Examining shifts in boreal carnivore species' resource selection in response to predator control to conserve woodland caribou (*Rangifer tarandus caribou*) in western Canada

by

Katherine Baillie-David
B.Sc. (Hons), University of Ottawa, 2017

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

MASTER OF SCIENCE

in the School of Environmental Studies

University of Victoria

Supervisory Committee

Examining shifts in boreal carnivore species' resource selection in response to predator control to conserve woodland caribou (*Rangifer tarandus caribou*) in western Canada

by

Katherine Baillie-David
B.Sc. (Hons), University of Ottawa, 2017

Supervisory Committee

Dr. Jason Fisher (School of Environmental Studies)
Co-Supervisor

Dr. John Volpe (School of Environmental Studies)
Co-Supervisor

Abstract

Predators play a critical role in regulating the structure and function of ecosystems by exhibiting top-down forces on lower trophic levels. Despite their important contributions in maintaining ecosystem health, lethal predator control remains a global wildlife management strategy to reduce predation on livestock, culturally and/or economically important species, and species at risk, as well as to reduce conflict with humans. Predator control has received criticism due in part to a paucity of rigorous research on the community-level impacts of this practice, beyond the target prey species. Specifically, there is a lack of understanding of the behavioural consequences of predator control on the wider ecological community. In this thesis, I used a multi-year camera trap dataset to evaluate how government-mandated grey wolf (*Canis lupus*) population reduction to conserve boreal woodland caribou (*Rangifer tarandus caribou*) could impact the resource selection of the carnivore community in northeast Alberta, Canada. In my second chapter, I investigated whether perceived persecution risk due to predator control may alter wolf habitat selection. I found that wolves switched from positively associating with roads before predator control to avoiding anthropogenic linear features and selecting for block features after predator control. These results suggest that lethal control may prompt wolves to prioritize local prey acquisition near block features over movement on linear features. In my third chapter, I examined whether coyote, lynx, and black bear exhibited shifts in co-occurrence with habitat features, competitors, and prey consistent with a release from top-down suppression in response to predator control. I found that predator control triggered unexpected behavioural changes among coyote and lynx consistent with a release from top-down suppression, but not among black bears. Non-apex predator response to predator control may depend on the strength of competition between the apex and non-apex predator, emphasizing the need to consider bottom-up processes when trying to understand the indirect effects of predator control. This research demonstrates that predator control can have trickle-down effects within the larger ecological community, specifically affecting how species utilize resources. As predator control continues to be a recommended wildlife management strategy, it is imperative to continue investigating its unintended consequences throughout the ecological community.

Table of Contents

List of Tables

List of Figures

Acknowledgments

I would like to thank the amazing people that make up my community, without whom this thesis would not have been possible.

Thank you to my supervisors, Dr. Jason Fisher and Dr. John Volpe, for providing me with immense support and guidance over the years. Jake, I am eternally indebted to you for providing me the opportunity to learn and grow as a scientist in your research group. From our discussions on ecological theory and statistics to the boisterous party banter to the heart to hearts, I have appreciated every conversation. John, thank you for being a source of steadfast support throughout this journey. I am very thankful for the insight you provided in developing this thesis.

For the thought-provoking discussions, care, and laughter, I thank my brilliant lab mates, past and present: Laura, Macgregor, Sandra, Nicole, Brianna, Becca, Sydney, Andrew L., Andrew B., Cat, Daniel, Wylie, Gillian, Mitch, Andrew W., and Desirée. Thank you to Team Pear for the fond memories of playing kick the can at Lake Cowichan and drinking our delicious homemade pear cider at the Pizza Slapdown.

A special thank you to the Christina Lake field crew: Luke, Sandra, Gillian, Laura, and Macgregor, as well as Amanda and Jillian from ABMI. Luke, Sandra, and Gillian, thank you for introducing me to the Conklin experience. I will never forget the times we spent cackling at the Conklin Corner.

Thank you to the School of Environmental Studies faculty and staff for your guidance and support throughout my time as a graduate student. A special thank you to Alina and Elaine for helping me navigate the administrative waters of grad school.

This project would not have been possible without financial support from the University of Victoria through graduate awards and the University of Victoria Fellowship, as well as a Mitacs Accelerate Internship with InnoTech Alberta. Thank you for providing funding and resources to support my work.

Finally, I would like to thank my family for all their love and reassurance over the last few years. Thank you to my mom, my dad, Gaston, Janette, and my sister, Alex, for supporting my curiosity for the natural world, and for your unwavering love throughout this journey. Lastly, I would like to thank my partner, Nathan, for every hug, snack, and word of encouragement – you made the darkest days so much brighter.

Chapter 1

An introduction to predator control in western Canada: conservation applications and ecological implications

1.1 Predator control as a wildlife management tool

Predators play a critical role in regulating the structure and function of ecological communities by exhibiting top-down forces on lower trophic levels (Hairston, Smith, & Slobodkin, 1960; Soulé et al., 1988; Terborgh & Estes, 2010). Despite their demonstrated importance in contributing to ecosystem health and biodiversity (Schmitz, 2007; Schmitz, Hawlena, & Trussell, 2010), predators are often perceived as negatively impacting humans by predating on livestock, culturally and/or economically important species, and species at risk, as well as directly conflicting with humans (Lennox, Gallagher, Ritchie, & Cooke, 2018). These issues are exacerbated by continued anthropogenic landscape change globally, which have resulted in widespread changes to predator-prey dynamics (Reynolds & Tapper, 1996).

The concept of predators as pest species that should be controlled due to resource competition with humans originated in Europe as early as 600 BC among herding and agricultural societies, eventually spreading to countries impacted by European colonization (Reynolds & Tapper, 1996). Predator control would later be used as a means of increasing hunter harvest of certain game species, particularly in colonial countries such as the United Kingdom (Tapper, 1992). Within the last century, the utility of predator control has evolved to conserve endangered prey species in the interest of preserving biodiversity, rather than directly serving the needs of humans (Reynolds & Tapper, 1996).

As society's understanding of the importance of biodiversity, and the role predators play in contributing to ecosystem health, has increased, so too has criticism for predator control as a staple in the wildlife management toolkit (Treves, Krofel, & McManus, 2016). From an ecological perspective, predator control has been criticized in part for lacking rigorous tests of community-level responses (Lennox et al., 2018; Treves et al., 2016). The origins of predator control, whereby predators were considered pests rather than important contributors to ecosystem regulation, have meant that research utilizing the method has predominantly focused on numerical responses of target livestock, game, or prey species (Reynolds & Tapper, 1996), and as such there is a knowledge gap on the potential side effects within the wider ecological community. Specifically, there is a paucity of information on the non-numerical responses among species.

While a reduction in an apex predator population can incite numerical shifts among the lower trophic levels via mesopredator release (Soulé et al., 1988), it is less well understood whether such a reduction could trigger changes to species behaviour (Treves et al., 2016). Following a reduction in the apex predator population, we might expect species in lower trophic levels to utilize resources, such as prey, forage, and refuge, differently when top-down pressures are decreased. Furthermore, there exists the possibility that surviving members of the apex predator community may shift resource associations in response to sudden population-wide persecution risk. We aimed to investigate these potential responses within the western Canadian boreal carnivore community following government-mandated predator control.

1.2 Predator control to conserve woodland caribou in western Canada

In western Canada, grey wolf (*Canis lupus*) control is a primary conservation strategy employed to curb the decline of woodland caribou (*Rangifer tarandus caribou*) (Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2014; Serrouya et al., 2019). Woodland caribou, a species particularly sensitive to landscape change due to their need for large areas of mature boreal forest, are threatened primarily by habitat loss as a result of resource extraction throughout the western Canadian boreal forest (Wittmer, McLellan, Serrouya, & Apps, 2007). The growing industrial footprint in the boreal forest has facilitated increased wolf predation of woodland caribou via two ecological mechanisms. Firstly, novel anthropogenic features are being added to the landscape due to oil and gas and forestry practices, which in turn facilitate wolf movement across the landscape (Dickie, Serrouya, McNay, Boutin, & Toit, 2017; Latham, Latham, Boyce, & Boutin, 2011; McKenzie, Merrill, Spiteri, & Lewis, 2012), leading to increased predation rates on caribou (James & Stuart-Smith, 2000). Second, increased population densities of moose (*Alces alces*) (Francis, Procter, Kuzyk, & Fisher, 2021) and white-tailed deer (*Odocoileus virginianus*) (Fisher & Burton, 2021; Fisher, Burton, Nolan, & Roy, 2020) due to greater forage subsidies provided by early seral vegetation on disturbance features supports greater wolf population densities. This leads to increased predation risk for caribou through an “apparent competition” relationship with moose and white-tailed deer (Holt, 1977; James, Boutin, Hebert, & Rippin, 2004; Latham, Latham, McCutchen, & Boutin, 2011).

Despite landscape change being the ultimate cause of woodland caribou population decline (Hebblewhite, 2017; Wittmer et al., 2007) and growing ecological and ethical concerns over the use of predator control (Treves et al., 2016), it continues to be the recommended short-term caribou recovery strategy among wildlife managers (Boutin et al., 2012; Hervieux et al., 2014; Serrouya et al., 2019) because alternative conservation methods, such as landscape restoration, apparent competitor control, maternal penning and translocation, are costly and can take decades to take effect (Boutin et al., 2012; Hebblewhite, 2017; van Rensen, Nielsen, White, Vinge, & Lieffers, 2015). As such, it is increasingly important to investigate the side effects of predator control.

1.3 Thesis overview

For this thesis, I used camera trap data collected before and after the onset of a government-mandated wolf control program in northeast Alberta aimed at conserving the East Side Athabasca and Cold Lake woodland caribou populations to pose questions about the behavioural effects of predator control. In my second chapter, I asked whether perceived risk of human persecution due to wolf control could alter the habitat selection of the surviving wolf population to avoid habitat with the potential to increase exposure risk. In my third chapter, I examined the behavioural responses of three focal non-apex predators: coyotes (*Canis latrans*), lynx (*Lynx canadensis*) and black bears (*Ursus americanus*). I sought to determine whether the focal non-apex predator species exhibited shifts in co-occurrence with habitat, competitors, and prey consistent with a release from top-down suppression in response to a reduction in the wolf population. In the fourth and final chapter, I summarize the findings from each data chapter, identify areas of future research, and suggest how this work advances our understanding of predator control as a global wildlife management strategy.

With this thesis, I provide novel insight into the side effects of predator control on the carnivore community in the Nearctic boreal forest using a multi-year camera trap dataset. Results may be used to inform wildlife managers on the effects of predator control being implemented in multi-carnivore systems experiencing disturbance-mediated shifts in predator-prey dynamics.

Chapter 2

Grey wolves (*Canis lupus*) shift selection of anthropogenic landscape features following predator control in the Nearctic boreal forest

2.1 Introduction

2.1.1 Predators as regulators of ecological communities

Predators play a disproportionate role in ecological communities as they have the ability to shape ecosystem structure and function through top-down processes, despite relatively low densities (Hairston et al., 1960; Soulé et al., 1988). Apex predators specifically regulate ecosystem structure through consumptive effects (e.g. predation) and non-consumptive effects (e.g. fear, competition) on both prey and mesopredators (Terborgh & Estes, 2010), thus impacting species abundance and distribution (Hairston et al., 1960; Soulé et al., 1988). Despite their importance in regulating ecological communities, predators are often perceived as negatively impacting humans by predating on livestock, culturally and/or economically valuable species, and species at risk, as well as directly conflicting with humans (Lennox et al., 2018). Consequently, predators have been historically and are currently controlled, whereby population sizes are reduced to achieve social, economic, or ecological objectives (Packer et al., 2009; Reynolds & Tapper, 1996).

2.1.2 Predator control and the potential for indirect effects

Although predator control has been found to exhibit short-term benefits for vulnerable prey populations (Boertje, Valkenburg, & McNay, 1996; Hayes et al., 2003; Hervieux et al., 2014; Serrouya et al., 2019), this management strategy has been criticized in part for lacking rigorous tests of community-level responses (Lennox et al., 2018; Treves et al., 2016). Past research on predator control has focused on species' numerical changes, particularly those of focal prey (D. E. Brown & Conover, 2011; Hayes et al., 2003; Hervieux et al., 2014) and mesopredator species (Berger, Gese, & Berger, 2008; Crooks & Soulé, 1999). However, there is less information on whether predator control could incite behavioural changes within the ecological community (Treves et al., 2016). By investigating behavioural responses, we can better understand how species' usage of resources required for survival, such as prey, forage, and refuge (McLoughlin, Morris, Fortin, Vander Wal, & Contasti, 2010), may shift following predator control. Thus, quantifying behavioural shifts is particularly important for the remaining apex predator population to understand how behavioural processes associated with predation of the target prey population might change in response to predator control, and could provide insight into the overall efficacy of predator control programs in recovering at-risk prey populations in a way that numerical changes alone cannot (Treves et al., 2016). One method of quantifying species' behavioural shifts is to examine their habitat selection.

Habitat selection is driven by internal factors such as movement ability (Avgar, Kuefler, & Fryxell, 2011) and animal personality (Leclerc et al., 2016; Stamps & Groothuis, 2010), and by external factors relating to resource acquisition and resource quality including forage availability (Langvatn & Hanley, 1993), competition (Morris, 2003; Rosenzweig, 1981) and predation (J. S. Brown, 1999; Gilliam & Fraser, 1987; Lima & Dill, 1990). Predator habitat use is driven largely by prey availability, in that predators select habitat that will maximize encounters with prey (Lima & Dill, 1990). Predators accomplish this by preferentially selecting areas with high densities of prey (Carbone & Gittleman, 2002) and/or their prey's preferred resources (Mitchell & Lima, 2002). In addition, predators will select habitat such as linear features that facilitate movement across the landscape (Avgar et al., 2011) to reduce search times and increase prey encounter rates (McKenzie et al., 2012). However, with human-induced mortality risk introduced into the system via predator control, habitat selection of the target predator could shift from selection based solely on prey availability to exhibiting a trade-off between prey acquisition and perceived risk avoidance (Lima & Dill, 1990; Rosenzweig, 1991). Anthropogenic landscape features have the potential to amplify this risk vs. reward trade-off in predator habitat selection (Lesmerises, Dussault, & St-Laurent, 2012). While anthropogenic features may be beneficial for predators by increasing movement rates, hence encounter and predation rates, (McKenzie et al., 2012), they may also be associated with increased detection by humans via reduced canopy cover, and thus, could increase the risk of human-induced mortality (Cristescu, Stenhouse, & Boyce, 2013; Llaneza, García, Palacios, Sazatornil, & López-Bao, 2016; Mysterud & Ostbye, 1999; Ordiz, StØEn, Delibes, Swenson, & Sveriges, 2011).

2.1.3 Case study – Grey wolf control to aid boreal woodland caribou recovery

The use of anthropogenic linear features to increase movement and promote prey encounters has been particularly well-documented among grey wolves (*Canis lupus*) in North America (Dickie et al., 2020; Dickie et al., 2017; A. D. M. Latham, M. C. Latham, M. S. Boyce, et al., 2011; McKenzie et al., 2012). However, the nature of wolves' usage of anthropogenic features following population reduction remains unknown. We examined this process in the Nearctic boreal forest of western Canada. Here, human disturbance on the landscape via oil and gas and forestry developments has resulted in an abundance of novel anthropogenic features on the landscape (Pickell, Andison, & Coops, 2013; Pickell, Andison, Coops, Gergel, & Marshall, 2015). These include linear features, such as seismic lines and pipelines, and block features, such as well sites and cutblocks.

This network of movement corridors has boosted predation rates on the grey wolf's preferred prey on this landscape – woodland caribou (*Rangifer tarandus caribou*) (James &

Stuart-Smith, 2000). The woodland caribou is one of the most threatened prey species in the north circumpolar region as a result of increased anthropogenic landscape change (Vors & Boyce, 2009), with population declines in the Canadian boreal forest primarily attributed to the loss of old-growth habitat due to increased industrial activity (Hebblewhite, 2017; Nagy-Reis et al., 2021). Furthermore, functional changes to the boreal ecosystem from human land-use activities have posed a significant threat to caribou populations (Boutin et al., 2012). In addition to grey wolf use of anthropogenic linear features as travel corridors, the replacement of old-growth forest with early seral forage on disturbed landscape features supports increased populations of apparent competitors such as white-tailed deer (*Odocoileus virginianus*) (Fisher & Burton, 2021; Fisher et al., 2020) and moose (*Alces alces*) (Francis et al., 2021), thereby bolstering grey wolf populations and increasing predation risk for caribou (Holt, 1977; James et al., 2004; A. D. M. Latham, M. C. Latham, M. S. Boyce, et al., 2011). Pursuant to recovery measures outlined in the Species at Risk Act's Recovery Strategy for boreal woodland caribou (Environment and Climate Change Canada, 2020), government-mandated wolf control programs were initiated across western Canada to help reverse boreal woodland caribou population decline and achieve self-sustaining populations (Alberta Environment and Parks, 2017; Serrouya et al., 2019).

2.1.4 Research question and hypothesis

We sought to understand how government-mandated wolf control in the highly industrialized Canadian boreal forest may alter habitat selection of the wolf population. We quantified wolf distribution using a multi-year camera trap dataset collected before and after the wolf population reduction program (Alberta Environment and Parks, 2017) and created habitat selection models for each period. We hypothesized that wolf control – which is largely done by aerial shooting (Bridger, 2019) – would trigger a trade-off in wolf habitat selection between prey acquisition and exposure risk, whereby wolves would adjust their selection of habitat features associated with their primary prey depending on the level of perceived risk from human persecution. Before wolf population reduction, we expected wolves to select primarily for landscape features that facilitate movement, the occurrence of their primary prey, or habitat associated with their primary prey. After the onset of wolf population reduction, we expected wolves to avoid natural and anthropogenic landscape features with lower canopy cover that would increase exposure risk to aerial gunning, at the expense of associating with primary prey.

2.2 Methods

2.2.1 Study area

Our study area consists of ca. 3500 km^2 of mixedwood boreal forest located approximately 350 km northeast of Edmonton, Alberta. The landscape is a mosaic of mixedwood, coniferous, and deciduous forest, as well as bogs, fens, lakes, and rivers. In addition, there is widespread human disturbance across the landscape from forestry and oil and gas exploration and extraction. Landscape features associated with these practices include seismic exploration lines, transmission lines, pipelines, roads, well sites, industrial camps, and cutblocks (Pickell et al., 2013; Pickell et al., 2015). The study area lies at the intersection of the Cold Lake and East Side Athabasca River (ESAR) caribou ranges (Appendix 1). Both the Cold Lake and ESAR caribou ranges have experienced consistent declines in population growth rates since monitoring began in 1999 (Alberta Sustainable Resource Development & Alberta Conservation Association, 2010; Hervieux et al., 2013).

In the winter of 2016/2017, the Government of Alberta initiated wolf population reduction within the Cold Lake and ESAR caribou ranges to help slow population decline (Alberta Environment and Parks, 2017). The standard procedure for wolf control programs conducted in western Canada has been to remove wolves annually during the winter months when aerial snow tracking is possible (Bridger, 2019). Aerial gunning via helicopter was the primary control method, which has been previously deemed the most efficient and humane control method for wolves as it facilitates rapid removal and reduces the risk of bycatch (Bridger, 2019). Between 2017 and 2020, 92 wolves were removed from the region containing the Cold Lake and ESAR caribou ranges (D. Hervieux, personal communication, March 18, 2021).

2.2.2 Camera trap array

Three years before the onset of wolf population reduction, we had deployed a camera array in the study area to examine mammals' response to landscape change (Fisher & Burton, 2018, 2021; Fisher et al., 2020; Wittische, Heckbert, James, Burton, & Fisher, 2021). We used a stratified random design, which aimed to capture the heterogeneity of natural and anthropogenic land cover types representative of an industrialized boreal forest landscape of northeast Alberta (Figure 2.1). Sampling locations were determined by overlaying a 1 km x 1 km cell grid across the study area in ArcGIS 10.2 Spatial Analyst (ESRI Inc, Redlands, CA). Grid cells were randomly selected (constrained by access and a minimum of 2-km apart) within strata defined by canopy cover, tree species, and topography.

Within each selected grid cell, one unbaited Reconyx PC900 Hyperfire infrared remote digital camera was placed on a tree facing an active game trail (Figure 2.2) to maximize detection probability of medium- to large-sized mammals (Fisher & Burton, 2018). Cameras were set to high sensitivity and no delay between triggers. While cameras were accessed primarily by roads and trails, the high density of these features across the study area means bias is reduced when landcover is analyzed at a radius of 250-m or more from the centroid of each cell (see multiscale analysis in (Fisher & Burton, 2018). "Site" is defined as the detection zone of an individual camera trap, and "study area" is defined as the ~3500 km^2 polygon surrounding all sites.

Camera traps operated across 61 sites from October 2011 to October 2014. After the onset of wolf population reduction, we capitalized on these existing data by re-deploying 60 cameras as close as possible to the original locations from October 2017 to October 2020. Sites were visited approximately once per year to collect camera data and service the camera traps.

Wolf control began in the winter of 2016/2017, thus we classified the camera data based on whether it was collected pre-control (2011-2014) or post-control (2017-2020). We processed camera trap images using Timelapse 2 version 2.2.2.4 (Greenberg, 2019; http://saul.cpsc.ucalgary.ca/timelapse/). Timelapse 2 provided a simple interface to efficiently record date, time, species identity, number of individuals, classifier identity, and comments (when necessary) for each image at each site. Timelapse files were exported as .csv files and imported into R (R Core Team, 2017) for analysis.

2.2.3 Wolf occurrence response variable

We considered wolf detection events as independent if they occurred a minimum of 30 minutes apart (Rovero & Zimmermann, 2016). We then summed wolf independent detection events by month to obtain a proportional binomial response variable, or "occurrence frequency", whereby a wolf was detected (1) or not (0) monthly at each site, which we deemed sensitive enough to detect variation in site use, while reducing zero-inflation induced by absences caused by movement (Neilson, Avgar, Burton, Broadley, & Boutin, 2018; Stewart, Fisher, Burton, & Volpe, 2018). Occurrence frequency was generated across 35 months pre-control (November 2011 – September 2014) and 35 months post-control (November 2017 – September 2020). Although cameras were operational in October of 2011, 2014, 2017 and 2020, they were treated as incomplete sampling months given that camera checks took place midway through each of these months. Consequently, October of 2011, 2014, 2017 and 2020 were excluded from analysis.

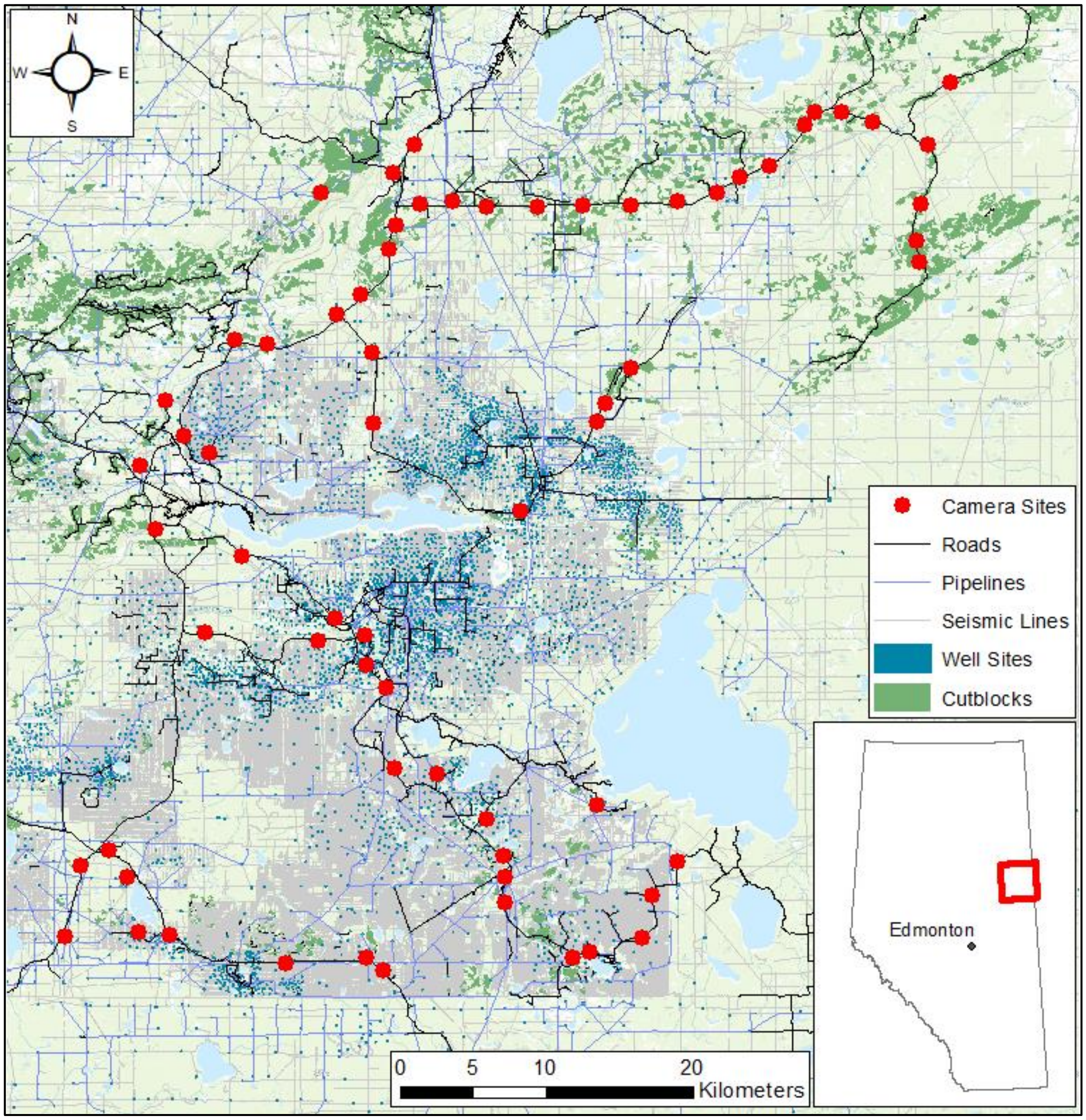


Figure 2.1 Map of camera trap locations within the study area.
The ~3500 km^2 study area is located approximately 350 km northeast of Edmonton, Alberta. The landscape has experienced significant disturbance from industrial practices, with high densities of features associated with oil and gas exploration and extraction and timber harvesting. These features include roads, pipelines, seismic lines, 3-D seismic lines, and cutblocks.

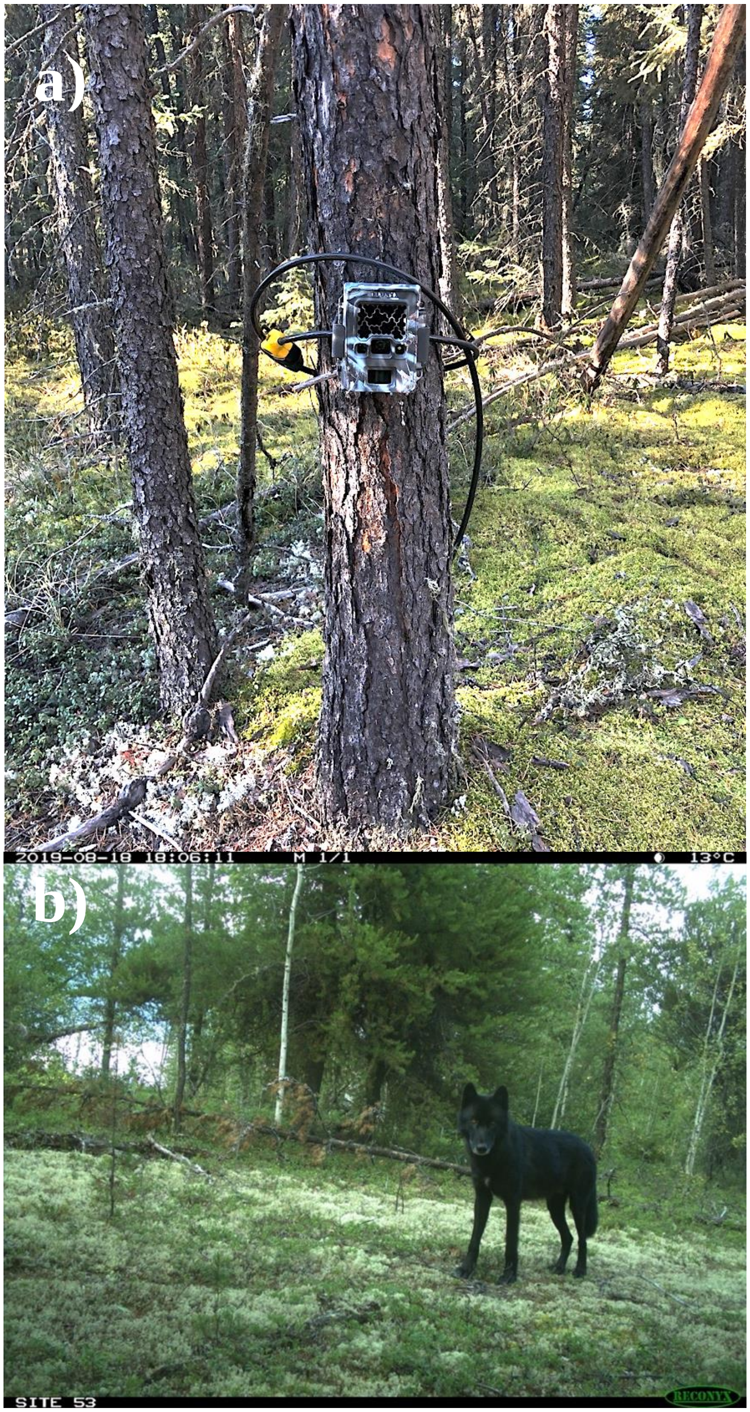


Figure 2.2 Camera trap set-up and example camera trap photo.
Photos of (a) a camera trap set-up at a site and (b) an example camera photo of the target species, the grey wolf (*Canis lupus*). Each site contained one unbaited Reconyx PC900 Hyperfire infrared remote digital camera fixed to a tree, approximately one metre off the ground, and facing an active game trail. Camera settings included one picture per trigger with no delay and high trigger sensitivity. Time-lapse was not set for the cameras during pre-control period; during the post-control period, time-lapse was set to take one picture per day at 12:00 PM.

2.2.4 Predictor variables

We quantified multiple habitat types and used those as our primary predictor variables to capture the heterogeneity in both natural and anthropogenic landcover across the study area. Natural landcover within the study area was quantified using Alberta Vegetation Inventory (Alberta Agriculture Forestry and Rural Economic Development, 2005). Applying standards used by Fisher and Burton (2018), natural landcover categorization was determined by canopy cover class, tree species, and moisture regime (Table 2.1). To quantify anthropogenic landcover within the study area, we used the Alberta Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory (Alberta Biodiversity Monitoring Institute, 2017a, 2017b, 2019). Given the growing industrial footprint throughout the study area, we accounted for temporal changes in anthropogenic landcover by calculating the amount of anthropogenic habitat classes from spatial data collected before (2010) and after (2016) the start of wolf population reduction.

We derived 20 anthropogenic and natural land cover classes to reflect landscape heterogeneity for both the pre-control and post-control time periods (Table 2.1). Land cover classes were then divided among three ecological mechanisms hypothesized to influence wolf occurrence: prey habitat, movement ability, and exposure risk (Table 2.2). We assumed all anthropogenic features and natural features with <6% crown closure (Table 2.1) would have greater exposure to human persecution risk via aerial gunning due to lower vegetation height and canopy cover relative to other natural features (Llaneza et al., 2016).

To represent the fourth ecological mechanism hypothesized to influence wolf occurrence, prey availability (Table 2.2), we generated occurrence variables for each of the wolves' primary prey species in this region – caribou, moose, and white-tailed deer. We calculated a proportional binomial variable, whereby a given prey species was detected (1) or not (0) monthly at each site.

We assessed collinearity among predictor variables by calculating variance inflation factor (VIF), and kept variable sets where VIF < 3 indicating a lack of collinearity among predictor variables (Zuur, Ieno, & Elphick, 2010). In addition, we jointly scaled pre-control and post-control predictor variables to allow for comparisons of coefficient estimates before and after wolf population reduction.

2.2.5 Statistical analysis

We modelled pre-control and post-control wolf occurrence to test whether habitat associations differed before and after the onset of wolf population reduction, and which associated ecological drivers most influenced observed patterns (Table 2.2). Given that wolf occurrence is a proportional binomial response variable, we used generalized linear models (GLM) (McCullagh & Nelder, 1989) with a binomial distribution (logit link function). All analyses were performed using R statistical software (R Core Team, 2017).

Species' habitat selection can vary depending on the spatial scale at which one quantifies available habitat. Furthermore, the relationship between spatial scale, landscape features and species' habitat selection is dependent upon the species and landscapes being considered (Fisher, Anholt, & Volpe, 2011; Levin, 1992). Therefore, we modelled wolf occurrence at multiple spatial scales to determine the scale at which habitat best explained wolf occurrence frequency. We first built global generalized linear models with the proportions of all natural and anthropogenic landcover variables at multiple spatial scales, defined as buffers around cameras with radii ranging from 250-2000 m surrounding sites, in 250-m intervals. To identify the best-supported spatial scale, we used model selection-based Akaike's Information Criterion corrected for small sample sizes (AICc); AICc weights of each candidate model were treated as evidence of the strength of habitat selection at that particular spatial scale (Burnham & Anderson, 2002).

Using the landcover variables at the best-supported spatial scale, as well as prey occurrence variables, we built competing models for both pre-control and post-control periods based on our hypotheses of the primary drivers of wolf occurrence (Table 2.2). Empirical support for each hypothesis was evaluated using AICc scores (Burnham & Anderson, 2002). We evaluated top models by generating diagnostics plots, calculating deviance explained, and using k-fold cross validation from the *boot* package (Canty & Ripley, 2021) in R to evaluate prediction error (Appendix A.3).

Table 2.1 Landcover types quantified within the study area.

We quantified 20 natural and anthropogenic habitat types to represent the landcover of the study area. We used a number of sources representing different time periods to account for landcover changes between pre-control (2011-2014) and post-control (2017-2020) time periods. AVI = Alberta Vegetation Inventory, 1987 – 2014; UALF = University of Alberta Linear Features Map Updated 2012; [1]ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2010; [2]ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2016; [3]ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2017; Aw = Aspen; Pb = Poplar; Bw = White birch; Sb = Black spruce; Sw = White spruce; Fb = Balsam fir; Lt = Larch/tamarack; d = Dry; m = Mesic; w = Wet; a = Aquatic. [4]Combined functionally similar landcover classes to reduce skew in distributions. [5]Omitted from both pre-control and post-control analysis to prevent collinearity with other variables.

Predictor variable	Pre-control source	Post-control source	Description
Upland Deciduous[4] Upland Mixedwood[4]	AVI AVI	AVI AVI	(Aw, Pb, Bw ≥ 70% canopy cover), 40-60% canopy cover, moisture = d or m
Lowland Deciduous[4] Lowland Mixedwood[4]	AVI AVI	AVI AVI	(Aw, Pb, Bw ≥ 70% canopy cover), 40-60% canopy cover, moisture = w or a
Upland Spruce	AVI	AVI	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = d or m
Lowland Spruce	AVI	AVI	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = w or a
Tamarack	AVI	AVI	Lt ≥ 70%
Pine[5]	AVI	AVI	Pj ≥ 70%
Upland Shrubs[5]	AVI	AVI	> 25% shrub cover; < 6% tree cover; moisture = d or m
Nonforest[5]	AVI	AVI	Areas with < 6% canopy
Open Wetland	AVI	AVI	< 6% crown closure; moisture = w or a
Water	AVI	AVI	Standing or flowing water
Cutblock	ABMI[1]	ABMI[3]	Forest harvest areas
Seismic Line	UALF	ABMI[3]	Traditional, single petroleum exploration line
3-D Seismic Line	UALF	ABMI[3]	3-D seismic petroleum exploration line, deployed in a high-density hashtag pattern
Pipeline	ABMI[1]	ABMI[2]	Petroleum pipelines, typically wide and grass-covered
Road	ABMI[1]	ABMI[3]	Combination of road and rail (hard surface or vegetated verge)
Trail	ABMI[1]	ABMI[3]	Combination of trails and truck trails
Well Site	ABMI[1]	ABMI[3]	Petroleum extraction sites, including well and surrounding area
Block Feature[5]	ABMI[1]	ABMI[3]	Combination variable including borrow pits, dugouts, sumps, industrial sites, other disturbed vegetation

Table 2.2 Candidate models to explain wolf occurrence.
Candidate models to test the relative effect of preferred prey habitat, relative abundance of prey, movement ability and landcover associated with exposure risk on monthly wolf occurrence before and after the onset of wolf population reduction.

Hypothesis – Wolf occurrence best explained by:	Predictor variables
Prey habitat	Upland Deciduous/Mixedwood Lowland Deciduous/Mixedwood Upland Spruce Lowland Spruce Tamarack Open Wetland Water Cutblock Well Site
Prey occurrence	Caribou Moose White-tailed deer
Movement ability	Trail Road Pipeline Seismic Line 3-D Seismic Line
Exposure risk	Open Wetland Water Cutblock Well Site Road Pipeline Seismic Line 3-D Seismic Line

2.3 Results

2.3.1 Effects of population reduction on wolf relative abundance and distribution

Although the spatial distribution of independent wolf detections only decreased by 25% post-control (pre-control: 92% of sites; post-control: 67% of sites) (Figure 2.3.b), the number of independent wolf detections decreased nearly four-fold in the post-control sampling period (pre-control: 509 detections; post-control: 122 detections) (Figure 2.3.a).

2.3.2 Effects of population reduction on drivers of wolf occurrence

Before population reduction, wolf occurrence was most strongly influenced by landscape features associated with movement ability (AICcw = 0.915, deviance explained = 0.11) (Table 2.3). After the onset of population reduction, wolf occurrence was driven predominantly by landscape features associated with exposure risk (AICcw = 0.986, deviance explained = 0.41) (Table 2.4). While wolf occurrence was strongly driven by anthropogenic features before and after population reduction, the direction of these relationships differed between sampling periods (Figure 2.4).

Wolves exhibited a positive association with roads ($\beta = 0.370$ [0.119, 0.621]) and a negative association with 3-D seismic lines ($\beta = -0.228$ [-0.373, -0.082]) before population reduction (Figure 2.4.a). Wolves did not respond strongly to trails ($\beta = 0.051$ [-0.009, 0.111]), pipelines ($\beta = -0.004$ [-0.123, 0.115]) or seismic lines ($\beta = -0.106$ [-0.244, 0.032]) before wolf reduction (Figure 2.4.a), but did respond negatively to roads ($\beta = -0.546$ [-0.939, -0.153]), seismic lines ($\beta = -0.568$ [-0.909, -0.227]) and pipelines ($\beta = -0.844$ [-1.261, -0.427]) after population reduction (Figure 2.4.b). In addition, wolves responded positively to anthropogenic block features after population reduction (Figure 2.4.b), including cutblocks ($\beta = 0.369$ [0.150, 0.588]) and well sites ($\beta = 0.519$ [0.268, 0.771]). Wolves did not respond strongly to open wetland (β = -0.076 [-0.349, 0.196]), water (β = 0.243 [-0.027, 0.513]) or 3-D seismic lines (β = 0.127 [-0.260, 0.514]) after wolf reduction.

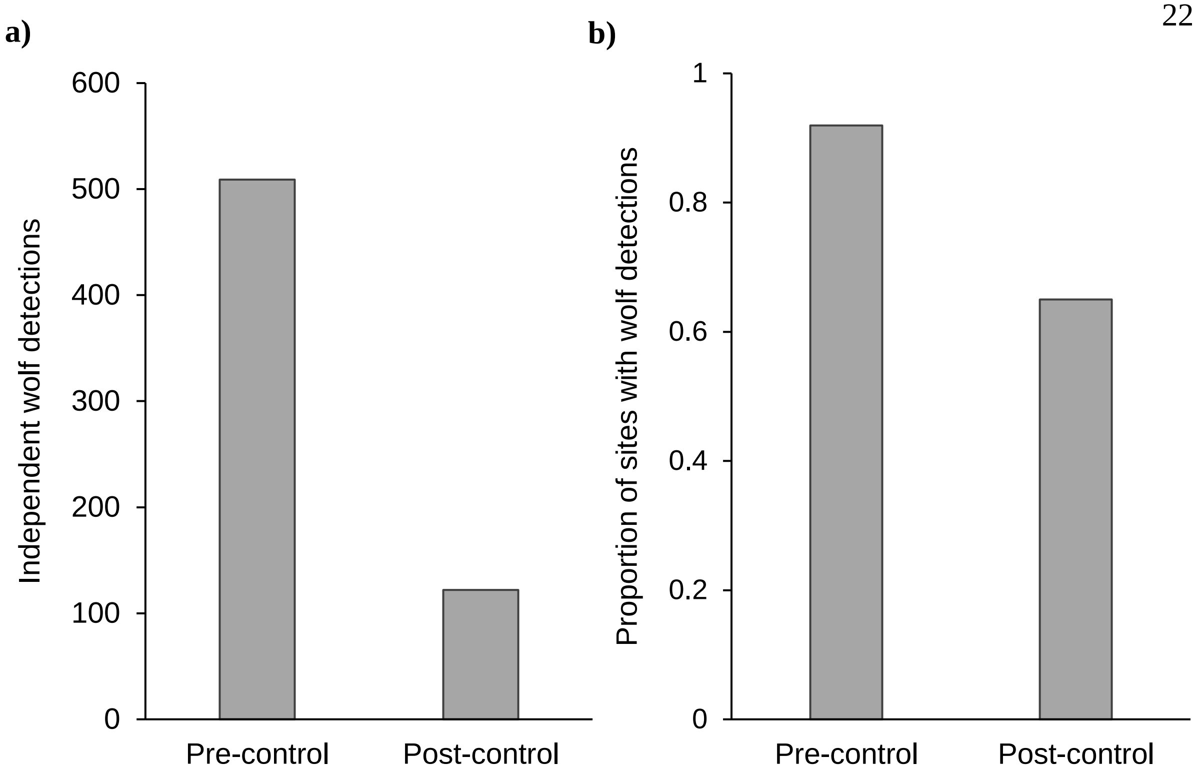


Figure 2.3 Grey wolf relative abundance and distribution during the pre-control and post-control sampling period in the Christina Lake study area.
Total number of independent wolf detections throughout the pre-control (November 2011 – September 2014) and post-control (November 2017 – September 2020) sampling periods, and (b) the proportion of sites in the pre-control and post-control sampling periods where wolves were independently detected.

Table 2.3 AICc table of pre-control and post-control candidate models of wolf occurrence. AICc scores for pre-control and post-control candidate models of monthly wolf occurrence. The table includes AICc, model intercept, log-likelihood, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported in each sampling period.

Sampling period	Hypothesis	Intercept	df	log-lik	AICc	ΔAICc	AICcw
Pre-control	Movement ability	-1.839	6	-183.795	381.1	0.00	0.915
	Exposure risk	-1.857	9	-182.755	387.0	5.85	0.049
	Prey habitat	-1.947	10	-181.694	387.7	6.58	0.034
	Null	-1.773	1	-195.508	393.1	11.96	0.002
	Prey occurrence	-1.787	4	-194.605	397.9	16.79	0.000
Post-control	Exposure risk	-2.698	9	-85.818	193.2	0.00	0.986
	Movement ability	-2.662	6	-94.113	201.8	8.58	0.014
	Prey occurrence	-3.940	4	-106.836	222.4	29.16	0.000
	Null	-3.178	1	-114.224	230.5	37.28	0.000
	Prey habitat	-3.514	10	-103.896	232.3	39.05	0.000

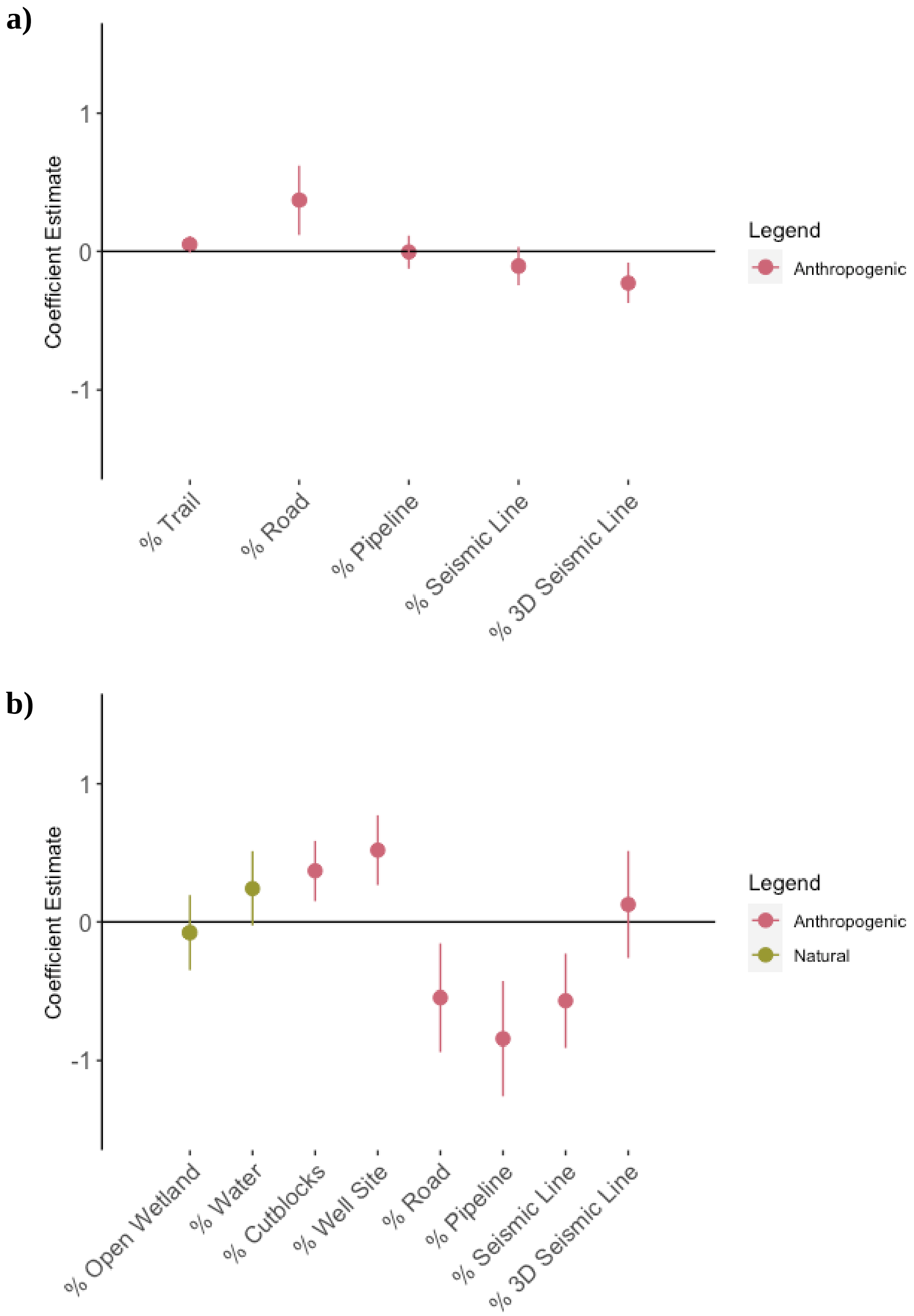


Figure 2.4 Coefficient plots of top-ranked pre-control and post-control wolf occurrence models.

Coefficient plots of top-ranked (a) pre-control and (b) post-control wolf occurrence models according to AICc scores. The top-ranked pre-control model was the movement ability model, which included the proportion of trails, roads, pipelines, seismic lines, and 3-D seismic lines as predictor variables. The top-ranked post-control model was the exposure risk model, which included the proportion of open wetland, water, cutblocks, well sites, roads, pipelines, seismic lines, and 3-D seismic lines as predictor variables.

2.4 Discussion

2.4.1 Wolves shifted habitat selection following population reduction

Our results show that government-mandated predator control triggered behavioural changes among the remaining wolf population in the Nearctic boreal forest. Following aerial gunning that removed 92 wolves over three years (D. Hervieux, personal communication, March 18, 2021), wolf habitat selection shifted: before population reduction, selection was driven primarily by movement corridors which facilitate prey acquisition; after reduction, by habitat features associated with greater exposure risk. These results suggest that predator control may trigger conditional habitat selection among the wolf population depending on the relative amounts of risk and reward available within a given habitat type.

2.4.2 Wolves avoided anthropogenic linear features following population reduction

Before the onset of population reduction, wolves responded most strongly to movement corridors. In particular, wolves were positively associated with the proportion of roads. However, following the onset of population reduction, wolves were most strongly influenced by landscape features associated with exposure risk. Specifically, wolves exhibited a clear avoidance of the proportions of anthropogenic linear features including roads, pipelines and seismic lines following wolf control.

Our results suggest that predator control may shift the perceived value of anthropogenic linear features for wolves. Predators are known to select habitat that decreases exposure risk to humans and, conversely, avoid habitat that increases exposure risk to humans in anthropogenic landscapes (Cristescu et al., 2013; Llaneza et al., 2016). However, predator associations with the landscape are not static, and can vary depending on their level of perceived risk relative to available resources (Cristescu et al., 2013; Llaneza et al., 2016; Llaneza, López-Bao, &

Sazatornil, 2012). For example, Scandinavian brown bears (*Ursus arctos*) shifted their resting site selection to sites with greater concealment and further from human settlements during the hunting season when detection risk by humans was highest (Ordiz et al., 2011).

While wolves in the highly-industrialized boreal forest of western Canada typically exhibit strong selection for anthropogenic linear features as travel corridors to facilitate prey acquisition (Dickie et al., 2017; McKenzie et al., 2012), our results suggest that human-induced mortality risk via predator control may introduce sufficient risk to these features for wolves to avoid them. Therefore, the value of anthropogenic linear features for wolves in this system is not fixed, but rather may depend on the level of perceived mortality risk.

2.4.3 Wolves selected anthropogenic block features following population reduction

Although we predicted wolves would avoid all anthropogenic features associated with exposure risk after population reduction, wolves only exhibited negative relationships with anthropogenic linear features. Contrary to our predictions, wolves responded positively to anthropogenic block features after population reduction, including cutblocks and well sites.

While anthropogenic block features are also associated with human persecution risk, we speculate that their utilization by wolves may be justified given that industrial landscape change has allowed these features to support high prey densities (James et al., 2004). Moose and white-tailed deer select well sites and cutblocks due to their availability of early seral forage (Fisher et al., 2020; Francis et al., 2021; A. David M. Latham et al., 2011), and Fisher and Ladle (2022) found that wolf occurrence frequency within anthropogenic block features was actually facilitated by the frequency of white-tailed deer occurrence. By selecting anthropogenic block features and avoiding anthropogenic linear features, wolves may be prioritizing local prey acquisition over movement in response to population reduction.

2.4.4 Implications for woodland caribou recovery

These observed behavioural shifts could potentially benefit woodland caribou recovery by limitation of the movement subsidy for wolves. Linear features promote wolf incursion into caribou habitat by increasing movement rates between foraging patches (DeMars, Boutin, & Börger, 2018; Dickie et al., 2017), ultimately reducing search time and increasing encounter rates with caribou (McKenzie et al., 2012). However, the likelihood of wolf-caribou encounters has been found to depend upon the cost associated with movement along linear features. Keim et al. (2021) found that by employing movement mitigations (i.e., soil mounding, tree planting and tree felling) on treatment seismic lines, wolves' mean intensity of use of linear features decreased and wolf-caribou encounters were reduced compared to control seismic lines.

We speculate that wolf avoidance of linear features after population reduction could lead to decreased wolf-caribou encounter rates via potential reductions in wolf movement rates across the landscape. Furthermore, wolf selection of anthropogenic block features associated with higher densities of apparent competitors (i.e., moose and white-tailed deer) – features which caribou avoid (James et al., 2004) – could indicate a potential decoupling in wolf-caribou co-occurrence in response to predator control. We strongly recommend future studies explicitly test whether predator control facilitates changes in (1) wolf movement rates and (2) spatiotemporal co-occurrence among wolves, caribou, and apparent competitors.

2.4.5 Caveats

While we attributed anthropogenic and natural habitat types with lower canopy cover and vegetation height as being more likely associated with exposure risk to human persecution (Llaneza et al., 2016), we did not explicitly measure exposure risk between habitat types and, therefore, cannot with certainty attribute variation in selection between these features to risk avoidance. Quantification of exposure risk among habitat types using GPS coordinates of individual wolves killed by aerial shooting would be necessary to attribute variable selection of these features to risk avoidance. However, such data was not available for analysis in this study.

Although we test a mechanism of human risk avoidance to explain wolf habitat selection in response to predator control, there exist alternate mechanisms that we were not able to directly test. Firstly, density dependence is a known driver of wolf resource selection (T. K. Fuller, Mech, L.D. & Cochrane, J.F. , 2003; Kauffman et al., 2007), particularly in areas of high prey density (Cubaynes et al., 2014). Unfortunately, wolf population density estimates before and after predator control were not available for analysis, and wolf population density estimation using camera trap data was beyond the scope of this study. However, if wolf response to predator control observed in our study were driven by density-dependence, we would not expect wolves to exhibit an avoidance of anthropogenic linear features post-population reduction, but rather an increased selection for these preferred features, due to reduced intraspecific competition for spatial resources (Cubaynes et al., 2014). Nevertheless, we recommend future studies with access to predator population density estimates before and after predator control explicitly test a density-dependent response relative to human risk avoidance.

Another possible mechanism contributing to observed habitat selection changes following wolf population reduction which we were unable to account for is the potential for change in social stability. Wolves are eusocial predators, meaning they form social groups (packs) in which breeding is limited to the alpha male and female and other pack members aid with raising pups (Brainerd et al., 2008; Wallach, Ritchie, Read, & O'Neill, 2009). Population reduction is known to disrupt wolf social stability with implications for demography (e.g., pack size, age structure, survival rates, genetic diversity, etc.) and behaviour (e.g., hunting skills, territory size, social behaviour, etc.) (Haber, 1996; Wallach et al., 2009). While it was beyond the scope of this research to identify wolves to the individual-level using camera traps, we recommend future studies attempt individual-level identification within the wolf population to generate a metric of social stability, ultimately allowing for differentiation between the influence of persecution risk and social dynamics on habitat selection in response to predator control.

Lastly, while it is possible that changes in wolf habitat selection could be attributed to changes in the availability of certain landscape features due to increasing industrial development within the study area between 2011 and 2020, we could not test for the relative impacts of predator control and landscape change in this study given that we did not have access to camera trap data collected over the same time period as our dataset from a structurally and functionally similar system unimpacted by predator control. However, in this instance, changes to the landscape throughout the study period may not outweigh the effects of an extensive population reduction. When population reduction rates are high, environmental factors (Rich et al., 2013) and prey availability (Boitani, 2003; T. K. Fuller, 1989; T. K. Fuller, Mech, L.D. & Cochrane, J.F. , 2003) are weaker determinants of wolf abundance and distribution than population reduction (Bassing et al., 2019). Previous literature indicates that only when wolf populations are subjected to lower reduction rates (~35%) do they respond more strongly to landscape change than population reduction (Bassing et al., 2019). However, targeted government-mandated wolf control programs in western Canada typically aim for a much higher population reduction rates (~80%) (Bridger, 2019). Furthermore, mean proportions of anthropogenic features did not differ strongly between the pre-control and post-control periods (Appendix A.1), however the differences were not explicitly tested. As such, we recommend that wildlife managers conducting predator control invest in research that implements a before-after control-impact (BACI) study design to allow for empirical testing of the relative effects of predator control and other environmental factors on the wolf population, as well as the broader mammal community.

2.4.6 Conclusion

Our research demonstrates that predator control can trigger behavioural shifts among the surviving wolf population. By avoiding landscape features that facilitate movement in favour of features known to support higher prey densities after the onset of population reduction, the perceived value of anthropogenic features for wolves may change in response to persecution risk from predator control. These behavioural changes could have positive implications for woodland caribou recovery, but further research is needed to test this.

Predator control remains a primary strategy in the wildlife management toolkit, despite being criticized for lacking rigorous tests of community-level responses (Lennox et al., 2018; Treves et al., 2016). Investigating the potential for behavioural shifts within the remaining apex predator population, and the implications for the recovery of the focal prey species, are imperative to better understand the efficacy of predator management strategies aimed at conserving species at risk. Therefore, we strongly recommend that all wildlife managers implementing predator control programs invest in rigorous and purposeful research to account for these possible indirect effects.

Chapter 3

Predator control prompts shift in competing carnivore species' spatial co-occurrence with competitors and prey in the Nearctic boreal forest

3.1 Introduction

3.1.1 Predators as regulators of ecological communities

Predators are critical components of functioning ecosystems – they exhibit top-down forces on lower trophic levels through consumptive (i.e., predation) and non-consumptive (i.e., fear, competition) effects (Hairston et al., 1960; Soulé et al., 1988; Terborgh & Estes, 2010), allowing them to regulate species abundance and distribution and contribute to the composition of ecological communities (Hairston et al., 1960; Soulé et al., 1988). Specifically, apex predators can suppress non-apex predators through direct competition via antagonism, kleptoparasitism, and direct killing (Linnell & Strand, 2000), as well as indirect competition, whereby apex predators outcompete non-apex predators for shared resources (Case & Gilpin, 1974).

To minimize risk of competition, non-apex predators can adopt behavioural traits that facilitate niche partitioning from the apex predator, thus promoting coexistence (Amarasekare, 2003; Chesson, 2000). Behavioural adaptations include differential use of space (Shigesada, Kawasaki, & Teramoto, 1979), time (Carothers & Jaksic, 1984), and/or food resources (R. Macarthur & Levins, 1967). Given the influence of apex predators on predators occupying lower trophic levels, a reduction in the apex predator population is expected to incite dramatic shifts in both numerical and behavioural trends of non-apex predator populations (Ritchie & Johnson, 2009; Soulé et al., 1988).

3.1.2 Predator control and the potential for community-wide consequences

Despite their integral role in ecological systems, predators are often perceived as negatively impacting human welfare (i.e., human-wildlife conflict) and resources (i.e., livestock, culturally and/or economically valuable species, and species at risk). As such, predators have been historically and currently lethally controlled, whereby population sizes are reduced to achieve social, economic, or ecological objectives (Lennox et al., 2018). While predator control has provided demonstrable short-term benefits to at-risk prey populations (Boertje et al., 1996; Hayes et al., 2003; Hervieux et al., 2014; Serrouya et al., 2019), it can also prompt indirect responses in non-target species (Ritchie & Johnson, 2009). Specifically, the reduction of an apex predator population is widely hypothesized to trigger "mesopredator release", whereby non-apex predators occupying one trophic level beneath the apex predator can increase in abundance and distribution following a reduction in apex predator density (Soulé et al., 1988).

Considerable research has been devoted to measuring whether non-apex predators exhibit numerical changes in response to reductions in apex predator population density (Berger et al., 2008; Crooks & Soulé, 1999; Elmhagen & Rushton, 2007; Palomares, Gaona, Ferreras, & Delibes, 1995). However, there is less information on whether a release from top-down suppression by the apex predator can incite behavioural changes among non-apex predators (Allen, Allen, Engeman, & Leung, 2013; Brook, Johnson, & Ritchie, 2012).

Following apex predator population reduction, we might expect non-apex predators to utilize resources required for survival, including prey, forage and refuge (McLoughlin et al., 2010), differently when top-down pressures are minimized. Furthermore, a decrease in competitive pressure from the apex predator could result in increased or novel predation opportunities for the non-apex predators, with potential negative impacts on prey populations. As such, quantifying behavioural changes among non-apex predators is critical to better understand the broader ecological impacts and overall effectiveness of predator control.

One method of identifying species' behavioural changes is to analyze their resource selection. Resource selection reflects a suite of behavioural decisions across space and time allowing an animal to maximize forage availability while reducing risk from competition and predation (Langvatn & Hanley, 1993; Lima & Dill, 1990; R. H. MacArthur & Pianka, 1966; Rosenzweig, 1981). As risk is reduced via control of the apex predator population, it may allow non-apex predators to access resources previously deemed too risky.

Despite the mesopredator release hypothesis describing non-apex predator responses to apex predator reduction as straightforward and predictable (Soulé et al., 1988), determining the degree of response of a non-apex predator to predator control, numerical or behavioural, poses an immense challenge for ecologists as non-apex predators can be driven simultaneously by a combination of top-down and bottom-up processes (Power, 1992; Prugh et al., 2009). To disentangle the effects of top-down and bottom-up limitations on non-apex predators, it is necessary to understand the strength and structure of interactions between apex predator, non-apex predator and prey species (Prugh et al., 2009). We sought to disentangle these signals by examining the western boreal carnivore community's response to grey wolf (*Canis lupus*) population control.

3.1.3 Case study – Grey wolf control to aid boreal woodland caribou recovery

The Nearctic boreal forest of western Canada is home to a diverse community of medium- to large-bodied carnivores including grey wolves, the apex predator, as well as coyotes (*Canis latrans*), Canada lynx (*Lynx canadensis*), and black bears (*Ursus americanus*). Woodland caribou (*Rangifer tarandus caribou*) face considerable threats from resource extraction practices in this region (Boutin et al., 2012; Hebblewhite, 2017).

The growing industrial footprint in the boreal forest has facilitated increased wolf predation of woodland caribou via two ecological mechanisms. First, oil and gas exploration and extraction, as well as forestry practices, are responsible for the addition of novel anthropogenic features to the landscape, such as roads, seismic lines, pipelines, well sites and cutblocks (Pickell et al., 2013; Pickell et al., 2015). These features can serve as movement corridors that wolves utilize to more efficiently travel across the landscape and access caribou habitat (Dickie et al., 2020; Dickie et al., 2017; A. D. M. Latham, M. C. Latham, M. S. Boyce, et al., 2011; McKenzie et al., 2012), which has been shown to increase predation rates on caribou (James & Stuart-Smith, 2000). Second, the conversion of old-growth forest to early seral vegetation through resource exploration and extraction provides forage subsidies for white-tailed deer (*Odocoileus virginianus*) (Fisher & Burton, 2021; Fisher et al., 2020) and moose (*Alces alces*) (Francis et al., 2021). Consequently, increased population densities of white-tailed deer and moose support greater wolf population densities, which increases predation risk for caribou and creates “apparent competition” between these three ungulate species (Holt, 1977; James et al., 2004; A. David M. Latham et al., 2011).

While habitat loss and fragmentation due to increased industrial activity across western Canada are recognized as the ultimate drivers of caribou population decline (Boutin et al., 2012; Hebblewhite, 2017; Wittmer et al., 2007), increased predation by wolves is a by-product of these landscape-level disturbances and is therefore considered the proximal cause (Boutin et al., 2012). As such, government-mandated wolf control programs have been initiated in multiple provinces in western Canada in an attempt to reverse woodland caribou population decline (Alberta Environment and Parks, 2017; Hervieux et al., 2014; Serrouya et al., 2019).

3.1.4 Research question and hypotheses

We asked whether non-apex predators exhibit behavioural shifts consistent with a release from top-down suppression in response to predator control in an anthropogenically disturbed boreal landscape, manifested as changes to habitat associations and prey and competitor co-occurrence. To achieve our goal, we generated three competing hypotheses and predictions that aimed to disentangle the influences of top-down and bottom-up processes on coyote, lynx, and black bear occurrence. In forming these competing hypotheses, we acknowledge that species at any given time can be influenced simultaneously by both top-down and bottom-up processes (Power, 1992; Prugh et al., 2009).

Our first hypothesis is that the spatial distributions of coyotes, lynx, and black bears are to some degree constrained by wolves. Relative body size and the degree of resource overlap are important determinants of the strength of competition exhibited between apex predators and non-apex predators (Caro & Stoner, 2003). If predator species share similar body sizes and resources (e.g., prey, habitat), they are more likely to exhibit strong interspecific competition (Donadio & Buskirk, 2006). Wolves and coyotes are similarly sized canids, with wolves being the larger, competitively dominant species (Berger & Gese, 2007; Merkle, Stahler, & Smith, 2009; Polis & Holt, 1992). In addition, they exhibit dietary overlap (Paquet, 1992), as both coyotes and wolves are known to predate white-tailed deer in the Nearctic boreal forest (James et al., 2004; Latham, Latham, Boyce, & Boutin, 2013). Lynx and black bears also exhibit dietary overlap with wolves, with lynx and wolves feeding on small-bodied mammals (Latham, 2009; Mark O'Donoghue et al., 1998), and black bears and wolves predating on ungulates (James et al., 2004; Zager &

Beecham, 2006). As such, we expect wolves are capable of suppressing coyotes, lynx, and black bears. Before wolf control, we predicted coyote, lynx, and black bear avoidance of wolves, preferred prey, or anthropogenic features. After reduction of wolf populations, we predicted coyote, lynx and black bear overlap with remaining wolves, preferred prey or anthropogenic features.

Our second hypothesis is that lynx are primarily suppressed by coyotes. Lynx feed on small-bodied mammals such as snowshoe hares and red squirrels (Squires & Ruggiero, 2007), and thus exhibit less dietary overlap with wolves, who predate primarily on ungulates including caribou, moose, and white-tailed deer. However, wolves have been observed feeding on smaller mammals including snowshoe hare, red squirrel, and beaver, but they are not their target prey (Latham, 2009; Latham, Latham, Knopff, Hebblewhite, & Boutin, 2013). While dominance hierarchies exist between apex predators and non-apex predators, they also occur among non-apex predators, with competitively dominant non-apex predators capable of suppressing subdominant non-apex predators (Levi & Wilmers, 2012). Lynx have been hypothesized to be more strongly limited by coyotes than wolves, as suggested by the among-predator cascade hypothesis (Levi & Wilmers, 2012; Ripple, Wirsing, Beschta, & Buskirk, 2011) due to the greater degree of niche overlap between coyotes and lynx and wolves and coyotes relative to wolves and lynx. Thus, wolves are expected to suppress coyotes, releasing lynx from suppression by coyotes. Conversely, if wolves are absent, coyotes are released from wolf suppression and exert suppression on lynx. Before wolf control, we predicted lynx overlap with coyotes or preferred prey. After wolf control, we predicted lynx avoidance of coyotes or preferred prey. There is little evidence that black bears compete directly with coyote and lynx in this system, therefore we did not test these interactions.

Our third hypothesis is that black bears are primarily limited by bottom-up processes. Bottom-up limitation may be a stronger behavioural driver if apex predator suppression is relatively weak. While black bear suppression by wolves is possible, given that both species prey on moose, caribou, and white-tailed deer (James et al., 2004; Zager & Beecham, 2006), black bears are omnivorous and regularly switch between animal and plant food sources (Bastille-Rousseau, Fortin, Dussault, Courtois, & Ouellet, 2011; Mosnier, Ouellet, & Courtois, 2008). Their predation strategy is more opportunistic (Bastille-Rousseau et al., 2011), with ungulate predation limited to the calving season (Bergerud, 1971). Thus, direct competition with wolves may be weaker relative to other non-apex predators, and black bears may be more strongly limited by forage and habitat availability irrespective of changes in wolf density (Borer et al., 2005; Fagan, 1997). We predicted black bears could overlap with prey, natural or anthropogenic landcover, and we would observe little to no change in the drivers of occurrence before versus after wolf control.

We tested the above hypotheses using a multi-year camera trap dataset collected before and after government-mandated wolf control. Camera traps are an increasingly common tool among ecologists to measure relative abundances, distributions, and behavioural patterns of multiple species across space and time in a relatively non-invasive manner (Burton et al., 2015; Caravaggi et al., 2017; O'Connell, Nichols, & Kāranta, 2011; Steenweg et al., 2017). Specifically, species detection rates across a camera trap array can provide insight into the spatial niche of species, and how co-occurring species may partition in space to reduce the likelihood of competitive or predatory interactions (Schoener, 1974).

This is the first study of which we are aware to measure shifts in the spatial associations of multiple boreal carnivores before and after the onset of predator control exclusively using camera trap data. By examining changes to non-apex predator spatial associations in response to predator control, we can better understand the potential indirect effects of predator control within the mammal community (Treves et al., 2016).

3.2 Methods

3.2.1 Study area

Our study area is in the western Nearctic boreal forest, 350 km northeast of Edmonton, Alberta, a ca. 3500 km^2 landscape of deciduous, coniferous and mixedwood forests; it also contains wetlands and water bodies including bogs, fen, lakes, and rivers. Anthropogenic disturbance is ubiquitous within the study area due to oil and gas exploration and extraction and forestry, providing a model landscape to examine disturbance effects on boreal mammals (Fisher & Burton, 2018, 2021; Fisher et al., 2020; Wittische et al., 2021). Landscape features associated with these practices include seismic lines, transmission lines, pipelines, roads, well sites, industrial camps, and cutblocks (Pickell et al., 2013; Pickell et al., 2015). The Cold Lake and East Side Athabasca River (ESAR) caribou populations, whose ranges converge within our study area (Appendix 1), have exhibited consistent declines in population growth rates since the onset of monitoring in 1999 (Alberta Sustainable Resource Development & Alberta Conservation Association, 2010; Hervieux et al., 2013).

In an effort to mitigate population declines in the Cold Lake and ESAR caribou populations, the Government of Alberta commenced wolf population reduction in their ranges in the winter of 2016/2017 (Alberta Environment and Parks, 2017). The standard procedure for wolf removal programs conducted in western Canada has been to remove wolves annually during the winter months when aerial snow tracking is possible (Bridger, 2019). Aerial gunning via helicopter was the primary removal method, which has been previously deemed the most efficient and humane removal method for wolves as it facilitates rapid removal and reduces the risk of bycatch (Bridger, 2019). Between 2017 and 2020, 92 wolves were removed from the Cold Lake and ESAR caribou ranges in our study area (D. Hervieux, personal communication, March

18, 2021). There are no data to indicate what percentage of the population was removed but based on increasingly required effort, it is believed the majority of the population was removed.

3.2.2 Camera trap array

We deployed a camera trap array in the study area three years prior to the onset of wolf population reduction to understand multi-species response to anthropogenic landscape change. We used a constrained stratified random design (Fisher & Burton, 2018; Fisher et al., 2020; Wittische et al., 2021), which captures the variation in natural and anthropogenic land cover within the industrialized boreal forest of northeast Alberta (Figure 3.1) while preventing collinearity among variables. A grid containing 1 km x 1 km cells was placed across the study area in Arc GIS 10.2 Spatial Analyst (ESRI Inc, Redlands, CA) to identify sampling locations. Grid cells were randomly selected (constrained by access and a minimum of 2-km apart) within strata defined by canopy cover, tree species, and topography.

One unbaited Reconyx PC900 Hyperfire infrared remote digital camera (Holmen, WI, USA) was placed within each selected grid cell, where each camera was secured to a tree facing an active game trail to maximize detection probability of medium- to large-sized mammals (Fisher & Burton, 2018). Cameras were set to high sensitivity and no delay between triggers. While camera sites were constrained to access via roads and trails, potential bias is reduced when landcover is analyzed at a radius of 250 m or more from the centroid of each cell, due to the high density of these features across the study area (see multiscale analysis in Fisher and Burton (2018). We defined “site” as the detection zone of an individual camera trap, and “study area” as the ~3500 km^2 polygon surrounding all sites.

From October 2011 to October 2014, camera traps operated across 61 sites. After the onset of wolf population reduction, we re-deployed 60 cameras as close as possible to the original locations from October 2017 to October 2020. Camera servicing and data collection occurred approximately once per year. Given wolf population reduction was initiated in the winter of 2016/2017, we partitioned the camera data based on whether it was collected pre-control (2011-2014) or post-control (2017-2020). We used Timelapse 2 version 2.2.2.4 (Greenberg, 2019; http://saul.cpsc.ucalgary.ca/timelapse/) to classify camera trap images. Timelapse 2 allowed us to record date, time, species identity, number of individuals, classifier identity, and comments (when necessary) for each image at each site in an efficient and consistent manner. We exported Timelapse files as .csv files and imported into them R (R Core Team, 2017) for analysis.

3.2.3 Carnivore occurrence response variables

We generated individual response variables for black bear, coyote, and lynx. We imposed a minimum threshold of 30 minutes between species' detection events in order to classify them as independent (Rovero & Zimmermann, 2016). Independent detection events were summed across months to obtain a proportional binomial response variable, or "occurrence frequency", where a species was detected (1) or not (0) monthly at each site, which we deemed sensitive enough to detect intra-annual variation in site use, while reducing zero-inflation induced by absences caused by movement (Neilson et al., 2018; Stewart et al., 2018). Despite cameras operating in October 2011, 2014, 2017 and 2020, camera checks occurred midway through each of these months. Therefore, we treated these months as incomplete and excluded them from analysis.

Except for black bear, species occurrence frequencies were generated across 35 months pre-control (November 2011 – September 2014) and 35 months post-control (November 2017 – September 2020). To account for winter hibernation, I only included months between April and

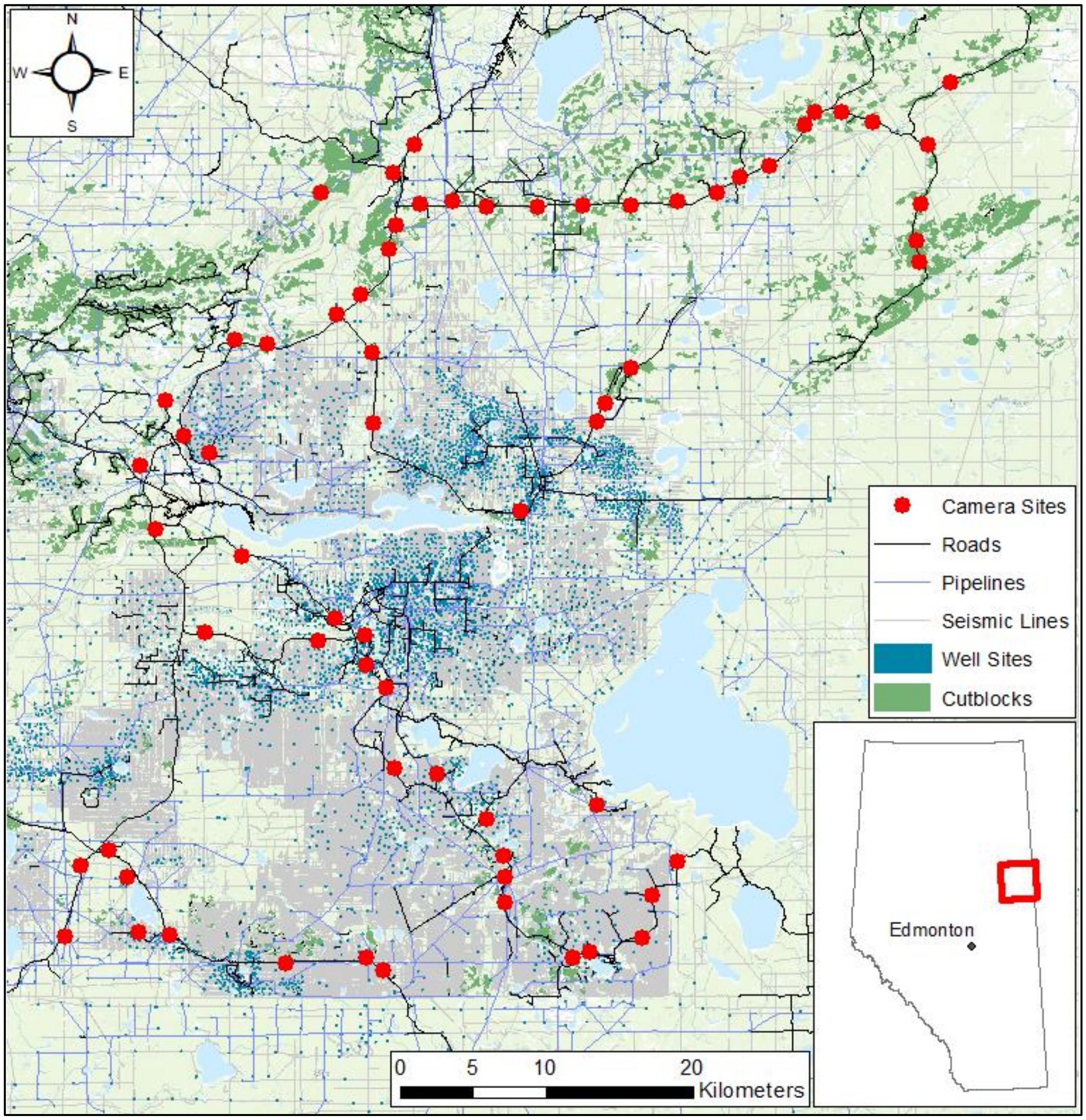


Figure 3.1 Map of camera trap locations within the study area.
Camera sites are represented by red dots. Natural resource extraction via forestry and oil and gas exploration in northeast Alberta has resulted in high densities of disturbance features across the study area. These features include roads, pipelines, seismic lines, 3-D seismic lines, and cutblocks.

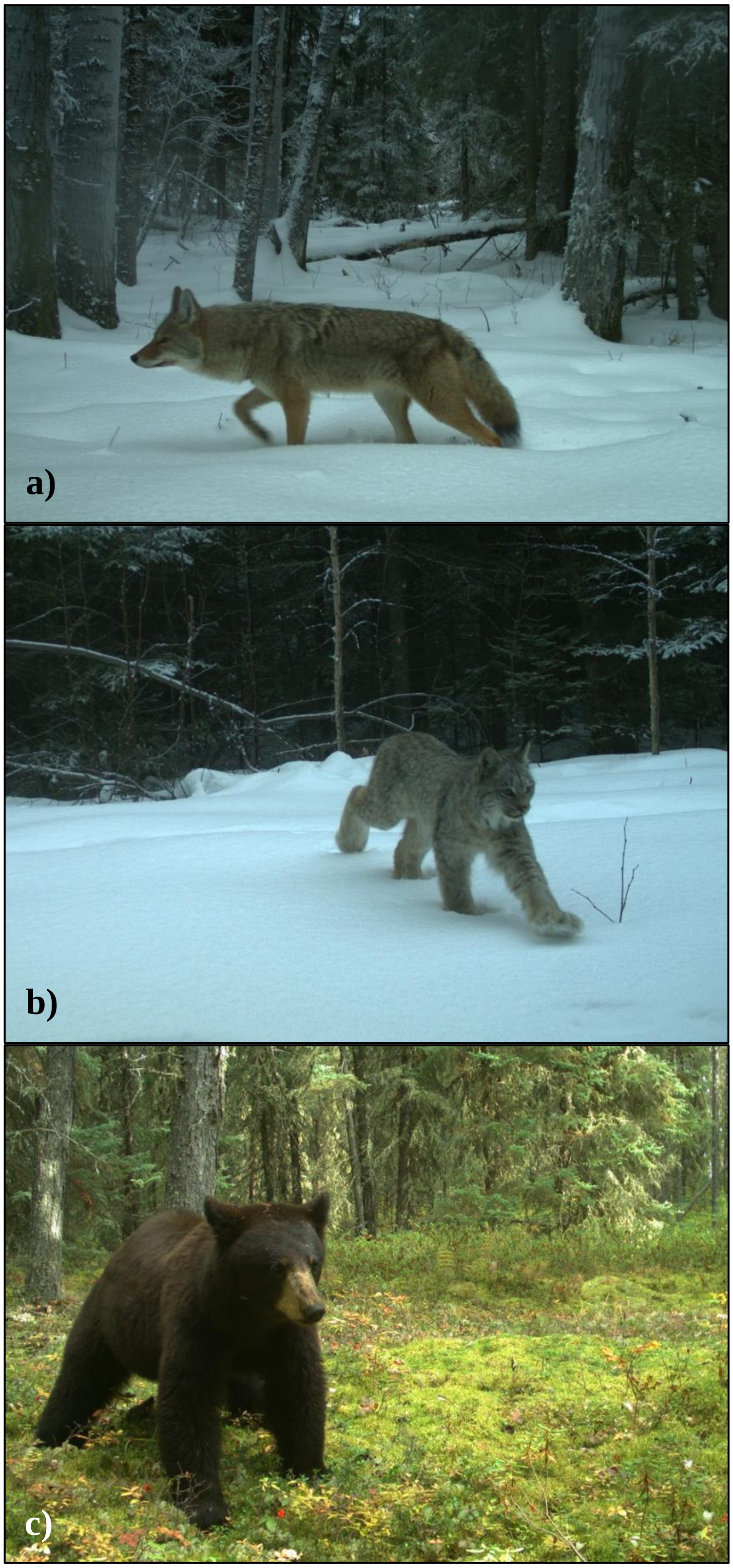


Figure 3.2 Camera trap photos of the focal non-apex predator species: (a) coyote (*Canis latrans*), (b) lynx (*Lynx canadensis*) and (c) black bear (*Ursus americanus*).

October when generating black bear occurrence frequency, resulting in a total sampling period of 20 months pre-control and 20 months post-control.

3.2.4 Predictor variables

Predictor variables were generated to represent the mechanisms hypothesized to influence subordinate carnivore occurrence on the landscape – natural landcover, anthropogenic landcover, apex predator occurrence, intraguild competition, and predation opportunities. We quantified a variety of habitat types to capture the heterogeneity of both natural and anthropogenic landcover across the study area. We quantified natural landcover within the study area using the Alberta Vegetation Inventory (Alberta Agriculture Forestry and Rural Economic Development, 2005). Natural landcover was classified based on canopy cover class, tree species, and moisture regime (Table 3.1). We used Alberta Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory (Alberta Biodiversity Monitoring Institute, 2017a, 2017b, 2019) to quantify the amount of anthropogenic landcover in the study area, and binned individual features into two broad categories: linear features and polygonal (block) features. Given the rapidly growing industrial footprint throughout the study area, we accounted for temporal changes in anthropogenic landcover by calculating the amount of anthropogenic habitat classes from spatial data collected before (2011) and after (2016) the start of wolf population reduction. We generated 12 natural and anthropogenic land cover classes to reflect landscape heterogeneity for both pre-control and post-control sampling periods (Table 3.1).

We generated predictor variables to represent apex predator occurrence and prey availability. We summed independent detections of multiple prey species into broad groups for each subordinate carnivore species based on their preferred prey species. Black bear prey species

Table 3.1 Natural and anthropogenic landcover types classified within the study area. I classified natural and anthropogenic landcover types within the study area into 12 bins. See Appendix B.1 for descriptions of individual variables comprising combination variables and data sources for each variable. Aw = Aspen; Pb = Poplar; Bw = White birch; Sb = Black spruce; Sw = White spruce; Fb = Balsam fir; Lt = Larch/tamarack; d = Dry; m = Mesic; w = Wet; a = Aquatic. [1]Combined functionally similar landcover classes to reduce skew in distributions. [2]Omitted from both pre-control and post-control analysis to prevent collinearity with other variables.

Predictor variable	**Description**
Upland Deciduous[1]	(Aw, Pb, Bw ≥ 70% canopy cover), moisture = d or m
Upland Mixedwood[1]	40-60% canopy cover, moisture = d or m
Lowland Deciduous[1]	(Aw, Pb, Bw ≥ 70% canopy cover), moisture = w or a
Lowland Mixedwood[1]	40-60% canopy cover, moisture = w or a
Upland Spruce	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = d or m
Lowland Spruce	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = w or a
Tamarack	Lt ≥ 70%
Pine[2]	Pj ≥ 70%
Upland Shrubs[1,2]	> 25% shrub cover; < 6% tree cover; moisture = d or m
Nonforest[1,2]	Areas with < 6% canopy
Open Wetland	< 6% crown closure; moisture = w or a
Water	Standing or flowing water
Linear Features	Combination of road, trail, pipeline, seismic line and 3-D seismic line
Block Features	Combination of well site and cutblock

consisted of white-tailed deer, moose and caribou (Zager & Beecham, 2006); coyote prey species included white-tailed deer, snowshoe hare and red squirrel (Latham, Latham, Boyce, et al., 2013; Mark O'Donoghue et al., 1998), while lynx included snowshoe hare and red squirrel (Mark O'Donoghue et al., 1998). To quantify apex predator and prey occurrence before and after population reduction, we used the same methods applied to subordinate carnivores and calculated both pre-control and post-control proportional binomial variables for wolves and each group of prey species, where a species was detected (1) or not (0) monthly at each site.

3.2.5 Data exploration

We calculated variance inflation factors (VIF) to assess collinearity among predictor variables. Predictor variable sets where VIF < 3, indicating a lack of collinearity, were retained (Zuur et al., 2010). We then scaled predictor variables from the pre-control and post-control datasets together to allow for accurate comparison of coefficient estimates before and after wolf population reduction.

3.2.6 Statistical analysis

We modelled pre-control and post-control coyote, black bear, and lynx occurrence to test the effect of predator control on non-apex predator resource selection and co-occurrence (Table 3.2). We modelled each non-apex predator species' proportional binomial response variable using a generalized linear model (GLM) (McCullagh & Nelder, 1989) with a binomial distribution (logit link function).

Species' habitat selection is subject to considerable variation when habitat is measured across a gradient of spatial scales. Variability in species habitat selection in relation to spatial scale is further dependent on the species and landscape in question (Fisher et al. 2011; Levin, 1992). To account for this variation, competing carnivore occurrence was modelled across a range of spatial scales to identify the spatial scale that best explained competing carnivore occurrence frequency. Firstly, we built core models consisting of the proportions of all natural landcover variables across a range of spatial scales. Spatial scales were defined as buffers surrounding camera sites ranging from 250 – 2000 m in radius, in 250-m increments. We used Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc) to identify the best-supported spatial scale, where we used AICc weights of each candidate model to determine the strength of natural landcover selection at each spatial scale (Burnham & Anderson, 2002). If models were ≤ 2 ΔAICc values from the top model, we selected the most parsimonious model.

We then built competing models using the core natural features model at the best-supported spatial scale for both pre-control and post-control periods. Candidate model sets were built to test the relative effects of apex predators, intraguild competitors and resource availability (i.e., natural and/or anthropogenic habitat and prey) on non-apex predator occurrence. We used AICc scores to evaluate empirical support for each model. If models were ≤ 2 ΔAICc values from the top model, we selected the most parsimonious model (Burnham & Anderson, 2002). Models were evaluated using diagnostic plots, calculating deviance explained, and using k-fold cross validation from the *boot* package (Canty & Ripley, 2021) in R to evaluate prediction error.

Table 3.2 Candidate model sets to explain non-apex predator occurrences.
Candidate model sets to test the relative effect of natural and anthropogenic habitat, as well as interspecific interactions with apex predators, competitors, and prey on subordinate carnivore occurrences. "Linear" is a combination variable of trails, roads, seismic lines, 3-D seismic lines and pipelines, and "Block" is a combination variable of cutblocks and well sites (See Table 3.1). Candidate model sets for coyote and lynx are identical – non-apex predator 1 is the responding species, and non-apex predator 2 is the intraguild competitor (e.g., when non-apex predator 1 is coyote, non-apex predator 2 is lynx and vice versa).

Species	Hypothesis – Non-apex predator occurrence is best explained by:	Predictor variables
Non-apex predator 1	Natural features	Significant natural habitat features from step 1 (Core model: CM)
	Anthropogenic features	Linear + CM Block + CM Linear + Block + CM
	Apex predator occurrence	Wolf + CM Wolf + Linear + CM Wolf + Block + CM Wolf + Linear + Block + CM
	Intraguild competitor occurrence	Non-apex predator 2 + CM Non-apex predator 2 + Linear + CM Non-apex predator 2 + Block + CM Non-apex predator 2 + Linear + Block + CM
	Prey occurrence	Prey + CM Prey + Linear + CM Prey + Block + CM Prey + Linear + Block + CM
Black bear	Natural features	Significant natural habitat features from step 1 (Core model: CM)
	Anthropogenic features	Linear + CM Block + CM Linear + Block + CM
	Apex predator occurrence	Wolf + CM Wolf + Linear + CM Wolf + Block + CM Wolf + Linear + Block + CM
	Prey occurrence	Prey + CM Prey + Linear + CM Prey + Block + CM Prey + Linear + Block + CM

3.3 Results

3.3.1 Effects of wolf control on non-apex predator relative abundance and distribution

Of the three focal non-apex predator species, only black bears exhibited increased independent detections following wolf control (pre-control: 628 detections; post-control: 1,027 detections) (Figure 3.3.e). Black bears were also the only non-apex predator species to be detected at a larger proportion of sites post-control (Figure 3.3.f). Conversely, coyote (pre-control: 867; post-control: 500) and lynx (pre-control: 662; post-control: 190) exhibited reductions in independent detections (Figure 3.3.a; Figure 3.3.c) and were detected at 10% and 32% fewer sites (Figure 3.3.b; Figure 3.3.d), respectively, after the onset of wolf control.

3.3.2 Coyote shifted from co-occurrence with competitor pre-control, to prey selection post-control

Before wolf control, coyote occurrence was best explained by intraguild interactions (AICcw = 0.789, deviance explained = 0.359; Table 3.3). Specifically, coyotes were more likely to co-occur with lynx (β = 0.389 [0.274, 0.508]), and occur at sites with higher proportions of industrial block features (β = -0.214 [-0.323, -0.105]) (Figure 3.4.a, Appendix B.5). However, after the onset of wolf control, coyote no longer co-occurred with lynx; instead, coyote occurrence was best explained by prey availability (AICcw = 0.561, deviance explained = 0.254; Table 3.3), exhibiting a strong positive relationship with the occurrence of their preferred prey (β = 0.966 [0.591, 1.341]) in addition to variance explained by the core model (Figure 3.4.b, Appendix B.6).

3.3.3 Lynx shifted from co-occurrence with competitor pre-control, to prey selection post-control

Lynx occurrence before wolf control was primarily explained by intraguild interactions, and afterwards shifted to selection for prey. With three models falling within 2 ΔAICc of the top model, the most parsimonious model (AICcw = 0.233, deviance explained = 0.398; Table 3.3) included coyote occurrence (β = 0.254 [0.155, 0.352]) and the core model (Figure 3.5.a, Appendix B.7). After wolf control, lynx occurrence increased with increasing prey availability (β = 0.431 [0.264, 0.597], Figure 3.5.b) (AICcw = 0.183, deviance explained = 0.328; Table 3.3, Appendix B.8).

3.3.4 Black bears selected for natural landcover before and after wolf control

Black bear occurrence was best explained by natural landcover before and after wolf control. Pre-control bear occurrence was explained equally by the top four models, with only the core model being retained in each of the top models (Table 3.3). The most parsimonious model was the natural features model (AICcw = 0.125, deviance explained = 0.248; Table 3.3).

Black bears occurred more frequently with increasing proportions of upland deciduous/mixedwood (β = 0.177 [0.059, 0.294]), upland spruce (β = 0.109 [0.042, 0.175]), lowland spruce (β = 0.200 [0.069, 0.331]) and water (β = 0.597 [0.277, 0.917]), and occurred less frequently with increasing proportions of tamarack (β = -0.526 [-1.005; -0.046]) before wolf control (Figure 3.6.a, Appendix B.9). After wolf control, five models fell within 2 ΔAICc of the top model (Table 3.3). The most parsimonious model contained only the core natural features model. Similar to the pre-control period, black bears occurred more frequently with increasing proportions of upland spruce (β = 0.151 [0.054, 0.248]) and water (β = 0.138 [0.021, 0.256]), and occurred less frequently with increasing proportions of tamarack (β = -0.524 [-0.776, -0.273]) (Figure 3.6.b, Appendix B.10). Black bears also exhibited a negative response to the proportions of upland deciduous/mixedwood (β = -0.150 [-0.258, -0.043]) and open wetland (β = -0.248 [-0.367, -0.129]) after wolf control (Figure 3.6.b, Appendix B.10).

3.3.5 Post-hoc analysis - Coyote co-occurrence with individual prey species

We conducted a post-hoc analysis to test a secondary hypothesis, which detailed a possible mechanism for the unexpected co-occurrence between coyote and lynx before wolf control. If coyotes seek to avoid competition with wolves before wolf control, as we initially hypothesized, we might expect coyotes to preferentially select small mammals (i.e., snowshoe hare and red squirrels) over white-tailed deer, given wolves primarily target white-tailed deer in this system (Wasser, Keim, Taper, & Lele, 2011). As such, coyote and lynx co-occurrence before wolf control may indicate mutual selection of small mammal prey as an indirect result of competition with wolves. To test our hypothesis, we developed a set of candidate models where each prey species was an individual predictor variable (Appendix B.12), rather than grouping white-tailed deer, snowshoe hare and red squirrel into a single predictor variable of prey availability as in the initial analysis.

We found that although coyote occurrence was best explained by both snowshoe hare and white-tailed deer occurrence before and after wolf control, the direction and effect sizes of the relationships differed between sampling periods. Before wolf control, coyote strongly selected for snowshoe hare occurrence ($\beta = 22.955$ [15.966, 29.944]) and avoided the occurrence of white-tailed deer ($\beta = -5.184$ [-8.116, -2.252]) (Appendix B.13.a). Conversely, coyote exhibited a stronger positive relationship with white-tailed deer occurrence ($\beta = 0.605$ [0.387, 0.823]) than snowshoe hare occurrence ($\beta = 0.362$ [0.245, 0.480]) after wolf control (Appendix B.13.b).

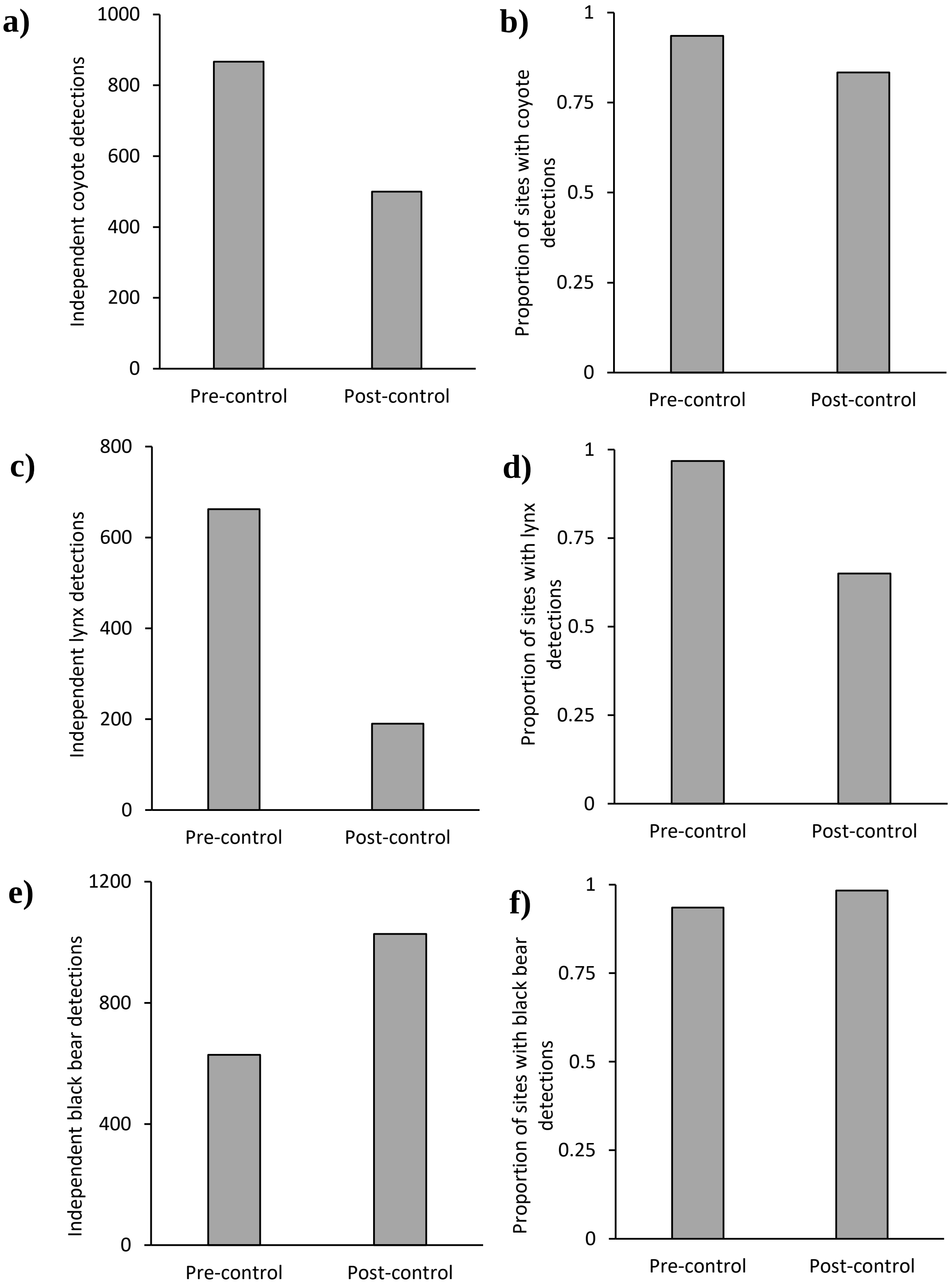


Figure 3.3 Relative abundances and distributions of non-apex predators before and after predator control.
Total number of independent (a) coyote, (c) lynx and (e) black bear detections throughout the pre-control (November 2011 – September 2014) and post-control (November 2017 – September 2020) sampling periods, and the proportion of sites in the pre-control and post-control sampling periods where (b) coyote, (d) lynx and (f) black bear were independently detected.

Table 3.3 Top-ranked pre-control and post-control models for each non-apex predator species.

Top-ranked pre-control and post-control models of coyote, lynx, and black bear occurrence. I included all models within 2 ΔAICc of the top model, but only the most parsimonious model was interpreted. See Appendices B.5 – B.10 for AICc tables of all pre-control and post-control models for each non-apex predator.

Species	Sampling period	Top models within 2 ΔAICc	df	log-lik	AICc	ΔAICc	AICcw
Coyote	Pre-control	Lynx + Block + CM	7	-207.916	431.9	0.00	0.789
	Post-control	Prey + CM	5	-180.626	372.4	0.00	0.561
		Prey + Block + CM	6	-180.356	374.3	1.93	0.213
Lynx	Pre-control	Coyote + Linear + CM	7	-183.789	383.7	0.00	0.457
		Coyote + CM	6	-185.738	385.0	1.35	0.233
		Coyote + Linear + Block + CM	8	-183.177	385.1	1.42	0.225
	Post-control	Prey + Linear + CM	5	-127.932	267.0	0.00	0.465
		Prey + Linear + Block + CM	6	-127.447	268.5	1.50	0.219
		Prey + CM	4	130.055	268.8	1.86	0.183
Black Bear	Pre-control	Linear + CM	7	-148.799	313.7	0.00	0.247
		Wolf + Linear + CM	8	-147.873	314.5	0.81	0.165
		Wolf + CM	7	-149.446	315.0	1.30	0.129
		CM	6	-150.755	315.1	1.36	0.125
	Post-control	CM	6	-151.372	316.3	0.00	0.242
		Linear + CM	7	-150.695	317.5	1.21	0.132
		Block + CM	7	-150.767	317.7	1.36	0.123
		Prey + CM	7	-150.851	317.9	1.53	0.113
		Wolf + CM	7	-151.021	318.2	1.87	0.095

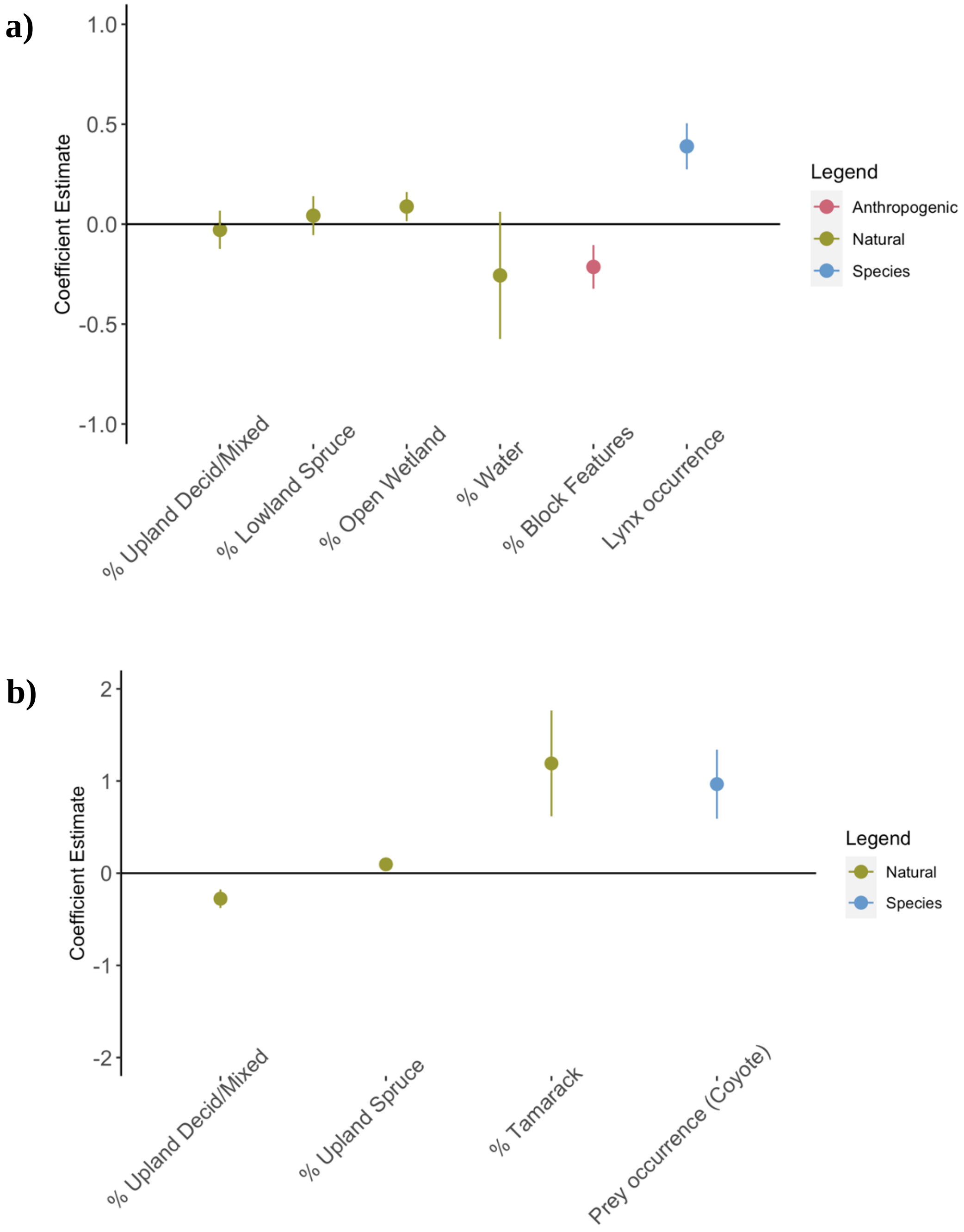


Figure 3.4 Coefficient plots of pre-control and post-control coyote occurrence models. Beta coefficient plots of most parsimonious (a) pre-control and (b) post-control coyote occurrence models. *Decid/Mixed = Decidous/Mixedwood.

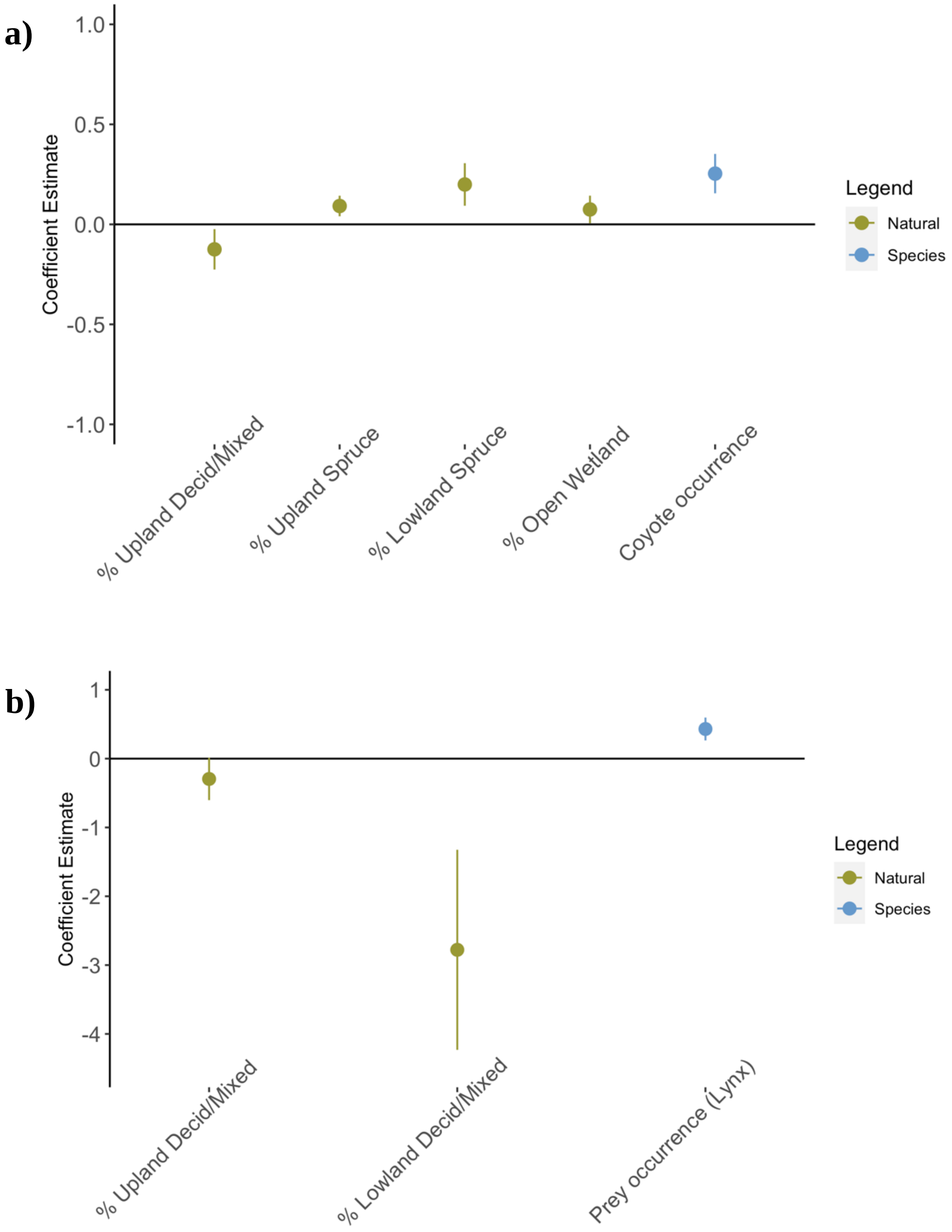


Figure 3.5 Coefficient plots of pre-control and post-control lynx occurrence models. Beta coefficient plots of most parsimonious (a) pre-control and (b) post-control lynx occurrence models. *Decid/Mixed = Decidous/Mixedwood.

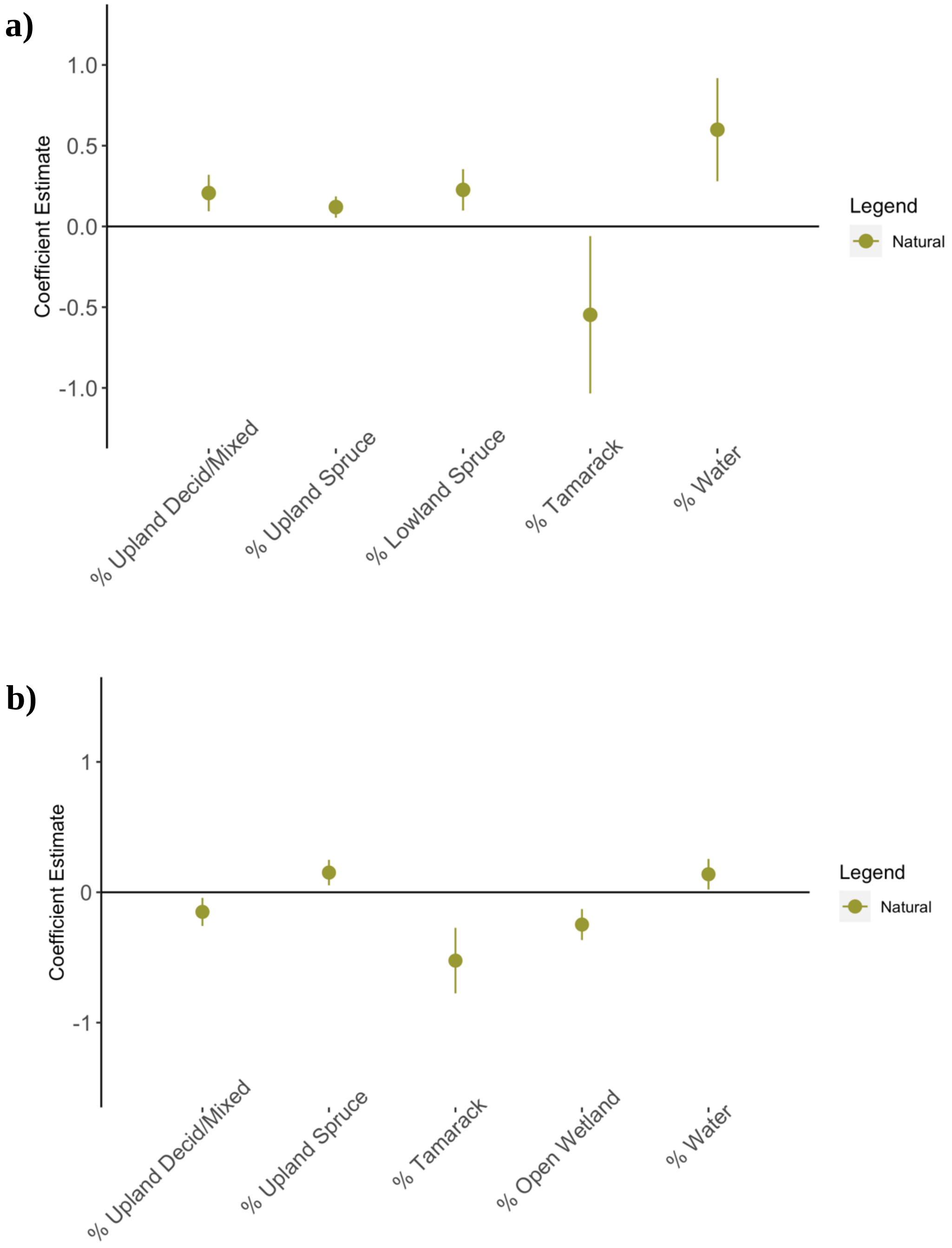


Figure 3.6 Coefficient plots of pre-control and post-control black bear occurrence models. Beta coefficient plots of most parsimonious (a) pre-control and (b) post-control black bear occurrence models. *Decid/Mixed = Decidous/Mixedwood.

3.4 Discussion

3.4.1 Non-apex predators exhibited variable shifts in behaviour following predator control

Non-apex predators did not exhibit behavioural shifts consistent with our *a priori* predictions that would indicate a release from wolf suppression in response to wolf control. Neither coyote, lynx, or black bear occurrences were influenced directly by wolf occurrence before or after the onset of wolf control. However, spatial distribution of coyote and lynx switched from being explained by their competitor, to being explained by prey availability. Black bear occurrence was consistently explained by natural landcover before and after wolf control. The lack of a direct response to wolf occurrence by the focal non-apex predators before and after wolf control indicates two possible scenarios: (1) wolf population reduction may be indirectly altering drivers of non-apex predator occurrence, and/or (2) there may be alternative ecological processes having a greater impact on non-apex predator occurrence than a reduction in wolf population density.

3.4.2 Wolf control may release subordinate predators from intraguild competition

In response to wolf control, coyote and lynx exhibited similar behavioural shifts. Before control they strongly spatially co-occurred, but did not co-occur after; instead, coyote and lynx were strongly positively associated with the occurrence of their preferred prey. Coyote and lynx reciprocal co-occurrence before wolf reduction, while not consistent with our *a priori* predictions associated with direct wolf suppression, may be evidence of indirect relationships resulting from top-down limitation by wolves. When faced with increased competition with wolves for prey, it may be energetically favourable for coyotes to partition from wolves in their resource use, even if it increases resource overlap and the potential for competition with lynx (R. H. MacArthur & Pianka, 1966; Sivy, Pozzanghera, Colson, Mumma, & Prugh, 2018).

In a post-hoc analysis, we tested the secondary hypothesis that top-down forces exhibited by wolves may indirectly result in spatiotemporal overlap between coyote and lynx, thus increasing the possibility of competition for prey. As predicted, coyotes co-occurred with snowshoe hare and even avoided the occurrence of white-tailed deer before wolf control. Conversely, while coyote co-occurred with both snowshoe hare and white-tailed deer after wolf control, coyote co-occurred more strongly with white-tailed deer, suggesting a potential reduction in the degree of competition for prey with lynx. However, we are cautious in inferring strong co-occurrence between coyote and snowshoe hare pre-control, as snowshoe hare occurrence appears relatively inflated. This large coefficient estimate may be due to the distribution of snowshoe hare monthly occurrence frequency being biased towards certain sites and months (i.e., winter) in the pre-control period. While the nature of the monthly occurrence frequency variable in this analysis does not allow for the inclusion of site and season random effects, we believe their inclusion in future analyses could account for the skew in pre-control snowshoe hare occurrence frequency distribution.

Overall, these results lend support to the hypothesis that wolves can exhibit top-down forces on coyotes and lynx in this system, which may indirectly drive resource overlap between coyotes and lynx when the wolf population is intact. Furthermore, our findings suggest that coyote and lynx may exhibit an indirect behavioural release from suppression following a reduction in the wolf population.

An among-predator cascade has been demonstrated for wolves, coyotes and red foxes (Levi & Wilmers, 2012), and while it has been suggested for wolves, coyotes and lynx (Ripple et al., 2011), it has yet to be tested. If an among-predator cascade were driving these relationships, we expected lynx to be suppressed by coyotes after wolf control, represented as an avoidance of coyotes or preferred prey. Our results did not indicate this. In fact, after wolf reduction, lynx responded positively to the occurrence of their preferred prey. Consequently, our results do not support coyote suppression of lynx via an among-predator cascade after the onset of wolf control.

3.4.3 Black bears did not exhibit a behavioural shift in response to wolf control

Black bear occurrence was primarily explained by the availability of natural landcover features both before and after wolf control, consistent with our resource limitation hypothesis. Black bears demonstrated consistent selection for increasing proportions of upland spruce and decreasing proportions of tamarack. These results corroborate previous work demonstrating black bears in this region avoiding lowland habitat in favour of upland habitat (Carter, Brown, Etter, & Visser, 2010; Czetwertynski, Boyce, & Schmiegelow, 2007; Latham, Latham, & Boyce, 2011; Tigner, Bayne, & Boutin, 2014). Vegetation is an important food source for black bears, and as such they are known to prioritize upland habitat with greater vegetation abundance given that lowland habitat, such as bogs and fens, are relatively unproductive (Bonan & Shugart, 1989; Mosnier et al., 2008; Tigner et al., 2014).

While wolves can exert competitive pressure on black bears, black bears’ ability to switch between animal and plant food sources may weaken the impact of this top-down pressure (Bascompte, Melián, & Sala, 2005; Thompson, Hemberg, Starzomski, & Shurin, 2007), represented as a consistent response to natural habitat before and after wolf control. Overall, our results suggest that black bears did not exhibit significant behavioural shifts in response to wolf control.

3.4.4 Caveats

Interspecific interactions were not directly measured, but rather inferred from co-occurrence data. While co-occurrence data is not a direct metric of species interactions (Blanchet, Cazelles, Gravel, & Jeffers, 2020), co-occurrence is a pre-requisite for interactions among species, thus signalling the possibility for interactions. Furthermore, the development of models that include the ecological mechanisms of species interactions allows one greater confidence in inferring the potential for species interactions from co-occurrence data (Blanchet et al., 2020), as we aimed to do in this study.

Species co-occurrences were measured at a monthly temporal scale, rather than finer-scale (e.g., weekly, daily) syntopy. We made this decision to reduce the likelihood of zero-inflation induced by absences caused by movement (Neilson et al., 2018; Stewart et al., 2018). To remain conservative, we limited our inference space to broad-scale spatiotemporal co-occurrence patterns between species.

Of the focal non-apex predator species, we recorded fewer coyote and lynx independent detections following wolf control than before the onset. While it was beyond the scope of this study to quantify numerical changes in response to predator control, we would expect non-apex predators such as coyote and lynx to exhibit increased relative abundance following release from wolf suppression (Soulé et al., 1988). These observed decreases could be attributed to slight differences in camera placement at sites among the two sampling periods, or animal movement patterns (Neilson et al., 2018; Stewart et al., 2018). Alternatively, these trends could be related to snowshoe hare relative abundance, which also exhibited a considerable reduction post-control (Appendix B.2). Snowshoe hare populations in the northern boreal forest experience boom-bust cycles repeating every 9-11 years (Keith, 1963; Krebs, Boutin, & Boonstra, 2001). Lynx and coyote densities are closely tied to the densities of their primary prey (Boutin et al., 1995; Krebs et al., 2001; M. O'Donoghue, Boutin, Krebs, & Hofer, 1997); for snowshoe hare, their population densities fluctuate 10-25-fold during these cycles (Boutin et al., 1995; Krebs et al., 2001). While outside the scope of this work, we believe these trends warrant investigation in future studies.

3.4.5 Conclusion

We found that non-apex predator species can exhibit behavioural changes consistent with a release of top-down suppression following apex predator control, but such changes are not experienced by all non-apex predator species. When the wolf population was intact, coyotes may have co-occurred with snowshoe hare to avoid competition with wolves, resulting in coyote and lynx spatial co-occurrence. By co-occurring with their preferred prey species after wolf control, whereby coyote switched from avoiding white-tailed deer to co-occurring with them, coyote and lynx may be indirectly released from top-down suppression by wolves. Conversely, black bears' consistent selection for natural features before and after the onset of wolf control suggests that an omnivorous diet may act as a buffer against competition with wolves for prey resources. Although apex predators serve a critical role in regulating the abundance and distribution of species at lower trophic levels (Estes et al., 2011; Hairston et al., 1960; Soulé et al., 1988), not all competitors are constrained by top-down forces to the same degree, and the constraints of resource limitation must be acknowledged if we are to better understand the degree to which individual predator species may be impacted by a reduction in the apex predator population.

Examining the potential for behavioural changes in response to predator control is arguably as important as examining numerical changes not only to better understand the community-wide impacts of predator control, but also the efficacy of the program in conserving the target species. The behavioural shifts observed within the coyote population in this study could have negative implications for woodland caribou recovery. Coyote have been observed predating on caribou calves in this system (Latham, Latham, Boyce, et al., 2013), and a reduction in competitive pressure from wolves following predator control could lead to increased opportunities to predate on larger-bodied prey species, including caribou. As such, we implore future studies to further examine coyote associations with caribou in the absence of wolves.

From an ecological perspective, predator control has been criticized in part for lacking rigorous tests of community-level effects (Lennox et al., 2018; Treves et al., 2016), yet it remains a popular conservation tool implemented worldwide (Packer et al., 2009; Reynolds & Tapper, 1996). As such, it is imperative to continue researching both the direct and indirect effects of predator control, and the broader consequences for ecosystem structure and function.

Chapter 4

Conclusions on the behavioural effects of predator control in the western Canadian boreal forest

4.1 Review of findings

As society's understanding of the importance of biodiversity, and the role predators play in contributing to ecosystem health, has increased, so too has criticism for predator control as a staple in the wildlife management toolkit (Treves et al., 2016). From an ecological perspective, predator control has been criticized in part for lacking rigorous tests of community-level responses (Lennox et al., 2018; Treves et al., 2016). While a reduction in an apex predator population can incite numerical shifts among the lower trophic levels via mesopredator release (Soulé et al., 1988), it is less well understood whether such a reduction could trigger changes to species behaviour. For this thesis, I used camera trap data collected before and after the onset of a government-mandated wolf control program in northeast Alberta aimed at conserving the East Side Athabasca and Cold Lake woodland caribou populations to pose questions about the behavioural effects of predator control.

In my second chapter, I asked whether perceived risk from human persecution as a result of wolf control could alter the habitat selection of the surviving wolf population to avoid habitat with the potential to increase exposure risk. I found that wolves selected for increasing proportions of roads before the onset of predator control, and switched to avoiding increasing proportions of roads, pipelines, and seismic lines after the onset of predator control. Furthermore, wolves selected for increasing proportions of anthropogenic block features after predator control began. This chapter suggests that the persecution risk that comes with predator control may shift the perceived value of anthropogenic features for wolves, prompting wolves to prioritize local prey acquisition in and around block features over movement on linear features.

In my third chapter, I examined the behavioural responses of three focal non-apex predators: coyotes, lynx, and black bears. I sought to determine whether the focal non-apex predator species exhibited shifts in co-occurrence with habitat, competitors, and prey consistent with a release from top-down suppression in response to a reduction in the wolf population. I found that predator control triggered behavioural changes among coyote and lynx consistent with a release from top-down suppression, but not among black bears. I posit that the varied responses among non-apex predators is dependent on the strength of competition between the apex and non-apex predator, emphasizing the need to consider bottom-up processes when trying to understand the impacts of predator control within the wider ecological community.

This work is the first of which we are aware to utilize camera trap data collected before and after the onset of a predator control program to explore its behavioural effects among multiple predator species in the boreal forest of western Canada. I believe the findings of my research demonstrate that the impacts of predator control are not limited to the target predator and prey species of conservation interest and can have trickle-down effects within the larger ecological community. In addition, my research demonstrates that predator control not only has the potential to shift species abundances, but also their behaviour, with the potential to negatively impact the recovery of the target prey species. While my research could contribute new knowledge to woodland caribou conservation efforts in western Canada, more broadly, my findings provide insight on the side effects of predator control in multi-predator systems experiencing disturbance-mediated shifts in predator-prey dynamics.

4.2 Future research

While I was only able to measure species occurrences three years before and three years after the onset of predator control in a single ecosystem, future research should acquire occurrence data within the same timeframe from a similar ecosystem that did not experience predator control. A paired predator control and non-predator control design would allow for more rigorous testing of the effects of predator control by comparing species responses in the treatment system to a control sample. Given that the camera traps used in my study were deployed before there was public knowledge of a government-mandated wolf control program in my study area, I was unable to coordinate a camera trap array in a non-predator control system to measure pre-control and post-control responses. As such, wildlife managers with the authority to implement these predator control programs should invest more resources into designing rigorous and purposeful research programs not only to measure the response of the species of conservation interest, but that of the larger wildlife community, and particularly those of species with the potential to hinder conservation outcomes following predator control (i.e., non-apex predators and apparent competitors).

Investigating prey species’ behavioural shifts in response to predator control would be a logical next step in this work; unfortunately, it was beyond the scope of this thesis. While fluctuations in apex predator densities are expected to impact prey population densities (Soulé et al., 1988), a reduction in the apex predator population could also enhance the ability of prey species to acquire resources, given the fear and stress predators are capable of inducing on prey populations (Boonstra, Hik, Singleton, & Tinnikov, 1998; Creel & Christianson, 2008). Future research should examine whether wolf population reduction elicits changes in resource associations and perceived risk from non-apex predators for caribou and apparent competitors (i.e., white-tailed deer and moose).

4.3 Conclusion

Despite the known importance of predators in contributing to ecosystem health and biodiversity (Schmitz, 2007; Schmitz et al., 2010), predator control continues to be a primary strategy for woodland caribou conservation in western Canada (Hervieux et al., 2014; Serrouya et al., 2019), and the management of livestock, game, and prey species of interest globally (Lennox et al., 2018; Packer et al., 2009). As such, it is increasingly important to devote more research efforts into understanding the myriad ways in which predator control can alter ecosystem structure and function.

Bibliography

Alberta Agriculture Forestry and Rural Economic Development. (2005). *Alberta Vegetation Inventory Interpretation Standards*. Edmonton, AB Retrieved from https://open.alberta.ca/dataset/c7ec0bd9-bd14-4d37-932f-82234f7b5e82/resource/23f8975d-e402-4cac-878a-f17ef5975ae4/download/2005-avi-abvegetation3-inventorystan-mar05.pdf

Alberta Biodiversity Monitoring Institute. (2017a). *Wall-to-Wall Human Footprint Inventory 2010*. Retrieved from: https://ftp-public.abmi.ca//GISData/HumanFootprint/2010/HFI_2010_v1.gdb.zip

Alberta Biodiversity Monitoring Institute. (2017b). *Wall-to-Wall Human Footprint Inventory 2016*. Retrieved from: https://ftp-public.abmi.ca//GISData/HumanFootprint/2016/HFI_2016.gdb.zip

Alberta Biodiversity Monitoring Institute. (2019). *Wall-to-Wall Human Footprint Inventory 2017*. Retrieved from: https://www.abmi.ca/home/data-analytics/da-top/da-product-overview/Human-Footprint-Products/HF-inventory.html

Alberta Environment and Parks. (2017). *Draft Provincial Woodland Caribou Range Plan*. Edmonton, AB: Alberta Environment and Parks Retrieved from https://open.alberta.ca/dataset/932d6c22-a32a-4b4e-a3f5-cb2703c53280/resource/3fc3f63a-0924-44d0-b178-82da34db1f37/download/draft-caribourangeplanandappendices-dec2017.pdf

Alberta Sustainable Resource Development, & Alberta Conservation Association. (2010). *Status of the Woodland Caribou (Rangifer tarandus caribou) in Alberta: Update 2010* Edmonton, AB Retrieved from https://open.alberta.ca/dataset/05cdc28e-5fbf-4906-9adf-eefbb26a2d1e/resource/9dd98304-0ddc-40cb-b94c-44158ca4bad8/download/4782681-2010-status-woodland-caribou-alberta-update-2010.pdf

Allen, B. L., Allen, L. R., Engeman, R. M., & Leung, L. K. P. (2013). Intraguild relationships between sympatric predators exposed to lethal control: predator manipulation experiments. *FRONTIERS IN ZOOLOGY, 10*(1), 39-39. doi:10.1186/1742-9994-10-39

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *6*(12), 1109-1122. doi:doi:10.1046/j.1461-0248.2003.00530.x

Avgar, T., Kuefler, D., & Fryxell, J. M. (2011). Linking Rates of Diffusion and Consumption in Relation to Resources. *The American Naturalist, 178*(2), 182-190. doi:10.1086/660825

Bascompte, J., Melián, C. J., & Sala, E. (2005). Interaction Strength Combinations and the Overfishing of a Marine Food Web. *Proceedings of the National Academy of Sciences - PNAS, 102*(15), 5443-5447. doi:10.1073/pnas.0501562102

Bassing, S. B., Ausband, D. E., Mitchell, M. S., Lukacs, P., Keever, A., Hale, G., & Waits, L. (2019). Stable pack abundance and distribution in a harvested wolf population. *The Journal of Wildlife Management, 83*(3), 577-590. doi:10.1002/jwmg.21616

Bastille-Rousseau, G., Fortin, D., Dussault, C., Courtois, R., & Ouellet, J.-P. (2011). Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography, 34*(4), 588-596. doi:10.1111/j.1600-0587.2010.06517.x

Berger, K. M., & Gese, E. M. (2007). Does Interference Competition with Wolves Limit the Distribution and Abundance of Coyotes? *The Journal of animal ecology, 76*(6), 1075-1085. doi:10.1111/j.1365-2656.2007.01287.x

Berger, K. M., Gese, E. M., & Berger, J. (2008). Indirect Effects and Traditional Trophic Cascades: A Test Involving Wolves, Coyotes, and Pronghorn. *Ecology (Durham), 89*(3), 818-828. doi:10.1890/07-0193.1

Bergerud, A. T. (1971). The Population Dynamics of Newfoundland Caribou. *Wildlife Monographs*(25), 3-55. Retrieved from http://www.jstor.org/stable/3830370

Blanchet, F. G., Cazelles, K., Gravel, D., & Jeffers, E. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters, 23*(7), 1050-1063. doi:10.1111/ele.13525

Boertje, R. D., Valkenburg, P., & McNay, M. E. (1996). Increases in Moose, Caribou, and Wolves Following Wolf Control in Alaska. *The Journal of Wildlife Management, 60*(3), 474-489. doi:10.2307/3802065

Boitani, L. (2003). Wolf conservation and recovery. In L. D. Mech & L. Boitani (Eds.), *Wolves: behavior, ecology, and concervation* (pp. 317–340). Chicago, Illinois, USA: University of Chicago Press.

Bonan, G. B., & Shugart, H. H. (1989). Environmental Factors and Ecological Processes in Boreal Forests. *Annual review of ecology and systematics, 20*(1), 1-28. doi:10.1146/annurev.es.20.110189.000245

Boonstra, R., Hik, D., Singleton, G. R., & Tinnikov, A. (1998). The Impact of Predator-Induced Stress on the Snowshoe Hare Cycle. *Ecological monographs, 68*(3), 371-394. doi:10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2

Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., . . . Halpern, B. S. (2005). What Determines the Strength of a Trophic Cascade? *Ecology (Durham), 86*(2), 528-537. doi:10.1890/03-0816

Boutin, S., Boyce, M. S., Hebblewhite, M., Hervieux, D., Knopff, K., Latham, M. C., . . . Serrouya, R. (2012). Why are caribou declining in the oil sands? *Frontiers in Ecology and the Environment, 10*(2), 65-67. doi:10.1890/12.WB.005

Boutin, S., Krebs, C. J., Boonstra, R., Dale, M. R. T., Hannon, S. J., Martin, K., . . . Schweiger, S. (1995). Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos, 74*(1), 69-80. doi:10.2307/3545676

Brainerd, S. M., Andrén, H., Bangs, E. E., Bradley, E. H., Fontaine, J. A., Hall, W., . . . Sveriges, l. (2008). The Effects of Breeder Loss on Wolves. *Journal of Wildlife Management, 72*(1), 89-98. doi:10.2193/2006-305

Bridger, M. (2019). *South Peace Caribou Recovery following Five Years of Experimental Wolf Reduction*. BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development Retrieved from https://www2.gov.bc.ca/assets/gov/environment/plants-animals-and-ecosystems/wildlife-wildlife-habitat/caribou/south_peace_caribou_recovery_following_five_years_of_experimental_wolf_reduction.pdf

Brook, L. A., Johnson, C. N., & Ritchie, E. G. (2012). Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology, 49*(6), 1278-1286. doi:10.1111/j.1365-2664.2012.02207.x

Brown, D. E., & Conover, M. R. (2011). Effects of Large-Scale Removal of Coyotes on Pronghorn and Mule Deer Productivity and Abundance. *The Journal of Wildlife Management, 75*(4), 876-882. doi:10.1002/jwmg.126

Brown, J. S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary ecology research, 1*(1), 49-71. Retrieved from http://www.evolutionary-ecology.com.ezproxy.library.uvic.ca/issues/v01n01/ggar1014.pdf

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach : with 31 illustrations* (2nd ed.). New York: Springer.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., . . . Stephens, P. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *The Journal of applied ecology, 52*(3), 675-685. doi:10.1111/1365-2664.12432

Canty, A., & Ripley, B. D. (2021). boot: Bootstrap R (S-Plus) Functions (Version 1.3-28). Retrieved from https://cran.r-project.org/web/packages/boot/boot.pdf

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., . . . Sollmann, R. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation, 3*(3), 109-122. doi:10.1002/rse2.48

Carbone, C., & Gittleman, J. L. (2002). A Common Rule for the Scaling of Carnivore Density. *Science (American Association for the Advancement of Science), 295*(5563), 2273-2276. doi:10.1126/science.1067994

Caro, T. M., & Stoner, C. J. (2003). The potential for interspecific competition among African carnivores. *Biological Conservation, 110*(1), 67-75. doi:10.1016/S0006-3207(02)00177-5

Carothers, J. H., & Jaksic, F. M. (1984). Time as a Niche Difference: The Role of Interference Competition. *Oikos, 42*(3), 403-406. doi:10.2307/3544413

Carter, N. H., Brown, D. G., Etter, D. R., & Visser, L. G. (2010). American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. *Ursus, 21*(1), 57-71. Retrieved from http://www.jstor.org.ezproxy.library.uvic.ca/stable/40962280

Case, T. J., & Gilpin, M. E. (1974). Interference Competition and Niche Theory. *Proceedings of the National Academy of Sciences - PNAS, 71*(8), 3073-3077. doi:10.1073/pnas.71.8.3073

Chesson, P. (2000). MECHANISMS OF MAINTENANCE OF SPECIES DIVERSITY. *Annual review of ecology and systematics, 31*(1), 343-366. doi:10.1146/annurev.ecolsys.31.1.343

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in ecology & evolution (Amsterdam), 23*(4), 194-201. doi:10.1016/j.tree.2007.12.004

Cristescu, B., Stenhouse, G. B., & Boyce, M. S. (2013). Perception of human-derived risk influences choice at top of the food chain. *PloS one, 8*(12), e82738-e82738. doi:10.1371/journal.pone.0082738

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature, 400*(6744), 563-566. doi:10.1038/23028

Cubaynes, S., MacNulty, D. R., Stahler, D. R., Quimby, K. A., Smith, D. W., Coulson, T., & Boutin, S. (2014). Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). *The Journal of animal ecology, 83*(6), 1344-1356. doi:10.1111/1365-2656.12238

Czetwertynski, S. M., Boyce, M. S., & Schmiegelow, F. K. (2007). Effects of Hunting on Demographic Parameters of American Black Bears. *Ursus, 18*(1), 1-18. Retrieved from http://www.jstor.org.ezproxy.library.uvic.ca/stable/20204063

DeMars, C. A., Boutin, S., & Börger, L. (2018). Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. *The Journal of animal ecology, 87*(1), 274-284. doi:10.1111/1365-2656.12760

Dickie, M., McNay, S. R., Sutherland, G. D., Cody, M., Avgar, T., & Loison, A. (2020). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *The Journal of animal ecology, 89*(2), 623-634. doi:10.1111/1365-2656.13130

Dickie, M., Serrouya, R., McNay, R. S., Boutin, S., & Toit, J. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology, 54*(1), 253-263. doi:10.1111/1365-2664.12732

Donadio, E., & Buskirk, S. W. (2006). Diet, Morphology, and Interspecific Killing in Carnivora. *The American Naturalist, 167*(4), 524-536. doi:10.1086/501033

Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters, 10*(3), 197-206. doi:10.1111/j.1461-0248.2006.01010.x

Environment and Climate Change Canada. (2020). *Amended Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada*. Ottawa: Environment and Climate Change Canada Retrieved from https://wildlife-species.canada.ca/species-risk-registry/virtual_sara/files/plans/Rs-CaribouBorealeAmdMod-v01-2020Dec-Eng.pdf

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Teknisk-naturvetenskapliga, f. (2011). Trophic Downgrading of Planet Earth. *Science, 333*(6040), 301-306. doi:10.1126/science.1205106

Fagan, W. F. (1997). Omnivory as a Stabilizing Feature of Natural Communities. *The American Naturalist, 150*(5), 554-567. doi:10.1086/286081

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and evolution, 1*(4), 517-528. doi:10.1002/ece3.45

Fisher, J. T., & Burton, A. C. (2018). Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment, 16*(6), 323-328. doi:10.1002/fee.1807

Fisher, J. T., & Burton, A. C. (2021). Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. *Ecology and evolution, 11*(2), 900-911. doi:10.1002/ece3.7103

Fisher, J. T., Burton, A. C., Nolan, L., & Roy, L. (2020). Influences of landscape change and winter severity on invasive ungulate persistence in the Nearctic boreal forest. *Scientific reports, 10*(1), 8742. doi:10.1038/s41598-020-65385-3

Fisher, J. T., & Ladle, A. (2022). Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. *The Science of the total environment, 822*, 153432. doi:10.1016/j.scitotenv.2022.153432

Francis, A. L., Procter, C., Kuzyk, G., & Fisher, J. T. (2021). Female Moose Prioritize Forage Over Mortality Risk in Harvested Landscapes. *The Journal of Wildlife Management, 85*(1), 156-168. doi:10.1002/jwmg.21963

Fuller, T. K. (1989). Population Dynamics of Wolves in North-Central Minnesota. *Wildlife Monographs*(105), 3-41. Retrieved from http://www.jstor.org/stable/3830614

Fuller, T. K., Mech, L.D. & Cochrane, J.F. . (2003). Wolf population dynamics. In L. D. M. L. Boitani (Ed.), *Wolves: Behavior, Ecology and Conservation* (pp. 161–190). Chicago, Illinois, USA: University of Chicago Press.

Gilliam, J. F., & Fraser, D. F. (1987). Habitat Selection Under Predation Hazard: Test of a Model with Foraging Minnows. *Ecology (Durham), 68*(6), 1856-1862. doi:10.2307/1939877

Haber, G. C. (1996). Biological, Conservation, and Ethical Implications of Exploiting and Controlling Wolves. *Conservation Biology*, *10*(4), 1068-1081. Retrieved from http://www.jstor.org.ezproxy.library.uvic.ca/stable/2387143

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community Structure, Population Control, and Competition. *The American Naturalist*, *94*(879), 421-425. doi:10.1086/282146

Hayes, R. D., Farnell, R., Richard, M. P. W., Carey, J., Dehn, M., Kuzyk, G. W., . . . O'Donoghue, M. (2003). Experimental Reduction of Wolves in the Yukon: Ungulate Responses and Management Implications. *Wildlife Monographs*(152), 1-35. Retrieved from http://www.jstor.org/stable/3830836

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation, 206*, 102-111. doi:10.1016/j.biocon.2016.12.014

Hervieux, D., Hebblewhite, M., DeCesare, N. J., Russell, M., Smith, K., Robertson, S., & Boutin, S. (2013). Widespread declines in woodland caribou (Rangifer tarandus caribou) continue in Alberta. *Canadian Journal of Zoology*, *91*(12), 872-882. doi:10.1139/cjz-2013-0123

Hervieux, D., Hebblewhite, M., Stepnisky, D., Bacon, M., & Boutin, S. (2014). Managing wolves (Canis lupus) to recover threatened woodland caribou (Rangifer tarandus caribou) in Alberta. *Canadian Journal of Zoology, 92*(12), 1029-1037. doi:10.1139/cjz-2014-0142

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology, 12*(2), 197-229. doi:10.1016/0040-5809(77)90042-9

James, A. R. C., Boutin, S., Hebert, D. M., & Rippin, A. B. (2004). Spatial Separation of Caribou from Moose and its Relation to Predation by Wolves. *The Journal of Wildlife Management, 68*(4), 799-809. doi:10.2193/0022-541X(2004)068[0799:SSOCFM]2.0.CO;2

James, A. R. C., & Stuart-Smith, A. K. (2000). Distribution of Caribou and Wolves in Relation to Linear Corridors. *The Journal of Wildlife Management*, *64*(1), 154-159. doi:10.2307/3802985

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters, 10*(8), 690-700. doi:10.1111/j.1461-0248.2007.01059.x

Keim, J. L., DeWitt, P. D., Wilson, S. F., Fitzpatrick, J. J., Jenni, N. S., & Lele, S. R. (2021). Managing animal movement conserves predator–prey dynamics. *Frontiers in Ecology and the Environment, 19*(7), 379-385. doi:10.1002/fee.2358

Keith, L. B. (1963). *Wildlife's ten-year cycle*. Madison: University of Wisconsin Press.

Krebs, C. J., Boutin, S. A., & Boonstra, R. (2001). *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford [UK]: Oxford University Press.

Langvatn, R., & Hanley, T. A. (1993). Feeding-Patch Choice by Red Deer in Relation to Foraging Efficiency. An Experiment. *Oecologia, 95*(2), 164-170. Retrieved from http://www.jstor.org/stable/4220423

Latham, A. D. M. (2009). *Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta.* (PhD). University of Alberta, Edmonton, Alberta. Retrieved from https://www.collectionscanada.gc.ca/obj/thesescanada/vol2/002/NR55419.PDF?is_thesis=1&oclc_number=743389794

Latham, A. D. M., Latham, M. C., & Boyce, M. S. (2011). Habitat selection and spatial relationships of black bears (Ursus americanus) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. *Canadian Journal of Zoology, 89*(4), 267-277. doi:10.1139/z10-115

Latham, A. D. M., Latham, M. C., Boyce, M. S., & Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications, 21*(8), 2854-2865. doi:10.1890/11-0666.1

Latham, A. D. M., Latham, M. C., Boyce, M. S., & Boutin, S. (2013). Spatial relationships of sympatric wolves (<i>Canis lupus</i>) and coyotes (<i>C. latrans</i>) with woodland caribou (<i>Rangifer tarandus caribou</i>) during the calving season in a human-modified boreal landscape. *Wildlife Research, 40*(3), 250-260, 211. doi:10.1071/WR12184

Latham, A. D. M., Latham, M. C., Knopff, K. H., Hebblewhite, M., & Boutin, S. (2013). Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography, 36*(12), 1276-1290. doi:10.1111/j.1600-0587.2013.00035.x

Latham, A. D. M., Latham, M. C., McCutchen, N. A., & Boutin, S. (2011). Invading White-Tailed Deer Change Wolf-Caribou Dynamics in Northeastern Alberta. *Journal of Wildlife Management, 75*(1), 204-212. doi:10.1002/jwmg.28

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J. E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia, 180*(3), 697-705. doi:10.1007/s00442-015-3500-6

Lennox, R. J., Gallagher, A. J., Ritchie, E. G., & Cooke, S. J. (2018). Evaluating the efficacy of predator removal in a conflict-prone world. *Biological Conservation, 224*, 277-289. doi:10.1016/j.biocon.2018.05.003

Lesmerises, F., Dussault, C., & St-Laurent, M.-H. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management, 276*, 125-131. doi:10.1016/j.foreco.2012.03.025

Levi, T., & Wilmers, C. C. (2012). Wolves-coyotes-foxes: a cascade among carnivores. *Ecology, 93*(4), 921-929. doi:10.1890/11-0165.1

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology (Durham), 73*(6), 1943-1967. doi:10.2307/1941447

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology, 68*(4), 619-640. doi:10.1139/z90-092

Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity & distributions, 6*(4), 169-176. doi:10.1046/j.1472-4642.2000.00069.x

Llaneza, L., García, E. J., Palacios, V., Sazatornil, V., & López-Bao, J. V. (2016). Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes. *Biodiversity and Conservation, 25*(8), 1515-1528. doi:10.1007/s10531-016-1134-6

Llaneza, L., López-Bao, J. V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity & distributions, 18*(5), 459-469. doi:10.1111/j.1472-4642.2011.00869.x

Macarthur, R., & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist, 101*(921), 377-385. doi:10.1086/282505

MacArthur, R. H., & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *The American Naturalist, 100*(916), 603-609. doi:10.1086/282454

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models* (2nd;2; ed. Vol. 37). London;New York;: Chapman and Hall.

McKenzie, H. W., Merrill, E. H., Spiteri, R. J., & Lewis, M. A. (2012). How linear features alter predator movement and the functional response. *Interface focus, 2*(2), 205-216. doi:10.1098/rsfs.2011.0086

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., & Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology, 79*(1), 4-12. doi:10.1111/j.1365-2656.2009.01613.x

Merkle, J. A., Stahler, D. R., & Smith, D. W. (2009). Interference competition between gray wolves and coyotes in Yellowstone National Park. *Canadian Journal of Zoology, 87*(1), 56-63. doi:10.1139/Z08-136

Mitchell, W. A., & Lima, S. L. (2002). Predator-Prey Shell Games: Large-Scale Movement and Its Implications for Decision-Making by Prey. *Oikos, 99*(2), 249-259. doi:10.1034/j.1600-0706.2002.990205.x

Morris, D. W. (2003). Toward an Ecological Synthesis: A Case for Habitat Selection. *Oecologia, 136*(1), 1-13. doi:10.1007/s00442-003-1241-4

Mosnier, A., Ouellet, J.-P., & Courtois, R. (2008). Black bear adaptation to low productivity in the boreal forest. *Écoscience (Sainte-Foy), 15*(4), 485-497. doi:10.2980/15-4-3100

Mysterud, A., & Ostbye, E. (1999). Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography. *Wildlife Society Bulletin, 27*(2), 385-394. Retrieved from http://www.jstor.org/stable/3783905

Nagy-Reis, M., Dickie, M., Calvert, A. M., Hebblewhite, M., Hervieux, D., Seip, D. R., . . . Serrouya, R. (2021). Habitat loss accelerates for the endangered woodland caribou in western Canada. *Conservation Science and Practice, 3*(7). doi:10.1111/csp2.437

Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere (Washington, D.C), 9*(1). doi:10.1002/ecs2.2092

O'Connell, A. F., Nichols, J. D., & Kāranta, K. U. s. (2011). *Camera traps in animal ecology: methods and analyses*. New York: Springer.

O'Donoghue, M., Boutin, S., Krebs, C. J., & Hofer, E. J. (1997). Numerical responses of coyotes and lynx to the snowshoe hare cycle [Lepus americanus]. *Oikos, 80*(1), 150-162. doi:10.2307/3546526

O'Donoghue, M., Boutin, S., Krebs, C. J., Zuleta, G., Murray, D. L., & Hofer, E. J. (1998). Functional Responses of Coyotes and Lynx to the Snowshoe Hare Cycle. *Ecology, 79*(4), 1193-1208. doi:10.2307/176736

Ordiz, A., StØEn, O.-G., Delibes, M., Swenson, J. E., & Sveriges, l. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia, 166*(1), 59-67. doi:10.1007/s00442-011-1920-5

Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D., . . . Nowell, K. (2009). Sport hunting, predator control and conservation of large carnivores. *PloS one, 4*(6), e5941-e5941. doi:10.1371/journal.pone.0005941

Palomares, F., Gaona, P., Ferreras, P., & Delibes, M. (1995). Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits. *Conservation Biology, 9*(2), 295-305. doi:10.1046/j.1523-1739.1995.9020295.x

Paquet, P. C. (1992). Prey Use Strategies of Sympatric Wolves and Coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy, 73*(2), 337-343. doi:10.2307/1382067

Pickell, P. D., Andison, D. W., & Coops, N. C. (2013). Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. *Forest Ecology and Management, 304*, 243-253. doi:10.1016/j.foreco.2013.04.031

Pickell, P. D., Andison, D. W., Coops, N. C., Gergel, S. E., & Marshall, P. L. (2015). The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. *Canadian Journal of Forest Research, 45*(6), 732-743. doi:10.1139/cjfr-2014-0546

Polis, G. A., & Holt, R. D. (1992). Intraguild predation: The dynamics of complex trophic interactions. In (Vol. 7, pp. 151-154). England: Elsevier Ltd.

Power, M. E. (1992). Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy. *Ecology (Durham), 73*(3), 733-746. doi:10.2307/1940153

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The Rise of the Mesopredator. *BioScience, 59*(9), 779-791. doi:10.1525/bio.2009.59.9.9

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria. Retrieved from https://www.r-project.org/

Reynolds, J. C., & Tapper, S. C. (1996). Control of mammalian predators in game management and conservation. *MAMMAL REVIEW, 26*(2-3), 127-155. doi:10.1111/j.1365-2907.1996.tb00150.x

Rich, L. N., Russell, R. E., Glenn, E. M., Mitchell, M. S., Gude, J. A., Podruzny, K. M., . . . Nichols, J. D. (2013). Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys: Estimating Occupancy of Wolf Packs. *The Journal of Wildlife Management, 77*(6), 1280-1289. doi:10.1002/jwmg.562

Ripple, W. J., Wirsing, A. J., Beschta, R. L., & Buskirk, S. W. (2011). Can restoring wolves aid in lynx recovery? *Wildlife Society Bulletin, 35*(4), 514-518. doi:10.1002/wsb.59

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *12*(9), 982-998. doi:doi:10.1111/j.1461-0248.2009.01347.x

Rosenzweig, M. L. (1981). A Theory of Habitat Selection. *Ecology, 62*(2), 327-335. doi:10.2307/1936707

Rosenzweig, M. L. (1991). Habitat Selection and Population Interactions: The Search for Mechanism. *The American Naturalist, 137*, S5-S28. doi:10.1086/285137

Rovero, F., & Zimmermann, F. (2016). *Camera Trapping for Wildlife Research*. Exeter, UK: Pelagic Publishing.

Schmitz, O. J. (2007). Predator Diversity and Trophic Interactions. *Ecology (Durham), 88*(10), 2415-2426. doi:10.1890/06-0937.1

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters, 13*(10), 1199-1209. doi:10.1111/j.1461-0248.2010.01511.x

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities. *Science (American Association for the Advancement of Science), 185*(4145), 27-39. doi:10.1126/science.185.4145.27

Serrouya, R., Seip, D. R., Hervieux, D., McLellan, B. N., McNay, R. S., Steenweg, R., . . . Boutin, S. (2019). Saving endangered species using adaptive management. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA, 116*(13), 6181-6186. doi:10.1073/pnas.1816923116

Shigesada, N., Kawasaki, K., & Teramoto, E. (1979). Spatial segregation of interacting species. *Journal of theoretical biology, 79*(1), 83-99. doi:10.1016/0022-5193(79)90258-3

Sivy, K. J., Pozzanghera, C. B., Colson, K. E., Mumma, M. A., & Prugh, L. R. (2018). Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos, 127*(4), 607-621. doi:10.1111/oik.04647

Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., & Hill, S. (1988). Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. *Conservation Biology, 2*(1), 75-92. doi:10.1111/j.1523-1739.1988.tb00337.x

Squires, J. R., & Ruggiero, L. F. (2007). Winter Prey Selection of Canada Lynx in Northwestern Montana. *Journal of Wildlife Management, 71*(2), 310-315. doi:10.2193/2005-445

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological reviews of the Cambridge Philosophical Society, 85*(2), 301-325. doi:10.1111/j.1469-185X.2009.00103.x

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., . . . Rich, L. N. (2017). Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment, 15*(1), 26-34. doi:10.1002/fee.1448

Stewart, F. E. C., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2018). Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere, 9*(2), e02112. doi:10.1002/ecs2.2112

Tapper, S. C. (1992). *Game Heritage. An Ecological Review from Shooting and Gamekeeping Records*. Fordingbridge: The Game Conservancy.

Terborgh, J., & Estes, J. A. (2010). *Trophic Cascades : Predators, Prey, and the Changing Dynamics of Nature*. Washington, UNITED STATES: Island Press.

Thompson, R. M., Hemberg, M., Starzomski, B. M., & Shurin, J. B. (2007). Trophic Levels and Trophic Tangles: The Prevalence of Omnivory in Real Food Webs. *Ecology (Durham), 88*(3), 612-617. doi:10.1890/05-1454

Tigner, J., Bayne, E. M., & Boutin, S. (2014). Black Bear Use of Seismic Lines in Northern Canada. *The Journal of Wildlife Management, 78*(2), 282-292. doi:10.1002/jwmg.664

Treves, A., Krofel, M., & McManus, J. (2016). Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment, 14*(7), 380-388. doi:10.1002/fee.1312

van Rensen, C. K., Nielsen, S. E., White, B., Vinge, T., & Lieffers, V. J. (2015). Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. *Biological Conservation, 184*, 127-135. doi:10.1016/j.biocon.2015.01.020

Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology, 15*(11), 2626-2633. doi:10.1111/j.1365-2486.2009.01974.x

Wallach, A. D., Ritchie, E. G., Read, J., & O'Neill, A. J. (2009). More than Mere Numbers: The Impact of Lethal Control on the Social Stability of a Top-Order Predator. *PloS one, 4*(9), e6861-e6861. doi:10.1371/journal.pone.0006861

Wasser, S. K., Keim, J. L., Taper, M. L., & Lele, S. R. (2011). The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. *Frontiers in Ecology and the Environment, 9*(10), 546-551. doi:10.1890/100071

Wittische, J., Heckbert, S., James, P. M. A., Burton, A. C., & Fisher, J. T. (2021). Community-level modelling of boreal forest mammal distribution in an oil sands landscape. *Science of The Total Environment, 755*(Pt 2), 142500. doi:10.1016/j.scitotenv.2020.142500

Wittmer, H. U., McLellan, B. N., Serrouya, R., & Apps, C. D. (2007). Changes in Landscape Composition Influence the Decline of a Threatened Woodland Caribou Population. *Journal of Animal Ecology, 76*(3), 568-579. doi:10.1111/j.1365-2656.2007.01220.x

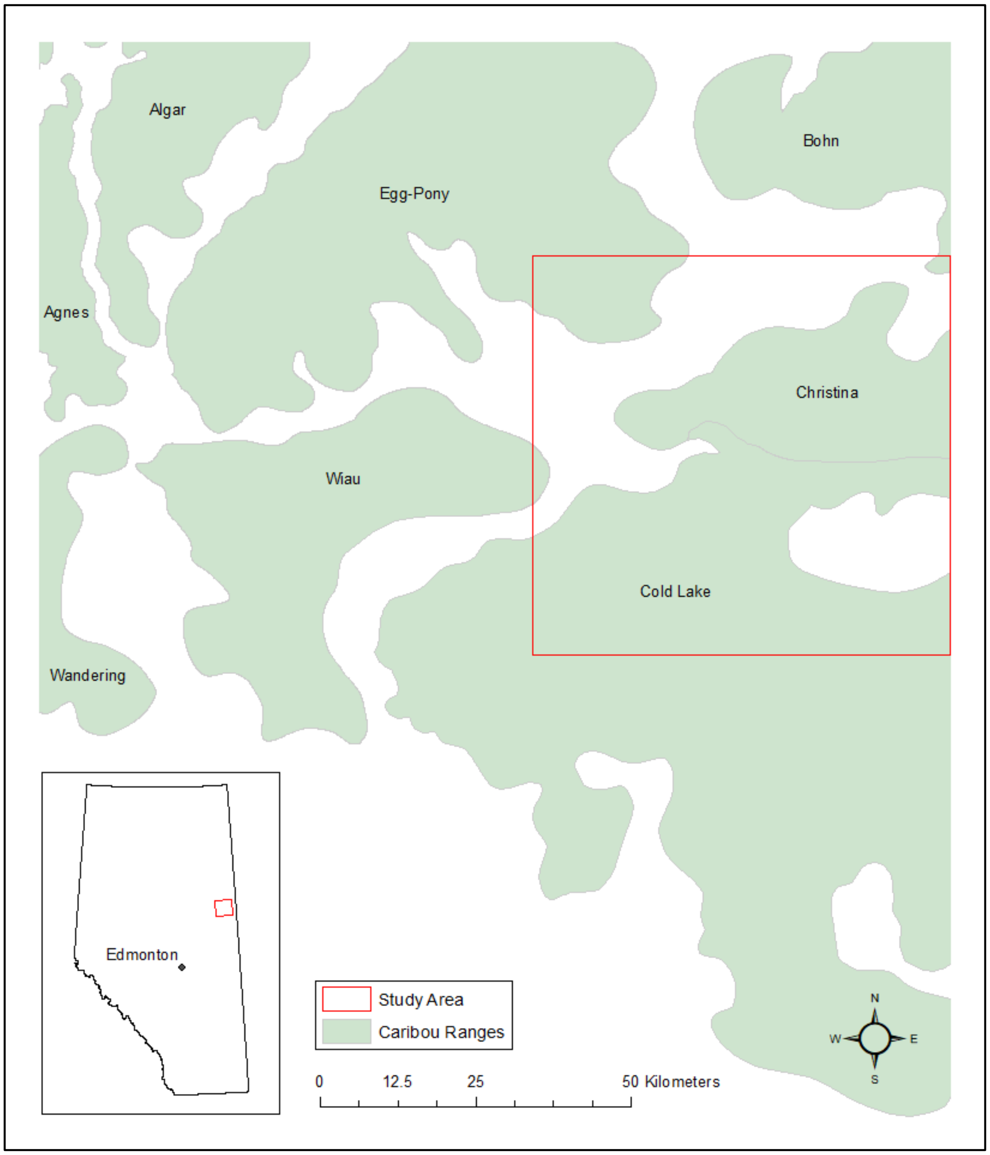
Zager, P., & Beecham, J. (2006). The Role of American Black Bears and Brown Bears as Predators on Ungulates in North America. *Ursus, 17*(2), 95-108. doi:10.2192/1537-6176(2006)17[95:TROABB]2.0.CO;2

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution, 1*(1), 3-14. doi:10.1111/j.2041-210X.2009.00001.x

Appendix

Appendix 1. Boreal woodland caribou ranges relative to the study area.

Our study area rests at the intersection of the East Side Athabasca River and Cold Lake caribou ranges. The East Side Athabasca River caribou range is comprised of seven sub-ranges: Agnes, Algar, Bohn, Christina, Egg-Pony, Wandering and Wiau.



Appendix A

Appendix A.1. Mean and standard deviation of landcover features.

Calculated the mean and standard deviation of percent landcover at the maximum spatial scale of analysis (2000 m) for pre-control vs. post-control sampling periods.

Landcover variable	**Mean (± SD)**	
	Pre-control	**Post-control**
Upland Deciduous/Mixedwood	24.38 (± 13.15)	20.25 (± 12.78)
Lowland Deciduous/Mixedwood	2.35 (± 3.14)	0.38 (± 0.39)
Upland Spruce	3.48 (± 3.69)	3.96 (± 3.35)
Lowland Spruce	33.13 (± 11.96)	30.90 (± 12.28)
Tamarack	7.27 (± 7.13)	5.61 (± 6.47)
Open Wetland	5.71 (± 3.86)	5.30 (± 4.07)
Water	2.47 (± 3.50)	2.33 (± 3.38)
Cutblock	6.52 (± 8.92)	8.48 (± 9.30)
Seismic Line	0.49 (± 0.21)	0.74 (± 0.32)
3-D Seismic Line	1.75 (± 2.18)	0.93 (± 1.41)
Pipeline	1.31 (± 1.02)	2.02 (± 1.93)
Road	0.43 (± 0.24)	1.88 (± 0.84)
Trail	0.27 (± 0.21)	0.11 (± 0.08)
Well Site	1.10 (± 1.23)	1.12 (± 1.59)

Appendix A.2. Best-supported spatial scale of pre-control and post-control global landcover models.

AICc table of pre-control and post-control global landcover models across eight spatial scales. Table includes AICc, delta (Δ) AICc and AICc weights for each model. Models are ranked from most-supported to least-supported for each sampling period. Landcover variables at the spatial scale with the greatest AICc weight were used to generate competing models to determine the drivers of wolf occurrence.

Sampling period	Spatial scale (m)	AICc	ΔAICc	AICcw
Pre-control	250	376.9	0.00	0.267
	2000	377.0	0.08	0.257
	1750	377.4	0.52	0.206
	1000	379.1	2.24	0.087
	500	379.6	2.71	0.069
	1250	379.8	2.97	0.061
	1500	380.1	3.24	0.053
	750	387.9	11.04	0.001
Post-control	500	180.4	0.00	1.000
	750	201.2	20.82	0.000
	1750	212.9	32.47	0.000
	1500	215.6	35.23	0.000
	2000	218.2	37.74	0.000
	1250	224.9	44.46	0.000
	1000	226.2	45.75	0.000
	250	230.4	49.96	0.000

Appendix A.3. K-fold cross validation of all competing pre-control and post-control wolf occurrence models.

K-fold cross-validation estimates of prediction error for each competing pre-control and post-control wolf model. The table includes model rank, the hypothesis associated with each model, and two different 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, 2017) in R statistical software.

Sampling period	**Model rank**	**Hypothesis**	**Raw cross-validation estimate of prediction error**	**Adjusted cross-validation estimate of prediction error**
Pre-control	1	Movement ability	0.01179939	0.01170374
	2	Exposure risk	0.01365484	0.01341489
	3	Prey habitat	0.03021203	0.02846875
	4	Null	0.01199093	0.01197058
	5	Prey occurrence	0.01247967	0.01242341
Post-control	1	Exposure risk	0.005908874	0.005622477
	2	Movement ability	0.004140348	0.004034524
	3	Prey occurrence	0.003133926	0.003118202
	4	Null	0.003159654	0.003154044
	5	Prey habitat	0.003981602	0.003910523

Appendix B

Appendix B.1. Landcover types quantified within the study area with data sources and descriptions.

We used a variety of sources representing different time periods to account landcover changes between pre-control (2011-2014) and post-control (2017-2020) time periods. AVI = Alberta Vegetation Inventory, 1987 – 2014; UALF = University of Alberta Linear Features Map Updated 2012; ^{1}ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2010; ^{2}ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2016; ^{3}ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2017.

Predictor variable	**Pre-control source**	**Post-control source**	**Description**
Upland Deciduous	AVI	AVI	(Aw, Pb, Bw ≥ 70% canopy cover), moisture = d or m
Upland Mixedwood	AVI	AVI	40-60% canopy cover, moisture = d or m
Lowland Deciduous	AVI	AVI	(Aw, Pb, Bw ≥ 70% canopy cover), moisture = w or a
Lowland Mixedwood	AVI	AVI	40-60% canopy cover, moisture = w or a
Upland Spruce	AVI	AVI	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = d or m
Lowland Spruce	AVI	AVI	(Sb, Sw, Fb ≥ 70% canopy cover), moisture = w or a
Tamarack	AVI	AVI	Lt ≥ 70%
Pine	AVI	AVI	Pj ≥ 70%
Upland Shrubs	AVI	AVI	> 25% shrub cover; < 6% tree cover; moisture = d or m
Nonforest	AVI	AVI	Areas with < 6% canopy
Open Wetland	AVI	AVI	< 6% crown closure; moisture = w or a
Water	AVI	AVI	Standing or flowing water
Cutblock	ABMI^1	ABMI^3	Forest harvest areas
Seismic Line	UALF	ABMI^3	Traditional, single petroleum exploration line
3-D Seismic Line	UALF	ABMI^3	3-D seismic petroleum exploration line, deployed in a high-density hashtag pattern
Pipeline	ABMI^1	ABMI^2	Petroleum pipelines, typically wide and grass-covered
Road	ABMI^1	ABMI^3	Combination of road and rail (hard surface or vegetated verge)
Trail	ABMI^1	ABMI^3	Combination of trails and truck trails
Well Site	ABMI^1	ABMI^3	Petroleum extraction sites, including well and surrounding area
Block Feature	ABMI^1	ABMI^3	Combination variable including borrow pits, dugouts, sumps, industrial sites, other disturbed vegetation

Appendix B.2. Mammal species' independent detections before and after wolf control.

Number of independent detections of all mammal species included in our analyses before and after wolf control. Pre-control data collected from October 2011 to October 2014, and post-control data collected from October 2017 to October 2020.

Species	**Independent Detections**	
	Pre-control	**Post-control**
Wolf	509	122
Coyote	867	500
Lynx	662	190
Black bear	628	1,027
Caribou	49	101
Moose	85	160
White-tailed deer	11,858	12,186
Snowshoe hare	4,196	1,893
Red squirrel	269	58

Appendix B.3. Mean and standard deviation of landcover features.

Calculated the mean and standard deviation of percent landcover at the maximum spatial scale of analysis (2000 m) for pre-control and post-control sampling periods.

Landcover variable	Mean (± SD)	
	Pre-control	Post-control
Upland Deciduous/Mixedwood	24.38 (± 13.15)	20.25 (± 12.78)
Lowland Deciduous/Mixedwood	2.35 (± 3.14)	0.38 (± 0.39)
Upland Spruce	3.48 (± 3.69)	3.96 (± 3.35)
Lowland Spruce	33.13 (± 11.96)	30.90 (± 12.28)
Tamarack	7.27 (± 7.13)	5.61 (± 6.47)
Open Wetland	5.71 (± 3.86)	5.30 (± 4.07)
Water	2.47 (± 3.50)	2.33 (± 3.38)
Linear Features	4.24 (± 2.65)	5.68 (± 2.82)
Block Features	7.62 (± 8.57)	9.60 (± 8.86)

Appendix B.4. Top core natural habitat models.

For each non-apex predator species and each sampling period, we included models within 2 ΔAICc of the top model. However, only the most parsimonious model was selected to build our candidate models. We reported AICc scores, delta (Δ) AICc, AICc weights, and the spatial scale associated with each model.

Species	Sampling period	Top models within 2 ΔAICc	AICc	ΔAICc	AICcwt	Spatial scale (m)
Coyote	Pre-control	Upland Deciduous/Mixedwood + Lowland Spruce + Open Wetland + Water	482.1	0.00	0.785	250
	Post-control	Upland Deciduous/Mixedwood + Upland Spruce + Tamarack	396.9	0.00	0.756	250
Lynx	Pre-control	Upland Deciduous/Mixedwood + Upland Spruce + Lowland Spruce + Open Wetland	408.0	0.00	0.984	250
	Post-control	Upland Deciduous/Mixedwood + Lowland Deciduous/Mixedwood + Upland Spruce	290.0	0.00	0.339	1500
		Upland Deciduous/Mixedwood + Lowland Deciduous/Mixedwood + Upland Spruce + Tamarack + Open Wetland	290.3	0.31	0.290	500
		Upland Deciduous/Mixedwood + Lowland Deciduous/Mixedwood	291.9	1.98	0.126	1750
Black Bear	Pre-control	Upland Deciduous/Mixedwood + Upland Spruce + Lowland Spruce + Tamarack + Water	315.1	0.00	1.000	250
	Post-control	Upland Deciduous/Mixedwood + Upland Spruce + Tamarack + Open Wetland + Water	316.3	0.00	0.991	500

Appendix B.5. AICc table of pre-control candidate models of coyote occurrence.

AICc scores for pre-control candidate models of monthly coyote occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
Lynx + Block + CM	7	-207.916	431.9	0.00	0.789
Lynx + Linear + Block + CM	8	-207.916	434.5	2.64	0.210
Lynx + CM	6	-216.182	445.9	13.99	0.001
Lynx + Linear + CM	7	-215.676	447.4	15.52	0.000
Wolf + Block + CM	7	-224.159	464.4	32.49	0.000
Wolf + Linear + Block + CM	8	-223.659	466.0	34.13	0.000
Block + CM	6	-229.972	473.5	41.57	0.000
Linear + Block + CM	7	-229.602	475.3	43.37	0.000
Prey + Block + CM	7	-229.776	475.6	43.72	0.000
Prey + Linear + Block + CM	8	-229.259	477.2	45.33	0.000
Wolf + Linear + CM	7	-231.192	478.5	46.55	0.000
Wolf + CM	6	-232.900	479.3	47.42	0.000
Linear + CM	6	-234.767	483.1	51.15	0.000
CM	5	-236.036	483.1	51.24	0.000
Prey + Linear + CM	7	-234.511	485.1	53.19	0.000
Prey + CM	6	-235.977	485.5	53.57	0.000
Null	1	-269.393	540.9	108.95	0.000

Appendix B.6. AICc table of post-control candidate models of coyote occurrence.

AICc scores for post-control candidate models of monthly coyote occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
Prey + CM	5	-180.626	372.4	0.00	0.561
Prey + Block + CM	6	-180.356	374.3	1.93	0.213
Prey + Linear + CM	6	-180.617	374.8	2.46	0.164
Prey + Linear + Block + CM	7	-180.347	376.8	4.48	0.060
Wolf + CM	5	-188.076	387.3	14.90	0.000
Lynx + CM	5	-188.095	387.3	14.94	0.000
Lynx + Block + CM	6	-187.266	388.1	15.75	0.000
Wolf + Linear + CM	6	-188.050	389.7	17.32	0.000
Lynx + Linear + CM	6	-188.053	389.7	17.33	0.000
Wolf + Block + CM	6	-188.067	389.7	17.36	0.000
Lynx + Linear + Block + CM	7	-187.244	390.6	18.28	0.000
Wolf + Linear + Block + CM	7	-188.040	392.2	19.87	0.000
CM	4	-194.079	396.9	24.52	0.000
Block + CM	5	-193.796	398.7	26.34	0.000
Linear + CM	5	-193.872	398.9	26.49	0.000
Linear + Block + CM	6	-193.613	400.8	28.45	0.000
Null	1	-214.388	430.8	58.48	0.000

Appendix B.7. AICc table of pre-control candidate models of lynx occurrence.

AICc scores for pre-control candidate models of monthly lynx occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
Coyote + Linear + CM	7	-183.789	383.7	0.00	0.457
Coyote + CM	6	-185.738	385.0	1.35	0.233
Coyote + Linear + Block + CM	8	-183.177	385.1	1.42	0.225
Coyote + Block + CM	7	-185.467	387.0	3.36	0.085
Linear + CM	6	-195.794	405.1	21.46	0.000
Wolf + Linear + CM	7	-194.543	405.2	21.51	0.000
Prey + Linear + CM	7	-195.325	406.7	23.07	0.000
Linear + Block + CM	7	-195.786	407.6	24.00	0.000
Wolf + Linear + Block + CM	8	-194.519	407.8	24.10	0.000
CM	5	-198.487	408.0	24.39	0.000
Wolf + CM	6	-197.502	408.5	24.88	0.000
Prey + Linear + Block + CM	8	-195.276	409.3	25.62	0.000
Prey + CM	6	-197.999	409.5	25.87	0.000
Block + CM	6	-197.999	410.4	26.77	0.000
Wolf + Block + CM	7	-197.312	410.7	27.05	0.000
Prey + Block + CM	7	-197.994	412.1	28.41	0.000
Null	1	-243.177	488.4	104.77	0.000

Appendix B.8. AICc table of post-control candidate models of lynx occurrence.

AICc scores for post-control candidate models of monthly lynx occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
Prey + Linear + CM	5	-127.932	267.0	0.00	0.465
Prey + Linear + Block + CM	6	-127.447	268.5	1.50	0.219
Prey + CM	4	-130.055	268.8	1.86	0.183
Prey + Block + CM	5	-129.206	269.5	2.55	0.130
Coyote + Linear + Block + CM	6	-133.255	280.1	13.12	0.001
Coyote + Linear + CM	5	-134.643	280.4	13.42	0.001
Coyote + Block + CM	5	-134.789	280.7	13.71	0.000
Coyote + CM	4	-136.679	282.1	15.11	0.000
Linear + CM	4	-140.255	289.2	22.26	0.000
Linear + Block + CM	5	-139.532	290.2	23.20	0.000
Wolf + Linear + CM	5	-140.255	291.6	24.65	0.000
Block + CM	4	-141.570	291.9	24.89	0.000
CM	3	-142.755	291.9	24.97	0.000
Wolf + Linear + Block + CM	6	-139.527	292.6	25.66	0.000
Wolf + CM	4	-142.671	294.1	27.09	0.000
Wolf + Block + CM	5	-141.549	294.2	27.23	0.000
Null	1	-167.243	336.6	69.58	0.000

Appendix B.9. AICc table of pre-control candidate models of black bear occurrence.

AICc scores for pre-control candidate models of monthly black bear occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
Linear + CM	7	-148.799	313.7	0.00	0.247
Wolf + Linear + CM	8	-147.873	314.5	0.81	0.165
Wolf + CM	7	-149.446	315.0	1.30	0.129
CM	6	-150.755	315.1	1.36	0.125
Linear + Block + CM	8	-148.694	316.2	2.45	0.073
Prey + Linear + CM	8	-148.713	316.2	2.48	0.071
Wolf + Linear + Block + CM	9	-147.737	317.0	3.29	0.048
Prey + CM	7	-150.579	317.3	3.56	0.042
Block + CM	7	-150.753	317.6	3.91	0.035
Wolf + Block + CM	8	-149.428	317.6	3.91	0.035
Prey + Linear + Block + CM	9	-148.594	318.7	5.01	0.020
Prey + Block + CM	8	-150.571	319.9	6.20	0.011
Null	1	-171.045	344.2	30.45	0.000

Appendix B.10. AICc table of post-control candidate models of black bear occurrence.

AICc scores for post-control candidate models of monthly black bear occurrence. The table includes the degrees of freedom (df), log-likelihood, AICc, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported.

Candidate models	df	log-lik	AICc	ΔAICc	AICcw
CM	6	-151.372	316.3	0.00	0.242
Linear + CM	7	-150.695	317.5	1.21	0.132
Block + CM	7	-150.767	317.7	1.36	0.123
Prey + CM	7	-150.851	317.9	1.53	0.113
Wolf + CM	7	-151.021	318.2	1.87	0.095
Prey + Block + CM	8	-150.107	319.0	2.71	0.062
Prey + Linear + CM	8	-150.131	319.1	2.76	0.061
Linear + Block + CM	8	-150.319	319.5	3.13	0.051
Wolf + Block + CM	8	-150.502	319.8	3.50	0.042
Wolf + Linear + CM	8	-150.535	319.9	3.56	0.041
Prey + Linear + Block + CM	9	-149.648	320.9	4.57	0.025
Wolf + Linear + Block + CM	9	-150.184	322.0	5.64	0.014
Null	1	-179.077	360.2	43.89	0.000

Appendix B.11. K-fold cross validation of top five models with lowest ΔAICc for each non-apex predator species and sampling period.

K-fold cross-validation estimates of prediction error for competing pre-control and post-control models for each non-apex predator species. The table includes species, sampling period, the top five models with the lowest ΔAICc, and two different 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, 2017) in R statistical software.

Species	Sampling period	Top five models with lowest ΔAICc	Raw cross-validation estimate of prediction error	Adjusted cross-validation estimate of prediction error
Coyote	Pre-control	Lynx + Block + CM	0.02137943	0.02105693
		Lynx + Linear + Block + CM	0.02486728	0.02423867
		Lynx + CM	0.02190036	0.02162410
		Lynx + Linear + CM	0.02253942	0.02215496
		Wolf + Block + CM	0.02404661	0.02371833
	Post-control	Prey + CM	0.01302576	0.01289821
		Prey + Block + CM	0.01402102	0.01383990
		Prey + Linear + CM	0.01256338	0.01245607
		Prey + Linear + Block + CM	0.01372683	0.01355111
		Wolf + CM	0.01549220	0.01520292
Lynx	Pre-control	Coyote + Linear + CM	0.01393161	0.01377762
		Coyote + CM	0.01480949	0.01460327
		Coyote + Linear + Block + CM	0.01403137	0.01386629
		Coyote + Block + CM	0.01522256	0.01498242
		Linear + CM	0.01473227	0.01463335
	Post-control	Prey + Linear + CM	0.005717815	0.005655814
		Prey + Linear + Block + CM	0.005968611	0.005875309
		Prey + CM	0.005198626	0.005179293
		Prey + Block + CM	0.005792457	0.005732719
		Coyote + Linear + Block + CM	0.006529590	0.006469612
Black Bear	Pre-control	Linear + CM	0.02093074	0.02064902
		Wolf + Linear + CM	0.02232278	0.02196232
		Wolf + CM	0.0261858	0.0253836
		CM	0.02233081	0.02202908
		Linear + Block + CM	0.02340571	0.02296201
	Post-control	CM	0.02443500	0.02415457
		Linear + CM	0.02722453	0.02674130
		Block + CM	0.02696145	0.02648102
		Prey + CM	0.02518643	0.02485473
		Wolf + CM	0.02455619	0.02425723

Appendix B.12. Coyote prey selection post-hoc analysis – AICc table

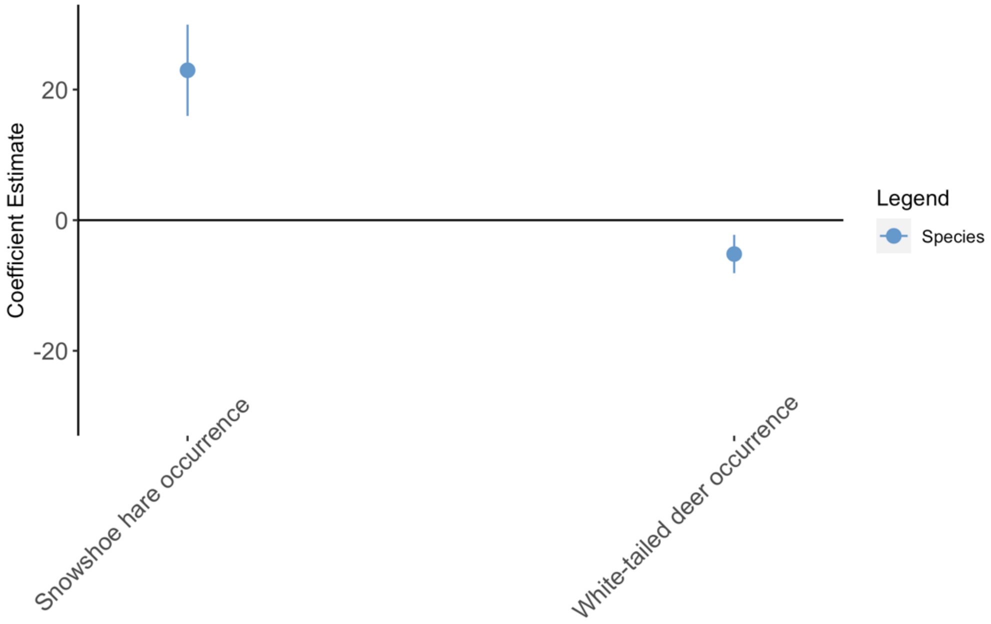
Pre-control and post-control candidate models of coyote prey selection analyzed post-hoc. We calculated variance inflation factors (VIF) to ensure there was no collinearity among predictor variables. We then analyzed candidate models at the best-supported spatial scale of coyote occurrence, which for both pre-control and post-control periods was 250 m. We modelled coyote's proportional binomial response variable using a generalized linear model (GLM) (McCullagh & Nelder, 1989) with a binomial distribution (logit link function). Predictor variables represent the monthly occurrence frequency of each prey species for both the pre-control and post-control periods. We used AICc scores to evaluate empirical support for each model. If models were ≤ 2 ΔAICc values from the top model, we selected the most parsimonious model (Burnham & Anderson, 2002).

Sampling period	**Candidate models**	**df**	**log-lik**	**AICc**	**ΔAICc**	**AICcw**
Pre-control	Snowshoe hare + White-tailed deer	3	-226.957	460.3	0.00	0.709
	Snowshoe hare + Red squirrel + White-tailed deer	4	-226.711	462.1	1.80	0.289
	Snowshoe hare	2	-234.309	472.8	12.49	0.001
	Snowshoe hare + Red squirrel	3	-234.245	474.9	14.58	0.000
	Red squirrel + White-tailed deer	3	-252.351	513.1	52.79	0.000
	White-tailed deer	2	-260.103	524.4	64.08	0.000
	Red squirrel	2	-260.885	526.0	65.65	0.000
	Null	1	-269.393	540.9	80.53	0.000
Post-control	Snowshoe hare + White-tailed deer	3	-190.993	388.4	0.00	0.548
	Snowshoe hare + Red squirrel + White-tailed deer	4	-190.034	388.8	0.38	0.452
	Snowshoe hare + Red squirrel	3	-204.768	416.0	27.55	0.000
	Snowshoe hare	2	-206.340	416.9	28.48	0.000
	White-tailed deer	2	-208.750	421.7	33.30	0.000
	Red squirrel + White-tailed deer	3	-208.670	423.8	35.35	0.000
	Null	1	-214.388	430.8	42.43	0.000
	Red squirrel	2	-214.352	432.9	44.50	0.000

Appendix B.13. Coyote prey selection post-hoc analysis – Beta coefficient plots

Beta coefficients plots of top (a) pre-control and (b) post-control coyote prey selection models.

a)



b)