The relative impacts of recreational activity and landscape protection on a Rocky Mountain mammal community

by

Laura Eliuk
BSc. Hons., University of Manitoba, 2018

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

MASTERS OF SCIENCE

in the School of Environmental Studies

University of Victoria

Supervisory Committee

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Abstract

Modern human expansion and landscape development has substantially restructured natural landscapes with cascading impacts on biodiversity, resulting in population declines and range contractions in many North American large mammal species. While conservation efforts through the establishment of protected areas (PA) mitigate stressors to wildlife by preventing further landscape disturbance, mammals are still impacted by high human use within PA, and ongoing landscape development outside PA boundaries. Comprised of a network of PA and unprotected areas, Canada's Rocky Mountains provide important habitat to a rich mammal community. The Rocky Mountains also support a range of human uses, including industrial development creating ongoing landscape disturbance, and recreational use of landscape features such as trails and roads. The relative importance of PAs in supporting mammal populations, as well as the relative impacts of recreational landscape use to mammals, are not well understood. In this thesis, I used wildlife camera arrays to investigate the relative impacts of recreation and landscape protection on a Rocky Mountain mammal community, assessing distributions of six species: wolves, grizzly bears, coyote, black bears, white-tailed deer, and mule deer. I chose to assess multiple species as species are expected to respond differently to disturbance, with wolves and grizzly bears being disturbance-sensitive while coyotes and white-tailed deer are more disturbance-tolerant. In my second chapter, within an unprotected region, I investigated whether motorized recreation influenced mammal distributions, weighing its importance against landscape disturbance, and natural landscape features. I found that wolves avoided areas of high motorized use; coyote, white-tailed deer, and grizzly bears were better explained by landscape disturbance features, and black bears and mule deer were best explained by natural landscape features. Recreational use can cause spatial displacement of wildlife, with the effect being constrained to more disturbance-sensitive species such as wolves. These results have important implications in managing habitat for disturbance sensitive species, but also emphasize the importance of minimizing and restoring ongoing landscape disturbance, as disturbance facilitates recreational use, and ultimately has a larger impact on the greater mammal community. In my third chapter, I investigated whether protected areas outweigh natural or anthropogenic landscape features in explaining species occurrence, across a range of PA and unprotected areas in the Rocky Mountains. I found that PAs best explained the occurrence of four out of six species:

wolves, grizzly bears, coyote, and mule deer. Wolves, grizzly bears, and mule deer had positive associations with PAs, while coyotes had negative associations. Black bears, white-tailed deer, and mammal diversity were best explained by anthropogenic landscape disturbance. These results underscore the importance of PAs in providing habitat for disturbance-sensitive predators, and demonstrate that anthropogenic landscape management and alteration are the driving factors determining species occurrence. This research has important implications for future landscape management. For disturbance-sensitive species, such as wolves, limiting the extent of motorized recreation is important; on a broader scale, the establishment of PAs is important for providing habitat for disturbance-sensitive top predator species, and ultimately reducing ongoing landscape alteration and restoring habitat is essential to mitigate ongoing impacts to mammal communities.

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Acknowledgments

It takes a village to make a thesis happen, and I am incredibly grateful for mine.

Thank you to my supervisors, Dr. Jason Fisher, and Dr. Eric Higgs, for the support, encouragement, and guidance throughout this process. Jake, thank you for believing in me from start to finish, especially when I couldn't believe in myself. Thank you for finding the right words to encourage me when stuck, supporting me through the ups and downs, and providing me with a world of opportunity on which to build the foundational skills and experiences that will carry me through my career.

Thank you to the ACME lab members past and present – Katie, Macgregor, Nicole, Sandra, Alina, Andrew L., Andrew B., Brianna, Becca, Sydney, Persia, Lilli – for all the discussions, R code, fieldwork trips, encouragement, support, and friendship. Thank you to Sandra for making my Bighorn dreams come true and being the greatest field partner I could ask for. Thank you to Nicole for helping with my trail cameras and commiserating with me through the writing process. Thank you to Andrew L. for helping with trail cameras, and for guiding and reassuring me through every step of data analysis. Thank you, Katie and Macgregor, for the companionship, affirmations, and laughs.

Thank you to my friends, at UVic and beyond, for making Victoria my home. Thank you especially to Maya and Ellyne, I am beyond lucky to have friends like you.

Thank you to my research partners in the Alberta Government and ABMI for facilitating and supporting my work, and teaching me about camera trapping. Thank you to Banff and Jasper Parks Canada staff for sharing data which made my research possible. Thank you to Hilary, Aerin, and the Yellowstone to Yukon Conservation Initiative's Alberta Team for welcoming me on as an intern and teaching me about landscape conservation.

For allowing me to commit full time to my research, I thank the University of Victoria, NSERC, MITACS, and the Canadian Mountain Network for financial support.

Finally, thank you to my family for the unconditional love and support. Mom and Dad, I couldn't do it without you; thank you for always being a phone call away, through every crisis and celebration. Thank you, Sam, for being my big brother and sharing my love for the wild. Thank you, Fred, for always putting a smile on my face. Thank you all for lifting me up and encouraging me to follow my dreams.

Dedication

To the love of the natural world and its wonders that inspires us to do this work:

"I've stood in some mighty-mouthed hollow
That's plumb-full of hush to the brim;
I've watched the big, husky sun wallow
In crimson and gold, and grow dim,
Till the moon set the pearly peaks gleaming,
And the stars tumbled out, neck and crop;
And I've thought that I surely was dreaming,
With the peace o' the world piled on top.

The summer—no sweeter was ever;
The sunshiny woods all athrill;
The grayling aleap in the river,
The bighorn asleep on the hill.
The strong life that never knows harness;
The wilds where the caribou call;
The freshness, the freedom, the farness—
O God! how I'm stuck on it all.

The winter! the brightness that blinds you,
The white land locked tight as a drum,
The cold fear that follows and finds you,
The silence that bludgeons you dumb.
The snows that are older than history,
The woods where the weird shadows slant;
The stillness, the moonlight, the mystery,
I've bade 'em good-by—but I can't.

There's a land where the mountains are nameless,
And the rivers all run God knows where;
There are lives that are erring and aimless,
And deaths that just hang by a hair;
There are hardships that nobody reckons;
There are valleys unpeopled and still;
There's a land—oh, it beckons and beckons,
And I want to go back—and I will."

- From "The Spell of the Yukon" by Robert Service

Chapter 1: Landscape change and large mammal species persistence in North America

One of the best-known conservation stories in North America is that of the North American Plains Bison (*Bison bison bison*). Once numbering upwards of 30 million animals ranging throughout North America, there are currently about 1500 wild bison in Canada in disjunct herds (Government of Canada, 2021). Though direct exploitation in the service of settlement and colonization caused initial numbers to plummet, landscape conversion for the purposes of urbanization, agriculture, and industry has and will continue to prevent bison from returning to much of their range. I began my career in wildlife ecology working in Prince Albert National Park, SK, which houses one of the only remaining free-ranging plains bison herds. Even within a large national park, this population faced issues. The Park had lost much of its grassland coverage to woody encroachment, reducing forage available to bison. The herd would leave the park to forage on agricultural lands, causing human-wildlife conflict issues and mortality. Park staff constructed electric fences to keep the herd within park boundaries, but the bison trampled these within a couple of months of their construction. A few years after I worked in this Park, a massive fire ripped through much of the herd's range, further complicating issues with their habitat. This experience shaped my thinking around wildlife conservation and restoration, ultimately leading me to pursue a master's thesis project studying how anthropogenic influences shape large mammal distributions. I was struck by how substantially we had altered the landscape from one that was suitable to bison, and how few tools we had to help this large, broad ranging animal persist on the modern landscape.

Bison are not a unique species in their story of population decline. Anthropogenic disturbance has modified over half of terrestrial land on earth, with cascading impacts on biodiversity (Williams et al., 2020). Large mammals in particular may require relatively large areas of relatively undisturbed habitat, and many species have faced population declines and range contractions in a rapidly changing world (Laliberte & Ripple, 2004). Within Canada, caribou herds in Alberta and BC have gone extinct or nearly so due to ongoing industrial threats (Hebblewhite, 2017), and predator species such as wolverine or grizzly bears have greatly reduced their ranges, persisting in low-disturbance northern and mountainous areas (Heim et al., 2017; Ripple et al., 2014; Sorensen et al., 2015). Conversely, select disturbance-tolerant species have experienced range expansions with changing landscapes. Coyotes have expanded their range around 40% since the 1950s, and white-tailed deer have expanded into northern boreal environments beyond their historic range, following forage subsidies on regenerating anthropogenic disturbance features, and milder winters under climate change (Fisher et al., 2020; Hody & Kays, 2018; Laliberte & Ripple, 2004; Latham et al., 2011).

Although anthropogenic drivers of landscape change are ongoing, there have also been measures to mitigate disturbance and preserve biodiversity. Almost fifteen percent of terrestrial land on earth is classified as protected areas, landscapes managed to preserve natural habitats for ecological integrity and human enjoyment (Maxwell et al., 2020). These areas are crucial in maintaining species biodiversity, and protecting species that are highly sensitive to human disturbance (Coetzee et al., 2014; Gaston et al., 2008). However, there are still issues with species conservation in protected areas. Many see high levels of human use, with potential negative effects on wildlife, or may not effectively conserve habitat for all species (Rogala et al., 2011; Watson et al., 2014; Wiersma & Nudds, 2009). Large mammals have still faced extinction risk within and around protected area boundaries (Hebblewhite et al., 2010; Parks & Harcourt, 2002).

The Rocky Mountains of western North America make up one of the largest remaining intact mountain ecosystems on earth, and are a key area for preserving biodiversity continentally across the western Cordillera (Hebblewhite et al., 2021). The region supports a diverse mammal population, serving as a refugia for many species that have been extirpated in other parts of North America (Hebblewhite et al., 2021; Heim et al., 2019; Laliberte & Ripple, 2004). The Rocky Mountains are also a popular tourism destination, providing important opportunities for recreation and wilderness enjoyment and providing economic benefit to the province (Alberta Government, 2022; Avantis, 2017). This landscape has changed rapidly in recent decades; though overall protected area coverage has increased (Hebblewhite et al., 2021), industrial development has accelerated through the Foothills and up to the boundaries of protected areas, causing forest loss, and reshaping the landscape through the introduction of industrial disturbance (Global Forest Watch Canada, 2014; Lee & Cheng, 2014; Maxwell et al., 2020). The Rocky Mountains are a complex, multi-use and multi-value landscape, providing crucial habitat to many species while also introducing stressors such as landscape alteration and high human recreational use. Through my research, and using a portion of Canada's Rocky Mountains as a study system, I sought to understand how different dimensions of human landscape use, landscape management, and landscape disturbance impact mammal species, and to identify the primary drivers of species distributions in complex human-use landscapes. I chose to focus on two aspects of human landscape use and management: firstly, recreational use, specifically motorized recreation, and its impact on mammal distributions; and secondly, landscape protection and how management boundaries influence mammal distributions across a broader landscape.

I approached my research into landscape use and management at two spatial scales in order to to examine different scales of human use and landscape management. My research spans protected areas, managed for conservation and enjoyment by people, and unprotected Crown lands, managed for multiple landscape uses, such as industrial development and recreational use. In my second chapter, I assessed the direct impact of intensity of human use on mammals within an unprotected region of the Rocky Mountains known as the Bighorn Backcountry, spanning roughly 8,000 km^2. I ask whether motorized recreational intensity causes spatial displacement of mammal species, and whether this is a stronger determinant of species distributions over linear disturbance features or natural landcover attributes. In my third chapter, I scaled up to assess the influence of landscape protection on species distributions over a much broader area spanning roughly 32,000 km^2 across the Rocky Mountains. I ask how protected areas influence mammal distributions across a broader landscape, and how their importance compares to anthropogenic landscape disturbance and natural habitat features.

I conducted my research using wildlife camera arrays deployed systematically across landscapes. Wildlife cameras are motion-triggered devices allowing for non-invasive capture of wildlife, making them a powerful research tool for surveying mammal communities (O'Connell et al., 2011). Wildlife camera use has grown in popularity over the last two decades, and the technology has been adopted into many mammal monitoring programs for estimating density, documenting rare species, modelling species' associations with their habitat, and many other methods that continue to develop (O'Connell et al., 2011). Along with collecting new data, I made use of existing wildlife camera arrays from previous studies and government monitoring programs, as many datasets already exist and may be leveraged to expand the scope of wildlife camera studies (Burton et al., 2015; Steenweg et al., 2017).

In examining how anthropogenic activity and management affects species distributions, I seek to provide insights into mammal conservation and highlight priority areas for landscape restoration and management.

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Chapter 2: The influence of motorized activity on mammal distributions in Alberta's Bighorn Backcountry

2.1 Introduction

Anthropogenic landscape alteration has substantially restructured natural landscapes across the globe, causing habitat loss and alteration that directly impacts species biodiversity. Human development has substantially altered over 58% of terrestrial land on earth (Williams et al., 2020) and has caused range contractions and population reductions across many large mammal species (Laliberte & Ripple, 2004). Along with inducing habitat loss and causing species declines, landscape change alters the ways in which species interact, potentially creating means for predators to more easily access prey (Barker et al., 2023; Dickie et al., 2017; McKenzie et al., 2012). Though many mammals are impacted by landscape change, the effects and extent of the impacts vary greatly within wildlife communities (Heim et al., 2019). Whereas some species avoid areas of high human density and have been substantially negatively impacted by landscape change– such as caribou, grizzly bears, or wolverine (Heim et al., 2017; Herrero, 2005; Hervieux et al., 2013) – other anthrophilic species such as coyote or white-tailed deer thrive in disturbed landscapes, and have used human disturbances to expand their ranges (Fisher et al., 2020; Heim et al., 2019; Hody & Kays, 2018; Latham et al., 2011).

Beyond altering habitat, landscape alteration has a secondary effect by facilitating human access to previously remote and inaccessible landscapes. Landscape change creates linear disturbances throughout forested areas, in the form of features such as roads, trails, seismic lines for oil exploration, pipelines, transmission lines, and others (ABMI, 2017; Hansen et al., 2010; Lee & Cheng, 2014). Throughout anthropogenically disturbed landscapes and at the fringes of wilderness areas, people make use of linear features for many means of travel and recreation, from non-motorized activities such as hiking, biking, and horseback riding, to motorized activities such as driving regular vehicles (cars, trucks, Sport Utility Vehicles/SUV’s, etc.) and off-highway vehicles (OHV’s) including ATV’s (All Terrain Vehicles), UTV’s (Universal Terrain Vehicles), snowmobiles, and other vehicle types.

Recreational use of wilderness landscapes is an important aspect of conservation, allowing people to gain an appreciation of natural landscapes and wildlife, and an incentive to protect landscapes. Outdoor recreation is often assumed to be compatible with conservation, but there is growing evidence that non-consumptive recreational activities (hiking, biking, OHV use, etc.) have negative behavioural effects on some mammals (Larson et al., 2016). Behavioural avoidance of motorized activity (OHV use) has been observed in wolverines (Heinemeyer et al., 2019; Scrafford et al., 2018), elk (Wisdom et al., 2018), grizzly bears (Ladle et al., 2018) and various other species (Salvatori et al., 2023). Behavioural avoidance of non-motorized activity, including activities such as hiking, biking, etc., has been observed in wolves, elk (Hebblewhite et al., 2005), wolverine (Heinemeyer et al., 2019), wolves and grizzlies (Naidoo & Burton, 2020), and various other species (Reed & Merenlender, 2008; Salvatori et al., 2023). It has been theorized that mammals may view anthropogenic noise – whether via motors or voices – as a form of predation risk, causing their avoidance (Frid & Dill, 2002). Alternatively, human use can also affect predator-prey interactions by creating “predator shields”, wherein predator species avoid high-use areas and ungulate prey do not, providing them relief from predators (Hebblewhite et al., 2005; Muhly et al., 2011; Rogala et al., 2011). Recreational use can also induce other behavioural changes, including increasing movement speeds when motorized use is prevalent, or inducing a shift to nocturnality in some species (Northrup et al., 2012; Olson et al., 2018).

Behavioural responses by wildlife to recreation in various forms have been well documented, but population-level responses remain poorly studied. Does sustained human use cause permanent displacement of wildlife from human-used areas, or are animals just moving aside and allowing people to pass before returning? Most studies have assessed behavioural responses (such as animal movement, (Larson et al., 2016)) rather than population-level responses such as spatial displacement from recreational areas. There is limited evidence of spatial displacement in top predators from recent studies: Naidoo and Burton (2020) found weekly spatial avoidance of cyclists in grizzly bears and wolves, and Salvatore et al. (2023) found negative spatial associations with hikers and bikers in large predators. Human activity has been found to pose “risky times” for many species, inducing increased movement and avoidance, but whether it is creating “risky places” (Droge et al., 2017) where species are avoiding areas of high activity altogether is unknown. A spatial/population effect that displaces species from a habitat is of greater concern for biodiversity conservation than an accommodating behavioural effect, as it contributes to habitat loss and further reduces habitat available to species. It is important to gain an understanding of whether recreational activity is inducing a spatial effect.

I assess the spatial influence of motorized recreation on mammal distributions in the eastern slopes and foothills of Alberta’s central Rocky Mountains, a region commonly referred to as the Bighorn Backcountry (BB). The BB, a pocket of mostly crown land situated between Banff and Jasper National parks, is part of the largest remaining intact mountain ecosystem on earth (Hebblewhite et al., 2021), and serves as important habitat to many mammal species (Weaver, 2017). Industrial activity is prevalent throughout the foothills, in the form of forestry, oil and gas extraction, and mining (Global Forest Watch Canada, 2014; Weaver, 2017). Historical and ongoing development has left an extensive network of linear access features throughout the area in the form of maintained and unmaintained roads, seismic lines and other cut lines, transmission and pipelines, along with official and unofficial recreational trail networks (Figure 2.1). The BB also has an extensive history and continuing popularity for use as a motorized recreation area (Alberta Wilderness Association, 2008).

To model the occurrence of both mammal species and human motorized use in the BB, I used two wildlife camera arrays: one on human use trails and roads, and one on wildlife trails (Figure 2.1). Wildlife cameras are a powerful tool allowing for long-term remote data collection (O'Connell et al., 2011; Steenweg et al., 2016). When set up effectively to maximize detection probability, they can facilitate the monitoring of several species simultaneously (Burgar et al., 2019; Rich et al., 2017). Sampling designs that adequately capture landscape variability allow for large-scale assessment of species' relationships to landscape variables (Burton et al., 2015). Wildlife cameras are also an effective tool for monitoring various types of human recreation on trails (Ladle et al., 2018; Naidoo & Burton, 2020) (Appendix Figure A1).

To investigate if and how motorized recreation affects species distributions, I assessed the distributions of six mammal species: grizzly bears (*Ursus arctos horriblis*), wolves (*Canis lupus*), black bears (*Ursus americanus*) coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginanus*) and mule deer (*Odocoileus hemionus*). I chose to assess multiple individual species as species are expected to show differing responses to human disturbance (Heim et al., 2019). These six species are detected frequently enough on wildlife cameras to use in analyses, while also filling different niches and responding differently to anthropogenic disturbance. I tested whether the spatial intensity of motorized recreation could predict species occurrence, or whether natural landscapes or linear disturbance features were stronger predictors of occurrence. In comparing the importance of human activity versus landscape disturbance, I sought to find out if there are different impacts between “footprint” and “footfall”, i.e., human’s use of landscape disturbance features versus the impact of the features themselves. I hypothesized that only species previously found to be sensitive to human activity, and shown to directly avoid areas of high human use, would be best explained by recreational intensity. I predicted that wolves and grizzly bears would spatially segregate from motorized recreation, a long-term outcome of behavioural avoidance of human activity (Ladle, 2017; Naidoo & Burton, 2020; Northrup et al., 2012; Rogala et al., 2011). Conversely I predicted that coyotes and white-tailed deer distributions would be positively explained by linear disturbances, as they are both species that have been found to thrive in human-disturbed landscapes, and have used the spread of anthropogenic disturbance to expand their ranges into previously unoccupied habitats (Hody & Kays, 2018; Nickel et al., 2020). I hypothesized that black bears and mule deer would be best explained by natural habitat features, having no clear behavioural response that could translate into a spatial response.

2.2 Methods

2.2.1 Study Area

This study encompassed the Bighorn Backcountry region of Alberta, in the foothills and front ranges of the Rocky Mountains (Figure 2.1). Roughly ~8000 km^2, this region contains the headwaters of the North Saskatchewan River. Elevations range from 900-3300 meters, and include alpine, subalpine, montane, and foothills natural subregions. Predominant vegetation species include lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*) at subalpine elevations, Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) at montane elevations, and aspen, white spruce, black spruce (*Picea mariana*), and lodgepole pine in the foothills (Natural Regions Committee, 2006). As part of the Canadian Cordillera and adjacent to a national protected area network, BB supports a diverse mammal community, with carnivore species such as grizzly bear (*Ursus arctos horriblis*), wolves (*Canis lupus*), coyotes (*Canis latrans*), martens (*Martes americana*), and ungulates such as elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) (Weaver, 2017). The Bighorn region is largely unprotected, with a handful of provincially protected areas: one Ecological Reserve (Kootenay Plains; 34 km^2), two Natural Areas (354 HA total), and thirty small Provincial Recreation Areas (5.2 km^2 total). Industrial development, including timber harvest, oil and gas exploration, and mining, is prevalent in the foothills along the eastern side of the study area (Figure 2.1). Parts of the landscape are managed with official trail networks and some restrictions on activity, but much of the area is unregulated and unprotected, allowing for widespread trail use. Popular with OHV users, high use and low compliance has been a long standing issue (Alberta Wilderness Association, 2008).

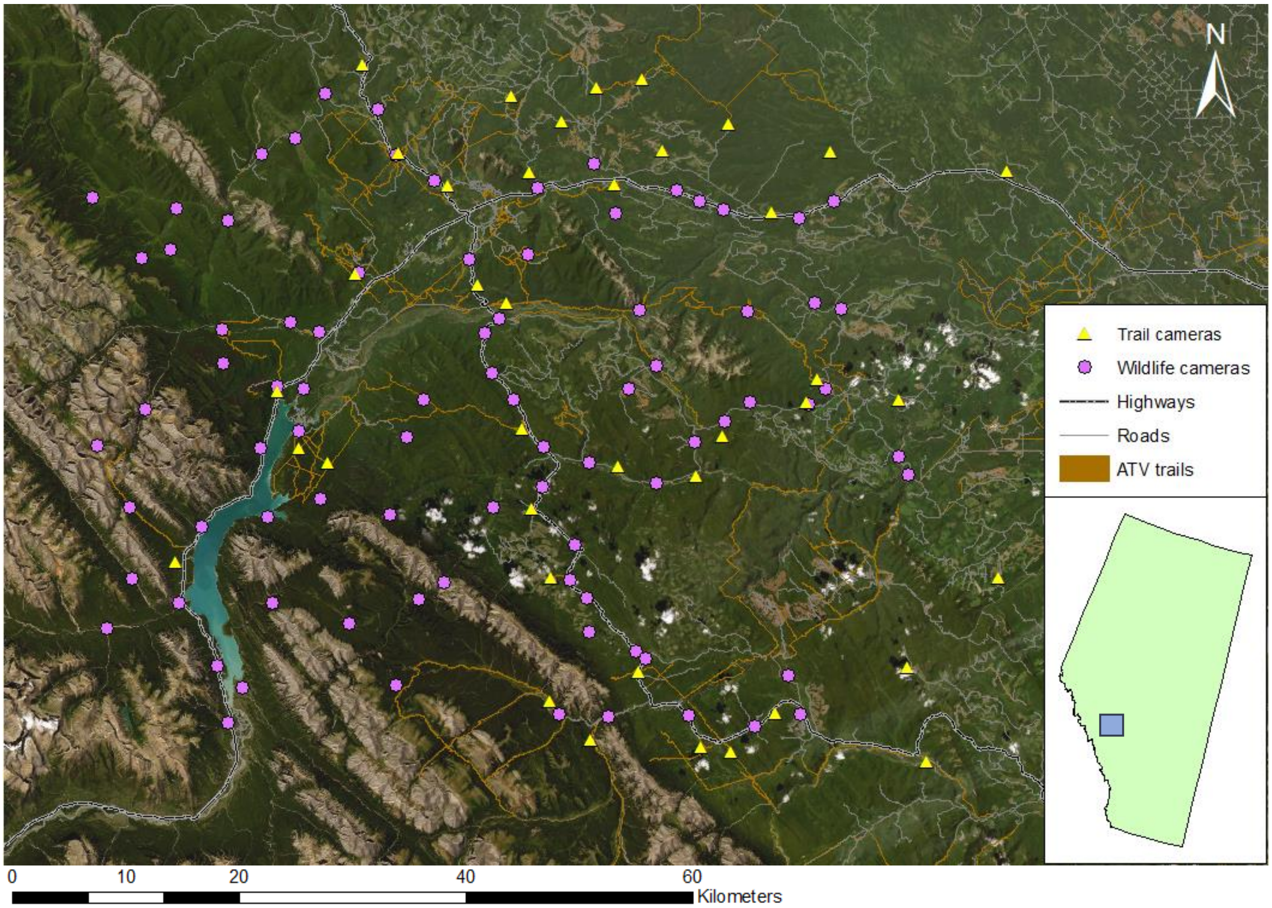

Figure 2.1. Map of the study area in the Bighorn Backcountry region of Alberta, showing the locations of all trail (yellow triangle) and wildlife (purple circle) camera sites. Thick grey lines show major highways through the study area; brown lines show ATV trails, and grey lines show roads. The inset map shows the location of the study region within the greater province of Alberta.

2.2.2 Wildlife and Trail Camera Data Collection

To survey wildlife across the region an array of 93 wildlife cameras was deployed using a systematic grid design (6 km^2 cells) with one camera (model PC900; RECONYX, Holmen, WI.) deployed per grid cell from October 2019-September 2020 (Figure 2.1). Camera sites were chosen to maximize species detectability, along game trails and cut lines. Commercial scent lure (O'Gorman's Long Distance Call; O'Gorman's Lures, Montana) was applied to trees opposite the wildlife camera to help draw in nearby species and increase species detection probabilities.

Cameras were placed at a minimum of 1 km apart. Due to camera malfunction and damage, eight sites were removed, leaving a total number of 83 functional sites and 27,692 trap days. Species detection events were considered independent when they occurred a minimum of 30 minutes apart (Rovero & Zimmermann, 2016); this was to help eliminate samples of same animal or group of animals photographed repeatedly over a short interval. The wildlife camera array yielded the following independent detection counts: 83 wolf, 68 grizzly bear, 189 coyote, 171 black bear, 1673 white-tailed deer, and 350 mule deer.

To survey motorized use of linear features, an array of 58 cameras (models HPX2 and PC900; RECONYX, Holmen, WI) were deployed using a systematic hexagonal grid design (2 km hexagon sides) with one camera per grid cell (Figure 2.1) from September 2020 – Sept. 2021. To adequately capture a range of activity across all feature types on the landscape, four linear feature classes were sampled: gravel roads, truck-trail-unimproved roads (legacy or minimal use industry roads), all-terrain vehicle (ATV) trails (officially maintained and unofficial) and seismic cut lines. As many grid cells had multiple of each type of feature running through them, I randomly assigned a feature type to each grid cell, generated a random point in each grid cell, and selected the closest feature of interest to the point to deploy a camera. I selected fifteen cells for each feature type. When deploying cameras in the field, some selected roads were gated, bermed off, or otherwise inaccessible; if this was found to be the case for a selected feature, we placed cameras on the next available feature of the same type in the grid cell. Cameras were placed a few meters off the road, and if possible, at an angle to maximize detectability of fast-moving objects. Due to camera theft, damage, and camera error, nineteen cameras were removed, leaving a total number of 39 functional sites. This resulted in 14,754 trap days, and 6896 independent OHV detections (Appendix Figure A1 for example images).

From both arrays, images were tagged using the Timelapse 2 image processing software (Greenberg, 2021) and imported into R (R Core Team, 2021) for analysis.

2.2.3 Modelling Motorized Activity Intensity

I used the data from the trail camera array to generate models predicting motorized recreation intensity along trail networks, which I then used to produce spatial layers representing intensity of motorized use across the landscape. The activity predictions generated from these models were used as covariates in wildlife models (section 2.2.4).

First, I separated the trail camera data into peak (July-September) and off (October-June) motorized recreation seasons, based on a histogram with counts of vehicle detections per month (Figure 2.2). I separated out data by seasons because patterns and intensity of motorized recreation may differ seasonally, with more people in the area and more trails available for use in the summer; mammal species' detection rates and spatial distributions may differ seasonally due to snow cover. I then summarized OHV detection events, including several types of motorized use (All OHV's, including ATV's, UTV's, snowmobiles, etc., dirt bikes, and regular vehicles) into daily bins to obtain a proportional binomial response variable, with vehicles being present (1) or not (0) daily at each site. For each season, I modeled motorized occurrence, using a proportional binomial response in a generalized linear model (GLM) with a binomial distribution (logit link function). I used a set of variables potentially affecting probability of trail use, based on study area attributes and previous studies on motorized use (Hornseth et al., 2018; Scrafford et al., 2018) (Table 2.1) in a set of models of increasing complexity and number of variables (Table 2.2). I used Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) to determine which set of trail covariates had the highest explanatory power. If top models were within 2 AICc of each other, the most parsimonious model was chosen.

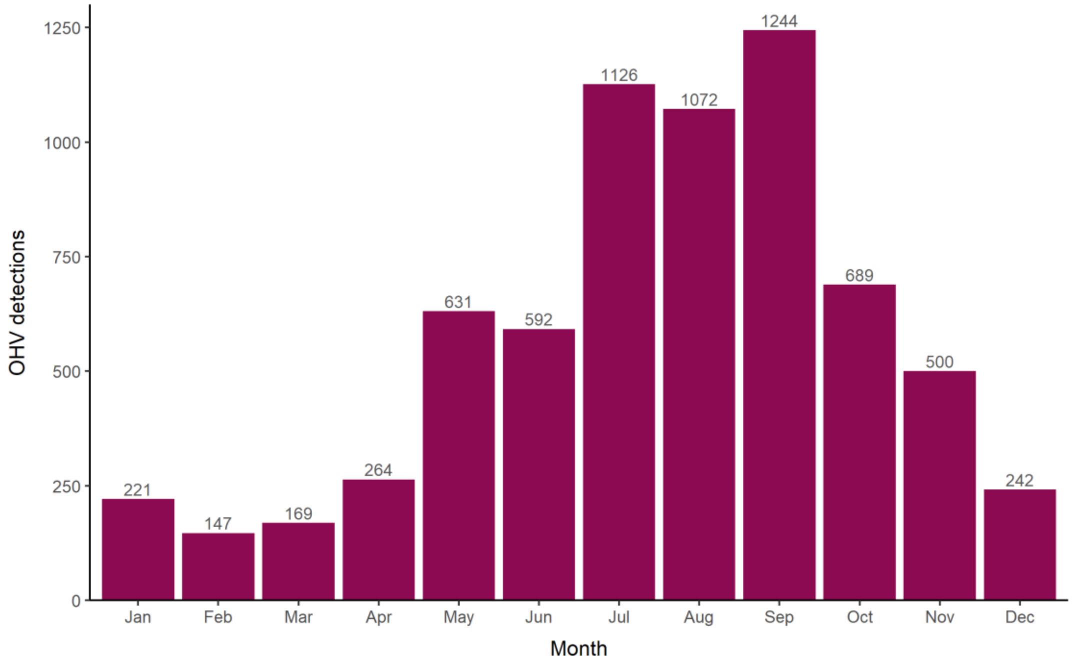

Figure 2.2. Histogram showing independent detections (>30min apart) of off-highway vehicles (OHVs) from the Bighorn Backcountry trail camera array, binned by month to show temporal patterns of recreation intensity.

Table 2.1. Description of covariates extracted at camera point locations used to model trail activity intensity in the Bighorn Backcountry region of Alberta.

Covariate	*Description*
Trail type 1	Type of linear feature: Gravel road, Truck-trail road, ATV trail, or cutline
Trail type 2	Same as above, but separating ATV trails into officially designated and unofficial
Distance to town	Distance in meters to the nearest town
Distance to highway	Distance in meters to the nearest highway
Distance to road	Distance in meters to the nearest road
Elevation	Elevation in meters
In PLUZ	Whether or not a site is within a Public Land Use Zone

Table 2.2. Candidate models used to determine the best supported set of predictors of motorized activity intensity in the Bighorn Backcountry, in peak and off seasons. Model covariates are described in Table 2.1. "Activity Model 5" was the top model predicting motorized intensity in the peak season, and "Activity Model 7" was the top model predicting motorized intensity in the off season.

Model name	*Covariates*
Activity Model 1	Trail type 1, distance to town, distance to highway
Activity Model 2	Trail type 2, distance to town, distance to highway
Activity Model 3	Trail type, distance to town, distance to highway, in PLUZ
Activity Model 4	Trail type 2, distance to town, distance to highway, in PLUZ
Activity Model 5*	**Trail type, distance to town, distance to highway, elevation**
Activity Model 6	Trail type, distance to town, distance to highway, distance to road
Activity Model 7$^{\Diamond}$	**Trail type 2, distance to town, distance to highway, distance to road, elevation**
	***** = peak season top model
	◊ = off season top model

The covariate estimates from the best-supported model for each season were then used to predict activity intensity across the landscape. I converted the trail and road network in the BB into points, with one point every 30 meters. At each point, I extracted the covariate values from the top models for peak and off seasons (Table 2.1). Using these covariate values and the coefficient estimates from the top models for each season (Figure 2.3), I used the *predict* function in R (R Core Team, 2021) to generate predicted motorized recreational intensity at each point. These point data with predicted recreational intensity were used in wildlife models, extracted to buffers around camera locations where wildlife occurrence was measured. The recreation variable I used in models was the maximum predicted activity within a buffer for each of three feature types: roads, ATV trails, and cutlines. I used the maximum value within each buffer because summing the values greatly inflated the activity estimates and introduced much variability among sites, and averaging the predicted recreation values diminished points of higher activity. I chose to keep the feature types separate because combining them resulted in increased spatial autocorrelation with linear features; including activity levels for each feature type also better represents the distribution of activity in an area.

A heat map of predicted motorized recreation intensity across the study area in peak and off seasons is shown in Figure 2.4. In the peak season, activity was spread out more throughout the study area, across all roads and trails; in the winter season, activity was more concentrated to industrial roads.

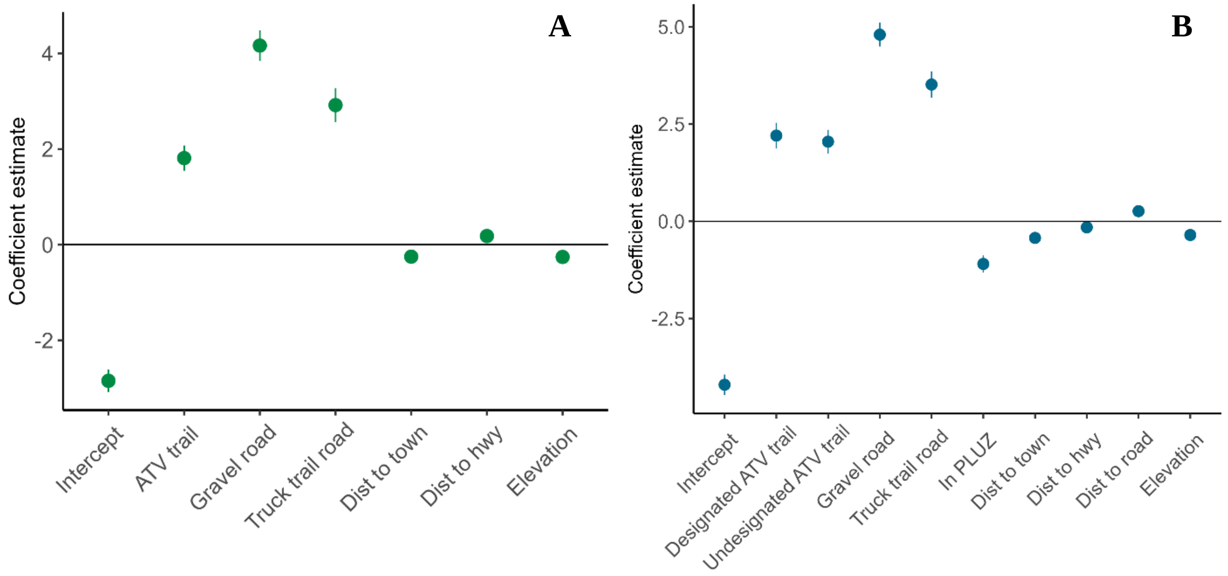

Figure 2.3. Coefficient estimates from the top models predicting motorized activity intensity in A) peak and B) off seasons in the Bighorn Backcountry region. Models are listed in Table 2.2, and covariates are explained in Table 2.1

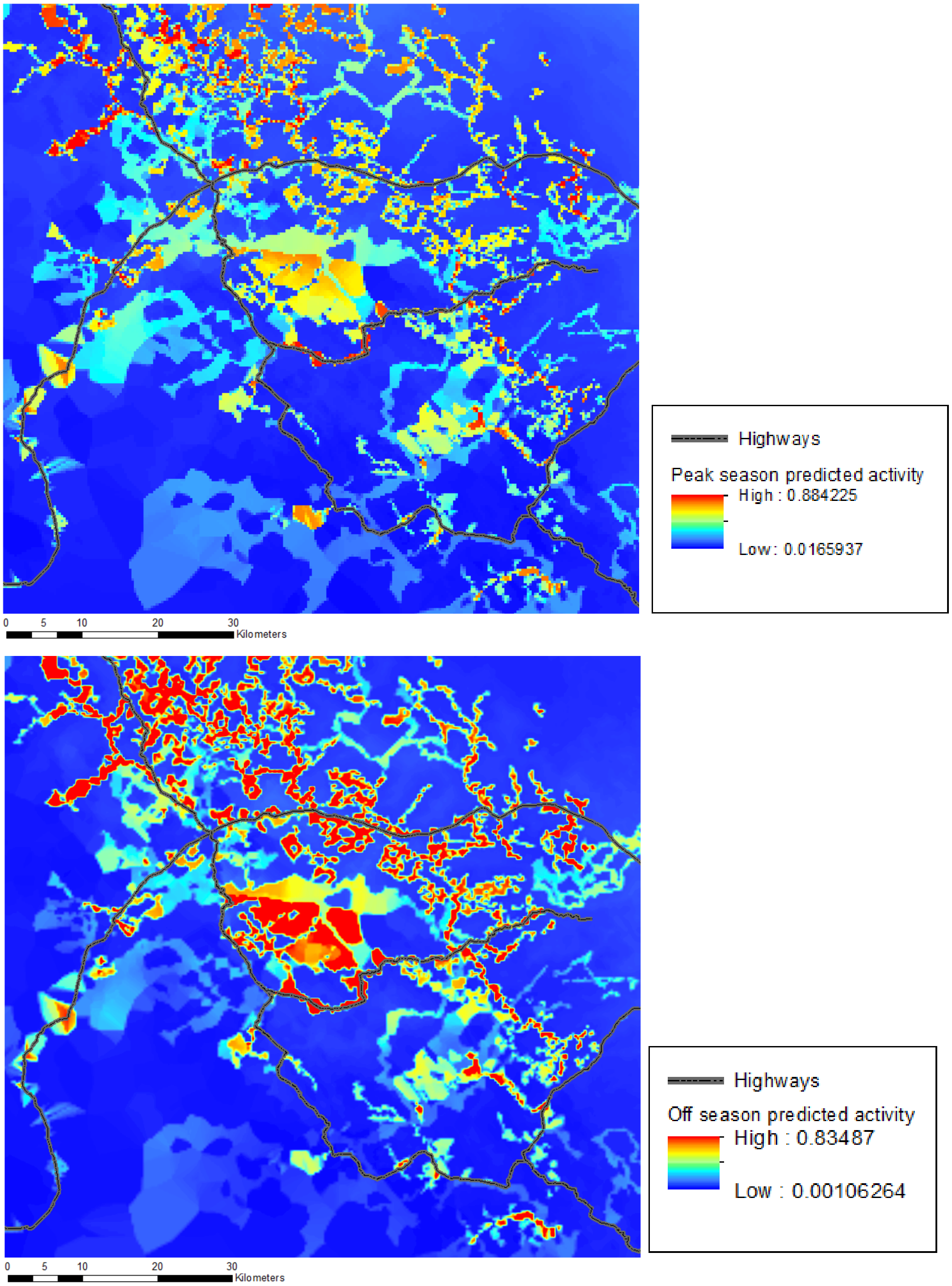

Figure 2.4. A visual representation of predicted motorized activity intensity in the Bighorn Backcountry region in A) peak (July-September) and B) off (October-June) seasons, generated by spatially kriging individual predicted activity points to produce an activity heat map. For spatial context, major highways are shown in thick grey lines.

2.2.4 Wildlife models - landscape covariates

To determine which landscape factors best supported the occurrence of wildlife species, I used three competing models with three corresponding sets of landscape covariates: an activity model, a linear disturbance model, and a natural landcover model (Tabled 2.3 and 2.4). Covariates were measured by building buffers (250m-2500m, in 250m increments) (Fisher et al., 2011) around wildlife cameras and extracting landcover variables within each buffer. For the activity model, I used the predicted peak activity on roads, cutlines, and ATV trails (Figure 2.4). For the linear disturbance features model, I obtained data on cutlines from ABMI's 2017 Human Footprint Inventory (ABMI, 2017), and I obtained road and ATV trail data from Government of Alberta staff (Table 2.3). For the natural landscape features model, I used a Landsat dataset classified into habitat types (Nijland et al., 2015) (Table 2.3). Variables were then scaled to have a mean of 0 and SD of 1 for more accurate comparisons of coefficient estimates.

2.2.5 Wildlife models - species response variables

To model wildlife occurrence, data were pooled between both arrays, the 39 trail sites and 83 off-trail sites, as the trail cameras were also effective in capturing wildlife (Appendix Figure A1). Four trail sites were removed for being within 1 km of a wildlife site, leaving 118 total sites. This resulted in 41,309 trap days and the following total independent detection counts: 285 wolf, 153 grizzly bear, 610 coyote, 287 black bear, 3530 white-tailed deer, and 525 mule deer. To account for detection differences between arrays, I included "Array" as a fixed effect in all models specifying whether the site was an on-trail or off-trail camera. For each species, I summarized independent detection events (detections >30 minutes apart) into weekly bins to obtain a proportional binomial response variable, with a species being detected (1) or not (0) weekly at each site. I chose to use a weekly bin across peak (July-September) and off (October-

June) seasons as this has been sensitive enough to detect variation in site use and providing a balanced distribution suitable for modelling in other mammal analyses (Fisher & Burton, 2018; Heim et al., 2017).

2.2.6 Wildlife model constructs

I modeled individual species occurrence using species' proportional binomial response in a generalized linear model (GLM) with a binomial distribution (logit link function) for both peak and off seasons. No off-season models were run for grizzly or black bears due to their winter dormancy. To determine the spatial scale at which landscape covariates best explained species occurrences, I used a global model with all variables from all models, measured at 20 spatial scales from 250-m to 2500-m radii at 250-m increments (Fisher et al., 2011). I used Akaike's Information Criterion corrected for small sample sizes (AICc) to determine which spatial scale had the strongest explanatory power for each species. The spatial scale with the lowest ∆AICc was used for further model selection. Once a spatial scale was selected, I measured my covariates at that scale for model selection. I used four competing models corresponding to different hypotheses (Tables 2.3 and 2.4): an activity model, with predicted motorized recreational intensity; a linear features model, including cover of linear disturbance features; a natural landcover model including coverage of natural habitat features; and a null model including only array. I used AICc to compare models in an information-theoretic framework for each species in peak and off seasons, choosing the top model as the one having the lowest AICc ranking (Burnham & Anderson, 2002). If top models were <2AICc apart, the most parsimonious model was considered the top model. K-fold cross validation was performed on all models using the *boot* package in R (Canty & Ripley, 2021).

2.2.7 Post hoc analysis – spatial scale contrast

Based on preliminary wildlife model results, I probed the role of spatial scale in determining the significance of motorized activity versus other landscape variables. I conducted a post-hoc analysis to determine if motorized activity best explained species occurrence when covariates were measured at larger scales (2000-meter buffer) as those models with covariates measured at smaller scales (250-meter buffer). To assess this, I used AIC_c to determine the best supported model out of the candidate models (Table 2.4) for each species at peak and off seasons at two spatial scales: a 250-meter covariate buffer, and a 2000-meter covariate buffer. I then compared the top supported models between spatial scales.

Table 2.3. Descriptions of each model covariate, grouped by model type, used in wildlife models.

Variable type	*Covariate*	*Description*
Motorized Activity	Predicted cutline activity	Highest predicted activity level on cutlines within buffer
	Predicted road activity	Highest predicted activity level on roads within buffer
	Predicted ATV trail activity	Highest predicted activity level on ATV trails within buffer
Linear Features	Roads	% cover of all roads and roadside berms
	Cutlines	% cover of seismic lines and other cutlines
	ATV trails	% cover of trails permitting motorized recreational use
	Highway	% cover of major gravel and paved highways
Natural landscape features	Coniferous forest	% cover of forest with conifer in over 80% of crown
	Mixed forest	% cover of broadleaf and mixed crown cover forest
	Wetland	% cover treed and open wetlands
	Herb/Shrub	% cover of herbaceous vegetation
	Shrub	% cover of shrubland
Array	Array	Fixed effect controlling for the two separate arrays used to detect wildlife: the off-trail wildlife camera array, and the on-trail array

Table 2.4. Competing hypotheses for factors explaining wildlife distributions in the Bighorn Backcountry region, and their corresponding model covariates and predictions for which species will be best supported by each model.

Model	*Hypothesis*	*Model covariates*	*Species predictions*
Activity	Species sensitive to human disturbance will avoid areas of high activity	Predicted road activity Predicted ATV trail activity Predicted cutline activity Array	Grizzly bear, Wolf
Anthropogenic features	Species that respond to landscape alteration; less impacted by human use	Roads Cutlines ATV trails Highways Array	White-tailed deer, coyote
Natural landcover	Species don't respond strongly to human activity and landscape use; select for natural habitat features	Coniferous forest Mixed forest Shrubland Herbaceous cover Wetlands Array	Black bear, mule deer
Array	Null model controlling only for the influence of array on species detection	Array	none

2.3 Results

2.3.1 Motorized recreation best explains wolf and mule deer occurrence

Motorized recreation intensity was the best-supported model predicting wolf occurrence (peak season $AICc_w$ = 1; off season $AICc_w$ = 0.99) (Table 2.5). In the peak season, wolves were negatively associated with road activity ($\beta_{predicted\_road}$ = -0.36±0.17, p = 0.0322) and ATV trail activity ($\beta_{predicted\_ATV}$ = -0.41±0.17, p = 0.0180), and positively associated with cutline activity ($\beta_{predicted\_cutline}$ = 0.95±0.21, p = 5.42E-06) (Figure 2.5). In the off season, wolves were again negatively associated with ATV trail activity ($\beta_{predicted\_ATV}$ = -0.39±0.17, p = 0.0178), and positively associated with cutline activity ($\beta_{predicted\_cutline}$ = 0.49±0.12, p = 0.0178) (Figure 2.6).

Along with wolves, mule deer were best explained by activity in the off season ($AICc_w$ = 1) (Table 2.5). Mule deer had a negative association with cutline activity ($\beta_{predicted\_cutline}$ = -0.59±0.18, p = 0.00105), opposite to wolves (Figure 2.6). In contrast, in the peak season mule deer were explained by natural landcover ($AICc_w$ = 1), having a negative association with mixed forests and wetlands (β_{Mixed_peak} = -0.61± 0.19, p = 0.0016; $\beta_{Wetland\_peak}$ = -0.81± 0.23, p = 0.0004) (Figure 2.6).

2.3.2 Grizzly bears, coyotes, and white-tailed deer were best explained by linear features

Linear features best explained the occurrence of grizzly bears (peak season $AICc_w$ = 0.97), coyotes (peak season $AICc_w$ = 1; off season $AICc_w$ = 0.99), and white-tailed deer (peak season $AICc_w$ = 1; off season $AICc_w$ = 1) (Table 2.5). Grizzly bears were negatively associated with highways ($\beta_{Highway}$ = -1.30±0.52, p = 0.0121), cutlines ($\beta_{Cutline}$ = -0.56±0.22, p = 0.013), roads (β_{Road} = -1.38±0.45, p = 0.002), and ATV trails (β_{ATV_trail} = -1.05±0.36, p = 0.0041) (Figure 2.5). Coyotes were positively associated with roads and ATV trails in both peak and off seasons ($\beta_{\text{Road\_peak}}$ = 1.25±0.24, p = 1.00E-07; $\beta_{\text{ATV\_trail\_peak}}$ = 1.04±0.15, p = 1.11E-12; $\beta_{\text{Road\_off}}$ = 0.25±0.036, p = 3.66E-12; $\beta_{\text{ATV\_trail\_off}}$ = 0.21±0.037, p = 6.55E-09) (Figure 2.5 and 2.6). White-tailed deer were positively associated with highways and ATV trails in both peak and off seasons ($\beta_{\text{Highway\_peak}}$ = 0.54± 0.094, p = 7.02E-09; $\beta_{\text{Highway\_off}}$ = 1.05± 0.079, p = 1.34E-39; $\beta_{\text{ATV\_trail\_peak}}$ = 0.51± 0.073, p = 5.16E-12; $\beta_{\text{ATV\_trail\_off}}$ = 0.50± 0.059, p = 2.59E-17) (Figure 2.5 and 2.6). White-tailed deer were also positively associated with cutlines in the peak season ($\beta_{\text{Cutline\_peak}}$ = 0.23±0.066, p = 0.00063) and roads in the off season ($\beta_{\text{Road\_off}}$ = 0.44± 0.069, p = 2.32E-10) (Figure 2.6).

2.3.3 Black bears were best explained by natural landcover

Natural landcover best explained the occurrence of black bears (AICc_w = 1.00) (Table 2.5). Black bears were positively associated with herbaceous landcover and mixed forests ($\beta_{\text{Herbaceous}}$ = 0.57± 0.15, p = 0.00011; β_{mixed} = 0.29± 0.097) and negatively associated with shrublands (β_{Shrub} = -0.81± 0.174, p = 3.23E-06) (Figure 2.5).

2.3.4 Wildlife detections on versus off trail, seasonal trends

To account for possible differences in species detections between wildlife and human use trails, an “Array” variable was included as a fixed effect, accounting for whether detections were on the trail camera array or the wildlife array. Most species (wolves, grizzly bears, coyotes, and white-tailed deer) had higher detection rates on human use trails; array was not significant for black bears or mule deer (Figure 2.5, Figure 2.6). For all species, the top model was consistent between seasons except for mule deer, which were best explained by natural landcover in the peak season and by human activity in the off season.

2.3.5 Motorized recreational activity is only a significant predictor at small spatial scales

To investigate whether there is a spatial scale-related pattern in the significance of activity, I conducted a post-hoc analysis to determine the best supported model at a 250-meter covariate buffer and at a 2000-meter covariate buffer for each species in peak and off seasons. At a 250-m buffer scale, predicted human activity was the top model for wolves at peak and off seasons, coyotes at peak season, and mule deer in the off season (Table 2.6). At a 2000-m buffer scale, linear features best explained most species occurrences (grizzly bears, coyote, black bear, white-tailed deer), with natural landcover being the top model for wolves and mule deer (Table 6). For detailed model results see Table A2 in the Appendix.

Table 2.5. Full AICc results from generalized linear models used to explain mammal species occurrence in peak and off seasons using different model sets. Covariates in each model are listed in Table 3. df is degrees of freedom; LL is the log-likelihood; ΔLL is delta log-likehlihood. K-fold cross-validation results for all models are listed in Table A1 in the Appendix.

Species	*Season*	*Model*	*AICc*	*dAICc*	*AICcw*	*df*	*LL*	*Δ LL*
Wolf	Peak	**Activity**	**151.20**	**0**	**1.00**	**5**	**-70.31**	**13.88**
		Linear features	169.50	18.3	0.00011	6	-78.34	5.85
		Array	172.50	21.3	2.37E-05	2	-84.19	0
		Landcover	178.52	27.32	1.17E-06	7	-81.72	2.48
	Off	**Activity**	**373.66**	**0**	**0.99**	**5**	**-181.56**	**19.13**
		Landcover	384.12	10.46	0.0053	7	-184.54	16.14
		Linear features	387.59	13.93	0.00094	6	-187.41	13.27
		Array	405.48	31.82	1.22E-07	2	-200.69	0
Grizzly bear	Peak	**Linear features**	**149.26**	**0**	**0.97**	**6**	**-68.23**	**22.79**
		Activity	156.41	7.158	0.027	5	-72.93	18.09
		Landcover	183.02	33.77	4.52E-08	7	-83.98	7.04
		Null	186.14	36.89	9.51E-09	2	-91.02	0.00
Coyote	Peak	**Linear features**	**256.19**	**0**	**1**	**6**	**-121.70**	**42.08**
		Landcover	320.64	64.45	1.01E-14	7	-152.79	10.99
		Activity	322.91	66.72	3.25E-15	5	-156.18	7.60
		Array	331.67	75.48	4.07E-17	2	-163.78	0
	Off	**Linear features**	**588.11**	**0**	**0.9912396**	**6**	**-287.66**	**36.46**
		Landcover	597.56	9.457	0.0087603	7	-291.26	32.87
		Activity	621.06	32.95	6.92E-08	5	-305.25	18.87
		Array	652.36	64.25	1.11E-14	2	-324.13	0
Black bear	Peak	**Landcover**	**326.42**	**0**	**1.00**	**7**	**-155.68**	**22.88**
		Linear features	347.30	20.88	2.92E-05	6	-167.25	11.30
		Array	361.22	34.8	2.77E-08	2	-178.56	0
		Null	364.22	37.81	6.18E-09	5	-176.83	1.72
White-tailed deer	Peak	**Linear features**	**638.59**	**0**	**1**	**6**	**-312.90**	**48.17**
		Activity	687.41	48.82	2.50E-11	5	-338.43	22.65
		Landcover	690.50	51.91	5.34E-12	7	-337.72	23.35
		Array	726.26	87.67	9.19E-20	2	-361.07	0
	Off	**Linear features**	**874.35**	**0**	**1**	**6**	**-430.80**	**152.61**
		Landcover	954.79	80.44	3.415E-18	7	-469.89	113.52
		Activity	1062.44	188.1	1.44E-41	5	-525.95	57.45
		Array	1170.91	296.6	4.00E-65	2	-583.41	0
Mule deer	Peak	**Landcover**	**422.77**	**0**	**1.00**	**7**	**-203.85**	**29.47**
		Linear features	447.44	24.68	4.38E-06	6	-217.32	15.99
		Array	470.75	47.98	3.81E-11	2	-233.32	0

		Activity	472.69	49.93	1.44E-11	5	-231.07	2.25
	Off	**Activity**	**413.88**	**0**	**1.00**	**5**	**-201.67**	**10.51**
		Landcover	425.78	11.89	0.0026	7	-205.37	6.81
		Linear features	428.47	14.59	0.00068	2	-212.18	0
		Array	429.00	15.11	0.00052	6	-208.11	4.07

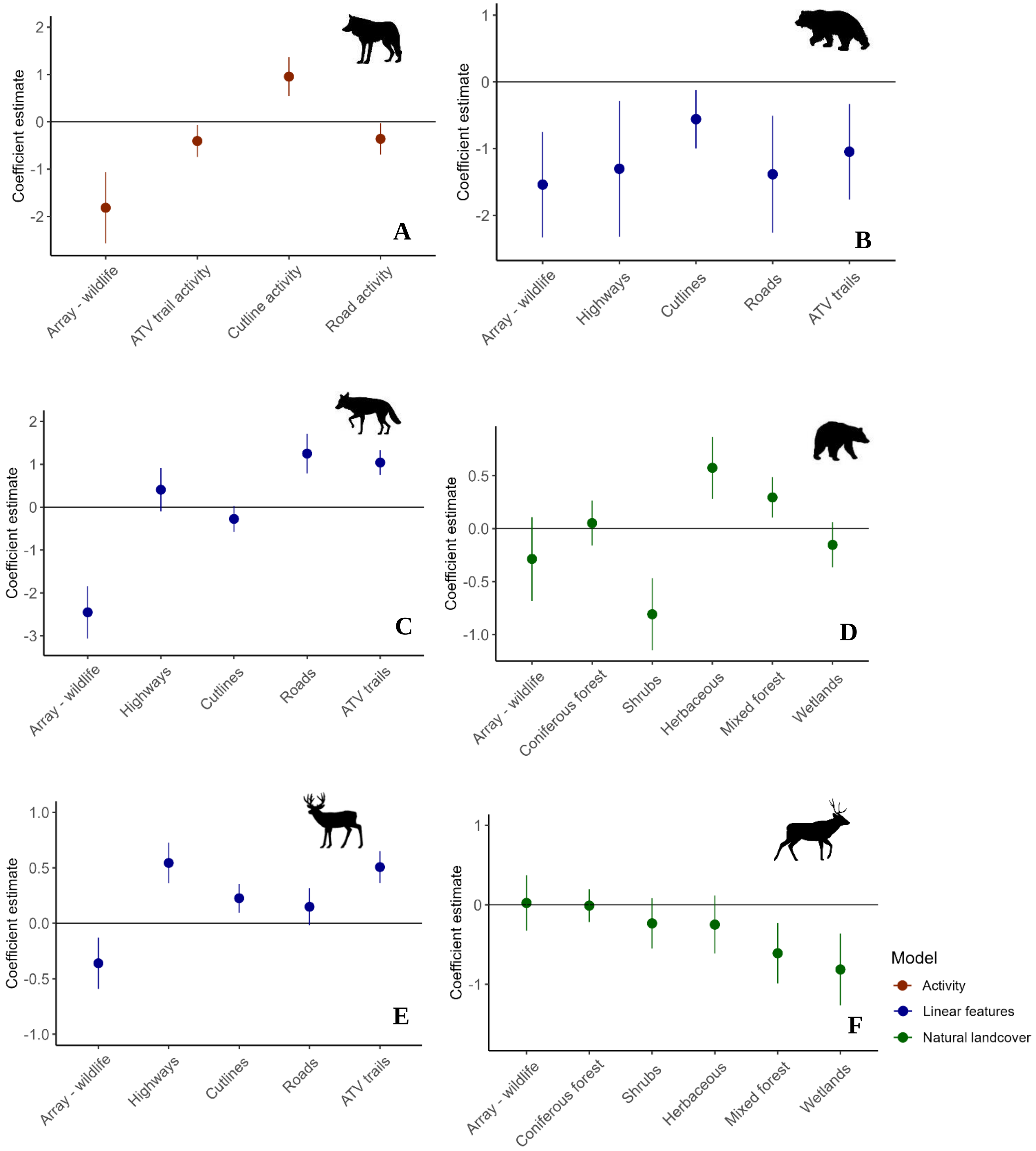

Figure 2.5. Coefficient plots of top ranked models in the peak season (June-October) for each of 6 species: A) wolf, B) grizzly bear, C) coyote, D) black bear, E) white-tailed deer, and F) mule deer.

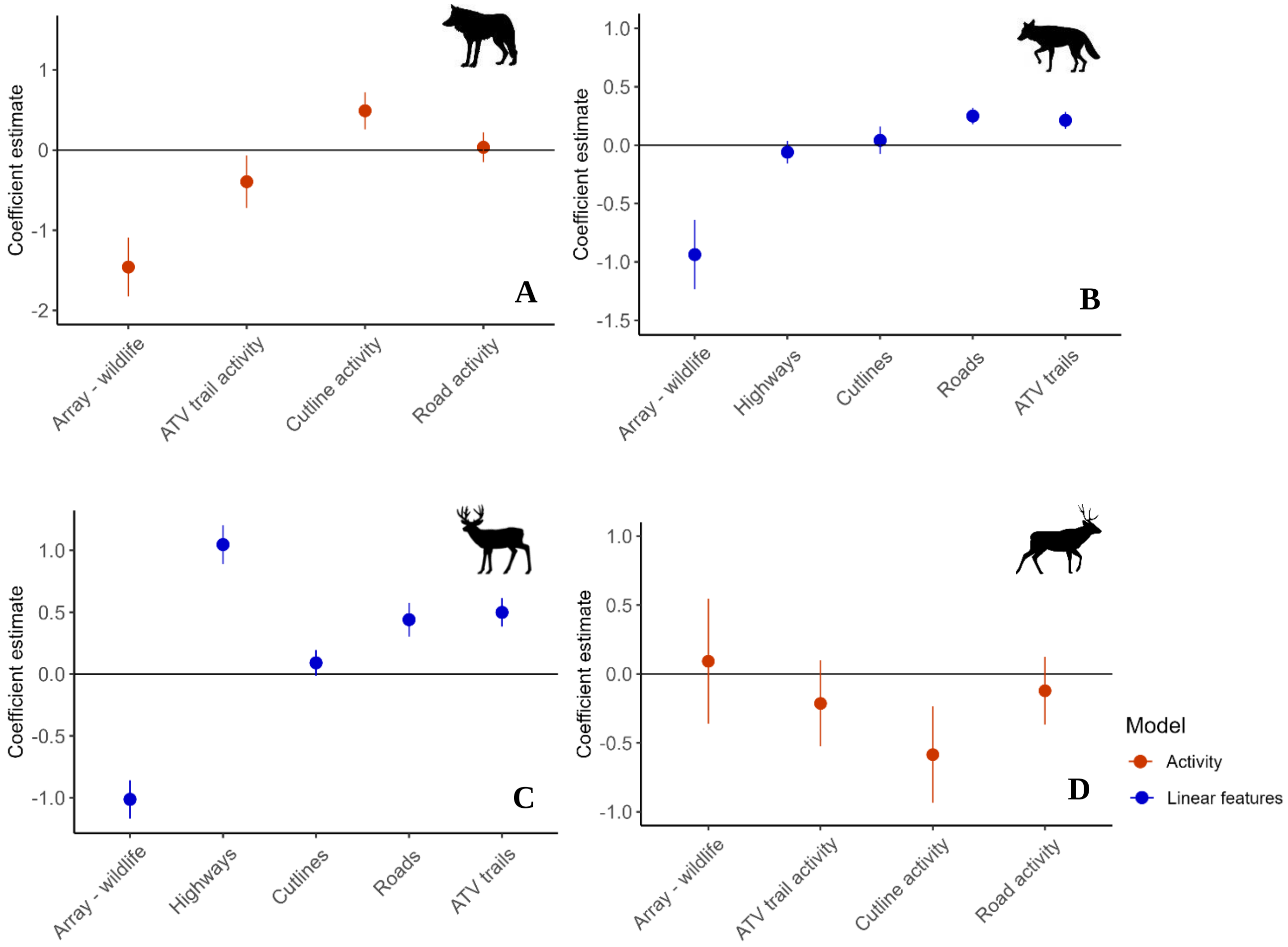

Figure 2.6. Coefficient plots of top ranked models in the off season (November-May) for each of 4 species: A) wolf, B) coyote, C) white-tailed deer, and D) mule deer.

Table 2.6. Top supported models from AICc analysis of generalized linear models used to explain mammal species occurrence in peak and off seasons using different model sets with covariates measured at a small buffer size (250-meter radius) and a large buffer size (2000-meter radius). Covariates in each model are listed in Table 3. Full AIC model selection results are listed in Table A2 in the Appendix.

Species	*Season*	*250m covariate buffer - top model*	*2000m covariate buffer - top model*
Wolf	Peak	Activity	Landcover
	Off	Activity	Landcover
Grizzly	Peak	Landcover	Linear features
Coyote	Peak	Activity	Linear features
	Off	Linear	Linear features
Black Bear	Peak	Linear features	Linear features
WTD	Peak	Linear features	Linear features
	Off	Linear features	Linear features
Mule Deer	Peak	Landcover	Landcover
	Off	Activity	Landcover

2.4 Discussion

Motorized recreation best explained the occurrence of wolves and mule deer, altering their spatial distributions; all other large mammals in this study were more affected by anthropogenic linear features, or variability in natural habitats. The spatial impact of motorised recreation was also constrained to smaller buffer sizes; at larger spatial scales, anthropogenic and natural landscape features were the predominant determinants of species distributions. In the question of "footprint versus footfall", there is a context-dependent influence of activity on linear features versus just linear features themselves. This effect seems to be significant only at smaller scales, and only for certain human disturbance-sensitive species. Neophobia, or fear of people, though shown to cause behavioural avoidance in many species (Hebblewhite et al., 2005; Larson et al., 2019; Naidoo & Burton, 2020), appears in the present study to be limited to most species temporarily avoiding human activity rather than abandoning areas completely. However, disturbance-sensitive species such as wolves may be disproportionately affected by recreation, and face indirect habitat loss in areas of high human use. Other studies investigating the role of motorized recreation have also posited that it is a finer scale disturbance primarily influencing species movement (Nickel et al., 2020; Scrafford et al., 2018), and that ultimately environmental landscape variables have a greater influence on species distributions (Naidoo & Burton, 2020). One implication is that management efforts should focus more on landscape alteration and restoration than regulating human activity to conserve most mammal species populations, but constraining the spatial extent of human activity may be important for conservation disturbance-sensitive species.

Landscape disturbance remains a major determinant of species distributions – in this study, linear disturbance features best explained three out of six species across peak and off seasons. Coyotes and white-tailed deer had positive associations with linear features, while grizzly bears had negative associations. Grizzly bears have been previously found to be negatively affected by anthropogenic disturbance (Nielsen et al., 2006; Sorensen et al., 2015), and have faced widespread range contractions (Laliberte & Ripple, 2004), whereas both coyote and white-tailed deer have increased in disturbed habitats (Hody & Kays, 2018; Latham et al., 2011). Anthropogenic disturbances have previously been found to be the major determinants of species occurrence in anthropogenically altered landscapes, with differential effects, positive and negative, across different species (Fisher & Burton, 2018; Heim et al., 2019; Shackelford et al., 2018; Suraci et al., 2021). Where the literature remains unclear on human activity effects, there is a large body of evidence to indicate that ongoing anthropogenic disturbance has substantial impacts on the mammal community (Laliberte & Ripple, 2004; Suraci et al., 2021; Tscharntke et al., 2012), causing species declines and altering predator-prey dynamics (Boutin et al., 2012; Fisher et al., 2022).

Wolves were the only species to consistently avoid areas with high motorized recreation intensity, avoiding high use roads and ATV trails in the peak season, and high use ATV trails in the off season. Wolves have been shown to be risk-averse towards people. They do not necessarily avoid anthropogenic disturbance (Pigeon et al., 2020), using linear features as a means of travel (Dickie et al., 2017). Wolves have, however, been found avoiding areas of high human use and human activity (Hebblewhite et al., 2005; Rogala et al., 2011). Throughout their range, wolves face mortality risk from human persecution (Baille-David, 2022; Hebblewhite & Whittington, 2020), perhaps explaining their risk aversion. Our findings are similar to Rogala et al. (2011), wherein wolves avoided areas of high human use at fine scales (<500m), though their study assessed the effects of hikers. Other risk-averse human avoiding species may show similar spatial responses to recreational use as wolves do; further investigation should be taken to see which species are impacted. I was only able to assess the impacts of motorized recreation in the present study; future research should assess whether similar patterns are found in areas of high intensity non-motorized use (ex. hiking, biking).

In contrast to their response to road and trail activity, wolves had a positive association with activity on cutlines. Cutline activity was generally lower than roads and ATV trails, potentially staying below thresholds wolves consider risky. Additionally, motorized activity on cutlines helps prevent vegetation regrowth, maintaining lines for travel (Hornseth et al., 2018; Pigeon et al., 2016). Cutlines with higher motorized activity levels are thus more likely to be better travel corridors. This effect may be heightened in the winter months, where motorized use of cutlines packs down snow, making for easier travel. Wolves' use of cutlines for more efficient travel has contributed to widespread declines of boreal caribou (*Rangifer tarandus caribou*) in industrialized landscapes by facilitating increased predation (Hebblewhite, 2017; Hervieux et al., 2014). Mule deer were the only other species with motorized activity as a best supported model, and only in the off season. The model results, however, do not indicate avoidance of motorized recreation; mule deer had no significant relationship to activity on roads or ATV trails, but were negatively associated with cutline activity, which had the lowest level of activity out of any features. This relationship may indicate that mule deer avoided high-activity cutlines to mitigate predation risk by wolves and suggests the hypothesis that human activity may be altering predator-prey interactions in this landscape. It is a somewhat opposite effect to the "predator shield" hypothesis posited by other studies, wherein predator avoidance of human activities provides prey with refugia close to areas of high human use or disturbance (Berger, 2007; Muhly et al., 2011; Rogala et al., 2011). In this specific case, human use of cutlines over the winter months provides them easier methods of travel, leading to avoidance by mule deer, a potential prey species.

Recreation is highly visible and prevalent in the Bighorn Backcountry and many other wilderness landscapes, but the impacts of this on species distributions have largely been unclear. This study demonstrates that for a disturbance-sensitive top predator, recreational use can cause spatial avoidance, and thus indirect habitat loss. This is important for the management of sensitive species, as recreational use may have a disproportionate impact on species with existing conservation threats and challenges. A management implication is that recreational use should be constrained to certain areas, rather than be widespread throughout a region, to manage habitat for sensitive species. In this study, due to data limitations, we were unable to assess the impacts of recreation on other neophobic species such as wolverine or caribou (Barrueto et al., 2022; M. Festa-Bianchet, 2011); the distributional impact of recreation should be assessed for these species as well to better understand the extent of spatial dislocation on the mammal community.

While managing for recreational use may be important, focusing conservation and restoration attentions and effort on mitigation may detract from a larger problem, which is ongoing industrial landscape conversion. The Bighorn is part of a large stretch of crown land areas in the foothills experiencing rapid and ongoing forest loss and landscape alteration in recent decades (Global Forest Watch Canada, 2014). Though ongoing human use, particularly motorized use, contributes to the maintenance of linear features by keeping them open and preventing regrowth (Hornseth et al., 2018; Pigeon et al., 2016), it is not the primary disturbance affecting most mammal distributions. Ongoing landscape disturbance affects the wider mammal community, while also expands the extent by which people can use the landscape, impacting disturbance-sensitive species. To manage habitat for disturbance-sensitive at-risk predators such as wolves, land managers should consider constraining motorized use to smaller spatial extents, but ultimately land management should also focus on limiting the footprint of ongoing development in order to minimize anthropogenic impact on mammal distributions.

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Chapter 3: The influence of protected areas on mammal distributions in Canada's Rocky Mountains

3.1 Introduction

Human development has substantially restructured landscapes, causing many cascading impacts on species diversity. Globally, 58% of terrestrial land has experienced moderate to intense pressure from anthropogenic landscape alteration (Williams et al., 2020). Anthropogenic landscape alteration takes place through conversion of natural landscapes to agricultural lands, urbanization, creation of roads, and industrial disturbances (Global Forest Watch Canada, 2014; Hansen et al., 2010; Williams et al., 2020). Historical and ongoing landscape change and human expansion has caused range contractions and population declines, and extinctions in many large mammal species (Cardillo et al., 2004; Laliberte & Ripple, 2004; Ripple et al., 2014). Landscape change also alters the ways in which species interact, and changes the structure of mammal communities (Ripple et al., 2014). Though most species are affected by landscape change, the ways in which they are affected vary. Many large carnivores are more negatively impacted by human activity and landscape change (Heim et al., 2019; Laliberte & Ripple, 2004), whereas for species such as white-tailed deer (*Odocoileus virginanus*) and coyotes (*Canis latrans*) that can thrive in disturbed environments, landscape change has allowed for substantial range expansions (Fisher & Burton, 2018; Hody & Kays, 2018; Nickel et al., 2020).

The influence of anthropogenic pressures on mammal communities varies greatly depending on the level of landscape protection. Protected areas (PAs) set aside for conservation and/or recreation – rather than landscape development –constitute *ca.* 15% of terrestrial land on earth (Maxwell et al., 2020). Globally, the PA network is key in maintaining species biodiversity (Coetzee et al., 2014), particularly mammal diversity (Baker, 2016; Chen et al., 2022). Many of the threats to species persistence, including ongoing industrial development and landscape change, hunting, poaching, and recreation, are regulated within PA boundaries (Gaston et al., 2008; Watson et al., 2014). In North America, PAs are instrumental in mitigating many of the anthropogenic mortality threats to at-risk species such as grizzly bears, wolverines, and wolves (Hebblewhite & Whittington, 2020; Heim et al., 2017; Lamb et al., 2020; Nielsen et al., 2004). The protection and maintenance of habitat patches with minimal human disturbance needed for broad-ranging mammal species is essential for their persistence (Laliberte & Ripple, 2004; Schneider, 2019; Stewart, Darlington, et al., 2019). Overall, the global PA network has helped greatly to mitigate the biodiversity crisis (Chen et al., 2022; Watson et al., 2014); still, more action is needed to ensure the protection of biodiversity, including protecting more landscapes, restoring degraded habitat, and developing a better understanding of how human activities inside and outside of PAS affect their ability to conserve species.

Though PAs are essential to maintaining biodiversity, their conservation effectiveness has been widely scrutinized. PA efficacy is dependent on area size, habitat quality within and surrounding the PA, and the level of human occupancy in the area (Gaston et al., 2008; Stewart, Volpe, et al., 2019; Wiersma & Simonson, 2010). Many PAs are expected to serve as economic and recreational spaces, with conservation being a competing priority (Watson et al., 2014). PAs that function as recreation centres may attract higher numbers of visitors to parks for ecotourism than those designated for conservation – possibly hindering their function in biodiversity conservation (Hebblewhite et al., 2005; Watson et al., 2014). Many PAs see high levels of human use (Buxton et al., 2019); even quieter forms of recreation, including non-motorized activities such as hiking, biking etc. can have strong impacts on mammal habitat use (Procko et al., 2022; Reed & Merenlender, 2008; Rogala et al., 2011) and change species interactions (Rogala et al., 2011). This was demonstrated during the COVID-19 pandemic, where the effects of park closures and reopening to the public altered how species used the landscape; animals were more likely to use roads and trails, and began avoiding human use areas more when parks were open to recreation (Anderson et al., 2023; Procko et al., 2022). Human use and activity within PAs can increase mortality risk for grizzly bears and wolves, through factors such as human-wildlife conflict or vehicle collisions (Cassidy et al., 2023; Nielsen et al., 2004). The effectiveness of PAs is also influenced by the larger environment around them (Hansen & DeFries, 2007), with species extinction risk increasing with increased disturbance around a PA (Parks & Harcourt, 2002). Landscape context is crucial; across a 5000-km^2 PA network, mammalian biodiversity was best explained by surrounding landscape disturbance, not by protected areas (Stewart, Volpe, et al., 2019). It can also be questioned whether PAs have been established in a way that effectively conserves habitat, defined as providing adequate niche space for all species in an area (Hanson et al., 2020). Some recently established PAs have anthropogenic disturbance densities within their borders that exceed thresholds for at-risk species of conservation concern (Smith et al., 2016). Considering these factors, the role of PAs in providing effective habitat to mammal species remains a prime area of research.

In this chapter, I investigated the role of protected areas in predicting mammal occurrence, and whether PAs could be a stronger predictor of species occurrence over landscape disturbance and natural landcover. The Rocky Mountains of Alberta are a part of the largest remaining intact mountain ecosystem on earth, and an important continental trans-boundary wildlife habitat and connectivity network (Hebblewhite et al., 2021). The Rocky Mountains provide important habitat to at-risk predators such as grizzly bears and wolverine (Barrueto et al., 2022; Steenweg et al., 2016), wolves (Hebblewhite & Whittington, 2020), and many other large mammals (Heim et al., 2019; Steenweg et al., 2019). While the Rocky Mountains have seen an increase in protected area coverage over the last three decades (Hebblewhite et al., 2021), the adjacent mountains and foothills in the eastern side of the range have concurrently seen a rapid acceleration in industrial development, mainly through forestry and oil and gas mining and exploration (Global Forest Watch Canada, 2014). The Foothills is comprised of a mosaic of crown land areas, national and provincial parks, and wildlands (Figure 3.1). The Rocky Mountains and Foothills are also very popular for tourism and recreation in Alberta, attracting nearly 5 million visitors in 2019 (Government of Alberta, 2019). This complex landscape has a wide variety of management, disturbance, and conservation efforts taking place while supporting a diverse mammal community, making it an excellent model system to examine the role of area protection in species distributions.

To measure mammal occurrence in Alberta's Rocky Mountains and Foothills, I combined serial mammal detection data from wildlife camera arrays deployed across PAs and unprotected areas (Figure 3.1). Wildlife cameras are an effective tool allowing for long-term remote data collection (O'Connell et al., 2011; Steenweg et al., 2016). When set up effectively to maximize detection probability, they can facilitate the monitoring of several species simultaneously (Burgar et al., 2019; Rich et al., 2017). Sampling designs that adequately capture landscape variability allow for large-scale assessment of species' relationships to landscape variables (Burton et al., 2015).

To assess the importance of PAs in determining mammal species distributions, I assessed the occurrence of six mammal species: grizzly bears (*Ursus arctos horriblis*), wolves (*Canis* *lupus*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), white-tailed deer (*Odocoileus virginanus*) and mule deer (*Odocoileus hemionus*). I chose to assess multiple species as responses to anthropogenic disturbance vary greatly; some species, such as grizzly bears and wolves, are sensitive to disturbance and have experienced population declines (Laliberte & Ripple, 2004), while coyotes and white-tailed deer thrive in disturbed areas and have used anthropogenic disturbance to expand into previously unoccupied habitats (Fisher et al., 2020; Hody & Kays, 2018; Nickel et al., 2020). Black bears can also use anthropogenic disturbance features such as roads for forage and travel (Brody & Pelton, 1989; Suraci et al., 2021). Mule deer, in contrast to WTD, have been negatively impacted by anthropogenic landscape change (Northrup et al., 2015). I also assessed mammal species diversity in the form of species richness, as there is mixed and scale-dependent evidence on how PAs influence mammalian diversity (Chen et al., 2022; Stewart, Volpe, et al., 2019). I hypothesized that protected areas would best explain the occurrence of species that are most sensitive to human disturbance, and respond most strongly to landscape management through area protection. I predicted that grizzly bears and wolves would select for protected areas, favoring the lower disturbance areas with more restricted levels of human activity. I hypothesized that anthropogenic landscape disturbance would be the driving factor shaping the occurrence of most mammal species in the Rocky Mountains, with species responding differentially to changed habitats. I predicted that landscape disturbance would best explain the occurrence of white-tailed deer, coyotes, black bears, and mule deer, with white-tailed deer and coyotes having positive relationships to most disturbance features, black bears selecting for roads, and mule deer avoiding disturbance features. I predicted that anthropogenic landscape disturbance would best explain species richness counts, as anthropogenic disturbance affects most mammal species distributions (Fisher & Burton, 2018).

3.2 Methods

3.2.1 Study Area

Mammals were surveyed across the central Rocky Mountains in Alberta, Canada, the front ranges of the Western Cordillera. The study area encompassed two national parks, various provincial parks, and developed crown land areas, spanning roughly 32,000 km^2 (Figure 3.1). Data were used from three regional camera arrays (Table 3.1): Jasper and Banff National Parks (NP), highly protected landscapes at the heart of the Rocky Mountains; Kananaskis Country (KC), a mosaic of provincially protected areas and crown land across the Rocky Mountains and Foothills; and the Bighorn Backcountry (BB), a region containing mostly crown land used for resource extraction and recreation stretching out from the Rocky Mountains into the Foothills. The study area encompasses a diverse range of habitats over multiple natural subregions, including alpine, subalpine, montane, and foothills. Predominant vegetation includes dwarf birch (*Betula nana*) and bog birch (*Betula pumila*) at high elevations, lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*) at subalpine elevations, Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*) at montane elevations, and aspen, white spruce, black spruce (*Picea mariana*), and lodgepole pine in the foothills (Natural Regions Committee, 2006). The region supports a diverse mammal community, with carnivore species such as wolverine (*Gulo gulo*), grizzly bear (*Ursus arctos horriblis*), wolves (*Canis lupus*), coyotes (*Canis latrans*), martens *(Martes americana*), and ungulates such as elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) (Weaver, 2017).

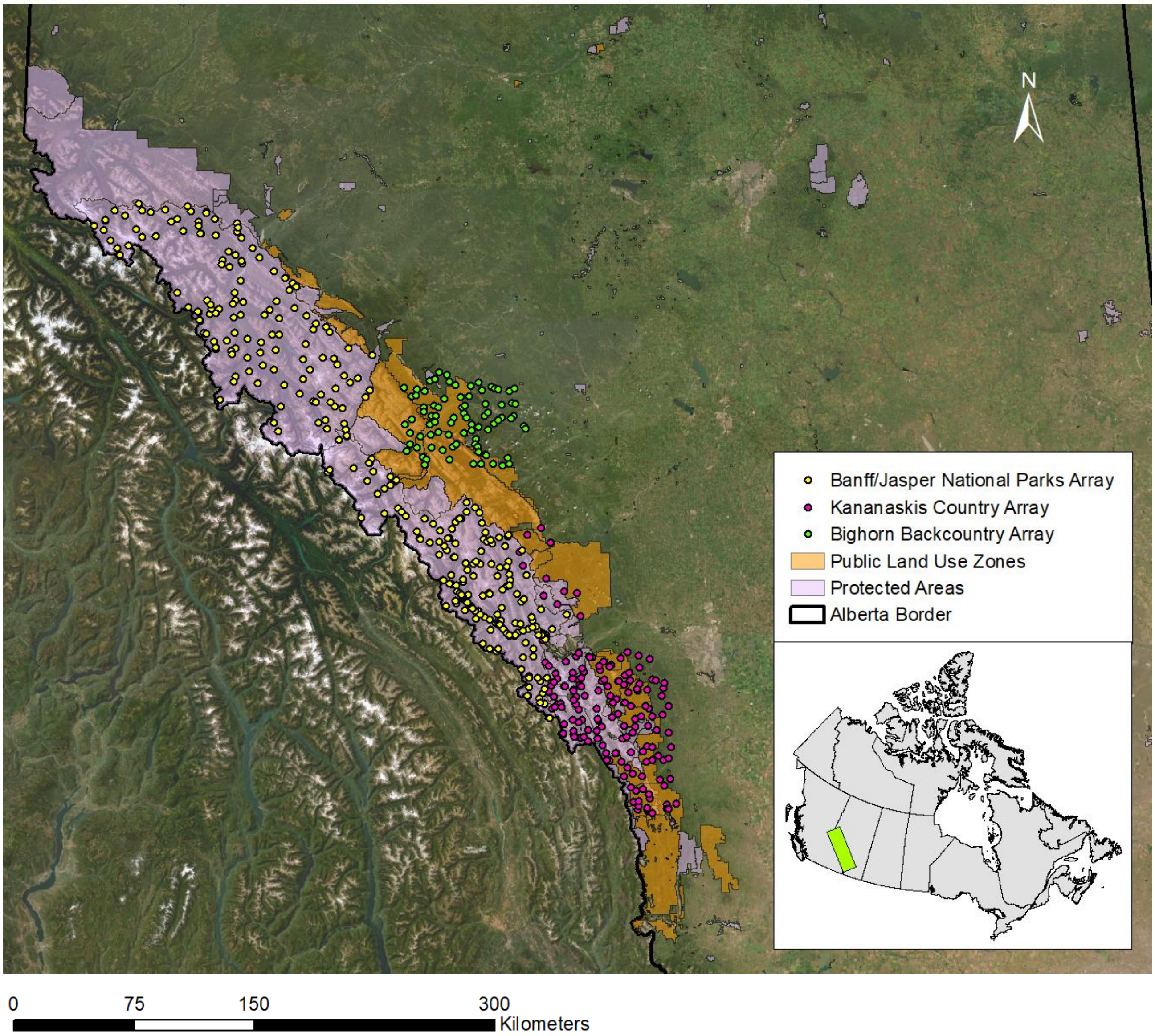

Figure 3.1. Map of the study area in Alberta's Rocky Mountains, showing the locations of protected areas (in purple), Public Land Use Zones (in orange) and wildlife cameras in Jasper and Banff National Parks (yellow), the Bighorn Backcountry (green), and Kananaskis Country (pink). The inset map shows the study area location within Canada.

Table 3.1. Average percent coverage landcover values in 2500-meter radius buffers around wildlife camera sites in each of the three study areas (Banff/Jasper National Parks (NP), Kananaskis Country (KC), and Bighorn Backcountry (BH)) used in this analysis.

		NP		*KC*		*BH*	
Covariate	*Definition*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Elevation	Elevation at camera sites (m)	1745.1	306.9	1618.2	216.1	1518.2	216.3
Anthropogenic landcover	% cover of all anthropogenic features, including all roads, cutlines, trails, cutblocks, wellsites, railways	0.8	1.6	7.9	10.0	11.7	13.2
Coniferous forest cover	% cover of coniferous forest with >80% crown coverage	46.2	22.7	49.7	25.8	68.0	17.7
Protected area cover	% cover of all PA types	97.2	9.0	49.1	46.2	2.7	8.5

3.2.2 Wildlife Camera Data

I used data from motion-activated camera traps (RECONYX models PC900, HPF2X; Reconyx, Holmen, WI), compiling data from three separate camera arrays (Figure 3.1; Table 3.2). Banff and Jasper National Parks have a long-term Ecological Integrity Monitoring array established in 2012 (Steenweg et al., 2019); I used years 2017-2018, including 186 camera sites. The KC array was established from 2012-2014, as a collaborative effort between University of Victoria and the Government of Alberta (Heim, 2015); I used data from 2013-2014, including 89 camera sites. The BB array was established in 2019 as a collaborative effort between University of Victoria and Innotech Alberta; I processed and used 2019-2020 data from this array, including 81 sites. Arrays had similar deployment designs; all studies used a systematic grid deployment design, with Banff and Jasper arrays using 10 km^2 grids, and KC and BB arrays using 6 km^2 grids. All cameras were spaced with a minimum of 1 km between sites. Cameras were placed on hiking trails and game trails in National parks and on game trails and seismic lines in the KC and BB to maximize probability of detection given presence. One year of continuous data was subset from each array for analysis, from October to the following September. Sites where cameras died early and sites that were <1 km apart, were omitted. The final analysis included 89 cameras from KC surveying 22,705 trap days, 81 cameras from BB surveying 25,756 trap days, and 186 cameras from Banff and Jasper National parks surveying 57,898 trap days, totaling 356 unique camera sites and 106,359 trap days. This resulted in the following independent detection counts: 1383 grizzly bear, 1191 wolf, 1095 coyote, 954 black bear, 4129 white-tailed deer, and 1295 mule deer (Table 3.2). Species richness counts ranged from 0-9 species per month, with an average of 2.25 species (sd =1.90) in the summer months (May-September) (Table 3.3). Camera data were process and tagged using Timelapse and Timelapse 2 software (Greenberg, 2021) and imported into R (R Core Team, 2021) for analysis.

3.2.3 Species response variables

Species detection events were considered independent when they occurred a minimum of 30 minutes apart (Rovero & Zimmermann, 2016); this was to help eliminate samples wherein the same animal or group of animals was photographed repeatedly over a short period of time. For each species in the analysis, I summarized independent detection events into monthly bins to obtain a proportional binomial response variable, with a species being detected (1) or not (0) monthly at each site. I chose to use a monthly bin across 12 months of data as this has been sensitive enough to detect variation in site use and providing a balanced distribution suitable for modelling in other mammal analyses (Fisher & Burton, 2018; Heim et al., 2017). For species richness, I used monthly bins, calculating the number of mammal species detected at camera sites within each month. For species richness counts, I included all observed mammal species except bats, domestic cows, and feral horses.

Table 3.2. Total counts of independent detections (detections that were ≥30 minutes apart), and proportion of months present (all months of occurrence summed across all camera sites for each array) for the three study areas used in this analysis – Kananaskis Country (KC) (89 sites), Bighorn Backcountry (BB) (81 sites), and Jasper and Banff National Parks (NP) (186 sites). Note: for bear species, proportion of months present includes summer months only to account for seasonal inactivity (May-September).

		Wolf	*Grizzly bear*	*Black bear*	*Coyote*	*White-tailed deer*	*Mule deer*
KC	Independent dets	67	277	267	705	1284	255
	Proportion months present	0.029	0.23	0.29	0.27	0.29	0.11
BH	Independent dets	82	66	171	189	1669	350
	Proportion months present	0.057	0.078	0.21	0.95	0.41	0.13
NP	Independent dets	1042	1040	516	201	1176	690
	Proportion months present	0.18	0.46	0.22	0.29	0.16	0.10
	Independent dets - total	**1191**	**1383**	**954**	**1095**	**4129**	**1295**

Table 3.3. Average monthly species richness counts in summer (May-September) and winter (October-April) seasons for the three study areas used in this analysis three study areas used in this analysis – Kananaskis Country (KC) (89 sites), Bighorn Backcountry (BB) (81 sites), and Jasper and Banff National Parks (NP) (186 sites) and across all arrays.

Array	*Species richness range*	*Species richness mean (summer)*	*Species richness SD (summer)*	*Species richness mean (winter)*	*Species richness SD (winter)*
Kananaskis Country (KC)	0-8	2.64	1.92	1.32	1.46
Bighorn Backcountry (BB)	0-6	1.74	1.31	1.4	1.36
Jasper and Banff (NP)	0-9	2.69	1.99	1.06	1.34
All arrays combined	0-9	2.25	1.9	1.02	1.21

3.2.4 Landscape covariates

To assess how landscape variables affected species occurrence, I used Landsat and administrative boundary landcover datasets. To account for possible scale dependence in explaining variability of each species, I extracted landscape feature variables from spatial data coverages (*q.v.*) in increasing buffer sizes from 250-m to 5000-m radii, at 250-m increments (Fisher et al., 2011). I did not consider overlapping buffers at larger buffer sizes to be problematic as they do not substantially alter the degree of autocorrelation between variables (Zuckerberg et al., 2020). To weigh evidence on contrasting models to assess which landcover attributes best explain species presence, I used three competing models using corresponding sets of landscape covariates: a protected areas model, an anthropogenic features model, and a natural landcover model. I also included a model containing season only as a null.

For the protected areas model, I extracted percent cover of PAs, as well as distance to PA boundary from both within and outside of PAs (Table 3.4; Figures 3.2 and 3.3). I obtained the PA boundary by dissolving together the boundaries from the continuous connected PA network, both national and provincial, across the Rocky Mountains. To generate this boundary variable, I eliminated small PA (Provincial Parks and Recreation Areas <7 km^2) scattered outside of the larger park complex to best represent the boundary between protected and unprotected areas (Figure 3.3). For PA coverage, I separated PA into different type classes (Figure 3.2), as not all PAs in this region function equally (Table 3.5). The various provincial PA and NP have differences in average spatial coverage, and widely varied management practices and human activity permissions (Table 3.5). I also included Public Land Use Zones (PLUZ) as an area type; though these areas are considered crown land and not explicitly PA, they still regulate activity and industrial development more than general crown lands (Province of Alberta, 2020). I obtained all PA coverage data from the Alberta Government Open Data Portal (https://open.alberta.ca/opendata). For the anthropogenic landscape features model, I obtained data on most linear and block features from ABMI's 2017 Human Footprint Inventory (ABMI, 2017). I also obtained trail data for Parks Canada and for Alberta provincial parks from government databases (pers. comm.) (Table 3.4). For the natural landscape features model, I used a Landsat dataset classified into habitat types (Nijland et al., 2015) (Table 3.4). In all models I included season as a fixed effect to account for seasonal variation in species detection, with most species having lower detectability in the winter. This variable had two levels, summer (May-September) or winter (October-April), to represent snow-free and snow-present periods in the Rocky Mountains. Because both black and grizzly bears are inactive over the winter months, I only used summer data, and thus did not include season in their models.

For all landscape variables, collinearity between variables was assessed, and variables with a collinearity of >0.7 (Zuur et al., 2010) were deemed too highly collinear and either combined with another variable if appropriate (ex. combining dense and moderate coniferous forest, transmission and pipelines) or removed from analysis. Variables were then scaled to have a mean of 0 and SD of 1 for more accurate comparisons of coefficient estimates.

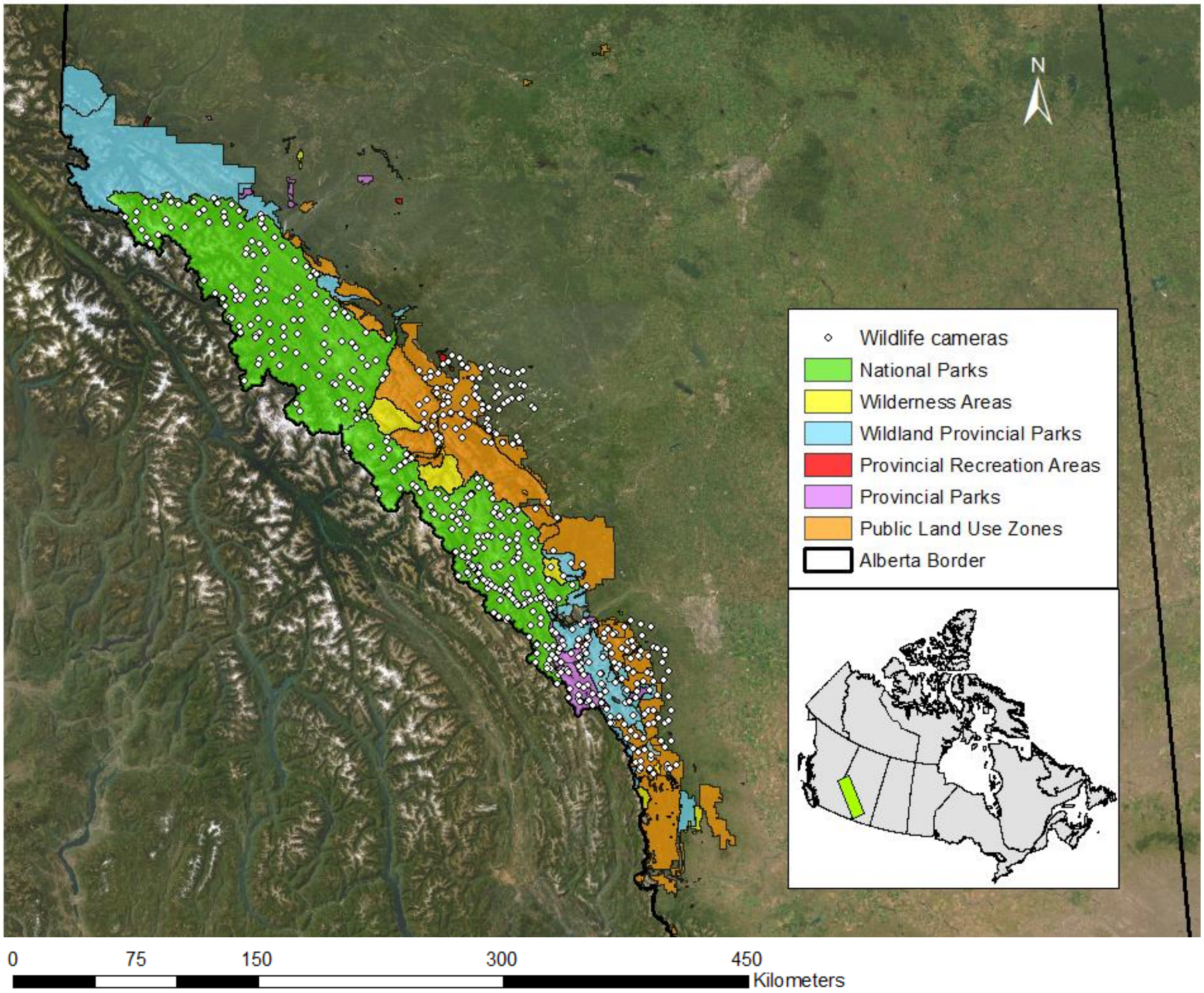

Figure 3.2. Map of the study area in Alberta's Rocky Mountains, showing the locations and coverage of the different protected area types and one crown land type (Public Land Use Zones) included in the wildlife models. All study camera sites are shown in white dots. The inset map shows the study area location within Canada.

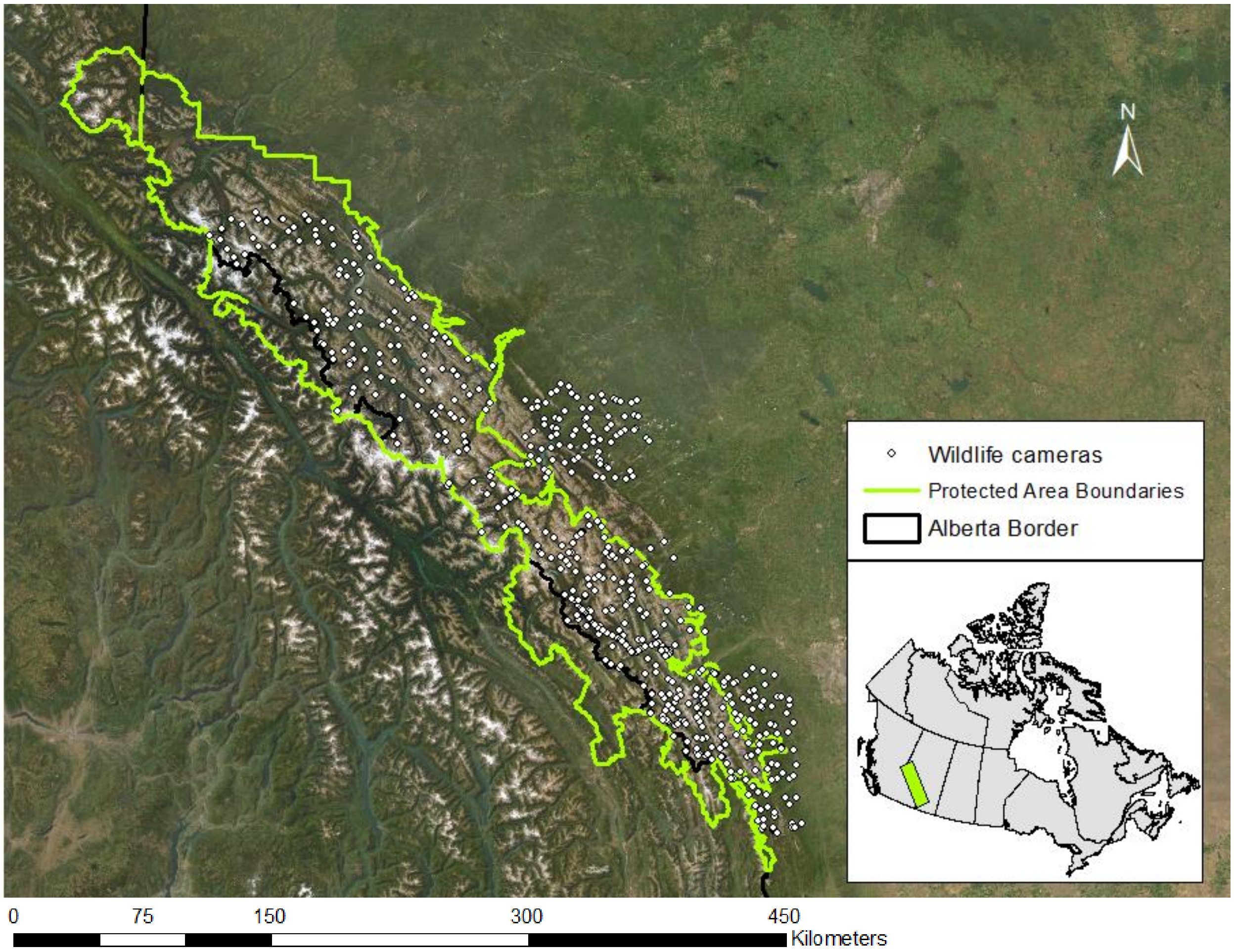

Figure 3.3. Map of the study area in Alberta's Rocky Mountains, showing the protected area boundary that is formed by the continuous set of national and provincial protected areas in the Rocky Mountains. Distance to boundary was a covariate included in the wildlife models. All camera study sites are shown in white dots. The inset map shows the study area location within Canada.

Table 3.4. Descriptions of each model covariate, grouped by model type, used in wildlife models.

Variable type	*Covariate*	*Description*
Anthropogenic features	Roads	% cover of all roads and roadside berms
	Well sites	% cover of all active and inactive well pads
	Cutblocks	% cover of forest harvest cutblocks
	Cutlines	% cover of seismic lines and other cutlines
	Pipelines	% cover of pipeline and transmission line features
	Motorized trails	% cover of trails permitting motorized recreational use
	Non-motorized trails	% cover of trails permitting non-motorized recreational use
	railways	% cover of railway tracks
Natural landscape features	Coniferous forest	% cover of forest with conifer in over 80% of crown
	Mixed forest	% cover of broadleaf and mixed crown cover forest
	Wetland	% cover treed and open wetlands
	Herb/Shrub	% cover of herbaceous and shrubland cover
Protected areas	Distance to PA boundary (in)	For sites inside of protected area boundary, distance to the continuous PA boundary formed by Alberta's Rocky Mountain PA complex (0 for sites outside of PA)
	Distance to PA boundary (out)	For sites outside of protected area boundary, distance to the continuous PA boundary formed by Alberta's Rocky Mountain PA complex (0 for sites inside of PA)
	PA type (NP, WA_all, PP, WPP, PRA, PLUZ)	% cover of each PA category type; see table X for PA type information
Season	Season	Fixed effect controlling for season, with two levels: summer (May-September) and winter (October-April)

Table 3.5. Descriptions of each protected area type used in the protected areas model, including area covered by each PA type in the study area, mean size of the PA types within the study area, and general characteristics of how each area type is managed. Information was obtained from national and provincial parks acts and regulations (Alberta Government, 2002, 2006, 2014, 2020; Government of Canada, 2023; Province of Alberta, 2020)

Variable name	*Area type*	*# in study area*	*Area coverage in study area (km^2)*	*Mean individual area size in study area (km^2)*	*Management characteristics*
NP	National Park	2	18,083	9041	Large parks; federally managed; focus on ecological conservation and facilitating public enjoyment and recreation; no hunting, no motorized activity, no plant removal; non-motorized recreation common
WA	Wilderness Areas, Ecological Reserves, Natural Areas, Heritage Rangelands	16	1,295	81	Small-medium sized parks; provincially managed; classified due to unique ecological characteristics; focus on ecological preservation; foot access only
WPP	Wildland Provincial Park; Willmore Wilderness Park	10	7,933	793	Large parks; provincially managed; focus on ecological conservation and backcountry recreation; nonmotorized recreation common, motorized recreation and hunting allowed in some parks
PP	Provincial Park	14	1,057	76	Small-medium parks; provincially managed; focus on facilitating front country recreation; nonmotorized recreation common, motorized recreation and hunting allowed in some parks
PRA	Provincial Recreation Area	123	123	1.3	Small areas; provincially managed; facilitating a wide range of recreational activities; often access points to adjacent crown lands
PLUZ	Public Land Use Zones	61	10,860	178	Large areas; provincially managed; crown land, not strictly PAs; new industrial development is not common, but sometimes allowed; facilitating human uses, including various types of recreation and hunting

3.2.5 Model constructs:

I modeled individual species occurrence using species' proportional binomial response in a generalized linear model (GLM) with a binomial distribution (logit link function). To model species richness, monthly richness count variables were used in a GLM with a Poisson distribution (log link function). To determine the optimal spatial scale with which to run models at for each species and for species richness, I used a global model with all variables from all models at spatial scales from 250-m to 5000-m radius at 250m increments. I used Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) to determine which spatial scale had the strongest explanatory power for each species. The highest ranked spatial scale was then used for analysis. If top models were within 2 AICc of each other, the smaller spatial scale model was chosen. To assess which set of landscape variables best explained species occurrence I used three competing models corresponding with different hypotheses (Table 3.4); a protected areas model, an anthropogenic landscape disturbance model, and a natural landcover model. I used AICc to compare models in an information-theoretic framework for each species and for species richness, choosing the top model as the one having the lowest AICc ranking (Burnham & Anderson, 2002). If top models were <2AICc apart, the most parsimonious model was considered the top model. K-fold cross validation was performed on all models using the *boot* package in R (Canty & Ripley, 2021).

3.3 Results

Protected area coverage best explained the occurrence of four out of the six assessed species: wolves ($AICc_w = 1$), grizzly bears ($AICc_w = 1$), coyotes ($AICc_w = 1$), and mule deer ($AICc_w = 0.999$). Conversely, the proportion of anthropogenic landscape features around camera sites best explained variability in occurrence of black bears ($AICc_w = 1$) and white-tailed deer ($AICc_w = 1$). Species richness counts were best explained by human features as well ($AICc_w = 1$). Natural landcover features were not the top model for any species in the analysis (Table 3.6). K-fold cross-validation estimates for all species and all models are listed in the appendix (Table B1).

3.3.1 Protected areas explained predator occurrences better than development or natural habitat

Wolves were positively associated with National Parks (NP; $\beta_{NP} = 1.71\pm0.21$, $p = 1.09E\text{-}15$), Wilderness Areas (WA; $\beta_{WA} = 0.18\pm0.04$, $p = 9.36E\text{-}06$), and Provincial Parks (PP; $\beta_{PP} = 0.42\pm0.13$, $p = 0.001$) (Figure 3.4). They were also positively associated with the Public Land Use Zones (PLUZ; $\beta_{PLUZ} = 0.36\pm0.12$, $p = 0.004$), a type of crown land outside of PAs subject to development. Grizzly bears were positively associated with NP ($\beta_{NP} = 0.55\pm0.2$, $p = 0.0049$), and negatively associated with WA ($\beta_{WA} = -0.17\pm0.7$, $p = 0.015$) (Figure 3.4).

Both wolves and grizzlies had significant relationships to distances in and out of PA boundary. Surprisingly, both species had negative relationships to increasing distance inside of PA boundary (wolves, $\beta_{DistanceIn} = -0.31\pm0.06$, $p = 2.72E\text{-}07$; grizzly bears, $\beta_{DistanceIn} = -0.42\pm0.08$, $p = 2.41E\text{-}08$); wolves, in spite of a strong positive association, also had a positive relationship with distance outside of PA boundary ($\beta_{\text{DistanceOut}}$ = 0.56±0.14, p = 3.40E-05) while grizzlies had a negative relationship with distance outside of PA boundary ($\beta_{\text{DistanceOut}}$ = -0.96±0.17, p = 4.64E-08) (Figure 3.6).

Though coyotes had protected areas as a top model, the relationships to PA were largely negative. Coyotes were negatively associated with WA (βWA = -0.19±0.06, p = 0.002), PP (β_{PP} = -0.20±0.08, p = 0.010), and NP (β_{NP} = -1.25±0.15, p = 5.41E-17) (Figure 3.2). Similarly to grizzlies, coyotes had a negative relationship to both distance inside and outside of PA boundary ($\beta_{\text{DistanceIn}}$ = -0.41±0.12, p = 0.001; $\beta_{\text{DistanceOut}}$ = -0.61±0.09, p = 3.26E-12) (Figure 3.4).

Mule deer were positively associated with WA (β_{WA} = -0.17±0.7, p = 0.015), and negatively associated with PP (β_{PP} = 0.42±0.13, p = 0.001) (Figure 3.4).

3.3.2 Anthropogenic landscape features – best explaining anthropophilic species and species diversity

Black bears had positive associations with the linear features roads and pipelines (β_{road} = 1.03±0.21, p = 5.74E-07; β_{pipeline} = 0.63±0.24, p = 0.008) and negative associations with wellsites and seismic lines (β_{well} = -0.64±0.27, p = 0.016; β_{seismic} = -0.32±0.14, p = 0.023) (Figure 4). White-tailed deer had positive associations with several linear features, including roads, pipelines, seismic lines, motorized trails, and railways (β_{road} = 0.68±0.06, p = 1.62E-26; β_{pipeline} = 0.14±0.07, p = 0.034; β_{seismic} = 0.35±0.05, p = 2.14E-11; $\beta_{\text{mototrail}}$ = 0.22±0.05, p = 1.40E-05; β_{railway} = 0.16±0.05, p = 0.001) (Figure 3.5).

Species richness counts were positively associated with pipelines, seismic lines and non-motorized trails (β_{pipeline} = 0.45±0.05, p = 1.27E-18; β_{seismic} = 0.12±0.03, p = 9.04E-05;

$\beta_{\text{nonmototrail}}$ = 0.09±0.01, p = 1.23E-33), and negatively associated with roads, wellsites, and cutblocks (β_{road} = -0.18±0.05, p = 0.00011; β_{well} = -0.23±0.06, p = 4.42E-05; β_{cutblock} = -0.06±0.02, p = 0.0034) (Figure 3.5).

Table 3.6. Full AICc results from generalized linear models used to explain mammal species occurrence and mammal species richness using different model sets. Covariates in each model are listed in Table 4. df is degrees of freedom; LL is the log-likelihood; ΔLL is delta log-likehlihood. K-fold cross-validation results for all models are listed in Table B1 in the Appendix.

Species	*Model*	*AICc*	*dAICc*	*AICcw*	*df*	*LL*	*Δ LL*
Wolf	**Protected areas**	**1805.61**	**0**	**1**	**10**	**-892.65**	**138.56**
	Anthropogenic landcover	1886.28	80.67	3.03E-18	10	-932.99	98.22
	Natural landcover	2044.60	238.99	1.27E-52	6	-1016.24	14.97
	Null	2066.44	260.83	2.30E-57	2	-1031.21	0
Grizzly bear	**Protected areas**	**1216.34**	**0**	**1**	**9**	**-598.91**	**147.84**
	Anthropogenic landcover	1249.61	33.27	5.97E-08	9	-615.55	131.21
	Natural landcover	1376.94	160.60	1.34E-35	5	-683.38	63.37
	Null	1495.52	279.18	2.38E-61	1	-746.76	0
Coyote	**Protected areas**	**1687.28**	**0**	**1**	**10**	**-833.48**	**208.95**
	Anthropogenic landcover	1713.53	26.25	1.99E-06	10	-846.61	195.83
	Natural landcover	1851.56	164.29	2.12E-36	6	-919.72	122.71
	Null	2088.88	401.61	6.20E-88	2	-1042.43	0
Black bear	**Anthropogenic landcover**	**1133.71**	**0**	**1**	**9**	**-557.60**	**60.87**
	Natural landcover	1162.80	29.09	4.83E-07	5	-576.31	42.15
	Protected areas	1236.29	102.58	5.31E-23	9	-608.89	9.58
	Null	1238.94	105.23	1.41E-23	1	-618.47	0
White-tailed deer	**Anthropogenic landcover**	**2587.01**	**0**	**1**	**10**	**-1283.35**	**290.02**
	Natural landcover	2727.11	140.10	3.78E-31	6	-1357.50	215.88
	Protected areas	2771.09	184.08	1.07E-40	10	-1375.39	197.98
	Null	3150.76	563.75	3.83E-123	2	-1573.37	0
Mule deer	**Protected areas**	**1692.25**	**0**	**0.999**	**10**	**-835.97**	**26.54**
	Natural landcover	1706.12	13.87	0.001	6	-847.00	15.51
	Anthropogenic landcover	1710.33	18.08	0.0001	10	-845.01	17.50
	Null	1729.04	36.79	1.02E-08	2	-862.51	0
Species richness	**Anthropogenic landcover**	**14084.86**	**0**	**1**	**10**	**-7032.41**	**155.19**
	Protected areas	14250.50	165.64	1.08E-36	10	-7115.23	72.37
	Natural landcover	14274.95	190.09	5.29E-42	6	-7131.47	56.13
	Null	14379.20	294.33	1.22E-64	2	-7187.60	0

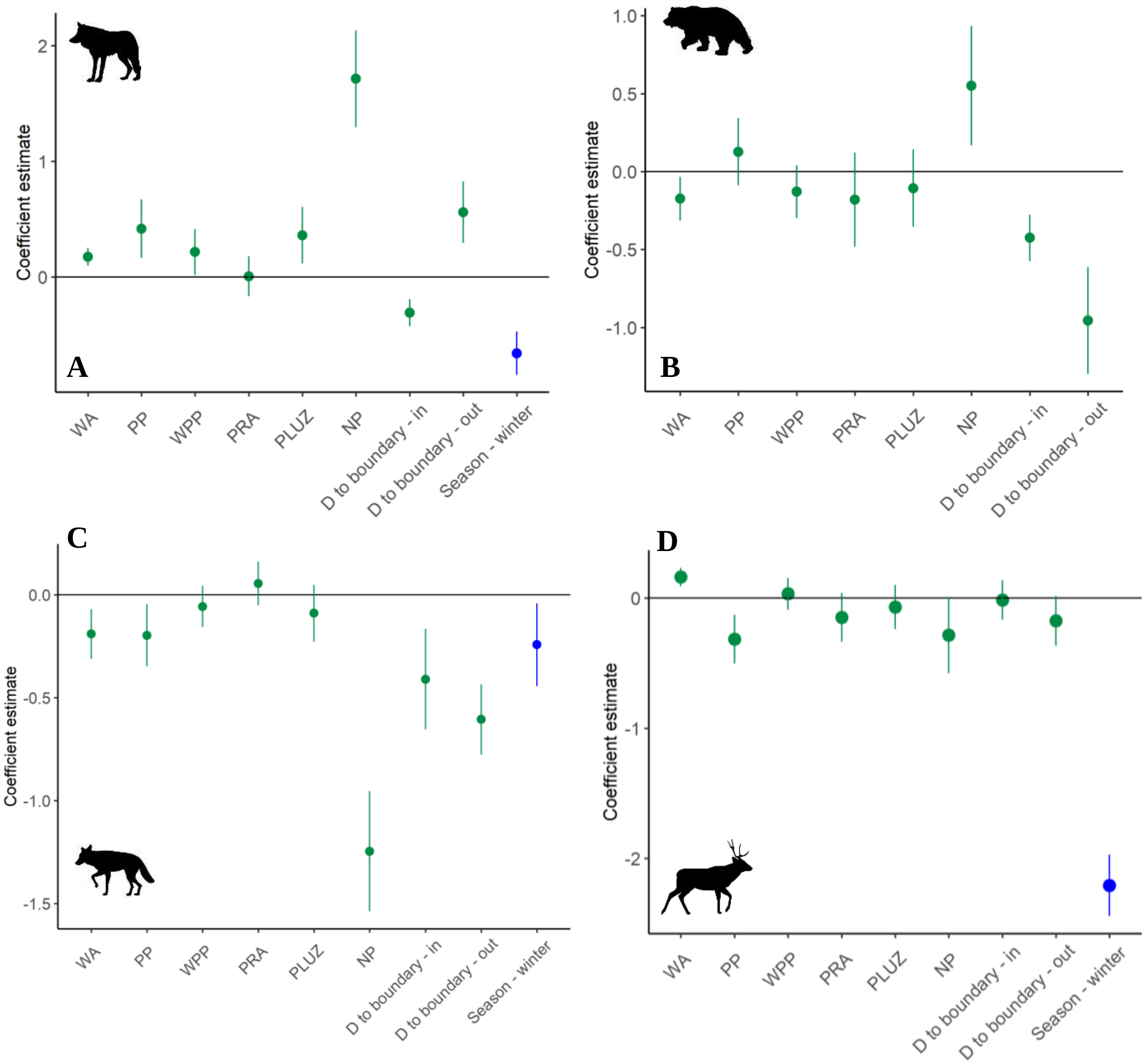

Figure 3.4. Coefficient plots from top ranked models for each of four species: A) wolves, B) grizzly bears, C) coyotes and D) mule deer, all species best explained by protected areas.

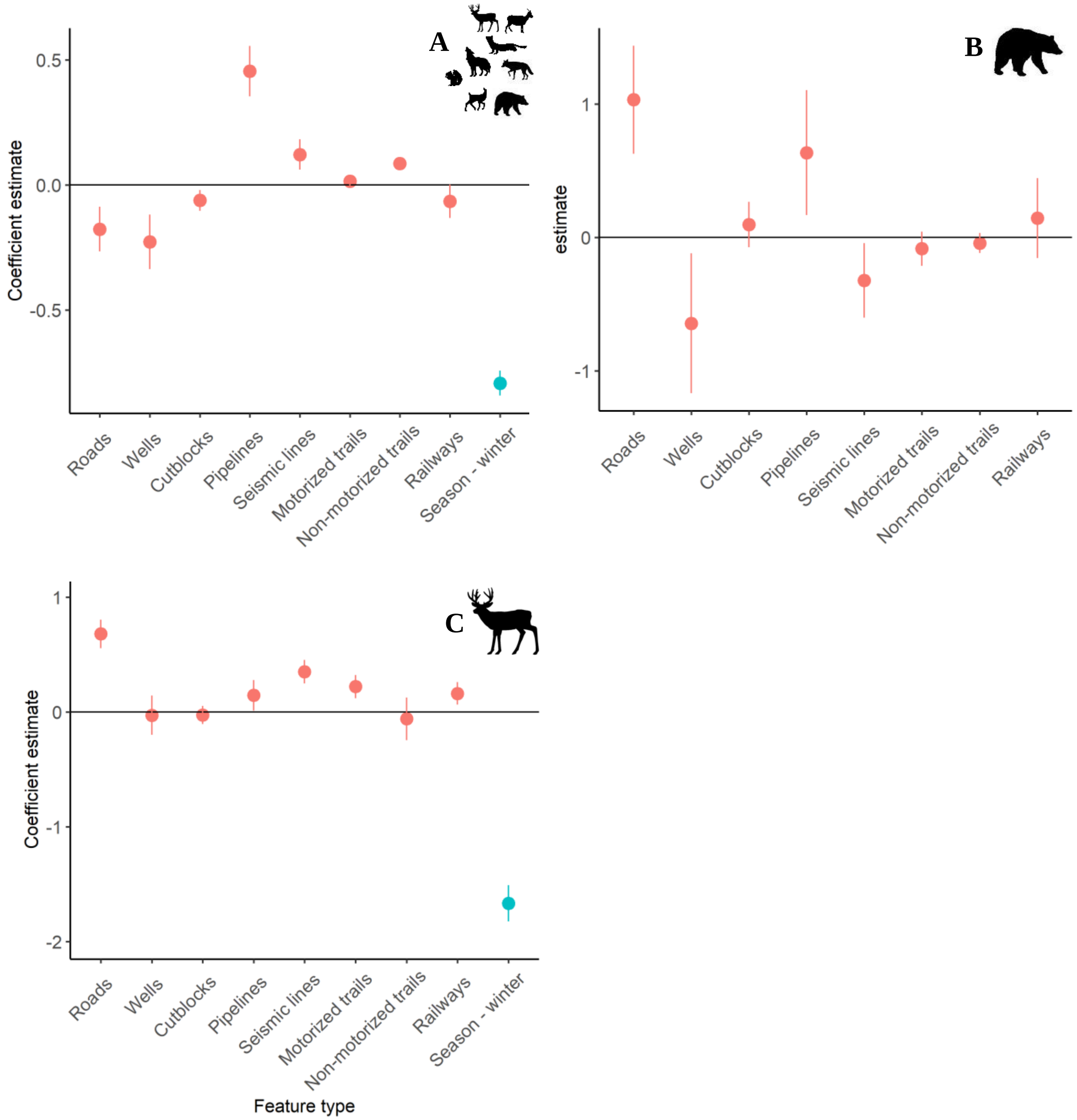

Figure 3.5. Coefficient plots from top ranked models for: A) species richness, B) black bears, and C) white-tailed deer, all variables best explained by anthropogenic landscape features.

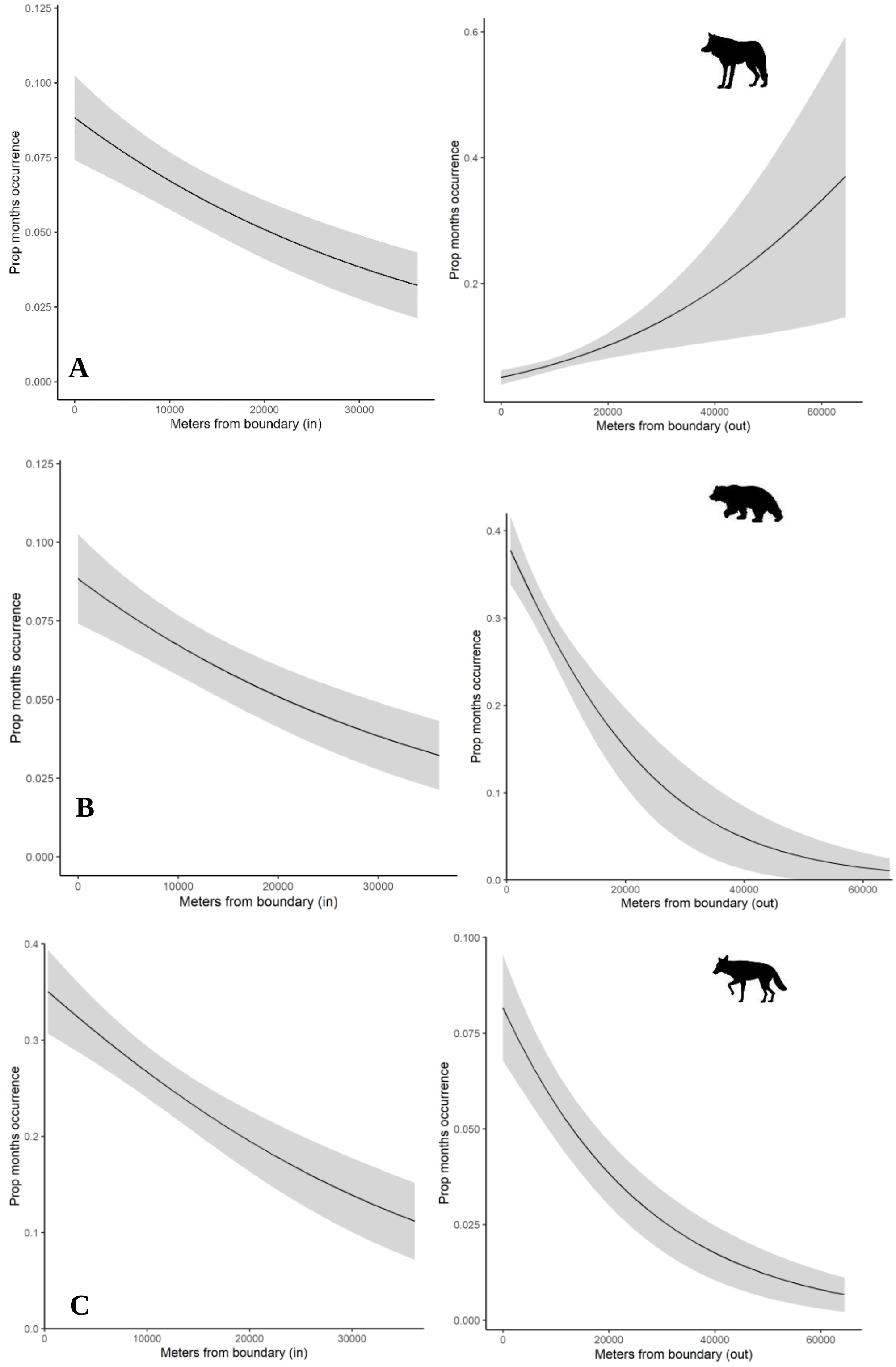

Figure 3.6. Response curves for (A) wolf, (B) grizzly bear and (C) coyote occurrence with increasing distance inside and outside of PA boundary, based on beta coefficient estimates from top-supported models explaining the occurrence of each species.

3.4 Discussion

Across the north-central Rocky Mountains and foothills in western Canada, I found that protected area coverage best explained the occurrence of four out of six mammal species. For these four species (wolves, grizzly bears, coyotes, mule deer), PA boundaries and the landscapes that they have resulted in are stronger determinants of occurrence over landscape features generated by anthropogenic disturbances, or natural landcover features. These protected areas represent the culmination of legislated decisions carried out through landscape management: minimal landscape development, little to no hunting, and various forms of human recreation, which taken together influenced species distributions. In this landscape, it is difficult to sample unprotected land that is as undisturbed as protected areas, so we cannot parse apart whether the major effect of PAs is purely the lack of disturbance, or the combination of management factors limiting human activity that are included with protected areas. We can only determine that all the factors involved in protected area establishment are strongly influential on mammal distributions.

For the remaining two out of six species (black bears and white-tailed deer), anthropogenic disturbances best explained their occurrence. Species richness counts were also best explained by anthropogenic disturbance. Overall, anthropogenic influences (PAs, landscape disturbance) explained species distribution better than natural habitat features did. My hypothesis that disturbance sensitive top predator species would be best explained by landscape protection and have positive relationships with parks was supported, as well as my hypothesis that disturbance-tolerant species (black bears, WTD) would be best explained by and have positive associations with anthropogenic features. I hypothesized that coyotes would be best explained by anthropogenic features; somewhat surprisingly, they were best explained by PA, but with negative associations to PA. Coyote have been shown to thrive in disturbance-heavy landscapes

(Heim et al., 2019; Šálek et al., 2015); this result is consistent as coyotes were found more often in areas without protection from landscape development. White-tailed deer were best explained by anthropogenic landscape features, with positive relationships to several anthropogenic feature types; this is consistent with past research finding that white-tailed deer thrive in disturbance-heavy landscapes (Darlington et al., 2022; Fisher et al., 2020; Latham et al., 2011). White-tailed deer and coyotes are both species that have expanded their ranges across North America, exploiting widespread land conversion (Hody & Kays, 2018; Latham et al., 2011).

All three carnivore species that were best explained by PAs showed significant relationships to PA boundary (Figure 3.6). Coyotes and grizzly bears showed selection for PA boundaries from both inside and outside of PAs, and wolves selected for PA boundary when inside of PAs. Taken together, these responses indicate some form of selection for the area around PA boundary. One explanation may be that PAs have been established such that optimal mammal habitat is concentrated around the PA network borders, in foothills and valley bottoms. Further into the PA network, the Rocky Mountains transition into higher alpine and rugged environments, with less forested habitat available. Further outside the PA network into the foothills, anthropogenic disturbance levels increase (Lee & Cheng, 2014; Weaver, 2017) (Figure 3.1). The PA border may be situated in optimal habitat, indicating that PAs themselves are not providing optimal mammal habitat. In Canada and many other regions, low productivity areas, including higher alpine areas are generally over-represented as PAs, whereas higher productivity and lower elevation areas are underrepresented (Martínez et al., 2006; Oldfield et al., 2004; Shrestha et al., 2010; Wiersma & Nudds, 2009). Canada’s PA system has also been shown to be sub-optimal in providing adequate habitat for all mammal species (Wiersma & Nudds, 2009). Though the Rocky Mountains provide important habitat to the mammal community, their coverage of rugged and higher alpine areas may not be ideal for many species, and some of their most valuable habitat may be concentrated at PA edges. Further research should investigate the environmental drivers behind species' selection for PA boundaries in this region, and to assess whether this trend extends across the western Cordillera.

Though this study found that PAs provide important habitat to sensitive top predator species, it also shows that there is valuable habitat for wolves outside of PAs. Wolves had a positive association to PLUZ, a public land classification that is common in Alberta's Eastern Slopes outside and along the borders of its PA network. PLUZ allow a variety of activities depending on the area, generally allowing hunting and various forms of motorized and non-motorized access, but most prevent new resource extraction leases from being established (Province of Alberta, 2020). They may also not attract the same visitation as officially established parks and protected areas, and can have average sizes that are larger than some provincial PA types (Table 3.5). Somewhat perplexingly, given their strong positive association with NP inside of PA boundaries, wolves also had increasing occurrence with distance outside of PA boundary. This also seems to indicate that some of the crown land areas around PA provide important habitat for wolves. One Scandinavian study found that carnivore species did not have higher densities within PA than outside, but the surrounding area was still heavily forested, meaning there may not be significantly better habitat inside of PA versus outside of it (Terraube et al., 2020). Other studies have also emphasized how critical the areas surrounding PA are in determining the relative importance of the PA to mammals (Hansen & DeFries, 2007; Wiersma & Simonson, 2010). These factors indicate that there is important conservation value in the management of non-PA crown land, and that crown lands surrounding PA should be considered when managing landscapes for habitat conservation, even for large PA networks like the Rocky Mountains.

Anthropogenic disturbances have been found to influence entire mammalian communities in different ways (Fisher & Burton, 2018; Heim et al., 2019); in this study, species richness was best explained by anthropogenic disturbance, with mixed positive and negative effects from different feature types. Though PAs were not a strong determinant of large mammal diversity, they were important in explaining the distribution of individual species, underscoring the importance of assessing individual species and their differing relationships to landscape features (Burgar et al., 2019; Fisher & Burton, 2018; Heim et al., 2019). PAs have clear global importance in retaining multi-taxa species diversity (Coetzee et al., 2014; Gray et al., 2016), but their effects in retaining mammalian diversity are mixed across studies (Chen et al., 2022; Stewart, Volpe, et al., 2019). Some of these differences may be due to scale. Chen et al. (2020) used wildlife camera data from all around the globe, encompassing a variety of mammalian communities and sizes of PA networks, and found that PAs supported mammal diversity, whereas Stewart et al (2019) assessed diversity across a network of small PA over just ~1500 km^2, and found that anthropogenic landscape disturbance better explained species diversity. At ~32,000 km^2, our study covers a much larger area and larger PAs than Stewart et al. (2019) yet finds a similar trend for some species. To assess the value of PAs in providing habitat to mammals individual landscapes, particularly in more northern regions with smaller species assemblages, diversity may be a poor indicator, as species have highly differing responses (Heim et al., 2019). Rather, is important to consider the importance of PAs for at-risk species such as grizzlies, wolves, wolverine, or caribou, as PAs are more critical in conserving these species (Barrueto et al., 2022; Hebblewhite et al., 2010; Herrero, 2005)

In this analysis, I separated out different PA types in Alberta to assess whether these management differences (Table 3.5) were influential to mammal distributions. PAs in vary widely in how they are managed; while new landscape disturbance is generally not permitted, human activity levels and types vary greatly. National Parks had the strongest influence in this study, with coyotes avoiding these PAs and grizzly bears and wolves selecting for them. National Parks are some of the largest, most highly protected, and longest-established PA (Table 3.5); though they attract high visitor numbers, they are restrictive in visitor activities. Beyond National Parks, wolves selected for Wilderness areas, Wildland Provincial Parks, Provincial Parks, and PLUZ, and mule deer selected for Wilderness Areas. For wolves and grizzly bears, they generally showed selection for larger protected areas, and for wolves, larger crown lands, regardless of other management factors. There may not be clear effects of differences between how different park types manage human activity; rather the relative size of the PA is more important.

This study demonstrated that the culmination of landscape management decisions that go into protected areas are key in providing habitat for large carnivores in Alberta's Rockies. At this broad of a scale (~32,000 km^2), PAs are the primary determinant of mammal species distributions. Anthropogenic landscape alteration is another major driver of species distributions, and the primary determinant of mammalian diversity. I emphasize the importance of scale in considering important habitat for mammals, as larger PA and management areas were important for grizzly bears and wolves. This study has also emphasized the importance of boundary habitat in the Rocky Mountains, implying that the most desirable place for mammal species is at the boundaries of PA and unprotected foothills. Landscape management efforts should also consider the importance crown lands at the borders of PA, as these habitats are important for mammal species.

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Chapter 4: Conclusions

4.1 Summary of findings

In an era of widespread and ongoing landscape alteration and human disturbance (Williams et al., 2020), where people are the dominant influence on the natural world (Steffen et al., 2007), it is crucial that we gain an understanding of how ongoing human disturbance and landscape use affects wildlife. Through this thesis, I have sought to understand how human landscape use and management affect large mammal species distributions through two independent but related studies. I assessed the roles of protected area coverage and motorized recreational activity in shaping mammal distributions. I provide insight into the broader influence of recreation on species distributions, and on the significance of protected areas for mammal species. I hope my findings will help guide future management decisions for species conservation in Western Canada and elsewhere. I also demonstrated the utility of scaling up camera trap research (Steenweg et al., 2017), combining similar data across study regions to ask questions at a broader scale, and leveraging camera data collected using different methods (on and off trail) to model both wildlife and human use of a landscape.

In Chapter 2, I investigated the relative importance of motorized recreational intensity in determining mammal species' spatial distributions, in comparison with anthropogenic linear disturbance features and natural landcover. I found that motorized recreation did have an affect on the spatial distributions of wolves, which avoided areas of high motorized use; most species were better explained by anthropogenic landscape alteration or natural landcover features. Additionally, the effects of motorized recreation were constrained to relatively small extents, only being significant when covariates were measured at 250-500 meter radii. Coyotes, white-tailed deer, and grizzly bears were best explained by linear disturbance features, with coyotes and white-tailed deer selecting for these features, and grizzly bears avoiding them. Black bears and mule deer were best explained by natural landcover attributes. I demonstrated that motorized recreation may be altering the distributions of disturbance-sensitive species such as wolves, but that landscape disturbance and habitat availability are drivers of most species distributions.

In Chapter 3, I investigated the relative importance of protected area coverage and proximity to protected area boundary in determining mammal species distributions, relative to anthropogenic landscape disturbance and natural landcover. I found that protected areas best explained four out of the six species assessed, including three out of the four carnivore species (wolves, grizzly bears, and coyotes). Wolves, grizzly bears, and mule deer exhibited selection for protected areas, whereas coyotes avoided national parks. All three carnivore species (coyote, wolves, and grizzly bears) showed selection for the protected area boundary region. Black bears and white-tailed deer were best explained by anthropogenic disturbances, as was total mammal species richness. This chapter demonstrated the importance of protected areas in shaping mammal distributions, particularly in providing habitat to more disturbance-sensitive predators such as wolves and grizzly bears. It also illustrated the significance of anthropogenic disturbance in explaining the distributions of more disturbance-tolerant mammals such as coyotes and white-tailed deer, and of overall diversity. Overall, at a broad scale, anthropogenic influences in the form of landscape management and landscape alteration were stronger drivers of species distributions than natural landcover features.

Taken as a whole, my thesis chapters illustrate a broad theme: the strongest determinants of species occurrence in the Rocky Mountains are landscape features that are anthropogenic

(anthropogenic disturbance, landscape management). Natural landcover attributes were rarely significant in explaining species distributions. Responses to anthropogenic influences are highly variable between species, but individual species responses were similar in both studies and thus at different spatial scales. Wolves were positively associated with protected areas, where human activity is regulated, and negatively associated with motorized recreation on crown lands. Grizzly bears were positively associated with protected areas, and negatively associated with linear disturbances. Coyotes were positively associated with anthropogenic disturbance, and negatively associated with protected areas. Black bear and mule deer occurrences were best explained by a mixture of natural and anthropogenic influences, with varying responses. For conservation and restoration efforts, I emphasize the importance of considering a broad scale for landscape management, and that the most substantial impact will come from minimizing ongoing landscape disturbance and restoring existing disturbed landscapes. Recreational use of landscapes impacts disturbance-sensitive species on a limited scale, meaning that widespread motorized recreational use may cause habitat loss for species such as wolves. Overall, landscape disturbance was a more significant driver of species distributions, and should be managed to prevent ongoing human access and habitat loss. Protected areas are important in providing habitat for mammals, particularly larger carnivore species, but size matters. Wolves and grizzly bears were positively associated with larger park types, such as National Parks, Wildland Provincial Parks and Provincial Parks, and even crown land management areas such as Public Land Use Zones (PLUZ).

4.2 Implications and future directions

Though landscape alteration and habitat loss are ongoing, there is increasing recognition of our influence and our need to mitigate it to protect and sustain biodiversity. In 2021, the United Nations declared it to be the Decade on Ecosystem Restoration, calling for global efforts to prevent, halt, and reverse ecosystem degradation across the globe. The most recent UN Biodiversity Conference, COP15, found that habitat restoration should be a top goal in the coming decade, as outlined in the Kumming-Montreal Global biodiversity framework (UN Environment Programme, 2022). The Government of Canada has set a goal of conserving 30 percent of the country's lands and waters by 2030, to fight biodiversity declines and increase our resiliency to climate change. The government plans to reach this goal through the implementation of new protected areas, as well as the establishment of Other Effective area-based Conservation Measures (OECM), lands with biodiversity value that are not primarily protected areas and may be managed for different purposes. Canada remains committed to reaching these goals, and other organizations, including provincial governments and conservation not-for-profit organizations are also working toward this aim. These conservation initiatives, if carried out effectively, will certainly be vital in conserving mammal populations. My work illustrates that PAs are important in supporting the persistence of large mammal species, as well as showing that there is conservation value in non-PA lands such as PLUZ. The effective establishment OECMs and PAs through conservation campaigns should be an effective way to conserve mammal habitat into the future. I emphasize the importance of protecting effective habitat, managing for recreation to protect disturbance-sensitive species, and minimizing ongoing landscape disturbance to keep large mammals on the landscape.

To expand on my research in Chapter 2, future studies could continue to make use of the Bighorn trail camera data set to better understand the influence of recreation. More fine-scale interactions could be investigated, such as assessing how recreation use affects how species use trails, or how species occurrences overlap temporally with recreation. My study method of modelling recreation spatially could also be repeated with non-motorized recreational activities, including equestrian use, biking, and hiking, to better understand the impacts of these forms of recreation. Parks Canada data from Banff and Jasper could be leveraged for this type of study as well, as these cameras are frequently deployed along human-use trails.

To expand on my research in Chapter 3, further research could be done into the specific factors within and outside of protected areas that are driving species occurrences. To investigate why some species are selecting for protected area boundaries, future studies could further investigate the effects of environmental and anthropogenic disturbance gradients around these boundaries. Studies could also explicitly include park management regulations into wildlife models, to assess the effects of hunting, or different types of recreation. More data sets could also be incorporated into the analysis to better represent the region. To understand the role of protected areas in a broader context, this study method should be repeated in different landscapes. This would aid in understanding whether the positive influence of protected areas on top predator species is context dependent. An example landscape could be surveying mammal occurrence inside and outside of a large northern boreal park such as Wood Buffalo National Park in Northwestern Alberta.

4.3 Caveats and limitations

Though my study illustrates the relative influences of anthropogenic activity and landscape management on mammal distributions, my conclusions have limitations and caveats. Across chapters two and three, I contained my inferences to six mammal species: wolves, grizzly bears, coyote, black bears, white-tailed deer, and mule deer. I designed my studies in this way to assess how different species are affected by anthropogenic influences, while ensuring I had selected species with enough detection data available to adequately conduct analyses. I was not able to make inferences on some of the more elusive or disturbance-sensitive species in these habitats, such as mountain caribou, wolverine, or cougar, as I did not have enough data to do so. To better understand the spatial impacts of motorized recreation, further studies should focus specifically on disturbance-sensitive species to determine if human use is spatially displacing species such as wolverine or caribou.

In Chapter 2, I used two separate camera arrays to assess both wildlife and human use of the landscape. These arrays were temporally separated by a year, with the wildlife array running from September 2019-2020, and the trail camera array running from September 2020-2021. I thus had to model the activity from 2020-2021 to use on models with the 2019-2020 wildlife data, and assume that patterns of activity were similar between years. Preferably, data could have been collected concurrently to capture activity patterns most accurately. Modelling activity from the trail cameras may have come with its own issues, as I could have missed variables that were important in explaining activity. Additionally, I lost many cameras due to human theft, camera error. This project was constrained by budget and equipment availability; ideally, I could have purchased security boxes for each camera, a metal housing that locks around a camera and screws into a tree to help prevent camera damage or theft. I was only able to use security boxes on a subset of cameras. I also would have preferred to use newer cameras, as some of the older PC900 model cameras in my study malfunctioned and didn’t collect data. Having a larger sample size of trail cameras may have facilitated better estimates of trail activity.

In Chapter 3, to compare species occurrence in and outside of protected areas, I had to combine camera arrays from different sources and assume that variability in camera trap sampling design did not have a significant influence on species detection probabilities. This assumption is commonly made in studies that synthesize camera trap data, but differences in camera trap sampling designs likely do affect detection probabilities (Burton et al., 2015; Kays et al., 2021). To improve the synthesis of camera array data in the future, practitioners should work towards developing a set of standardized best practices so that data may be synthesized and compared (Steenweg et al., 2017).

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Appendix

Figure A1. Example photos from trail cameras in the Bighorn Backcountry, showing both recreational off-highway vehicle use as well as wildlife species occurrence, including wolves (top right) and grizzly bears (bottom right). Cameras were placed on roads, trails, and cutlines throughout the study area.

Table A1. K-fold cross-validation estimates of prediction error for each model explaining species occurrence in peak and off seasons, listed in order of increasing ΔAIC value. The table includes two estimates of prediction error. The first is the raw cross-validation estimate of prediction error. The second is the adjusted cross-validation estimate of prediction error, which is designed to compensate for the bias introduced by not using leave-one-out cross-validation. K- fold cross validation performed using the cv.glm function in the boot package (Canty &Ripley, 2021) in R (R Core Team, 2021).

Species	*Season*	*Models (in order of ΔAIC value)*	*Raw cross-validation estimate of prediction error*	*Adjusted cross-validation estimate of prediction error*
Wolf	Peak	Activity	0.00348	0.00343
		Linear features	0.00401	0.00398
		Array	0.00401	0.00399
		Landcover	0.00443	0.00437
	Off	Activity	0.00232	0.00231
		Landcover	0.00274	0.00271
		Linear features	0.00295	0.00291
		Array	0.00284	0.00284
Grizzly bear	Peak	Linear features	0.00239	0.00236
		Activity	0.00270	0.00267
		Landcover	0.00527	0.00506
		Array	0.00293	0.00292
Coyote	Peak	Linear features	0.0143	0.0140
		Landcover	0.0180	0.0178
		Activity	0.0177	0.0176
		Array	0.0157	0.0157
	Off	Linear features	0.00671	0.00665
		Landcover	0.00763	0.00753
		Activity	0.00781	0.00773
		Array	0.00742	0.00740
Black bear	Peak	Landcover	0.0133	0.0131
		Linear features	0.0137	0.0136
		Array	0.0139	0.0138
		Activity	0.0141	0.0141
White-tailed deer	Peak	Linear features	0.0584	0.0578
		Activity	0.0634	0.0632
		Landcover	0.0665	0.0661
		Array	0.0702	0.0701
	Off	Linear features	0.0264	0.0262
		Landcover	0.0272	0.0270
		Activity	0.0327	0.0325
		Array	0.0324	0.0323
Mule deer	Peak	Landcover	0.0248	0.0247

	Linear features	0.0268	0.0267
	Array	0.0271	0.0270
	Activity	0.0282	0.0281
Off	Activity	0.0106	0.0106
	Landcover	0.0110	0.0110
	Linear features	0.0109	0.0109
	Array	0.0110	0.0110

Table A2. Full AICc results from generalized linear models used to explain mammal species occurrence in peak and off seasons using different model sets. Covariates in each model are listed in Table 3. df is degrees of freedom; LL is the log-likelihood; ΔLL is delta log-likehlihood.

Species	*Spatial Buffer*	*Season*	*Model*	*AICc*	*dAICc*	*AICcw*	*df*	*LL*	*ΔLL*
Wolf	Small (250 m)	Peak	**Activity**	**149.53**	**0**	**1.00**	**5**	**-69.48**	**14.72**
			Array	172.50	22.97	1.03E-05	2	-84.19	0.00
			Linear features	177.62	28.09	7.96E-07	6	-82.40	1.79
			Landcover	179.47	29.95	3.14E-07	7	-82.19	2.00
		Off	**Activity**	**373.66**	**0**	**0.99**	**5**	**-181.56**	**19.13**
			Landcover	384.12	10.46	0.0053	7	-184.54	16.14
			Linear features	387.59	13.93	0.00094	6	-187.41	13.27
			Array	405.48	31.82	1.22E-07	2	-201	0.00
	Large (2000 m)	Peak	**Landcover**	**157.62**	**0**	**0.67**	**7**	**-71.26**	**12.93**
			Activity	159.08	1.47	0.32	5	-74.26	9.94
			Linear features	167.12	9.51	5.79E-03	6	-77	7.04
			Array	172.50	14.88	3.94E-04	2	-84.19	0.00
		Off	**Landcover**	**377.54**	**0**	**0.97**	**7**	**-181.26**	**19.43**
			Linear features	384.74	7.19	0.027	6	-185.99	14.70
			Activity	396.06	18.52	0.00009	5	-192.76	7.92
			Array	405.48	27.93	8.38E-07	2	-201	0.00
Grizzly bear	Small (250 m)	Peak	**Landcover**	**157.62**	**0**	**0.67**	**7**	**-71.26**	**12.93**
			Activity	159.08	1.47	0.32	5	-74.26	9.94
			Linear features	167.12	9.51	0.0058	6	-77.16	7.04
			Array	172.50	14.88	0.00039	2	-84.19	0
	Large (2000 m)	Peak	**Linear features**	**149.26**	**0**	**0.97**	**6**	**-68.23**	**22.79**
			Activity	156.41	7.16	0.027	5	-72.93	18.09
			Landcover	183.02	33.77	4.52E-08	7	-83.98	7.04
			Array	186.14	36.89	9.51E-09	2	-91.02	0.00
Coyote	Small (250 m)	Peak	**Activity**	**295.93**	**0**	**0.98**	**5**	**-142.69**	**21.10**
			Linear features	304.27	8.34	0.02	6	-145.74	18.04
			Landcover	320.63	24.70	4.26E-06	7	-152.79	11.00
			Array	331.67	35.74	1.71E-08	2	-163.78	0
		Off	**Linear features**	**614.73**	**0**	**0.83**	**6**	**-300.98**	**23.15**
			Landcover	617.91	3.18	0.17	7	-301.43	22.69
			Activity	640.18	25.44	2.48E-06	5	-314.81	9.31
			Array	652.36	37.62	5.61E-09	2	-324.13	0
	Large (2000 m)	Peak	**Linear features**	**251.31**	**0**	**1**	**6**	**-119.26**	**44.52**
			Activity	321.24	69.94	6.51E-16	5	-155.34	8.44
			Landcover	323.56	72.25	2.04E-16	7	-154.25	9.53
			Array	331.67	80.36	3.54E-18	2	-163.78	0
		Off	**Linear features**	**607.17**	**0**	**0.97**	**6**	**-297.19**	**26.93**

			Landcover	614.23	7.06	0.028	7	-299.59	24.54
			Array	652.36	45.19	1.49E-10	2	-324.13	0
			Activity	656.39	49.23	1.99E-11	5	-322.92	1.20
Black bear	Small (250 m)	Peak	**Linear features**	**353.01**	**0**	**0.58**	**6**	**-170.11**	**8.45**
			Landcover	353.74	0.73	0.40	7	-169.34	9.22
			Activity	360.38	7.37	0.014	5	-174.91	3.65
			Array	361.22	8.21	0.0095	2	-178.56	0
	Large (2000 m)	Peak	**Landcover**	**334.10**	**0**	**1.00**	**7**	**-159.52**	**19.04**
			Linear features	349.37	15.26	4.85E-04	6	-168.29	10.27
			Array	361.22	27.12	1.29E-06	2	-179	0.00
			Activity	364.60	30.50	2.38E-07	5	-177.02	1.54
White-tailed deer	Small (250 m)	Peak	**Linear features**	**685.23**	**0**	**0.99**	**6**	**-336.22**	**24.85**
			Landcover	694.39	9.17	1.01E-02	7	-339.67	21.41
			Activity	702.48	17.26	1.77E-04	5	-345.96	15.11
			Array	726.26	41.03	1.22E-09	2	-361	0.00
		Off	**Linear features**	**1005.22**	**0**	**1.00**	**6**	**-496.23**	**87.17**
			Landcover	1042.77	37.55	7.01E-09	7	-513.88	69.53
			Activity	1078.76	73.54	1.07E-16	5	-534.12	49.29
			Array	1170.91	#####	1.05E-36	2	-583	0.00
	Large (2000 m)	Peak	**Linear features**	**639.23**	**0**	**1**	**6**	**-313.22**	**47.85**
			Landcover	690.30	51.06	8.16E-12	7	-337.62	23.45
			Activity	694.78	55.55	8.68E-13	5	-342.11	18.96
			Array	726.26	87.02	1.27E-19	2	-361	0.00
		Off	**Linear features**	**874.37**	**0**	**1**	**6**	**-430.81**	**152.60**
			Landcover	967.58	93.22	5.73E-21	7	-476.29	107.12
			Activity	1068.55	#####	6.80E-43	5	-529.01	54.39
			Array	1170.91	#####	4.03E-65	2	-583	0.00
Mule deer	Small (250 m)	Peak	**Landcover**	**470.73**	**0**	**0.40**	**7**	**-227.83**	**5.49**
			Array	470.75	0.02	3.95E-01	2	-233.32	0.00
			Linear features	472.88	2.15	1.36E-01	6	-230	3.27
			Activity	474.18	3.45	7.09E-02	5	-231.81	1.51
		Off	**Activity**	**413.88**	**0**	**1.00**	**5**	**-201.67**	**10.51**
			Landcover	425.78	11.89	0.0026	7	-205.37	6.81
			Array	428.47	14.59	0.00068	2	-212.18	0
			Linear features	429.00	15.11	0.00052	6	-208.11	4.07
	Large (2000 m)	Peak	**Landcover**	**425.26**	**0**	**1.00**	**7**	**-205.10**	**28.22**
			Linear features	448.24	22.98	0.00	6	-217.72	15.59
			Array	470.75	45.48	0.00	2	-233	0.00
			Activity	471.77	46.51	0.00	5	-230.61	2.71
		Off	**Landcover**	**403.23**	**0**	**1.00**	**7**	**-194.10**	**18.09**
			Activity	425.94	22.71	0.00	5	-207.70	4.49
			Linear features	428.23	25.00	0.00	6	-208	4.46
			Array	428.47	25.25	0.00	2	-212.18	0.00

Table B1. K-fold cross-validation estimates of prediction error for each model explaining species occurrence and species richness, listed in order of increasing ∆AIC value. The table includes two estimates of prediction error. The first is the raw cross-validation estimate of prediction error. The second is the adjusted cross-validation estimate of prediction error, which is designed to compensate for the bias introduced by not using leave-one-out cross-validation. K- fold cross validation performed using the cv.glm function in the boot package (Canty & Ripley, 2021) in R (R Core Team, 2021).

Species	*Models (in order of ∆AIC value)*	*Raw cross-validation estimate of prediction error*	*Adjusted cross-validation estimate of prediction error*
Wolf	Protected areas	0.0388	0.0387
	Human features	0.0401	0.0401
	Natural landcover	0.0439	0.0438
	Season	0.0442	0.0441
Grizzly bear	Protected areas	0.0822	0.0820
	Human features	0.0854	0.0852
	Natural landcover	0.0993	0.0992
	Null	0.1116	0.1116
Coyote	Protected areas	0.0365	0.0364
	Human features	0.0375	0.0374
	Natural landcover	0.0384	0.0384
	Season	0.0436	0.0436
Black bear	Human features	0.0688	0.0686
	Natural landcover	0.0736	0.0734
	Protected areas	0.0801	0.0798
	Null	0.0789	0.0788
White-tailed deer	Human features	0.0736	0.0734
	Natural landcover	0.0797	0.0795
	Protected areas	0.0804	0.0802
	Season	0.0955	0.0955
Mule deer	Protected areas	0.0412	0.0411
	Natural landcover	0.0412	0.0411
	Human features	0.0421	0.0420
	Season	0.0418	0.0417
Species richness	Anthropogenic	2.286	2.285
	Protected areas	2.288	2.287
	Landcover	2.351	2.350
	Season	2.368	2.367