in a heterogeneous mountain environment? (ii) Is there significant similarity among multi-species response to human footprint features, irrespective of biophysical features? (iii) Are there generalities in species-specific response to biophysical and anthropogenic features? (iv) Do biotic interactions play a relative role in explaining spatial occurrence patterns among multiple carnivores?

Carnivore community occurrence was hypothesized to change as a function of biophysical features and anthropogenic landscape alteration ("human footprint"), in two ways. First, I predicted similarity in response among assemblages of carnivores within this community to increasing density of human footprint, despite the biophysical features. Second, I predicted that human footprint, together with biophysical features and the presence or absence of competing and co-occurring carnivores (heterospecifics), makes the landscape more suitable for some medium-sized, or "meso", carnivore species.

3.1 Methods and Materials

3.1.1 Background

Sampling methods for surveying and monitoring wide-ranging carnivore species include snow tracking, aerial surveys, telemetry, and traditional mark-recapture techniques (Gittleman 2001). These techniques are often financially and logistically unfeasible to effectively survey multiple species of carnivores across the large spatial scales at which these species operate. Non-invasive genetic tagging (NGT) has been an alternative effective approach to surveying wide-ranging terrestrial carnivores, including grizzly bears (Kendall *et al*. 2009, Mowat *et al*. 2005) and wolverine (Copeland *et al.* 2010, Magoun *et al.* 2011), but can be subject to detection underestimation bias (Dreher *et al.* 2009). The addition of infrared remote camera (IRC) traps is an increasingly popular technique used to sample and monitor low density species (Thompson 2004, O'Connell *et al.* 2011) provides an independent way of validating underestimation bias (Fisher and Bradbury 2014). Combining IRC and NGT improves our ability to collect robust abundant data on single and multiple species at a reasonable cost and across large areas (Thompson 2004, Long *et al.* 2008, O'Connell *et al.* 2011).

Study design must consider the species of interest and the spatial scale of ecological processes under investigation (Weins 1989). Wide-ranging large-sized carnivores are being threatened by pervasive human development occurring at landscape scales (Ripple *et al.* 2014); however, there remains no single known spatial or temporal scale at which ecological distribution patterns and factors influencing those patterns should be studied for multiple carnivore species. As human landscape alteration continues to expand across large areas – those which carnivores must navigate – we might predict anthropogenic impacts to be evident at the community level. Though all species are expected to respond differently to landscape changes (Gittleman 2004), the range of spatial extent to which an organism may respond is determined largely by its mobility (Holling 1992). Since wide-ranging carnivore species share characteristic mobility requirements, we might further predict these species to be responding similarly to human landscape alteration at a spatial scale represented by the distribution scale of a single species within their guild.

The wolverine (*Gulo gulo*), though relatively small in body size within the medium-large sized carnivore guild, can occupy home ranges that span from a few hundred square kilometers to greater than one thousand square kilometers (Hornocker and Hash 1981 and others), a spatial extent of landscape use that represents the distribution scale for many co-occurring species within the carnivore guild. Furthermore, there is considerable evidence to suggest wolverine occurrence patterns at a large landscape scale are driven by both biophysical and anthropogenic landscape factors (May *et al.* 2006, Krebs *et al.* 2007, Inman *et al.* 2012, Fisher *et al.* 2013). Assuming this is true, we can expect the scale of wolverine habitat selection to be an appropriate proxy for study design to examine multiple medium-large sized carnivore species occurrence in relation to biophysical landscape features and factors representing large-scale human landscape alteration.

During the winter seasons of 2010-2013, I used a multi-method approach combining non-invasive genetic tagging (NGT) and infrared remote camera (IRC) trapping effective at simultaneously surveying a suite of mammalian carnivores in mountain environments (Fisher *et al.* 2011, Fisher and Bradbury 2014). I used the IRC trap data collected from this multi-method approach to model spatial multi-carnivore occurrence patterns in relation to landscape variables. I used these models to evaluate the relative roles of biophysical landcover and human footprint factors in affecting carnivore community occurrence across a heterogeneous mountain environment in the central region of the Canadian Rocky Mountains.

3.1.2 Study Area and Land Use

In collaboration with national park-based research efforts focused on wolverine population demographics and genetics (Clevenger and Barrueto 2014; Clevenger *et al.* 2011, *unpubl. data*), carnivore occurrence was surveyed throughout the central Canadian Rocky Mountains within a complex of National Parks and eastward into the provincially managed region of Kananaskis Country (Figure 1). The National Parks complex included Banff, Yoho and Kootenay National Parks. We also surveyed just beyond the boundary of the Kananaskis Country region and north into the Ghost Wilderness area, areas that were included as the greater Kananaskis Country region for this study's purposes. Therefore, the regional study area was comprised of two contiguous study areas - the National Parks complex and the Kananaskis Country region – representing a mosaic of mountain topography with varying degrees of landscape protection and density of human landscape alteration.

National Parks are federally protected from resource extraction, off-road motorized recreation, and trapping. Within the Parks complex, the Trans-Canada Highway and Canadian Pacific Railway bisect Banff and Yoho National Parks through the main river valley bottom. Human impacts in the Banff-Bow Valley are spatially restricted to existing recreational trails, lease areas, and two town sites. Activities within the National Parks complex include non-motorized recreational hiking, biking, and camping, human impacts. In contrast, land management units designated as protected areas, wildland parks, and public land use zones partition land use activities in the Kananaskis Country region. The various management units encourage conservation of natural and cultural heritage while providing for economic land use practices. Furthermore, human impacts in the Kananaskis Country region are subject to expansion and include non-motorized (e.g. hiking, biking, skiing, equestrian) and motorized (e.g.

off-road vehicles, snowmobile, and motorbike) recreation, trapping, and various types of resource extraction (e.g. oil and gas exploration, mining, timber harvest, and agriculture).

Ecological characteristics of both the National Parks complex and the Kananaskis Country region (Figure 3.1) fall within the Rocky Mountain Natural Region (Natural Regions Committee 2006). The Rocky Mountain Natural Region is home to a native suite of large mammalian carnivore and ungulate species that include: wolverine *(Gulo gulo)*, Grizzly and Black bear (*Ursus arctos* and *Ursus americanus*), cougar (*Puma concolor*), wolf (*Canus lupus*), Mountain goat (*Oreamnos americanus*), moose (*Alces alces*), elk (*Cervus elphus*) and deer (*Odocoileus sp.*). This natural region is classified by three Subregions: Alpine, Subalpine, and Montane. The Alpine Natural Subregion occurs above treeline and is dominated by low growing vegetation adapted to harsh climatic conditions. Occurring at mid-elevation, the forested slopes of the Subalpine Subregion varies in condition depending on aspect but is generally sheltered from the extreme conditions experienced at higher elevations. The subalpine subregion is dominated by Engelmann spruce (*Picea englemannii*), Subalpine fur (*Abies lasiocarpa*), and Subalpine larch (*Laryx lyallii*). On the lower front ranges of the Rocky Mountains, the montane natural subregion is dominated by mixed forests of Douglas-fir (*Pseudotsuga menziesii*), Trembling aspen (*Populus tremuloides*), and Lodgepole pine (*Pinus contorta*).

While Alpine and Subalpine dominate the Parks complex with areas of Montane found in the main valley bottom corridors, Kananaskis Country transitions from Alpine and Subalpine into Montane and is bordered to the east by Foothills Parkland. The convergence of natural subregions in the Kananaskis Country region provides for increased biodiversity compared with the central regions of the Rocky Mountains to the west. Topography across both regions is rugged, with high peaks and steep-sloped ridges trending to low elevation foothills in the east, spanning an elevation gradient from a low point of 825m to above 3600m. The west-east gradient of varied landscape protection and increasing anthropogenic activity overlaying this topographically rugged and naturally complex study area provides a unique opportunity to investigate the relative effects of biophysical and anthropogenic factors that may explain patterns of carnivore community occurrence occurring across a large spatial scale.

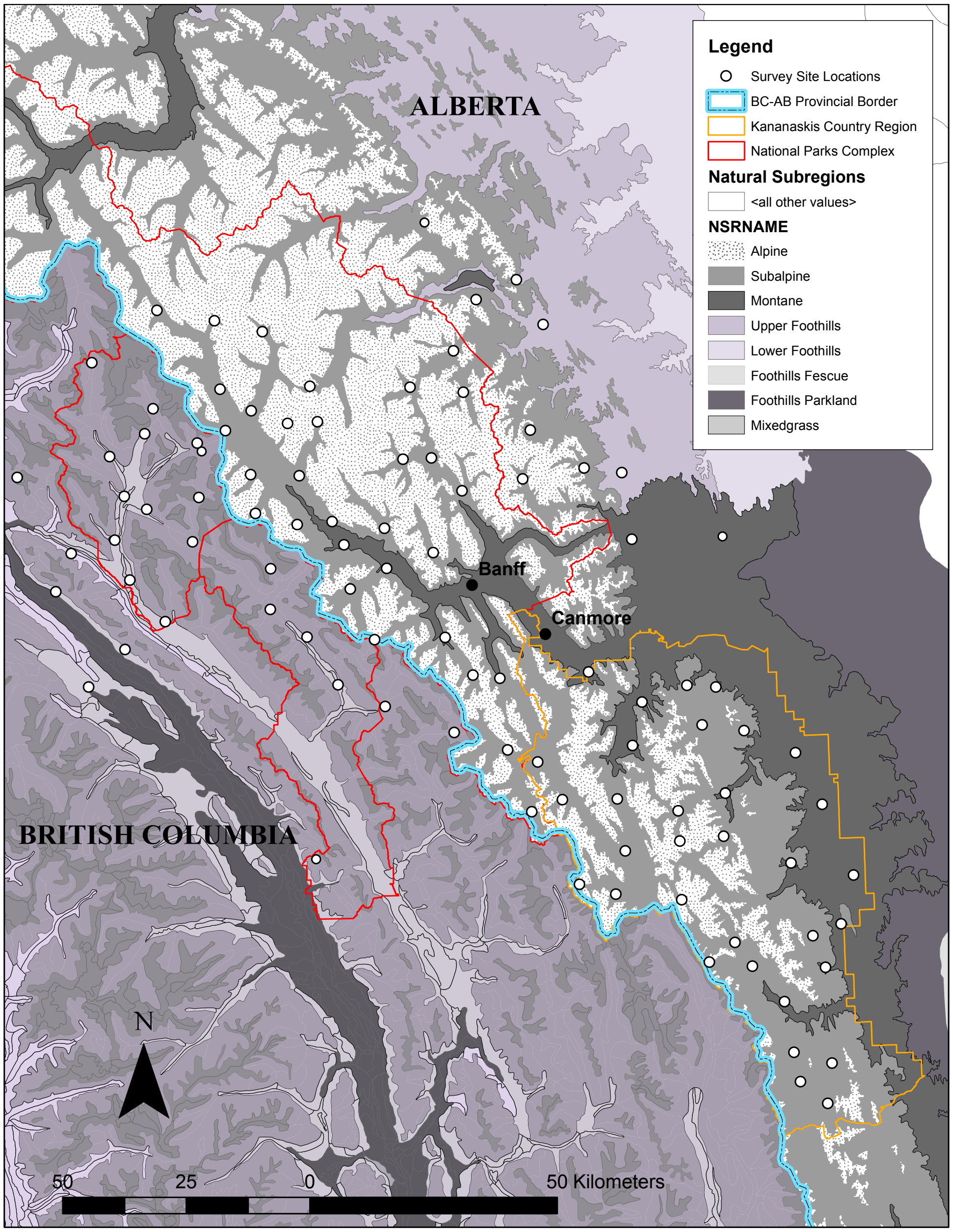


Figure 3.1 Map of natural subregions and park boundaries

Maps the point locations used to survey species occurrence (white dots) throughout the regional study area and across various Natural Subregions. The regional study area is situated along the Canadian Rocky Range, crossing a provincial boundary between British Columbia and Alberta and falls within National and Provincial Park boundaries.

3.1.3 Sampling Design

We surveyed multi-carnivore occurrence using a systematic grid-based sampling design (Figure 16), generated in ESRI ArcGIS 9.3 (Environmental Systems Research Institute 2009). Our systematic study design is a probabilistic approach that minimizes bias by spreading survey efforts uniformly across a large spatial area and allows for generalizations to be made from our analysis of random surveys to the broader population in the region (MacKenzie and Royle 2005).

To effectively survey wide-ranging carnivores the study design encompassed approximately 15,000 square kilometers and included repeat survey periods that reflect average individual movements (MacKenzie 2006). Sampling unit (grid cell) size can influence estimates of species occurrence and occupancy and is recommended to be no smaller than the minimum home-range size, but large enough to have a reasonable probability of detecting that species if it is present within a single survey (Gompper *et al.* 2006). Given that the minimum home range size of female wolverines is estimated between 100-150km^2 (Banci 1994), a 10x10km^2 (100km^2) grid cell size matches the spatial scale of the ecological process under investigation (Wiens 1989) and is the suggested scale to survey wolverine populations (Koen *et al.* 2008). Since the National Park complex is covered by a substantial proportion rock and ice, a slightly larger cell size of 12x12km^2 (144km^2) was plotted over the regional study area and assumed unlikely to reduce sampling success (Clevenger and Barrueto 2014).

Approximately 43 grid cells were plotted in the Kananaskis Country region; an adjacent 48+ grid cells were defined in the National Parks complex – a total of than >91 grid cells included in this regional study area (Figure 3.2). Each grid cell is considered one sampling unit; therefore, 91 units were surveyed to ask questions about multi-species occurrence. One survey site was placed within each sampling unit with each site a minimum of 6,000m apart from adjacent sites to facilitate sampling independence among sampling units, thereby reducing pseudoreplication. We determined site locations largely by logistics and accessibility, but generally they were placed at mid-elevation drainages, travel corridors, and at sites with escape cover and evidence of animal movement to facilitate animal detection. Subjectivity at the site level serves to maximize probability of detection, but does not affect our probabilistic design, since statistical inference occurs at the scale of the grid cell (MacKenzie *et al.* 2006). We accessed sampling sites by ground (ski, snowmobile, 4x4 vehicle) or helicopter.

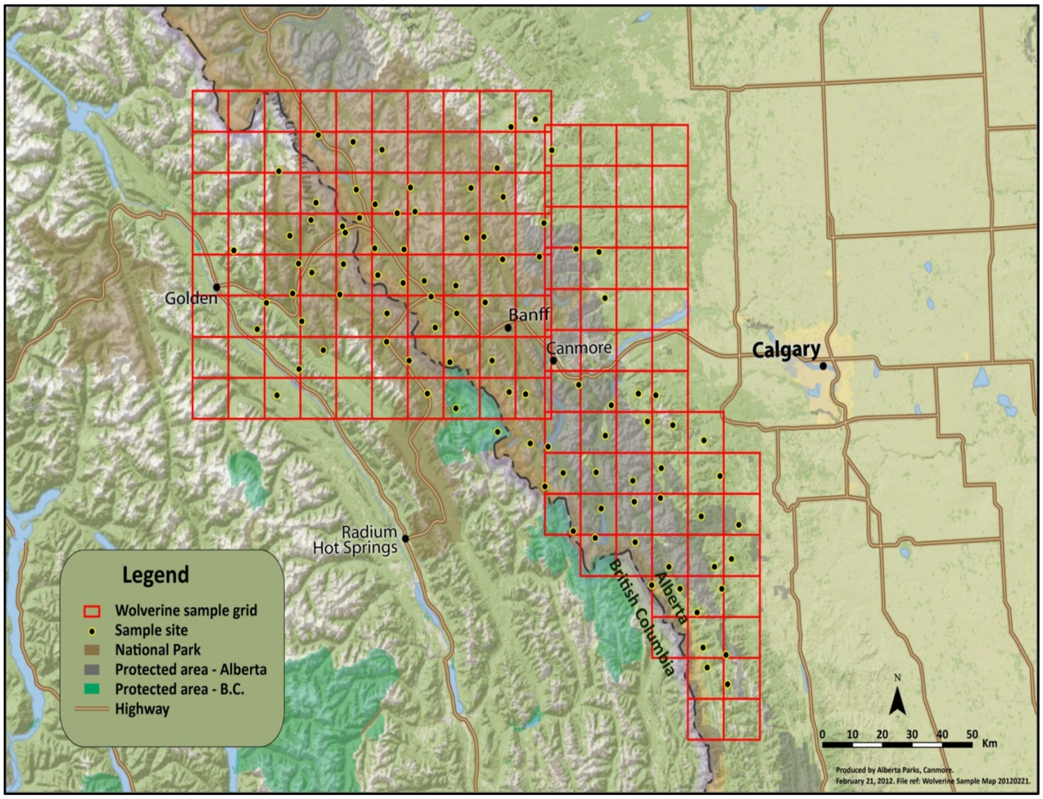


Figure 3.2 Map of systematic grid overlay and survey site locations

Shows the grid-based study design used to survey species occurrence throughout the regional study area. Individual sample, or survey, sites (black dots) are nested within the grid cells, or survey units, outlined in red. The sample grid of 12km x 12km cells stretches across the Rocky Mountain Range from Golden, BC to the eastern slopes of Alberta, representing a west-east gradient of variable land use practices within and adjacent to protected areas boundaries.

3.1.4 Field Collection

At each site we simultaneously deployed infrared camera traps (IRC's) and non-invasive genetic trapping (NGT) (Figure 3.3). We deployed Reconyx RM30 or PM30 infrared-triggered digital cameras (Reconyx, Holmen, Wisconsin, USA) and positioned these facing the hair trap. I used digital photographs to identify species occurrence. We used an attractant-based survey technique that lured carnivores to the site by both a bait (beaver carcass) and scent lure. The beaver carcass was secured 2m above ground on a limbed tree trunk. We loosely wrapped the tree trunk below the bait with Gaucho® barbed wire (Bekaert, Brussels, Belgium), as per (Fisher and Bradbury 2014). As an addition attractant, we smeared approximately one tablespoon of O'Gorman's LDC Extra scent lure (O'Gorman's Co., Montana, USA) on a rag and hung high on an adjacent tree to increase scent dispersal. The bait and lure attracted animals to the site, moved into view of the camera trap, and for some such as marten, lynx and wolverine, climbed the baited tree leaving hair on the barbed wire. We did not analyze hair samples collected by species other than wolverine for the broader scope of this study. I used camera images to identify multi-carnivore species occurring at each site.

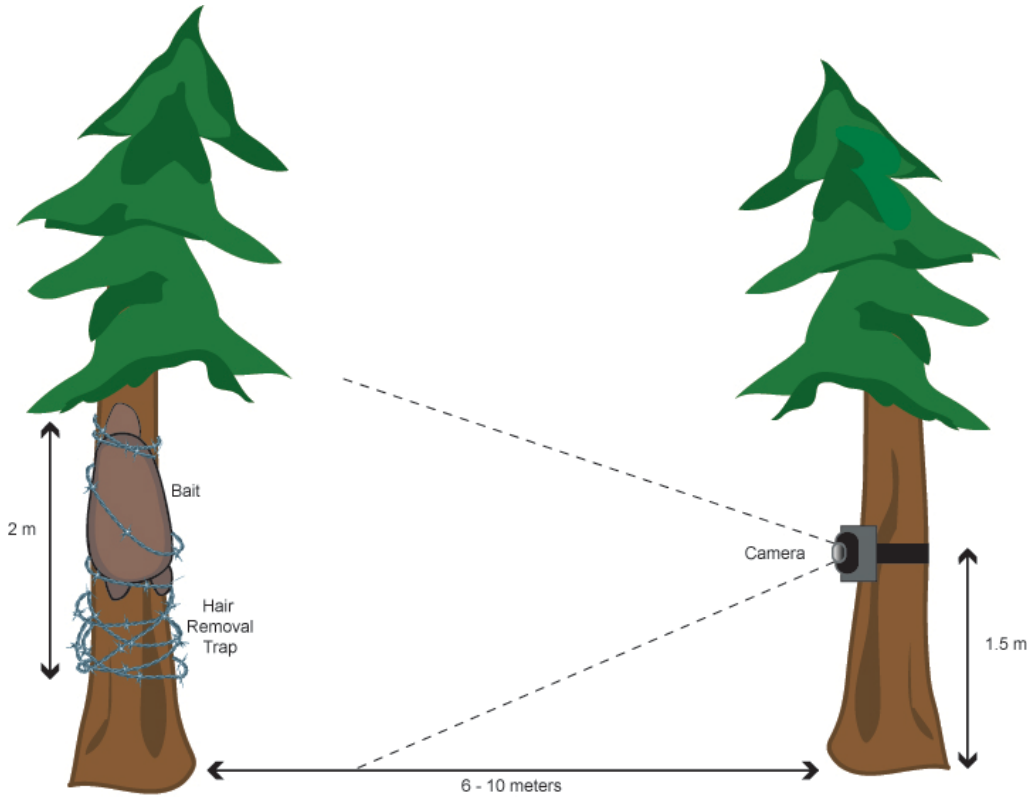


Figure 3.3 Illustration of multi-method survey approach

Multi-method approach used to sample multi-carnivore occurrence that combines remote camera trapping and non-invasive genetic tagging. The hair trap (located on the tree on the left) consisted of barbed wire loosely wrapped around a baited tree. The digital camera (located on the opposite right) was positioned on a tree 6-10m away to photograph the hair trap and the area around it.

The attractant-based sampling technique was conducted across three years (2010-2013) within the National Parks complex (2010-11 and 2012-13) and across two consecutive years within the Kananaskis Country region (2010-11 and 2011-12) during mid-December to mid-April. Using remote camera imagery, species occurrence data from the second and most spatially extensive (2012-13 and 2011-12, respectively) sampling seasons for each area was used to answer questions about carnivore distribution patterns for this study. We sampled all sites at monthly intervals, a survey duration that satisfies random sampling assumptions (a member of a population having an equal and independent chance of being detected (Koen 2008). During each sampling survey we replenished the bait and scent lure and uploaded the camera images.

3.1.5 Image-based Occurrence

Camera imagery (Figure 3.4) provided species presence-absence data that I used as the response variable in regression and multivariate models against explanatory variables quantifying biophysical and anthropogenic landscape features. I classified all images as a count of species detection (1) or non-detection (0) across each monthly survey. I then summed counts of detection for each species across the three monthly surveys, yielding a 0-3 index of species presence-absence use for each sampling unit. Due to logistic constraints, the number of monthly surveys was restricted to two for 26, or 28 percent, of the 91 survey sites included in these analyses. The total number of surveys was calculated by the number of sites multiplied by the number of survey periods (e.g. 26 sites * 2 survey periods = 52 surveys; 64 * 3 survey periods = 195 surveys; total = 246 surveys). The proportion of occurrence for each species was calculated by dividing the total number of species detections by the total number of surveys (eg. 50 coyote detections / 246 surveys).

I also modeled species presence-absence, or detection/non-detection, data (0-1) against UTM easting coordinates (Universal Transverse Mercator projected coordinate system, Map Datum: NAD 83, Zone 11) to evaluate spatial patterns of occurrence probability for each carnivore species across the regional study area and in relation to one another. I compared the proportion of occurrence among species to examine for variation in occurrence and detection patterns between species and across the regional study area.

Figure 3.4 Remote camera image of coyote detection a survey site

Remote camera imagery from Kananaskis Country captures coyote, one species of the suite of carnivore species that were found to occur throughout the central Rocky Mountains regions of Alberta, during the winter season of 2011-2012.

3.1.6 Occupancy Estimation and Two-Species Co-occurrence

Detection/non-detection data can be used to estimate occupancy, which allows empirical quantification of the probability of detecting a species if it is in the area (MacKenzie 2006, Royle 2006, Fisher and Bradbury 2014). Occupancy (ψ, or *psi*) estimates the probability of species occurrence, adjusting for imperfect detection, when the detection probability (p), the probability a species is detected given it is present, is less than 1 (MacKenzie 2006, Royle 2006, Nichols *et al.* 2008). Occupancy models are analogous to simultaneous generalized linear models on serial detection data to estimate both ψ and p. For wide- ranging and elusive species, imperfect detection in surveys is often a concern and has led to the increased use of occupancy modeling to understand species spatial distribution patterns (MacKenzie *et al.* 2002, MacKenzie 2006). Accounting for imperfect detection, I compared estimated ψ and p between carnivore species detected and across the regional study area. I compared estimates with unadjusted, or naïve, detection rates to assess underestimation bias can that lead to erroneous inferences about species detection patterns (MacKenzie 2006).

In addition, estimated ψ and p can be used to model two-species carnivore co-occurrence (φ), or the probability that two species co-occur at the same site, which identifies non-random patterns of species co-occurrence (MacKenzie et al 2006). The two-species co-occurrence model estimates occupancy of two species, as well as conditional occupancy given the presence of the heterospecific (described in Appendix A, Hines 2006). A positive co-occurrence pattern between two species is suggested if φ is greater than 1, when species co-occur more than expected. Conversely, if φ is less than one it suggests species co-occur less than expected and therefore avoidance may occurring between the two species modeled. No effect of one species on the other is assumed when the φ is equal to 1. Conditional parameters assume that species A is dominant and species B is subordinate and therefore models the presence of species A as a covariate in relation to the presence or absence of species B. For example: a two-species model to evaluate co-occurrence between wolf and coyote using the condition parameters p^A would estimate the probability of detecting coyote (subordinate species "B") given wolf (dominant species "A") is absent. I used single-season two-species co-occurrence models (standard and conditional) to detect for non-random species co-occurrence patterns (Presence v.4.9 software, Hines 2006).

3.1.7 Quantifying Landscape Covariates

I used ESRI ArcGIS 9.3.1 software and digital map inventories (ABMI Human Footprint Map 2010, and National and Alberta Provincial Parks' geo-databases) to acquire spatial data to measure biophysical and anthropogenic landscape features around each sampling point. Measured landscape features included those hypothesized to be important for a community of large ranging carnivores and having spatial data available with continuous coverage across the regional study area. We quantified the proportion of each landscape variable by creating circular buffers around each sampling point, across 20 spatial scales ranging from 500m up to 10,000m (q.v. 2.1.10).

We obtained a 16 class landcover raster dataset (McDermid *et al.* 2009) to quantify the average percent area of natural land-cover classes for each spatial buffer around each sampling point. Topographic ruggedness, measured as the mean elevation difference over an area, was quantified using a topographic ruggedness index (Riley *et al.* 1999). We calculated persistent spring snow as the number of years over a 12-year period an area was covered by snow during the spring (defined between the 14th of April and the 15th of May) using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data (Copeland *et al.* 2010, Hall and Riggs 2007). Persistent spring snow can be used as a surrogate for annual snow pack that has been found to influence space use patterns for species better adapted to travelling across deep snow packs, such as wolverine (Copeland *et al.* 2010, Brodie and Post 2010), or less adapted to deep soft snow packs, such as wolves (Telfer and Kelsall 1984, Seip 1992).

We separated anthropogenic or "human footprint" features (ABMI Human Footprint Map 2010) into 12 composite classes (Appendix B, highlighted in blue). We used spatial layers from a Parks Canada database (Parks Canada 2014) to summarize the human footprint features found within the National Parks Complex, features described by the ABMI Human Footprint Map (2010). To accurately model human footprint features across the regional study area, we buffered spatial layers from the Parks Canada database to meet the same spatial extent of layers described by the ABMI Human Footprint Map (2010). The 12 human footprint classes were then grouped into two main categories: block or linear features. Block features were measured as percent area of urban footprint (eg. town boundaries and recreational lease areas) and industrial footprint (eg. oil well and mining sites, timber harvest cut-blocks, and cleared or cultivated areas). Linear features were calculated as the mean density (km/km^2) of each linear feature class (eg. roads, cutlines, pipelines, seismic lines, and recreational trails) within the spatial buffers. Only linear loud recreational features were quantified from areas within the Kananaskis Country region since off-road motorized recreation is not permitted in the National Parks. Lastly, I summed monthly presence-absence (detection/non-detection) of carnivore species (listed in Table 3.1) was summed across the study period (0-3) to test for effects of heterospecific occurrence.

3.1.8 Parameter Simplification

I estimated multicollinearity to remove collinear variables from models and therefore reduce imprecise parameter estimation and type II errors (Zuur *et al.* 2013). I evaluated collinearity among proposed landscape covariates using Pearson correlation coefficient (r^2) matrices and multi-panel scatterplots to detect relationships among variables. I used variance inflation factor (VIF) estimation to evaluate the degree of collinearity among covariates (Belsey *et al.* 1980, Craney and Surles 2002). A stepwise approach to VIF estimation reduced the number of variables to those with VIF < 5. A tolerance level of VIF < 3 is preferred (Craney and Surles 2002), however; a VIF < 5 enabled retention of variables hypothesized to be ecologically meaningful for this suite of carnivore species (described in Table 3.1). Using this stepwise approach, I excluded four collinear variables from model specification (Table 3.2). To further reduce the number of model parameters, I also excluded two wetland cover types (treed and open wetlands) from the saturated global model having no *a priori* hypotheses to suggest these landscape variables to be important factors explaining multi-carnivore occurrence. However, two collinear snow-related variables were retained in the global model. These snow-related variables represent different measures of snow cover that may vary in their relative their biological importance and habitat associations with individual or multiple carnivore species.

Table 3.1 List of landscape variables

Landscape variables hypothesized to explain multi-carnivore occurrence across the regional study area found in the Canadian Rocky Mountains of Alberta.

Category	Landscape Variable	Description
Landcover	DENSECON	>70% crown closure; >80% coniferous
	MIXED	21-79% coniferous
	OPENCON	<30% crown closure; >80% coniferous
	SHRUB	shrub cover, represents avalanche path cover.
	HERB	herb cover
	REGEN	regenerating portions of the landscape
	SNOW.ICE	perennial, or permanent, snow and ice cover
Human Footprint	BLOCKURB	Blocks of urban footprint (eg. towns, developed recreational lease areas)
	LINROAD	Linear road features including paved and unpaved transportation
	LININD	Linear industrial cutlines (eg. seismic lines, powerlines)
	LINREC_Q	quiet linear recreational features (designated hiking trails)
	LINREC_L	loud linear recreational features (designated ATV and snowmobile trails)
Abiotic	TRI	topographic ruggedness index, average elevation difference in a given area
	SP.SNOW	number of years (out of 12) an area was snow covered during spring months
Biotic	WOLF	wolf occurrence
	COUG	cougar occurrence
	COYO	coyote occurrence
	LYNX	lynx occurrence
	BOBC	bobcat occurrence
	FOX	red fox occurrence
	MART	*American* marten occurrence
	WOLV	wolverine occurrence

Note: DENSECON, dense conifer cover
MIXED, Mixed forest Cover
OPENCON, Open conifer cover
SNOW.ICE, Perennial snow and ice over
BLOCKURB, Urban block shaped features
LINROAD, Linear roads
LININD, Linear industrial cutlines
LINREQ_Q, Quiet linear recreational trails
LINREQ_L, Loud linear recreational trails
TRI, Topographic ruggedness index
SP.SNOW, Annual spring snow cover

Table 3.2 List of collinear landscape variables

Collinear landscape variables excluded from model specification using a stepwise approach of variance inflation factor (VIF) estimation and a tolerance level of VIF < 5.

Category	Excluded Landscape Variable	Description	Collinear Landscape Variable
Landcover	BROAD	>60% crown closure, >75% broadleaf	Mixed Forest Cover (MIXED)
	BARREN	<6% vegetation cover	Persistent Spring Snow (SP. SNOW) and Topographic Ruggedness (TRI)
Human Footprint	BLOCKIND	Blocks of industrial footprint (eg. well and mine sites, cutblocks, disturbed vegetation)	Linear Industrial Features (LININD)
Abiotic	ELEV	Elevation (m) of survey site location	Persistent Spring Snow (SP. SNOW) and Topographic Ruggedness (TRI)

Note: BROAD, broad leaf forest cover
BARREN, barren ground
BLOCKIND, industrial block shaped features
ELEV, Elevation (m)

3.1.9 Characteristic Scale of Habitat Selection

Determining the appropriate scale of species habitat selection is of fundamental importance to understanding the ecological mechanisms driving species distributions (Levin 1992). The appropriate scale a species may be responding can be selected based on the researchers point of view that considers key research questions, focal organism, and the time period of study (Wiens 1989, Wiens *et al.* 1993). Alternatively, scale may be selected based on a species point of view that considers microsites, home range, to geographic range (Elith and Leathwick 2009). Since we are examining occurrence patterns for a community of mobile carnivore species influenced by landscape-scale human development, the scale of interest must include the maximum extent of area assumed to affect these species. Fisher *et al.* (2011) found landscape variables measured from the 250m to the 5000m scale to best explain occurrence patterns driving a suite of medium-large sized carnivore species, including those detected during this study. A 2500m scale was selected to examine relationships between landscape variables and multi-carnivore occurrence patterns, a scale encompassing the range of spatial extents found to drive the carnivore species found within the community of interest (Fisher *et al.* 2011).

3.1.10 Multi-Species Ordination

I used multivariate analyses to simultaneously test for relationships between multi-species occurrence and biophysical and anthropogenic landscape factors. Ordination is a heuristic approach that graphically summarizes complex relationships (McCune *et al.* 2002) by rearranging the data to find similarity among an assemblage of objects using as few descriptors as possible (Matthiopoulos 2011). Constrained ordination moves beyond evaluation of a single set of interdependent variables (i.e: unconstrained ordination) to reveal structures in one data set that are related to structures in another data set (Borcard *et al.* 2011). Redundancy analysis (RDA), a method of constrained ordination, is an extension of regression analysis that models a single set of multivariate dependent (or response) variables to generate a series of linear combinations that best explain the variation in the response data from the variation in a single set of explanatory data (Borcard *et al.* 2011, McGarigal *et al.* 2000). Give the species occurrence data being modeled, I chose RDA as the appropriate ordination approach to examine similarities among multiple species occurrence patterns in relation to a reduced selection of landscape variables.

I modeled the species occurrence index (0-3) as the response matrix against the explanatory matrix, a simplified set of biophysical and anthropogenic landscape variables measured at a 2500m scale (Table 3.1) as the explanatory matrix. A global model including all response and explanatory variables may weaken model resolution if a great deal of variation exists within carnivore species assemblage or landscape covariates. In an effort to reduce model complexity and increase partitioning of variance across species and landscape variables, I grouped response and explanatory matrices into subsets by: species predicted sensitivity levels to human-related disturbance and according to species body size, suggested to influence that spatial scale of habitat selection (Fisher *et al.* 2011), and landscape variables related to biophysical or anthropogenic environmental conditions (Table 3.3). Though numerous models with various species and landscape variable combinations could be specified, 11 different RDA models were examined using a combination of response and explanatory matrix sets hypothesized to be most ecologically important for the carnivore community under investigation (Table 3.4). Each response matrix subset was made up of species assemblages extracted from the community and landscape that was sampled simultaneously.

I applied a hellinger transformation to the response matrices for each species set, a method of assigning low weight to rare species when community data is sampled over variable environmental gradients and inherently are subject to a greater proportion of zeros (Legendre and Gallangher 2001). I compared the relative strength of model fit, or the amount of variation in the response matrix that is explained by the amount of variation in the explanatory matrix, across models by calculating the r-squared and adjusted r-squared value using Ezekiel's formula (Ezkeil 1930, Borcard *et al.* 2011) for each model. I used scree plots to examine for a descending trend in the order of magnitude of eigenvalues (measures of variance of axes) expected from ordination analyses (McGarigal *et al.* 2000). I reported the total variation explained by each model, the proportion of variance explained in the data for the constrained (measured) variables, the unconstrained (unmeasured) variables, and by the first two canonical axes for each model. Non-parametric permutation tests appropriate for ecological data - data subject to non-normal distributions - generated a reference distribution of the chosen F-statistic under the null hypothesis to measure the significance of association for each model. Using a significance level of 0.001, the null hypothesis being tested is that there is no (linear) relationship between the response data matrix and the explanatory data matrix (Borcard *et al.* 2011). Therefore, a relatively higher F-statistic (>1) with a significance value (Pr(>F)) at or below 0.001 suggests that there may be a significant relationship between the response and explanatory variables included in the specified model. I plotted point-vector biplots for each model to interpret the strength and direction of associations by examining the similarity among species and importance of explanatory variables in relation to species occurrence patterns in ordination space. Point-vector biplots graphically represent scaling of species in ordination space in relation to landscape variables indicated by the length and angle of vectors relative to the axes (Quinn and

Keough 2002). Since the greatest amount of variation can be explained by the first two axes, I examined biplots representing scaling of species in ordination space for axis 1 (RDA 1) and axis 2 (RDA2).

Table 3.3 Multi-species redundancy model subsets

Describes a subset of multi-species redundancy models used to relate carnivore occurrence patterns to biophysical and anthropogenic landscape variables in the central Rocky Mountain region of Alberta.

Matrix	**Subset**	**Variables**
Global response	All species	WOLF + COYOTE + FOX + COUGAR + LYNX + BOBCAT + WOLVERINE + MARTEN
Global explanatory	All landscape factors	DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW + BLOCKURB + LINROAD + LININD + LINREC
Species (response)	Sensitive	LYNX + WOLVERINE + MARTEN
	Tolerant	WOLF + COUGAR + COYOTE + BOBCAT + FOX
	Large body size	WOLF + COYOTE + COUGAR + WOLVERINE
	Medium body size	FOX + LYNX + BOBCAT + MARTEN
Landscape (explanatory)	Biophysical	DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW
	Anthropogenic	BLOCKURB + LINROAD + LININD + LINREC

Table 3.4 Lists the combination of multi-species redundancy models

Lists the combination of multi-species redundancy models used to relate carnivore occurrence patterns to biophysical and anthropogenic landscape variables in the central Rocky Mountain region of Alberta.

Model No.	Response Matrix Set	Explanatory Matrix Set	Model Variables
1, Global	all	all	WOLF + COYOTE + FOX + COUGAR + LYNX + BOBCAT + WOLVERINE + MARTEN + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW + BLOCKURB + LINROAD + LININD + LINREC
2	all	anthropogenic	WOLF + COYOTE + FOX + COUGAR + LYNX + BOBCAT + WOLVERINE + MARTEN + BLOCKURB + LINROAD + LININD + LINREC
3	all	biophysical	WOLF + COYOTE + FOX + COUGAR + LYNX + BOBCAT + WOLVERINE + MARTEN + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW
4	sensitive	anthropogenic	LYNX + WOLVERINE + MARTEN +BLOCKURB + LINROAD + LININD + LINREC
5	tolerant	anthropogenic	WOLF + COUGAR + COYOTE + BOBCAT + FOX + BLOCKURB + LINROAD + LININD + LINREC
6	mega	all	WOLF + COYOTE + COUGAR + WOLVERINE + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW + BLOCKURB + LINROAD + LININD + LINREC
7	meso	all	FOX + LYNX + BOBCAT + MARTEN + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW + BLOCKURB + LINROAD + LININD + LINREC
8	mega	anthropogenic	WOLF + COYOTE + COUGAR + WOLVERINE + BLOCKURB + LINROAD + LININD + LINREC
9	meso	anthropogenic	FOX + LYNX + BOBCAT + MARTEN + BLOCKURB + LINROAD + LININD + LINREC

10	mega	biophysical	WOLF + COYOTE + COUGAR + WOLVERINE + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW
11	meso	biophysical	FOX + LYNX + BOBCAT + MARTEN + DENSE + MODERATE + OPEN + MIXED + HERB + SHRUB + REGEN + BARE + TRI + SP.SNOW

3.1.11 Species Distribution Modeling

Since the ability to detect generality among species associations within complex ecological communities is inherently difficult to detect using multivariate analyses (McCune *et al.* 2002), I selected generalized linear models (R version 3.0.2, R Core Team 2013) – a form of species distribution modeling – to further examine for generality among species associations. I used generalized linear models (GLMs) to explicitly test multiple competing hypotheses describing species-specific responses to biophysical and anthropogenic landscape variables. GLMs are a family of models that deal with non-normal distributions by transforming, or generalizing, response data using a log-link function specified by an error distribution (Matthiopoulos 2011). Using a binomial distribution, I modeled species-specific presence-absence over three survey periods (0, 1) for each of the 91 sampling locations against biophysical and anthropogenic covariates, the same explanatory variables used in the RDA analyses. In addition to the explanatory variables included in the multivariate analyses, the occurrence of heterospecifics was then added to the each best-fit species-specific landscape model and examined for improved model-fit with the additional biotic variable. Violation of assumptions were investigated by extracting model residuals using three diagnostic plots: (1) simple residuals against predicted values, (2) Q-Q plot using standardized deviance residuals, (3) and an approximate Cook's distance; as well as, examining for over- and under-dispersion by calculating the deviation of a dispersion statistic from 1 to determine if the Poisson distribution is appropriate for the data (Matthiopoulos 2011, Zuur *et al.* 2013). I examined for outliers in the data for both the response and explanatory variables using Cleveland plots Zuur *et al.* 2010). I standardized all measured explanatory variables by subtracting the mean from the individual values and then dividing by the standard deviation for accurate comparison of parameter effect size. I standardized all measured landscape variables retained for these analyses to a common scale by subtracting the mean from the individual values and then dividing by the standard deviation, a calculation that allows for comparison of parameter effect size (Zuur *et al.* 2010). Explanatory variables were measured at the 2500m scale and grouped within candidate model sets specified according to the type of influence hypothesized to explain ecological mechanisms influencing species-specific carnivore occurrence (Table 3.5).

I examined for generalities among species-specific response by first defining models according to four model sets that represented biophysical and anthropogenic landscape features: landcover, topography, climate and human footprint. With no a priori hypotheses to predict the variables that might best explain species-specific occurrence over space, I used a stepwise progression of model simplification to select the best-fit, or minimum adequate, model (Crawley 2007) for each model set. This approach uses maximum likelihood estimation (MLE) and the principle of parsimony to evaluate the relative support for alternative hypotheses by estimating the model that best explains species-specific occurrence while balancing bias and variance, retaining only variables that improve model fit (Burnham and Anderson 2002). Using an Information-Theoretic approach, I compared Akaike Information Criterion (AIC) scores within and across model sets. A low AIC score indicates a more parsimonious and best-fit model relative to alternative models considered (Anderson 2008). I ranked models using differences in AIC values (ΔAIC) and weight of evidence (AIC_w). ΔAIC calculates the difference between the minimum AIC value of the best-fit model from the AIC value of each alternative model (Burnham and Anderson 2002). The further deviation from the minimum AIC value the less plausible the alternative model best-fits the data among the candidate set. AIC_w approximates the probable likelihood of a model by weighting the strength of evidence in favour of alternative models within a candidate model set (Anderson *et al.* 2000).

I then added the presence-absence (0, 1) of a heterospecific, a biotic explanatory variable, to the parameters retained in each minimum adequate, or best fit model, across four biophysical and anthropogenic candidate model sets for each species (Table 3.5). The heterospecific included with each best-fit species-specific landscape model was selected based on predicted competitive dominance. For example, if the response variable was coyote I selected wolf as the heterospecific. Model weight was then compared to those without the inclusion of the heterospecific to infer the relative influence of interspecific interactions with biophysical and anthropogenic landscape factors. Lastly, prey species were included to the best-fit models for each species. Prey was measured as the total number, or count, of monthly presence or absence (0-3) across two groups: (1) ungulates (moose, elk, deer) and (2) small mammals (Snowshoe hare *(Lepus americanus)* and Red squirrel *(Sciurus vulgaris)*).

Table 3.5 List of single-species distribution models

Single-species distribution models used to describe carnivore occurrence patterns in the central Rocky Mountain region of Alberta.

Species	**Model Set**	**Model No.**	**Model variables**
Fox	Landcover	1	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	2	TRI
	Climate	3	SP. SNOW
	Human Footprint	4	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	5	Best Model Variable(s) + COYOTE
Coyote	Landcover	6	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	7	TRI
	Climate	8	SP. SNOW
	Human Footprint	9	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	10	Best Model Variable(s) + WOLF
Bobcat	Landcover	11	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	12	TRI
	Climate	13	SP. SNOW
	Human Footprint	14	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	15	Best Model Variable(s) + COYOTE
Lynx	Landcover	16	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	17	TRI

	Climate	18	SP. SNOW
	Human Footprint	19	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	20	Best Model Variable(s) + WOLF
Cougar	Landcover	21	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	22	TRI
	Climate	23	SP. SNOW
	Human Footprint	24	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	25	Best Model Variable(s) + WOLF
Wolf	Landcover	26	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	27	TRI
	Climate	28	SP. SNOW
	Human Footprint	29	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	30	Best Model Variable(s) + COYOTE
Marten	Landcover	31	DENSE + MODERATE + OPEN + MIXED + SHRUB + HERB + REGEN + BARE
	Topography	32	TRI
	Climate	33	SP. SNOW
	Human Footprint	34	BLOCKURB + LININD + LINROAD + LINREC
	Best Model + Heterospecific	35	Best Model Variable(s) + COYOTE

3.2 Results

3.2.1 Carnivore Occurrence among Species and across Space

Variation among species – Across sites and over survey periods sampled, remote camera imagery detected eight medium- and large-sized carnivore species known to occur in the central region of Alberta's Rocky Mountains; these include: Grey wolf (*Canis lupus*), cougar (*Puma concolor*), coyote (*Canis latrans*), lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), Red fox (*Vulpes vulpes*), American marten (*Martes americana*), and wolverine (*Gulo gulo*). As predicted, we found the proportion of occurrence (sum of species detections / 246 total surveys) to vary among carnivore species (Figure 3.5). Wolverine and marten were detected in greater proportions compared to the other carnivore species detected. Wolverine, marten and coyote had the highest proportion of occurrences. The proportions of wolverine and marten occurrences were 2.34 and 3.52 times greater than coyote, respectively (Figure 3.5).

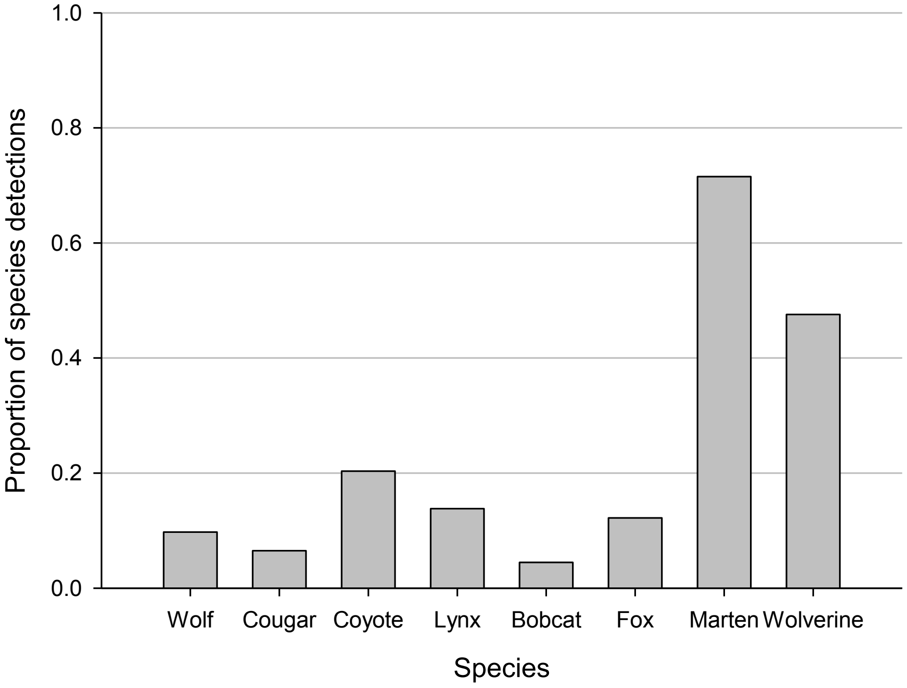


Figure 3.5 Graphs proportion of carnivore species detections

Compares the proportion of carnivore species detections from all sites and sessions surveyed throughout the regional study area (National Parks complex and Kananaskis Country region, Alberta).

Further supporting our predictions, carnivore occurrence also varied across space. First, the proportion of species occurrence, among all species detected, varied between the two study areas (Figure 3.6). The proportion of wolf, cougar, coyote, lynx, and fox occurrence increased eastward into Kananaskis Country region. Bobcat was not detected in the National Parks complex but was detected in the Kananaskis Country region. In contrast, the proportion of wolverine and marten decreased in Kananaskis Country. Conversely, the remaining 6 species detected increased in their proportion of occurrence in the Kananaskis Country region. The spatial variation of species occurrence between the two study areas was strongest for coyote and wolverine. The proportion of coyote detections increased by 13.54 times and the proportion of wolverine detections decreased by 8.19 times in the more developed region of Kananaskis Country compared to species detections found in the protected areas complex of Banff National Park (Figure 3.6).

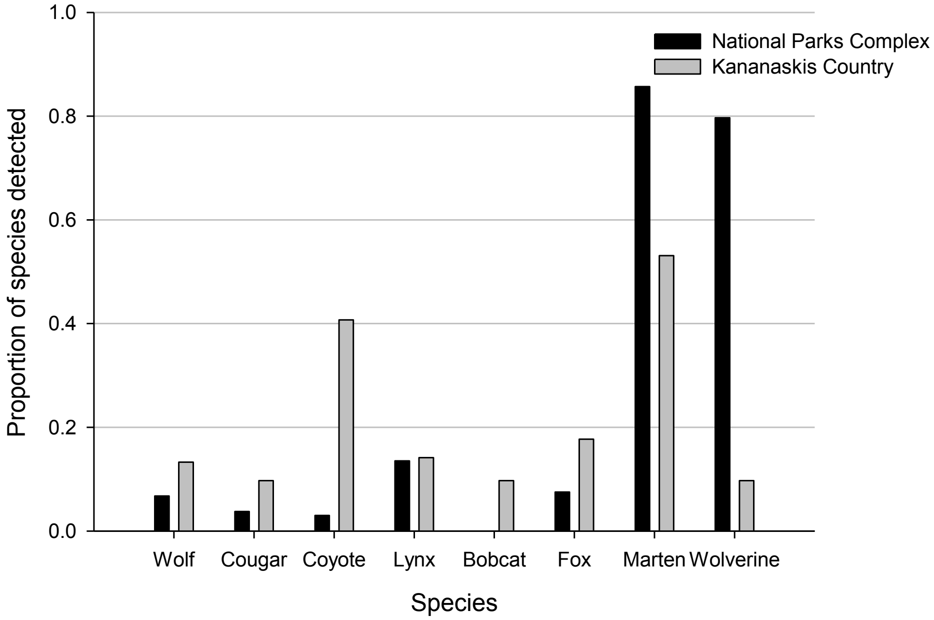


Figure 3.6 Graphs the proportion of carnivore species detections across study areas

Compares the proportion of carnivore species detections by species across the two study areas found within the regional study area, with the National Parks complex is highlighted by the black bars and the Kananaskis Country region is highlighted by the grey bars.

Variation among species and across space – When modeling the probability of carnivore occurrence against UTM east coordinates, the spatial patterns of occurrence varied among species along the west-east gradient from Banff National Park to Kananaskis Country (Figure 3.7). The probability of cougar, red fox, and wolf occurrence increased marginally across the west-east spatial gradient. The probability of bobcat occurrence displayed a sharp peak within the west-central region of Kananaskis Country. Cougar, red fox, and wolf showed a slight positive spatial response; while, the probability of coyote occurrence was the only spatial pattern to show a steady increase across the west-east gradient. The probability of lynx occurrence showed a slight decrease across the eastern-most coordinates. The probability of wolverine occurrence declines across a spatial gradient from within the protected areas of the National Parks complex to the more developed areas of the Kananaskis Country region. The probability of marten occurrence also decreased eastward, however; the relative magnitude of the decrease is weaker than found for wolverine. Presence-absence data used to compare spatial distribution patterns and model species-specific occurrence probabilities (Figure 3.7) are illustrated for each species across the regional study generated in ESRI ArcGIS 9.3 (Environmental Systems Research Institute 2009) (Appendix C).

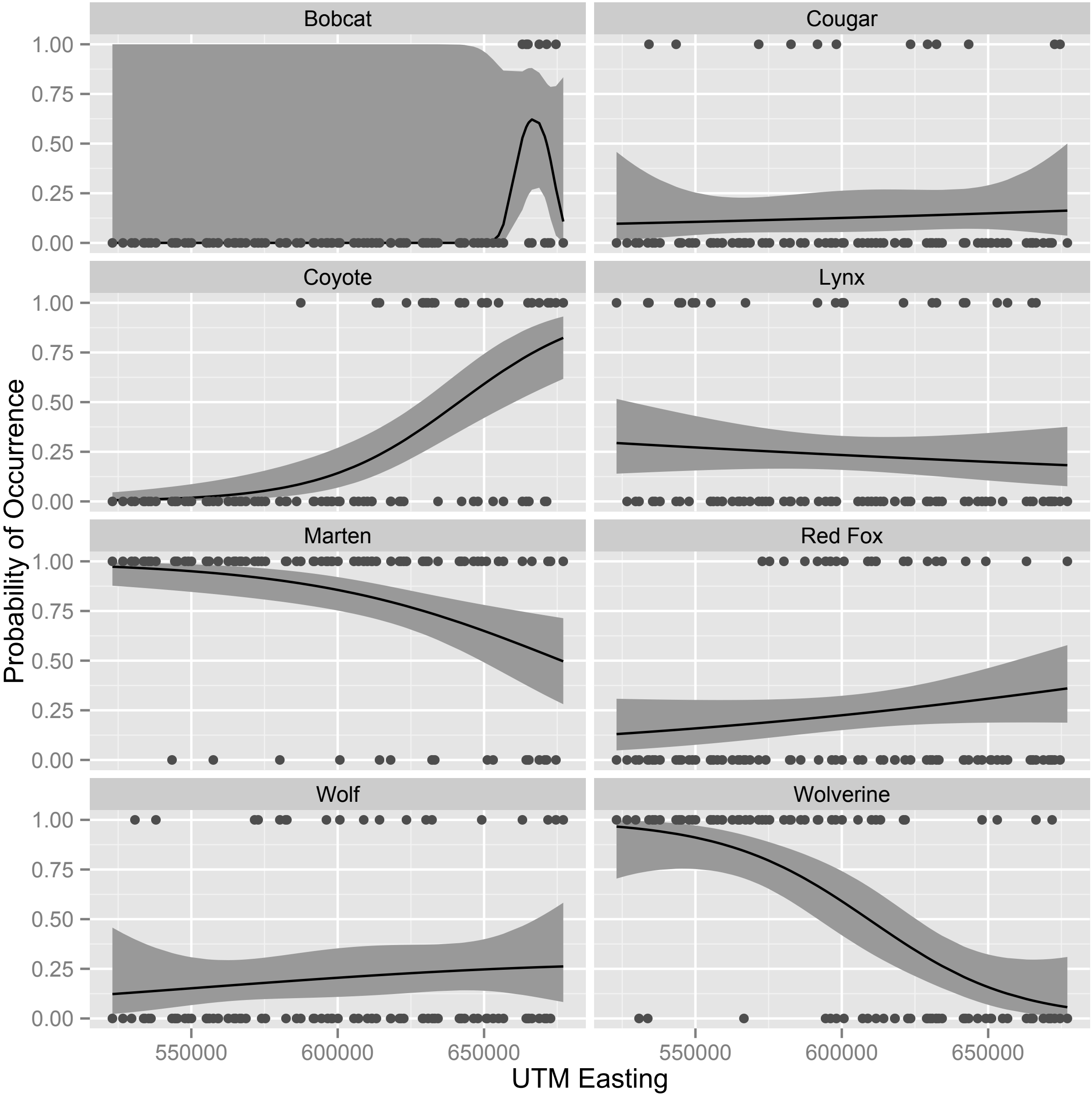


Figure 3.7 Spatial patterns of multiple carnivore occurrence probability

Compares carnivore occurrence probability for each species modeled across UTM east coordinates (Map Datum: Nad 83, Zone 11) from the west boundary of the National Parks complex to the east boundary of the Kananaskis Country region.

3.2.2 Estimating Species Occupancy across Space

Modeling Species Occupancy – After accounting for detection probability, species occupancy mirrored naïve (unadjusted) occurrence for all species except lynx and wolf (Figure 3.8). Occupancy of lynx and wolf was higher in the National Parks than in Kananaskis Country – the opposite pattern suggested by naïve occurrence rates – suggesting underestimation bias for these two species in the National Parks complex.

Most carnivore species were detected with low probability (<50%) across the study area. Though detection rates for cougar in the National Parks complex were too low to estimate occupancy, all other felid species had >50% chance of occupying an area across both study areas. Similarly, canid species had less or close to 50% chance of occupying an area, however; this did vary across space for coyote and wolf. While wolf occupancy was greatest within the National Parks complex, coyote occupancy was greatest in the more developed regions of Kananaskis Country. Marten was detected more than all other species and occupancy was greatest within the National Parks complex. The probability of wolverine to occupy an area was also greatest within the National Parks complex.

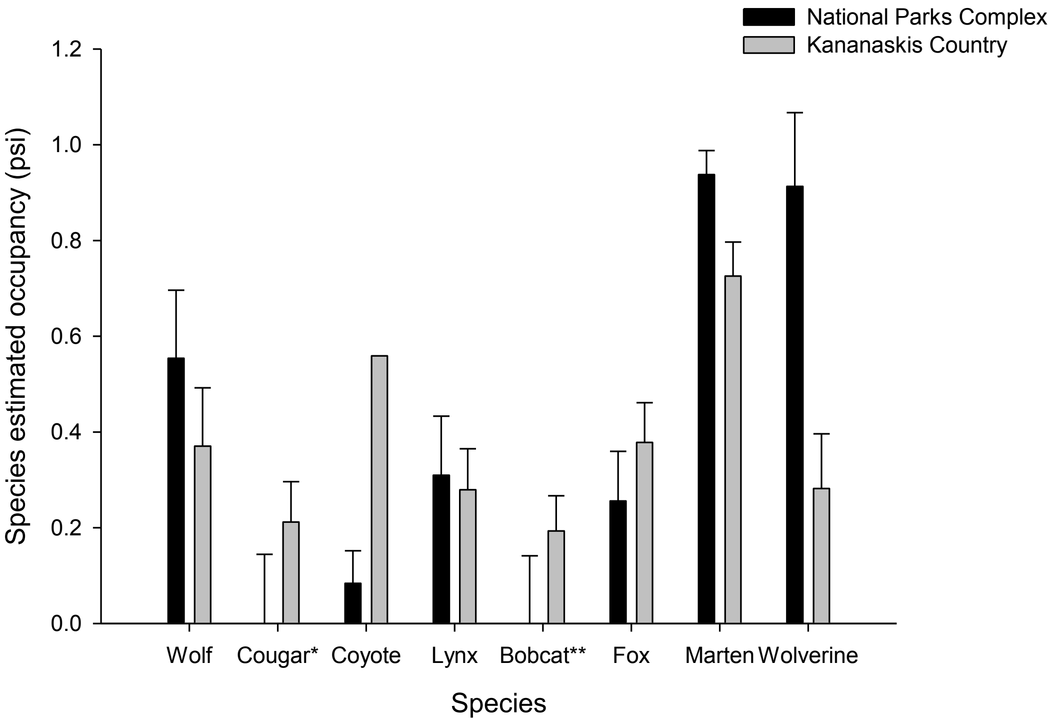


Figure 3.8 Graphs carnivore occupancy across study areas

Shows species occupancy (ψ / psi) and standard error estimates for each carnivore species across the two study areas within the regional study area. The National Parks complex is highlighted in "black" and the Kananaskis Country region is highlighted in "grey".

*Cougar occurrence counts were to low in the National Parks Complex to estimate occupancy (psi).
** Bobcat occurrence was only detected in the Kananskis Country region.

Two-species Co-occurrence – I was unable to reliably examine non-random patterns of co-occurrence using the standard or conditional two-species co-occurrence occupancy models. All models performed poorly with significantly high standard error estimates and confidence intervals. The poor model results were likely due to low detection rates used to compute occupancy parameters for both species being modeled (MacKenzie pers. comm. 2011).

3.2.3 Drivers of carnivore community occurrence patterns

Carnivore: all species ~ landscape association – The global model, which ordinated all carnivore species in relation to all biophysical and anthropogenic landscape variables, explained 49% of the total variation in the data (model no. 1, Table 3.6). Out of the total variation explained by RDA model 1 only 29.69% of the variation was explained by the constrained, or measured, landscape variables. Therefore, 70.31% of the variation in the data was explained by the unconstrained, or unmeasured, variables not included in this comprehensive model. The first two axes of the RDA model 1, expressed 59.67% and 14.01% of the total variation, respectively.

When examining for relationships using the point-vector bi-plots, most carnivore species were relatively clustered in ordination space along RDA axis 1 in relation to a combination of biophysical and anthropogenic explanatory variables (Figure 3.9), but with poor strength of association (adj. $r^2 = 0.178$, Pr(>F) = 0.005) (Table 3.6). However, wolverine and coyote were distinctly separated in ordination space and responding most dissimilarly to explanatory variables. Wolverine was situated on the far left side, or negative end, of RDA axis 1 and most closely associated to three landcover types. Opposite to wolverine, coyote was situated on the positive side of RDA axis 1 and was strongly associated to linear industrial features. Similar to wolverine, marten was isolated in their response to explanatory variables and disassociated from all human footprint features.

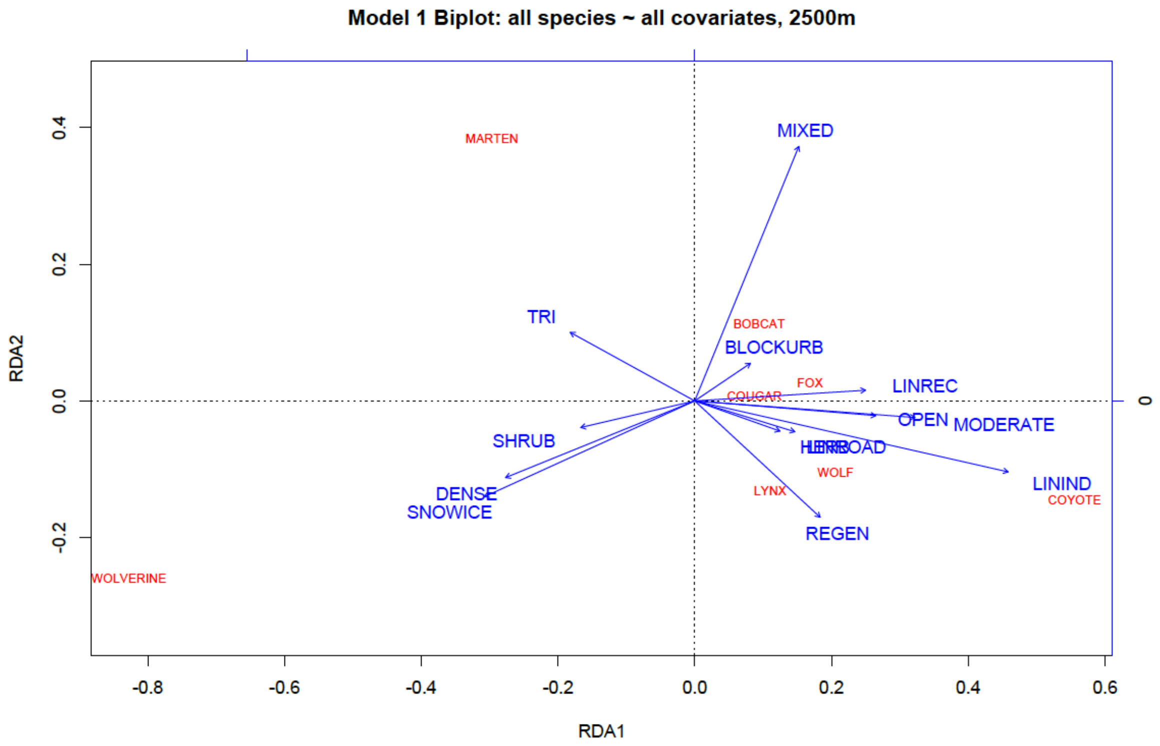


Figure 3.9 RDA biplot of all species modeled with all explanatory variables

Point vector biplot graphically represents the scaling of all carnivore species occurrence (response matrix) in ordination space in relation to all of the landscape variables (explanatory matrix) measured at the 2,500m scale. For interpretation, correlation strength is indicated by the length of the arrows and angle of vectors relative to the axes.

Strength of association among species and in relation to explanatory variables did not improve significantly when reducing model complexity, separating biophysical and anthropogenic explanatory variables across models 2 and 3 (Table 3.6). In model 2, only a few of all carnivore species clustered in relation to anthropogenic landscape features while a high degree of separation was shown among all others. In model 3, no clustering was found for any of the carnivore species in relation to biophysical landscape features. Though the pattern of species assemblages shifted slightly across these reduced models, the loading patterns of wolverine and coyote remained on opposite ends in ordination space and along RDA 1. Similarly, wolverine and marten remained uniquely dissimilar in their association among the carnivore community and in response to both the biophysical and anthropogenic explanatory variables.

Carnivore: by sensitivity ~ anthropogenic landscape association – The amount of variation explained and the strength of species associations decreased when reducing both the number of response variables according to their predicted sensitivity and tolerance to anthropogenic explanatory variables (Table 3.6). No strong clustering of species was found in either model 4 or 5 when examining how different species assemblages might similarly respond to human footprint. In model 4, all sensitive species were separated in ordination space. And again, the loading pattern of wolverine and marten did not associate these species with any of the anthropogenic landscape features. In model 5, wolf and cougar were closely organized to each other in ordination space but with weak association to any of the anthropogenic explanatory variables. The loading pattern of coyote remained on the positive end of RDA axis 1 in relation to linear industrial features.

Carnivore: by body size ~ landscape association – When further examining for relationships among species grouped according to body size – a trait hypothesized to influence how species operate across large spatial scales – the greatest amount of total variation was explained (52.66%) in models 6, 8 and 10 that included a subset of large-body sized, or mega, carnivores compared with all other models tested (Table 3.6). The best model fit having significant strength of association and the greatest amount of variation explained by the constrained variables was demonstrated by model 10, which included 4 large-body sized species and biophysical explanatory variables (adj. r^2 = 0.390, Pr(>F) = 0.001) (Table 3.6). Though there was an increase in variation explained and overall model strength by the inclusion of biophysical explanatory variables, a high degree of separation and dissimilarity in response was observed among the 4 mega-species in ordination space with weak associations between all explanatory variables across all three top models (shown by model 6 biplot, Figure 3.10). However, one consistent pattern remained with wolverine and coyote on opposite ends of RDA axis 1 and coyote closely associated with linear industrial features (Figure 3.10).

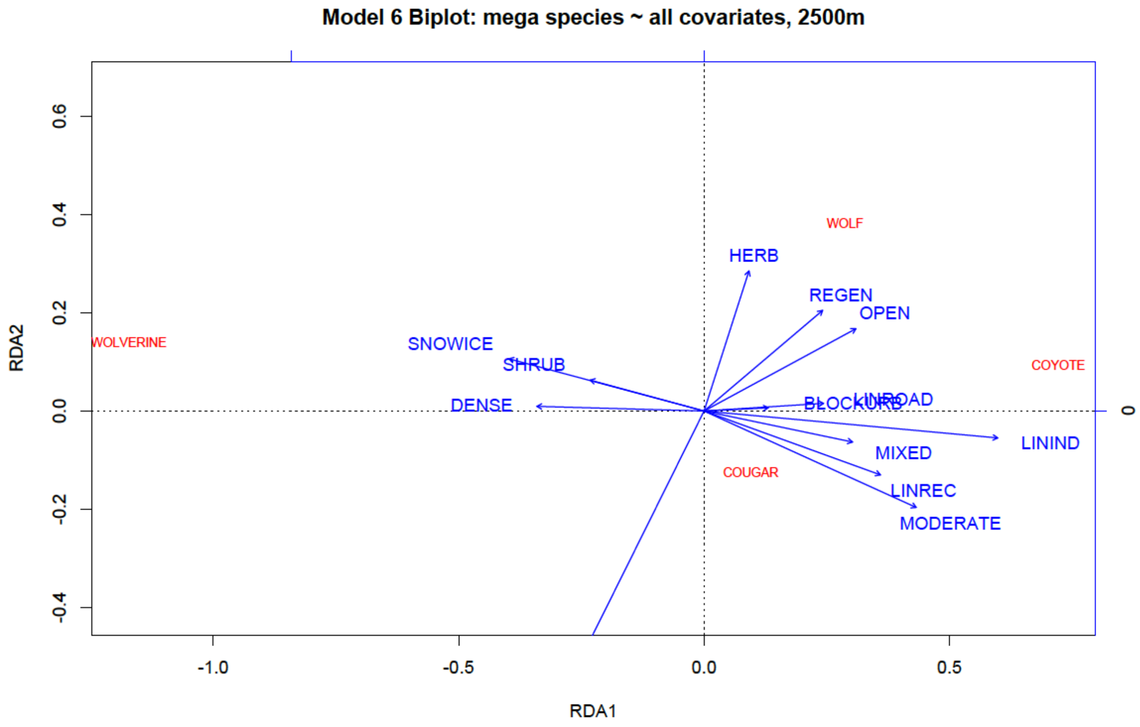


Figure 3.10 RDA biplot of large-body sized carnivores modeled with all explanatory variables

Point vector biplot graphically represents the scaling of a subset of large body sized (mega) carnivore species occurrence (response matrix) in ordination space in relation to all of the landscape variables (explanatory matrix) measured at the 2,500m scale. For interpretation, correlation strength is indicated by the length of the arrows and angle of vectors relative to the axes.

Overall, these multivariate analyses explained little variation in the response data by the constrained explanatory variables with poor model strength. Most carnivores species, regardless of their groupings, seemed to be responding dissimilarly to a variety of both biophysical and anthropogenic landscape variables. A single prevailing pattern revealed across all models tested was the high degree of dissimilarity in response between occurrence of wolverine and coyote.

Table 3.6 Summarizes all RDA model output and RDA model variation explained

Compares the amount of variation explained by each model tested using redundancy analysis using an F-statistic with a significant level of 0.001.

Model No.	Matrix Sets	No. of Var.	Total Inertia	Constrained Proportion	Unconstrained Proportion	R-Sq	R-Sq (adj)	df	F	Pr(>F)
1, global	all species + all covariates	22	0.4939	0.2969	0.7031	0.30	0.18	13	2.50	0.005
2	all species + anthropogenic	12	0.4939	0.1128	0.8872	0.11	0.07	4	2.73	0.005
3	all species + biophysical	18	0.4939	0.2777	0.7223	0.28	0.20	9	3.46	0.005
4	sensitive + anthropogenic	7	0.3183	0.0955	0.9044	0.10	0.05	4	2.27	0.015
5	tolerant + anthropogenic	9	0.4766	0.0935	0.9064	0.09	0.05	4	2.22	0.004
6	mega + all covariates	18	0.5266	0.3440	0.6560	0.34	0.23	13	3.11	0.001
7	meso + all covariates	18	0.3695	0.2305	0.7695	0.23	0.10	13	1.77	0.007
8	mega + anthropogenic	8	0.5266	0.1606	0.8394	0.16	0.12	4	4.11	0.002
9	meso + anthropogenic	8	0.3695	0.0661	0.9338	0.07	0.02	4	1.52	0.131
10*	mega + biophysical	14	0.5266	0.3879	0.6121	0.39	0.32	9	5.70	0.001
11	meso + biophysical	14	0.3695	0.1522	0.8478	0.15	0.06	9	1.62	0.033

*Model with most variation explained by constrained, or measured, explanatory variables.

3.2.4 Drivers of species-specific occurrence

There were no generalities among species response to landscape variables using a generalised linear modeling analysis (Table 3.7). Landcover features best described the probability of feline (bobcat, lynx, and cougar) and fox occurrence. The probability of wolf occurrence was best described by climate. The probability of wolverine occurrence was best described by a combination of factors. However, the landcover features retained in the best-fit models differed across these species, as did the direction and magnitude of the relationships (Table 3.8). Although coyote and marten showed similar responses to human footprint features, linear industrial features inversely described occurrence patterns for these two species. While coyote occurrence probability was positively associated to linear industrial features, marten was negatively associated to this anthropogenic landscape variable. Contrasting coyote but similar to marten, wolverine showed a strong negative association with linear industrial features. Uniquely, wolf occurrence probability was best described by persistent spring snow, with a strong negative association.

The inclusion of heterospecifics to the best-fit landscape model further improved model fit for the three felid species and marten. However, species associations with heterospecific occurrence differed among all species by the magnitude and direction of the relationships (Table 3.8), similar to those described between species and landcover features. Conversely, the addition of a heterospecific did not improve model fit among the canids (fox, coyote, or wolf). In addition, no improved fit was found when modeling lynx and cougar as heterospecifics in relation to bobcat and lynx. It is important to note that the inclusion of a heterospecific only improved model fit by ≤ 2 ΔAIC for bobcat, cougar and wolf; therefore, the relative strength of heterospecific occurrence in relation to biophysical and anthropogenic landscape variables for these three species is weak (Arnold 2010). However, consistent improved model-fit with the inclusion of a canid heterospecific suggests that the probability of large-sized canid occurrence (coyote or wolf) may be an influential variable driving a host species within the carnivore community found throughout this regional study area. Finally, there was no improved fit observed with the inclusion of prey counts to the best-fit models across all carnivores.

Table 3.7 Model support for single-species distribution models

Shows all single-species distribution model selection for each carnivore species detected within the regional study area. Models were ranked using AIC, Akaike information criterion. The best-fit model set is indicated by ΔAIC = 0 and AIC weight = 1.00. Also see section 1.2.4 (Chapter 1) for wolverine distribution model selection.

Species	**Model**	**Model Variable**	**AIC**	**ΔAIC**	**AIC (within species set)**
Fox	**Landcover**	**HERB**	**99.99**	**0.00**	**0.51**
	Topography	TRI	104.59	4.60	0.05
	Climate	SP.SNOW	104.17	4.18	0.06
	Human Footprint	LINROAD	101.92	1.93	0.19
	Landcover + Coyote	HERB + COYOTE	101.97	1.98	0.19
Coyote	Landcover	DENSE + OPEN + SHRUB + REGEN + BARE	96.04	6.28	0.03
	Topography	TRI	108.57	18.81	0.00
	Climate	SP.SNOW	97.33	7.57	0.02
	Human Footprint	**LININD**	**89.76**	**0.00**	**0.69**
	Human Footprint + Wolf	LININD + WOLF	91.72	1.96	0.26
Bobcat	Landcover	DENSE + MODERATE + SHRUB + HERB	60.93	0.58	0.37
	Topography	TRI	66.84	6.49	0.02
	Climate	SP.SNOW	65.13	4.78	0.05
	Human Footprint	LINROAD + LINREC	64.64	4.29	0.06
	Landcover + Coyote	**DENSE + MODERATE + SHRUB + HERB + COYOTE**	**60.35**	**0.00**	**0.50**
Lynx	Landcover	DENSE + MODERATE +	97.94	10.20	0.01

		HERB			
	Topography	TRI	98.97	11.23	0.00
	Climate	SP.SNOW	98.80	11.06	0.00
	Human Footprint	INTERCEPT	98.85	11.11	0.00
	Landcover + Cougar	**DENSE + MODERATE + HERB + WOLF**	**87.74**	**0.00**	**0.98**
Cougar	Landcover	DENSE + MODERATE + BARE	68.09	0.35	0.39
	Topography	TRI	74.20	6.46	0.02
	Climate	SP.SNOW	72.29	4.55	0.05
	Human Footprint	BLOCKURB	71.43	3.69	0.07
	Landcover + Wolf	**DENSE + MODERATE + BARE + WOLF**	**67.74**	**0.00**	**0.47**
Wolf	Landcover	BARE	94.51	14.51	0.00
	Topography	TRI	85.01	5.01	0.06
	Climate	**SP.SNOW**	**80.00**	**0.00**	**0.68**
	Human Footprint	LININD	94.44	14.44	0.00
	Climate + Coyote	SP.SNOW + COYOTE	81.87	1.87	0.27
Marten	Landcover	DENSE + MIXED + SHRUB + BARE	84.82	9.28	0.01
	Topography	TRI	87.18	11.64	0.00
	Climate	SP.SNOW	88.63	13.09	0.00
	Human Footprint	LININD	84.27	8.73	0.01
	Human Footprint + Coyote	**LININD + COYOTE**	**75.54**	**0.00**	**0.97**

Table 3.8 Single-species model support for best-fit explanatory variables

Estimated β parameters for variables retained in the best-fit model for each carnivore species.

Species	Parameter	Estimate	SE	z-value	Pr(>IzI)
Fox	HERB	0.7821	0.3485	2.244	0.0248
Coyote	LININD	1.3838	0.3712	3.728	0.0001
Bobcat	DENSE	-0.9066	0.6559	-4.817	0.1159
	MODERATE	-0.8059	0.4321	-1.865	0.0622
	SHRUB	-0.3269	0.3703	-0.883	0.3774
	HERB	0.4897	0.3575	1.370	0.1707
	COYOTE	1.3461	0.8481	1.587	0.1125
Lynx	DENSE	0.5208	0.3446	1.511	0.1307
	MODERATE	0.7647	0.3507	2.180	0.0292
	HERB	0.6174	0.3106	1.987	0.0468
	WOLF*	-17.7901	1431.54	-0.012	0.9900
Cougar	DENSE	1.9705	0.8220	2.397	0.0165
	MODERATE	2.9262	1.0827	2.703	0.0068
	BARE	2.5282	1.0106	2.502	0.0123
	WOLF	1.2304	0.7904	1.557	0.1195
Wolf	SP.SNOW	-1.4911	0.4708	-3.167	0.0015
Marten	LININD	-0.1123	0.2726	-0.412	0.6804
	COYOTE	-2.1448	0.6752	-3.177	0.0014

*Indicates high standard error

3.3.0 Discussion

When surveying multiple carnivores across a west to east gradient of increasing human land use in a complex mountain environment, I predicted to find (1) variation in species spatial occurrence patterns and (2) similarity in response among carnivore community members in relation to anthropogenic disturbance. As predicted, carnivore detection and occurrence probability did vary among species and across space. However, the variation in response to landscape alteration – as well as biophysical features – was not uniform among members of this carnivore guild, contradicting our predictions. Instead, a significant degree of dissimilarity was found across all species and the variation in the relationship between occurrence and landscape variables was poorly explained, even after reducing model complexity. Different responses among species might be considered surprising considering the growing body of literature that describes wide-ranging terrestrial carnivores as particularly sensitive to human-caused habitat disturbance (Woodroffe 2000, Gittleman 2001, Crooks 2002, Crooks *et al.* 2011). The differential response to landscape features may be explained by ecological processes that this study was unable to explicitly examine; however, further hypotheses could be made from the spatial patterns of occurrence observed.

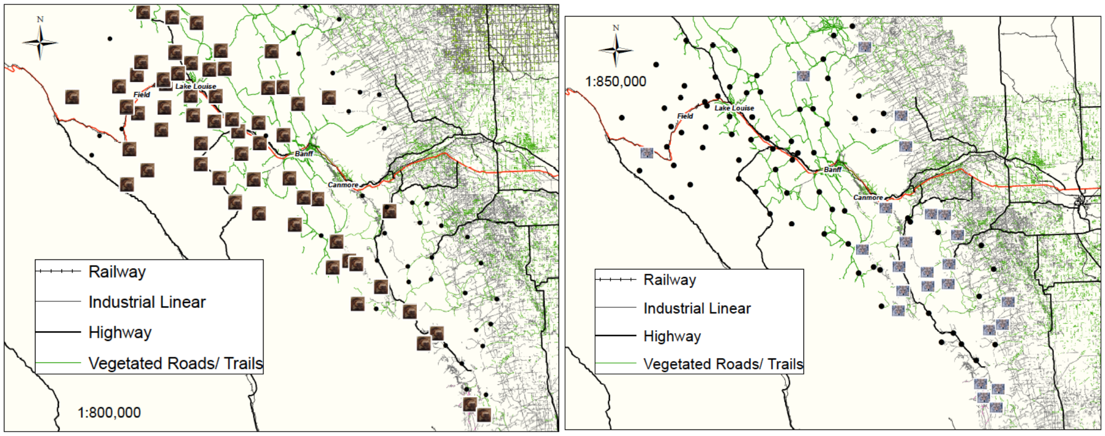
If carnivores are indeed responding dissimilarly, the varied occurrence patterns among species likely reflects differential habitat selection and space use across a naturally heterogeneous landscape found in the south-central Rocky Mountain region. Deriving from niche theory, a given species will select for a range of environments that optimize recruitment and regional persistence according to their life history traits (Fischer and Lindenmayer 2007). The range of environmental features utilized by different species defines an organism's multi-dimensional niche space (Grinnell 1917) and these different requirements permit spatial co-existence among potential competitors (Hardin 1960). Therefore, the persistence of a diverse suite of carnivores detected throughout this study area suggests spatial competitive co-existence – an ecological process requiring species to differ in their response to the environment (Linnell and Strand 2000, Amarasekare 2003). Where habitat condition for these mobile carnivores is altered by stochastic or anthropogenic events, modification of space use can occur to maximize foraging opportunity while minimizing risk (Elith and Leathwick 2009, Kolowski and

Holekamp 2009). Altered space use resulting from habitat disturbance and increased interspecific competition can further constrain a species realized niche space (Crooks 2002, Crooks *et al.* 2011); thus, influencing individual occurrence patterns and the extent of local and regional population-level distribution.

An alternative hypothesis is that carnivores persisting in the central region of the Canadian Rocky Mountains are responding as predicted to anthropogenic landscape alteration; however, species response to disturbance have yet to be expressed sufficiently to be detected by occurrence patterns at a large spatial scale. Mounting evidence suggests the threats of habitat loss and degradation on local communities often go unrecognized or are underestimated due to a temporal lag in population-level effects, or extinction debt (Hanski and Ovaskainen 2002, Kuussaari *et al.* 2009). Extinction debt is the time taken for a community of species to reach a new equilibrium after an environmental disturbance, a debt that is gradually paid over time as local extinctions are realized (Tilman *et al.* 1994)

Though empirical studies are lacking, our current knowledge suggests that long-lived species with low extinction and colonization rates – such as terrestrial carnivores – are more likely to experience delayed effects of recent disturbance, effects difficult to detect over short periods of time (Kuussaari *et al.* 2009). The delay in effects extend beyond just carnivores and have been observed at other trophic levels; for example, Vellend (2006) found extinction debt in some forest plants to persist for more than a century after forest fragmentation (Vellend *et al.* 2006). Since prolific landscape alteration occurring along Alberta's eastern slopes is relatively recent and ongoing, our challenge in uncovering similarity in response among carnivores may therefore be rooted in time and within the basic principles of extinction debt theory. Over a period of only 12 years (2000-2012), 6.8% of the forest cover was lost to expanding industrialized land use practices along the Foothills Natural Subregions of Alberta (Global Forest Watch Canada 2014). The rapid pace of industrialized disturbance in this region may trigger the predicted responses by the carnivore community and realized over the coming decades, a type of response that is not yet detected in this system. However, early indication of such insidious effects from increasing human footprint was revealed when I examined spatial occurrence patterns of two species, wolverine and coyote.

While wolverine occurrence patterns declined towards the more human-altered areas along Alberta's eastern slopes, coyote occurrence increased in the areas altered by extensive linear industrial features (Figure 3.11). A notable and consistent dissimilarity in response to biophysical and anthropogenic landscape features was observed between these two species. My research supports evidence that wolverine negatively respond to increasing human land use activities (May *et al.* 2006, Krebs *et al.* 2007, Fisher *et al.* 2013); and conversely, coyote positively respond to human altered landscapes (Atwood *et al.* 2004, Gehrt *et al.* 2009, Cove *et al.* 2012, Šálek *et al.* 2014). The differential response to landscape alteration may depend on these species relative ability to adapt to the habitat change according to the range of their niche requirements (Weaver et al. 1996, Crooks 2002, Rauset *et al.* 2012). Using several hundred spatial replicates from the French Breeding Bird Survey, Devictor *et al.* (2008) found woodland birds with less specialized (or generalist) habitat requirements to respond positively to human-caused habitat disturbance and were distributed more evenly and in greater densities across altered landscapes (Devictor *et al.* 2008). Following spatial competition theory, as more generalist species better adapted to habitat change expand their distribution patterns and increase in relative density, increased interspecific interactions are likely to exaggerate the adverse effects of habitat disturbance for some species within the carnivore community (Amarasekare 2003). We might therefore infer that the negative relationship observed between wolverine and coyote is an indirect effect of landscape alteration, an effect limiting wolverine distribution to the more undisturbed areas and favouring coyote distribution with human expansion.



Panel A. **Panel B.**

Figure 3.11 Contrasts spatial patterns of occurrence between wolverine and coyote

Contrasts the spatial pattern of occurrence, or detection, of wolverine (Panel A) and coyote (Panel B) in relation to linear features (railway, road, highway, and vegetation roads and trails) generated in ESRI ArcGIS 9.3 (Environmental Systems Research Institute 2009).

Though still poorly understood, increased rates of coyote occurrence and relative abundance in human dominated landscapes have been attributed to their generalist characteristics that include flexibility to exploit diverse habitat types and food items as well as to occupy various home range sizes within disjunct, or fragmented, habitat patches (Riley *et al.* 2003, Atwood *et al.* 2004, Gehrt 2007, Gehrt *et al.* 2009). Human-altered landscapes are also known to positively influence coyote densities by indirectly mediating interference competition where wolves – being the apex predator – are reduced or eliminated (Arjo and Pletscher 1999, Hebblewhite *et al.* 2005, Berger and Gese 2007). The role of the apex predator in a community can be defined by its position at or near the top of the food web (Sergio *et al.* 2014), limiting population abundance of smaller 'meso-predators' through competitive intra-guild interactions (Ritchie and Johnson 2009). Liberation of meso-predators from interference interactions through the reduction or removal of a top predator can be explained by the "meso-predator release hypothesis" (Litvaitis and Villafuerte 1996, Crooks and Soulé 1999, Gehrt and Clark 2003, Prugh *et al.* 2009). In relatively undisturbed areas where wolf and coyote home ranges overlap, large scale spatial and temporal segregation of these species allows for coexistence (Arjo and Pletscher 1999, Newsome and Ripple 2014) with depressed coyote densities in areas of high wolf presence due to increased vigilance, decreased rest, and a higher risk of direct predation (Switalski 2003). In this case, a weakened effect of top-down control by coyote can occur where wolves are sporadically distributed (Newsome and Ripple 2014).

Spatial patterns of canid occurrence in our study suggest the latter, with wolves occurring sporadically across the regional study area and some spatial overlap existing between coyote and fox occurrence (Appendix C). The degree of spatial overlap among the medium and large-sized members within this community suggests the presence of competitive co-existence; however, the increasing trend in coyote occurrence towards the more human-altered landscapes leads us to assume that this community may be experiencing early stage cascade effects of meso-predator release. If my predictions are correct, the carnivore community along the eastern slopes of Alberta's Rocky Mountains may be experiencing a temporal lag of distribution scale effects. As human land use activities expand over space and time, we might then expect to find the indirect effects of human footprint to amplify interspecific interactions therefore further reducing suitable habitat along current range boundaries for some large carnivores, especially the more sensitive species such as wolverine.

3.4.0 Caveats

Though my methods successfully detected the full compliment of carnivores persisting in the central region of the Canadian Rocky Mountains and described spatial patterns of occurrence across individual species, inherent challenges arose in revealing similarities among community members in relation to biophysical and anthropogenic landscape factors. These challenges are often faced by landscape ecologists when investigating the naturally complex and interacting landscape effects on species (Didham *et al.* 2012, Betts *et al.* 2014), including issues of scale and the use of single- versus multi-species approach to study design. The difference in detection probability among species that I observed may be a product of the use of a single spatial scale of investigation, a species-specific sampling scheme, or simply reflect the intrinsic natural variation in species relative abundance (Royle 2006).

Following recommendations by Levin (1992), this study selected a large spatial scale to match the landscape-level human disturbance that may be influencing ecological processes for mobile carnivores. With no single known spatial scale at which to test responses of multiple species in relation to landscape factors, I modelled species occurrence with landscape covariates at a single spatial scale (2500m) that encompassed the range of spatial extents that influence habitat selection of members within this carnivore community by Fisher *et al.* (2011). Within the range of spatial extents of habitat selection, Fisher *et. al* (2011) also related variation in species-specific scales of habitat selection to body size and cautioned the risk of flawed inferences and conclusions using scales that do not reflect a species-specific scale of response to landscape structure. To account for variation in habitat selection according to body size, I modeled subsets of carnivore assemblages according to medium and large sized carnivores.

To meet the objectives of this study we used a single-species approach to study design, with wolverine as a proxy for surveying multiple large-ranging carnivore species. Betts *et al.* (2014) argue that uncovering cross-species generalities in relation to human disturbance, such as habitat loss and fragmentation, must consider a more “species-centered approach” to distribution modelling that accounts for the different ways species perceive and respond to abiotic and biotic factors. Finding from this study suggest that uncovering generalities in response to human disturbance may require either the inclusion of differential niche requirements or long-term monitoring strategies that consider temporal lags and extinction debt.

3.5.0 Interpreting non-uniform responses to habitat disturbance

Habitat disturbance is accepted as the primary threat to biological diversity across taxonomic communities worldwide (Ewers *et al.* 2010), and therefore general response to increasing human landscape alteration across a guild of carnivore species is a logical prediction. However, the combination of species biological variability and landscape complexity makes a strong argument against a uniform community-level response (Didham *et al.* 2012). The lack of a uniform response observed among species detected in our study, despite the exhaustive analytic techniques applied, supports this argument. Consistent dissimilarity in spatial occurrence patterns and associations to landscape features between wolverine and coyote further imply that the direct and indirect effects of pervasive human-caused landscape alteration may be differentially shaping habitat condition that is beneficial for, or tolerated by, some species and detrimental for others. However, the context and magnitude of change may differ among species, leading to changes in where these species occur in the landscape, and in their relative densities.

In the case of coyote, the geographic range has expanded significantly north-east across the United States and Canada with increasing human settlement and land use activities (Gompper 2002). Therefore, the increasing spatial patterns of this species found along the more altered landscapes suggests this region along Alberta's eastern slopes region may be on the leading edge of a pre-existing phenomenon of meso-predator release. Attention to the severity of lag effects resulting from habitat disturbance on carnivore communities might prevent local extinction of the more sensitive species before the debt is realized and local population diversity is beyond a state of recovery.

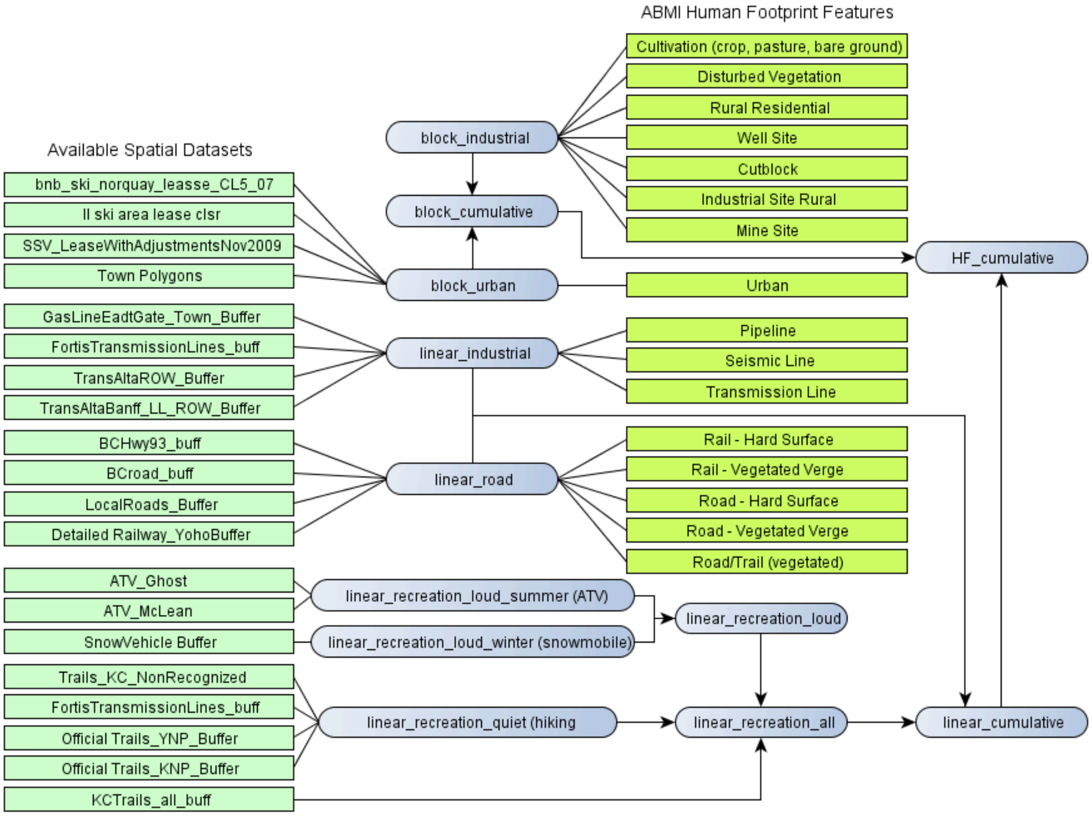
APPENDIX A

Lists and describes the Two-Species Co-occurrence occupancy parameters defined by Hines (2006).

Type	Parameter	Description
Standard	ψA	probability that the area is occupied by species A
	ψB	probability that the area is occupied by species B
	φ	species co-occurrence (ψAB/(ψA*ψB)), (ψAB=probability that area is occupied by both species)
	pA	probability of detecting species A, given species B is not present
	pB	probability of detecting species B, given species A is not present
	rA	probability of detecting species A, given both are present
	rB	probability of detecting species B, given both are present
	λ	species co-detection (rAB/(rA*rB)), (rAB=probability of detecting both species, given both are present)
Conditional	ψA	probability that the area is occupied by species A
	ψBA	probability that the area is occupied by species B, given species A is present
	ψBa	probability that the area is occupied by species B, given species A is not present
	pA	probability of detecting species A, given species B is not present
	pB	probability of detecting species B, given species A is not present
	rA	probability of detecting species A, given both are present
	rBA	probability of detecting species B, given both species are present, and species A was detected
	rBa	Probability of detected species B, given both are present, and species A was not detected.

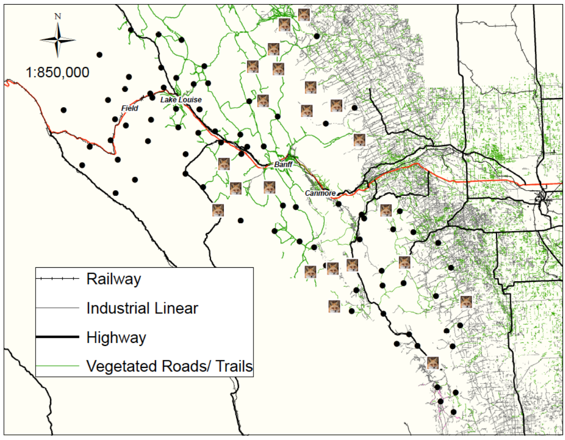
APPENDIX B

Flow chart (Kent Richardson, Alberta Innovates – Technology Futures) shows the data input used to create 12 human footprint categories hypothesized to influence wolverine occurrence by merging available spatial datasets and ABMI human footprint Features dataset in ESRI ArcGIS 9.3.

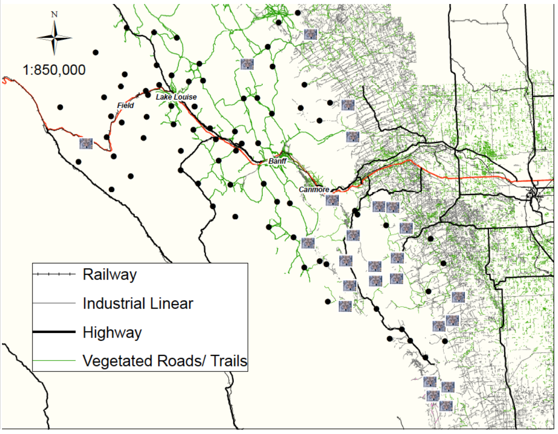


APPENDIX C

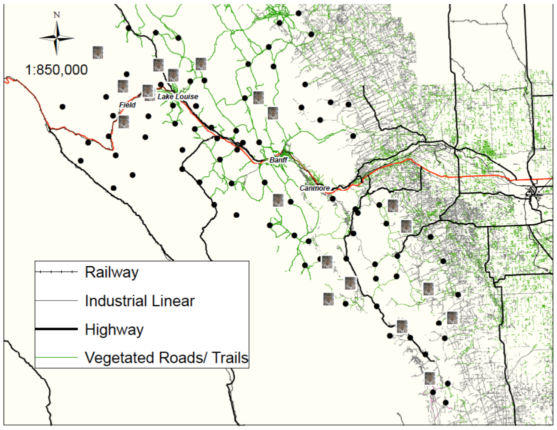
Shows the variation in spatial distribution species presence-absence across the eight carnivore species detected throughout the central region of the Canadian Rocky Mountains.



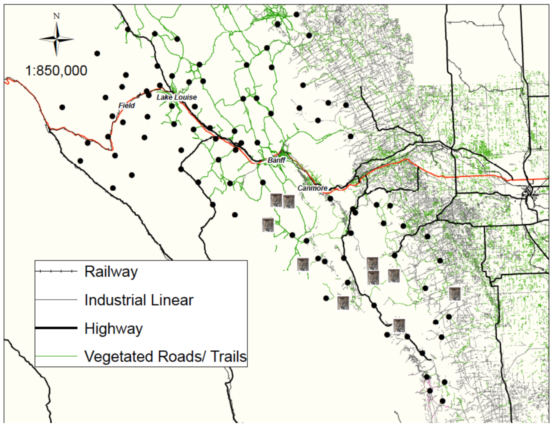
Coyote



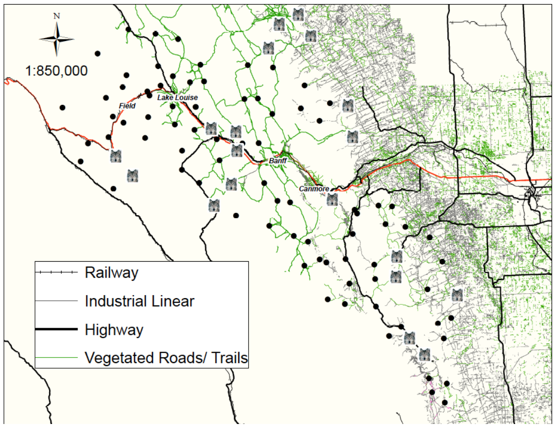
Fox



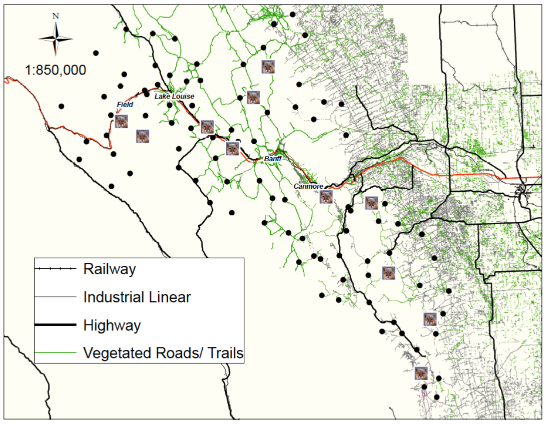
Lynx



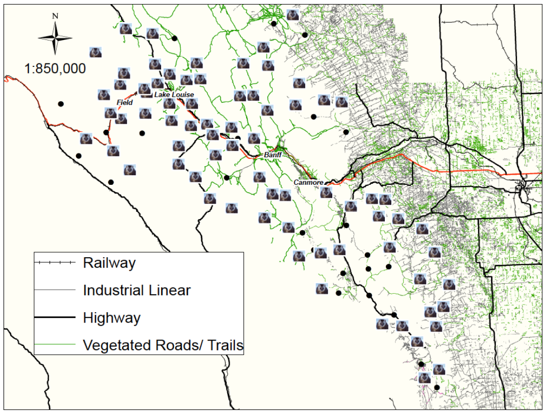
Bobcat



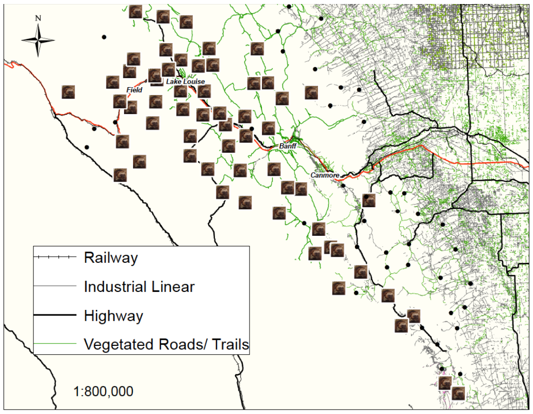
Wolf



Cougar



Marten



Wolverine

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Chapter 4: Present Conclusions and Future Implications – Competitive Co-existence in Human-Altered Landscapes?

Through top-down processes carnivores are recognized within the scientific community as species with the potential to influence ecological systems in disproportionate ways relative to their body mass (Estes *et al.* 1998, 2011, Post *et al.* 1999, Myers *et al.* 2007). Despite this recognition, terrestrial carnivores worldwide remain some of the most vulnerable species to impacts of human-caused landscape change (Ripple *et al.* 2014). Though conservation biologists are striving to better understand how changes to landscape structure and abiotic conditions influence individual carnivore species, there remains an under-appreciation of the other key biological components occurring at the community level (Linnell and Strand 2000), such as intra-guild interactions. Non-random effects of competitive interactions on co-occurrence patterns within carnivore guilds is a widespread and highly influential phenomenon more recently documented in empirical studies (Palomares and Caro 1999, Gotelli and McCabe 2002, Caro and Stoner 2003, Amarasekare 2003). For example, as an apex predator wolves can have a profound effect on other members within a canid community (Peterson 1995), limiting coyote and in turn altering fox density through competition (Hebblewhite et al. 2005, Berger and Gese 2007, Newsome and Ripple 2014). Therefore, changes to one species through human-caused habitat change can have a cascading effect on other members within carnivore communities (Hebblewhite *et al.* 2005, Prugh *et al.* 2009, Estes *et al.* 2011).

While there is growing interest to explore the role of interspecific interactions occurring within carnivore communities, the inherent difficulty and a reliance on single-species methods, notably telemetry, in studying large carnivores has often limited ecologists to intensive sampling efforts with a single-species focus (e.g. Nielsen *et al.* 2006). Focal species expected to respond more adversely to human activity are selected as ecological indicators to investigate landscape-scale impacts of human disturbance (Noss *et al.* 1996, Power *et al.* 1996, Carroll *et al.* 2001). If interspecific interactions are indeed a significant factor driving carnivore occurrence, simultaneous study of multiple co-occurring species will be more likely to inform ecological theory on the complex spectrum of influential factors driving spatial co-existence for carnivores in human-altered landscapes (Amarasekare 2003).

When examining survey results of a focal carnivore species selected for this study – the wolverine – I revealed a declining spatial pattern of occurrence in relation to increasing human land use activity and landscape alteration. Over the past few decades, literature has shown wolverine to be adversely affected by human activity and landscape alteration (May *et al.* 2006, Krebs *et al.* 2007, Fisher *et al.* 2013), supporting my results. In particular, wolverine occurrence in my study was negatively associated with linear industrial features, mirroring the same negative relationship found for wolverines north of our study area (Fisher *et al.* 2013). Since industrial development has been linked to significant habitat change along Alberta's eastern slopes (Global Forest Watch Canada 2014), this pervasive and declining spatial pattern of occurrence in relation to increasing density of industrialized landscape alteration may not be surprising.

Also supporting literature from the northern United States, I identified persistent spring snow cover as an important factor influencing wolverine occurrence. However, contrasting single-factor climate-focused predictions that suggest wolverine distribution is limited by deep snow packs (Copeland *et al.* 2010, Inman *et al.* 2012), wolverines in the central region of the Canadian Rocky Mountains appear to be driven by the cumulative effects of multiple and interacting abiotic and biotic factors. Included in these cumulative effects were human footprint, landcover, climate, and the occurrence of meso-canids – with a strong negative association between wolverine and coyote. While our current understanding of wolverine ecology supports associations found between the anthropogenic and abiotic factors, the biotic association between wolverine and meso-canids was unexpected. A seemingly sympatric but segregated spatial pattern of occurrence observed between wolverine and coyote led me to infer that human-caused changes to habitat condition are increasing competitive interactions and may be influencing this negative relationship in areas subject to increased human disturbance. Though it is difficult to explicitly detect for competitive interactions using species occurrence data (Hastings 1987), the biology of these two species and their known differential responses to human impacted environments made a strong case to support these inferences. The signal found relating wolverine occurrence with the presence or absence of a heterospecific (coyote and fox), led me to ask if this was consistent throughout the carnivore community, and whether there is a similarity in response among multiple carnivore species to anthropogenic landscape features throughout the south-central region of the Canadian Rocky Mountains.

Across all eight carnivores detected, occurrence patterns varied between individual species, across space, and in relation to biophysical and anthropogenic landscape factors. In contrast to my predictions, I was unable to reveal a uniform response among multi-species carnivore occurrence along a gradient of human landscape alteration. The variation in occurrence patterns and non-uniform response might be attributed to the natural variation in species habitat selection and differential abilities to adapt to human-altered landscapes (Crooks 2002, Crooks *et al.* 2011, Rauset *et al.* 2012). For example, I found a consistent and distinct dissimilarity in response between wolverine and coyote, two species known to respond inversely to human disturbance (Krebs *et al.* 2007, Fisher *et al.* 2013, Šálek *et al.* 2014). Alternatively, we might predict the dissimilarity in response by wolverine and coyote represents early stages of a broader trend leading to shifting carnivore community composition over time. If so, generality in response across the carnivore guild under investigation may be difficult to detect at this stage due to a delay in response, or temporal lag, to landscape-scale habitat disturbance. More simply, it may be too early to see the effects of recent and rapid human disturbance on most species.

At present, the diverse suite of carnivores detected throughout the regional study area suggests these species are co-existing at the large landscape-scale in the central Rocky Mountains (Linnell and Strand 2000). However, evidence of spatial segregation was particularly evident for two of these species – wolverine and coyote – with strong dissimilarity in occurrence patterns and response to human land-use features. Though competitive co-existence requires species to differ in their response to the environment (Amarasekare 2003), changes to that environment resulting in increased interspecific interactions can undermine the spatial mechanisms that allow for co-existence (Murrell and Law 2003, Soulé *et al.* 2003). Thus, the ongoing and prolific human land use practices occurring along Alberta's eastern slopes may be directly shaping occurrence patterns through changes to habitat condition as well as indirectly shifting mechanisms driving spatial co-existence, encouraging competitive exclusion for some species more than others.

Taken together, my findings emphasize the importance of incorporating a community-level approach to understanding the full suite of ecological mechanisms driving spatial patterns of individual and multiple carnivore species. It also extends caution to managers that effects of rapid and extensive human-caused landscape change may be slow to realize for some species and stresses the need for large-scale and long-term monitoring programs to effectively understand and mitigate local and regional population declines. Conclusions from this research are best summed by paraphrasing a statement made by Ewers and Didham (2006); *"human-caused changes to our environment occurring across large spatial scales is a recent phenomenon in evolutionary time and the long-term impacts of these changes may not yet be shown themselves."*

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