Seismic consequences: large mammal community dynamics in a boreal working landscape

by

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Seismic consequences: Large mammal community dynamics on a boreal working landscape

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the degree of       Master of Science
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Abstract

Anthropogenic landscape change modifies the face of our planet, creating new playing fields on which wildlife communities respond to altered landscapes. Individual species react to disturbance, which trigger subsequent responses in their interactions with other species and thus propagate effects across ecological communities. In Alberta’s boreal forest, resource extraction has created a working landscape: a heterogeneous mosaic of natural and industrial features. The most pervasive industrial features are seismic lines – long trails cut for oil and gas exploration. Mammal community responses to seismic lines have contributed to population declines for the iconic woodland caribou (*Rangifer tarandus caribou*), thus motivating mitigation strategies in the form of habitat restoration. Although restoration is promised to recover caribou and restore landscape functionality, effective restoration should change wildlife responses to seismic lines, yet such responses are rarely evaluated. Further, interspecific interactions on the working landscape must be analyzed to understand how differential behavioural responses across species influence community dynamics.

Using camera traps in northern Alberta, I investigated how large mammals respond to human landscape change at the behavioural and community levels. I first examined seismic line use by caribou, caribou predators, and caribou apparent competitors following restoration. Three years after treatment, white-tailed deer (*Odocoileus virginianus*) preferred unrestored seismic lines over restored lines, while wolves (*Canis lupus*) strongly preferred human-use lines but did not avoid restored lines. Caribou did not respond to restoration over the study period, instead preferring seismic lines in lowland habitat. I then explored interspecific interactions, assessing how distribution of wolves influenced occurrences of black bear (*Ursus americanus*), coyote (*Canis latrans*), and lynx (*Lynx canadensis*) at three spatiotemporal scales. All three species
showed positive associations with wolves on at least one spatiotemporal level, and black bear occurrences decreased with increasing linear density while coyote and lynx occurrences increased. Overall, I demonstrated how anthropogenic landscape change – even when implemented for conservation – induces behavioural responses that can affect community interactions and thus ripple across ecological hierarchies. These results illustrate the value of multi-species monitoring to improve understanding of community interactions, especially when making single-species management decisions that ultimately influence wildlife communities as a whole.
Lay summary

As humans modify landscapes to meet our resource demands, we induce changes in wildlife communities. In Alberta’s boreal forest, seismic lines – long trails cut for oil and gas exploration – create novel landscape features unlike any that occur naturally. These trigger behavioural and population responses across the mammal community, and ultimately contribute to declining populations of woodland caribou (*Rangifer tarandus caribou*). My work used camera traps to observe large mammals in order to assess community responses to human landscape change. I investigated whether seismic line restoration implemented for caribou conservation re-established separation between caribou, their predators, and other prey species. I also analyzed patterns in seismic line use by predators, thus expanding my scope beyond caribou conservation to consider community interactions. My thesis highlights the value of understanding both behavioural and community-level responses to disturbance, which can inform multi-species wildlife management on a human-modified landscape.
Preface

This thesis uses camera trap data collected as part of the Algar Wildlife Monitoring Project, a partnership between the Wildlife Coexistence Lab at UBC and the Applied Conservation Macroecology Lab at InnoTech Alberta (ITA). The project was funded by members of the Canadian Oil Sands Innovation Alliance (COSIA) led by Nexen Energy (now CNOOC), with contributions from ConocoPhillips, Shell Canada, Canadian Natural, and Suncor Energy. Cole Burton (UBC) developed the sampling design for camera trap monitoring, with input from Jason Fisher (ITA) and the Silvacom restoration team (led by John Peters). Cole Burton and Joanna Burgar (UBC) managed field work preparations, with support from me. Field data collection was conducted by Cole Burton, Luke Nolan (ITA), Joanna Burgar, and me, with support from Andrew Underwood at ITA, Brett Sarchuk and Andrew Braid from Environmental Monitoring and Science Division (EMSD) of Alberta Environment and Parks, Jason Fisher and Gillian-Chow Fraser. GIS data was provided by Daiyuan Pan and Andrew Underwood at ITA, Rob Serrouya at the Alberta Biodiversity Monitoring Institute, and John Peters at Silvacom. Joanna Burgar and I processed and managed all camera trap data, and Nisha Raghukumar scored images for snow presence. All methods for wildlife monitoring were approved by the Canadian Council of Animal Care administered by UBC (protocol A17-0035).

Chapter 2 has been adapted for a publication co-authored by Cole Burton, Joanna Burgar, and Jason Fisher, and will be submitted to Biological Conservation. Cole Burton and Jason Fisher developed the original research question, and I refined specific hypotheses. All co-authors provided chapter edits and feedback. Site prescriptions and restoration treatments were completed by Silvacom. Chapter 3 will also be prepared as a paper co-authored by Cole Burton and Jason Fisher. I performed all data analysis and wrote the original drafts of each chapter, with
edits and feedback from my committee members, Cole Burton, Jason Fisher, and Jeanine Rhemtulla, as well as Joanna Burgar.
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Chapter 1: General introduction

1.1 Ecological hierarchies and responses to human landscape change

Amidst global biodiversity loss and ongoing landscape change, a critical question for ecologists is whether communities are resilient to the level of change imposed by anthropogenic disturbances (WWF, 2018). Resilient wildlife communities are those that are able to absorb change and persist without fundamentally altering their overall nature (Holling, 1973). Due to the interconnected nature of ecological systems, resilience depends on how the effects of change propagate throughout ecological hierarchies (Jorgensen & Nielsen, 2013; Peterson, Allen, & Holling, 1998). Each level of the hierarchy – organism, population, community – is regulated through its relationships with the levels above and below, creating feedback systems that ultimately form the ecosystem’s response to change (MacMahon, Phillips, Robinson, & Schimpf, 1978; Peterson, 2000). Theoretical research suggests that preserving biodiversity fosters ecological resilience to disturbances (Holling, 1973; Jorgensen & Nielsen, 2013; Peterson et al., 1998); however, such concepts are difficult to apply to real-world wildlife management issues. Therefore, practical assessments of resilience require study of responses to change on multiple ecological levels.

The boreal forest of northern Alberta provides a unique landscape on which to examine such hierarchical responses to landscape change. Shared between industrial development and biodiversity, it is a heterogeneous mosaic of both anthropogenic and natural landscape features – a working landscape, modified by humans and utilized by wildlife (Kremen & Merenlander, 2018; Tscharntke et al., 2012). Widespread natural resource extraction creates novel ecological patterns and alters existing relationships, introducing a new form of disturbance to the boreal ecosystem (Pickell, Andison, Coops, Gergel, & Marshall, 2015). Cutblocks for forest harvesting
make up the largest anthropogenic disturbances by area, whereas access roads and energy infrastructure produce a network of linear disturbances across the forest (Pasher, Seed, & Duffe, 2013). In particular, seismic lines – wide trails cut for seismic exploration of oil reserves – are relatively low-impact but stretch across entire landscapes to affect abiotic processes at multiple spatial scales (Dabros et al., 2018; Pattison et al., 2016). These low-intensity, spatially extensive disturbances create a unique opportunity to examine how the boreal ecosystem responds to pervasive landscape change across hierarchical levels.

Industrial disturbances have particular effects for the boreal mammal community, contributing to population declines for species at risk (Hebblewhite, 2017), expansion of invasive species (Dawe, Bayne, & Boutin, 2014), and altered spatial ecology of apex predators (Latham, Latham, Boyce, & Boutin, 2011; McKenzie, Merrill, Spiteri, & Lewis, 2012). Though conservation efforts to mitigate serious consequences have been implemented, such interventions create additional human modifications to which boreal species must respond. One such intervention is habitat restoration. Despite being intended for ecosystem benefit, restoration needs to be investigated for its ability to re-establish landscape functionality (Dabros et al., 2018). Further, research into the consequences of anthropogenic disturbances in northern boreal forests is in its infancy, and commonly focuses only on species or interactions of special concern (e.g. woodland caribou; Burgar, Burton, & Fisher, 2018; Fisher & Burton, 2018). To fully understand the effects of human landscape change on the boreal mammal community, multilevel studies should assess responses of multiple populations, as well as how those responses translate into changes within the mammal community.

Ecological processes occur at various spatial and temporal scales, creating challenges for tracking changes across ecological hierarchies (Levin, 1992; Peterson, 2000). Additionally, the
complexity of ecosystems produces emergent properties that cannot be explained by the sum of their individual components, making relationships and responses difficult to translate between levels (Holling, 2001; Peterson, 2000). Fortunately, recent advances in camera trapping for biodiversity monitoring address some of these challenges. Camera traps are remotely-triggered cameras designed for non-invasive observation of wildlife (O’Connell, Nichols, & Karanth, 2011). Most camera trap models use passive infrared sensing technology to capture an image when a difference in temperature is detected, thus detecting homoeothermic animals as they pass through the field of view (Welbourne, Claridge, Paull, & Lambert, 2016). Camera trap images and videos are increasingly used for behavioural research at the individual level (Caravaggi et al., 2017), but they can also be scaled-up to monitor population and community interactions via coordinated sampling across entire landscapes (Burton et al., 2015; Steenweg et al., 2017). Further, time-stamped images and relatively inexpensive monitoring provide the means for temporal sampling at both fine and coarse scales (Burton et al., 2015; Frey, Fisher, Burton, & Volpe, 2017). Recently, camera traps have been used to assess species’ responses to anthropogenic change, offering a useful monitoring technique to evaluate human impact (Fisher & Burton, 2018; Steenweg et al., 2017; Stewart et al., 2016). Through cross-scale monitoring of multiple species on changing landscapes, camera traps provide a promising methodology for tracking responses across ecological hierarchies, thereby assessing ecological resilience in an applied setting.

1.2 Thesis objectives and hypotheses

To explore community resilience to human landscape change in an applied ecological setting, I assessed large mammal responses to anthropogenic disturbance across hierarchical levels. I investigated effects of industrial development on the boreal working landscape, examining
responses of species at risk as well as the broader mammal community with which they interact. I did this by 1) testing boreal mammal responses to linear disturbance and habitat restoration at the population level, and 2) examining strength and direction of interspecific interactions to reveal relationships and responses at the community level. By assessing effects of landscape change at two hierarchical levels, I examined how responses transfer from populations to communities, thus taking the first steps in addressing the boreal mammal community’s resilience to change.

In my second chapter, I examined population-level responses to seismic line disturbances and restoration to address conservation concerns for a boreal species at risk. Industrial development in the boreal forest has detrimental consequences for the woodland caribou (*Rangifer tarandus caribou*), causing habitat fragmentation and intensified predator-prey dynamics that contribute to drastic population declines (Boutin, Boyce, & Hebblewhite, 2012; Hebblewhite, 2017). Of all disturbance types in Alberta’s boreal forests, seismic lines are the most common, prompting calls for their restoration to reduce threats for caribou (Dabros et al., 2018). Seismic lines fragment caribou habitat, facilitate predator (wolves *Canis lupus* and black bears *Ursus americanus*) movements across the landscape, and may enhance apparent competition from white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*; Dickie, Serrouya, McNay, & Boutin, 2016; Dyer, O’Neill, Wasel, & Boutin, 2002; Latham, Latham, McCutchen, & Boutin, 2011). While habitat restoration shows promise for its benefits to the broader wildlife community (Dabros et al., 2018), the effects of restoration must be monitored for their impact on caribou, and their key predators and apparent competitors. I examined whether habitat restoration influenced line use by caribou, caribou predators, and caribou competitors in the three years following restoration to assess how landscape change for conservation purposes affected boreal mammal populations at
the behavioural level. I hypothesized that restoration would decrease line use by caribou predators and competitors by creating movement barriers and decreasing early seral vegetative browse, and consequently increasing line use by caribou. I used camera traps deployed across four seismic line treatments (restored with site-preparation and planting, naturally regenerating, human-use, and control) to detect mammal line use, and compared the effect of treatment to those of other environmental factors for a detailed examination of how these species used seismic lines on a boreal working landscape.

In my third chapter, I expanded to community relationships on the working landscape by investigating interspecific interactions for three non-apex boreal predators: black bears (*Ursus americanus*), coyotes (*Canis latrans*) and Canada lynx (*Lynx canadensis*). Industrial landscape change creates a novel playing field on which boreal mammals interact, presenting new pressures and factors that may influence species’ relationships (Valiente-Banuet et al., 2015). Although numerous studies have explored how wolves have incorporated linear features into their spatial ecology (Dickie, Serrouya, McNay, & Boutin, 2016; Latham et al., 2011), the responses of non-apex predators are less well studied (but see Fisher & Burton, 2018 and Tigner, Bayne, & Boutin, 2014), and it is unknown how these predators interact under effects of anthropogenic disturbances. Using co-occurrences from camera traps as a proxy for interspecific interactions, I assessed which interactions governed non-apex predators’ use of the working landscape. I used segregation of occurrences as evidence of competition (Karanth et al., 2017), and overlap as evidence of facilitation (Cusack et al., 2016). As a primary hypothesis, I predicted that top-down influences from apex predators (wolves) would produce spatial or spatiotemporal relationships between wolves and each of the three non-apex predators. Alternatively, non-apex predator occurrences could also be more influenced by their prey, or by an intraguild competitor. To
address multiple potential scales of interspecific interactions during my sampling period (Fahrig, 1992), I examined co-occurrences at the spatial scale (site-level relative abundance across the entire survey period) and both coarse and fine spatiotemporal scales. Further, I analyzed effects of interacting species in addition to existing habitat influences and assessed for interactions between co-occurrences, season, and level of anthropogenic disturbance.

In the final chapter, I summarize results from each data chapter and synthesize conclusions in light of current research. I also reflect on the strengths and limitations of these analyses and suggest promising areas for future study.

1.3 General Methods

1.3.1 Study system

My study is located within the Algar sub-range of the East Side Athabasca River (ESAR) caribou range, approximately 70 km southwest of Fort McMurray, Alberta, Canada. The ESAR range covers a total area of 13,160 km$^2$ with an estimated minimum population of 227 caribou that is considered not self-sustaining (Government of Alberta, 2017). The 570 km$^2$ study area is bounded to the north and west by the Athabasca River, and has linear feature density of 1.1 km/km$^2$, including 523.6 km of seismic lines (Fig. 1.1; Alberta Biodiversity Monitoring Institute, unpublished data). In 2011, a habitat restoration program commenced in the area with the objective of restoring seismic lines in critical caribou habitat, providing an opportunity to quantify the effects of habitat restoration on boreal mammals (Silvacom & Nexen, 2015). Further, the Algar landscape allowed the study of community dynamics on a relatively low-disturbance landscape compared to other areas of northeastern Alberta, serving as a comparison to research conducted in caribou ranges with higher intensity anthropogenic disturbances (Fisher & Burton, 2018; Government of Alberta, 2017).
The Algar study area is predominantly a lowland coniferous landscape, with patches of upland deciduous forest alongside the Athabasca River and smaller tributaries. Dominant forest cover consists of mature black spruce (*Picea mariana*) and tamarack (*Larix laricina*) wetlands. Upland forest stands include aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). Primary shrub species are Labrador teas (*Ledum spp.*), willows (*Salix spp.*), and birch (*Betula spp.*). This lowland landscape is representative of the greater western boreal forest that is critical for carbon sequestration (Bradshaw, Warkentin, & Sodhi, 2009).

The large mammal community within this ecosystem is comprised of two large predators, grey wolves (*Canis lupus*) and black bears (*Ursus americanus*), as well as a suite of meso-carnivores, including Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), fisher (*Pekania pennanti*), American marten (*Martes americana*), and red fox (*Vulpes vulpes*). Prey species include moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), woodland caribou (*Rangifer tarandus caribou*), beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*), and small mammals such as red squirrels (*Tamiasciurus hudsonicus*), muskrats (*Ondatra zibethicus*) and voles (*Microtus spp.*).

### 1.3.2 Camera trap sampling design and implementation

We deployed Reconyx PC900 HyperFire camera traps (Reconyx, Holman, WI) along seismic lines between November 2015 and 2017. The Algar landscape is most readily accessible by helicopter in early spring and late autumn (April and November – when ground conditions are frozen with minimal snow cover). We installed the first 24 camera traps in November 2015, followed by a second deployment of 36 cameras in November 2016, resulting in a total of 60 cameras (Fig. 1.1).
The Algar Caribou Habitat Restoration Program restored seismic lines in the Algar study area between 2012 and 2015, treating 148 km of line segments with site preparation and planting (SPP) and designating 192 km as ‘natural regeneration protection’ (NatRegen). Line segments were defined as a continuous section of line at least 200 m long within similar ecological conditions (Silvacom & Nexen, 2015). For a more comprehensive study of how large mammals used this landscape, we additionally classified other seismic line segments as ‘Human-use’ and ‘Control’ for a total of four seismic line treatments (Fig. 2.1; Burton, Burgar, Tattersall, & Fisher, 2017). My sampling unit was the line segment within the field of view of the camera, which is a sample of the larger line segment of the same seismic line treatment. Entire seismic lines cannot be considered the sampling unit as these could be many kilometres long and cross more than one treatment and landcover type, therefore displaying different effects on wildlife along their length.

Camera station locations were selected using a stratified random design, with line segments randomly selected within four seismic line treatments. When stations were deployed on different treatments on the same seismic line, cameras were set up at least 500 m apart to increase the probability of independent detections between stations (Burton 2014; Tigner, Bayne, & Boutin, 2014; 2015). In some cases, line segment proximity resulted in cameras of different line treatments to be less than 500 m apart (minimum distance 338 m). Mapping individual species’ detections at adjacent sites did not indicate any spatial dependence.

We set all cameras to take one image per trigger, with one second lag between triggers and no quiet periods. Camera traps also took time-lapse images every 24 hours at noon to test camera function and record background conditions (i.e. vegetation, snow). Cameras were deployed from November 2015 to April 2018. During the April and November 2017 site visits
we recorded field data such as seismic line characteristics and broad vegetation measurements (types of vegetation present and height of tallest on-line vegetation; see Appendix 1 for field data collection sheet).

1.3.3 Project data management

I processed camera trap images using Camelot (Hendry & Mann, 2017; https://gitlab.com/camelot-project/camelot) and camtrapR within R statistical software (Niedballa, Sollmann, Courtiol, & Wilting, 2016; R Core Team 2018; www.r-project.org). Together, these programs allowed for streamlined and organized data management that adhered to metadata standards outlined by Forrester et al. (2016). CamtrapR included functions for basic image management and summarization (image renaming, detection summaries), while Camelot provided a camtrapR-compatible interface for recording deployment and image identification data. I processed images by identifying species, sex, age, and behavior (wherever possible). I then summarized detection events in camtrapR record tables, treating detection events as independent when occurring at least 30 minutes apart to follow standard practice (Rovero & Zimmermann, 2016). Both of my research chapters use camera trap data from November 2015 to April 2018, for a total of 30 months of detection data for 16 mammal species (Fig. A2.1).
Figure 1.1 The Algar study area, camera trap locations, and seismic line treatments from the Algar Caribou Habitat Restoration Program in northeastern Alberta. Forest cover classifications were based on moisture regime and forest data from the Alberta Vegetation Inventory (AVI; Alberta Vegetation Interpretation Standards, 2005).
Chapter 2: Boreal mammal seismic line use varies with restoration treatments: applying habitat restoration to caribou conservation

2.1 Introduction

2.1.1 Energy development in northern Alberta

In the last 200 years, humans have become the most powerful transformative force on Earth, resulting in a new geologic epoch known as the Anthropocene (Crutzen & Stoermer, 2000). More than 75% of the Earth’s terrestrial surface has now been modified by humanity’s efforts to acquire resources (Venter et al., 2016). Such drastic transformations trigger responses in wildlife, altering their habitat use, movement rates, and temporal activities (Fisher & Burton, 2018; Frey et al., 2017; Tucker et al., 2018). Further, they modify abiotic processes as well (Vitousek, Mooney, Lubchenco, & Melillo, 1997), thus disrupting multiple interacting landscape processes. While restoration is recommended to mitigate the worst of these effects, the proposed solutions can be costly (e.g. Hebblewhite, 2017) and are rarely evaluated for their efficacy. Without a clear understanding of whether restoration reinstates these processes, these solutions may merely be another anthropogenic disturbance altering landscape functionality.

In northern Alberta, the boreal forest ecosystem has been transformed into a working landscape in which biodiversity competes for space with largescale industrial development. Oil and gas extraction over the last 50 years is the primary driver of land transformation, generating a novel landscape unlike any produced through natural processes (Pickell et al., 2015). Belowground exploration and in situ drilling create a vast network of linear corridors, of which seismic lines are the most common (Lee & Boutin, 2006; Pickell et al., 2015). Seismic lines are cleared paths cut through the forest in preparation for seismic exploration of oil reserves. While recent technological advances allow for low-impact seismic (LIS) lines that are less than 5 m
wide, conventional seismic lines (those cut before mid-1990s) were 5 – 10 m wide to accommodate for large machinery (Dabros et al., 2018).

The site-level disturbance effects of conventional seismic lines include vegetation removal and soil compaction, altering temperature and moisture regimes that ultimately results in a new vegetation structure (Dabros et al., 2018). At the landscape level, individual seismic lines constitute a relatively small land area, but are up to five times longer in total length than roads or rail lines. This high density disturbance fragments habitats by increasing the number and decreasing the size of forest patches, while increasing the amount of forest edge (Pattison et al., 2016). The resulting landscape patterns are without any natural analogue, and therefore have uncertain recovery trajectories (Pickell et al., 2015). Once cut, conventional seismic lines are often converted into access trails, but even those that are deactivated experience very low rates of vegetative regeneration (Lee & Boutin, 2006). Recovery is particularly slow in lowland ecosites (i.e. bogs and fens with low productivity), which are the dominant cover type in northeastern Alberta (van Rensen, Nielsen, White, Vinge, & Lieffers, 2015). The result of decades of petroleum exploration is an extensive network of ‘legacy’ seismic lines that are predicted to remain on the landscape for over 50 years. Such widespread and persistent disturbance patterns alter how animals use the landscape, which can have cascading influences on their interactions and the resulting community structure (Fisher & Burton, 2018).

2.1.2 Consequences for caribou

Most dramatic of these consequences is ongoing and precipitous declines in the woodland caribou (*Rangifer tarandus caribou*; hereafter caribou). Federally listed as threatened in 2002, caribou have declined across Canada. In Alberta, this is due to new landscape configurations formed by seismic exploration (Environment Canada, 2012). Not only do seismic lines cause
fragmentation of preferred caribou habitat, they also exacerbate harmful interactions between caribou and other large mammals. Widespread replacement of mature forest with early seral vegetation has facilitated the northward expansion of white-tailed deer (*Odocoileus virginianus*; Dawe, Bayne, & Boutin, 2014). Increasing populations of boreal deer contribute to growing predator populations, thus enhancing predation pressures on native species via a process known as apparent competition (Dawe et al., 2014; Holt, 1977; Latham, Latham, McCutchen, & Boutin, 2011). Linear corridors also influence movement and behavior of the apex predator grey wolf (*Canis lupus*; Dickie, Serrouya, McNay, & Boutin, 2016). Within the boreal forest, caribou have historically mitigated predation risks from wolves by spatially separating from moose (*Alces alces*; James, Boutin, Hebert, & Rippin, 2004) and spatiotemporally avoiding wolves (Latombe, Fortin, & Parrott, 2014). However, the prevalence of seismic lines and intensified apparent competition make predator avoidance difficult within this fragmented landscape, decreasing the effectiveness of such strategies (Dyer, O’Neill, Wasel, & Boutin, 2002). Seismic lines facilitate wolf movement within lowland caribou habitat, increasing their encounter rate with caribou and thus likely increasing their predation rate (Whittington et al., 2011). In addition, black bear (*Ursus americanus*) use of seismic lines could contribute to caribou calf mortality by increasing caribou encounter rates with this opportunistic predator (Latham, Latham, & Boyce, 2011; Tigner, Bayne, & Boutin, 2014). As caribou prefer lowland bog and fen habitats where natural regeneration of seismic lines is negligible, these dynamics are predicted to persist, posing a lasting threat to boreal caribou populations (van Rensen et al., 2015).

In response to boreal caribou declines, Environment Canada (2012) released its *Recovery Strategy for the Woodland Caribou*, outlining primary causes of population decline and recommending counter actions. It determined that for a population to have 60% probability of
sustaining itself, only 35% of caribou habitat within that range could be disturbed from both natural (i.e. fire) and anthropogenic causes. Komers and Stanojevic (2013) reported anthropogenic disturbances across 78% of Alberta’s boreal forest by 2008. In its 2017 draft range plan, Alberta outlined an integrated land management approach to reaching federal habitat goals by balancing environmental, economic, and social priorities through strategic land planning. This approach is aimed at achieving caribou conservation on the working landscape while also addressing human energy needs. A central aspect of this plan is collaboration between government, industry, and indigenous stakeholders to implement widespread caribou habitat restoration (Government of Alberta, 2017). Given their widespread footprint and lack of natural regeneration, seismic lines are a high priority restoration target for restoration of ecological processes and reduction in caribou predation rates (Bentham & Coupal, 2015; Environment Canada, 2012).

2.1.3 Seismic line restoration approaches

A number of seismic line restoration initiatives have already been implemented across Alberta (Bentham & Coupal, 2015; Pyper, Nishi, & McNeil, 2014). These projects generally take two approaches that address the threats imposed on caribou by linear corridors. Structural restoration re-establishes natural vegetation composition on lines, thus facilitating forest regeneration. Functional restoration, on the other hand, focuses on line-blocking techniques that impedes line use as movement corridors (Pyper et al., 2014). While many functional restoration techniques have implications specific to caribou and their predators, structural restoration has extensive benefits for a broader wildlife community (Dabros et al., 2018). Caribou are considered an umbrella species, suggesting that focusing conservation efforts on their habitat
needs will have ancillary benefits for the boreal ecosystem as a whole (Bichet, Dupuch, Hebert, Le Borgne, & Fortin, 2016).

The Algar Caribou Habitat Restoration Program was initiated to implement seismic line restoration measures in the Algar region of northern Alberta (OSLI, 2012). The project’s objectives aimed to address both structural and functional restoration by simultaneously promoting vegetative regeneration and providing movement barriers for predators (Silvacom & Nexen, 2015). Treatments included site preparation with mounding and addition of course woody material (i.e. dead and damaged trees) where available, as well as planting of black and white spruce seedlings (*Picea mariana* and *P. glauca*, respectively). These treatments began in 2012 and completed in 2015 (Silvacom & Nexen, 2015). In addition, we categorized three other seismic line types in this area for comparison. These included seismic lines that were considered to be regenerating naturally (i.e. vegetation heights of 1.5m or more), those left as human-use lines for left open for industrial or trapper access, and those that were recommended for site preparation and planting but were set aside as untreated control lines within the wildlife monitoring program (Fig. 2.1; Silvacom & Nexen, 2015). While vegetative regeneration through site preparation and planting (SPP) and natural regeneration (NatRegen) has previously been successful, wildlife responses to seismic line treatments has not yet been assessed (Bentham & Coupal, 2015; Pyper et al., 2014). This program is a landscape-scale experimental manipulation to test wildlife responses, providing a unique opportunity to investigate whether habitat restoration initiatives can re-establish wildlife aspects of landscape functionality.

### 2.2 Objectives and hypotheses

In order to aid in caribou population recovery, successful restoration of seismic lines for caribou conservation needs to result in increased line use for caribou and decreased line use for
their predators and competitors. In this chapter, I tested the effect of structural seismic line restoration on use of lines by five large mammal species: wolves, black bears, white-tailed deer, moose, and caribou (Fig. 2.2). My objectives were to:

1) Compare mammal seismic line use across four line treatment types to assess the effects of restoration on use of lines by caribou, their competitors, and predators in the 3-6 years immediately following restoration, and

2) Examine the strength of seismic line treatments relative to other factors that are known to influence line use by at least one of the target species, so as to provide additional environmental context to treatment effects.

I hypothesized that the four seismic line treatments represented four stages in line regeneration, and that mammals would respond accordingly. From least restored to most, I therefore predicted the stages to be human-use lines, control, SPP, and NatRegen, where we broadly considered the first two treatments to be unrestored seismic lines and the second two treatments to be restored seismic lines. I further expected the effect of natural regeneration to be stronger than SPP given the latter treatment’s recent application (one to three years prior to when monitoring began; Fig. 2.1).

I hypothesized that seismic line restoration would restore movement barriers for predators, resulting in less frequent use. I also hypothesized that restoration replaces early seral browse species for deer and moose, resulting in less frequent use by caribou apparent competitors. In summary, I predicted that wolves, black bears, white-tailed deer, and moose would use restored lines less frequently than unrestored lines. Using control lines as the reference level (where they are neither regenerating nor experiencing ongoing human activity), use of SPP and NatRegen lines should be less than control whereas use of human-use lines
should be greater. Conversely, I expected the reduction of predators and apparent competitors to benefit caribou, such that they would use SPP and NatRegen lines more frequently and human-use lines less frequently relative to control lines.

I further predicted that the effect of seismic line treatment on mammal line use would be greater than or equal to the effect of other landscape features influencing line use. Caribou have previously shown a strong preference for wetland forest habitats that provide spatial separation from habitat preferred by their predators and competitors (James, Boutin, Hebert, & Rippin, 2004; Latham, Latham, & Boyce, 2011; Latham, Latham, McCutchen, & Boutin, 2011). I therefore expected that caribou would prefer seismic lines in lowland forest, while deer, moose, wolves and black bears would prefer upland habitat. Seismic line use is also likely to be seasonally-dependent, varying with the presence of snow (Latham, Latham, Boyce, & Boutin, 2011). Finally, I hypothesized that local and site-level seismic line characteristics such as vegetation height, line width, and line density would affect mammal line use (Dickie, Serrouya, DeMars, Cranston, & Boutin, 2017; Fisher & Burton, 2018; McKenzie et al., 2012; Tigner et al., 2014).
Figure 2.1 Examples of the four seismic line treatments within the Algar study area. The top row displays control lines (a) and human-use lines (b), both considered unrestored. The bottom row shows site preparation and plant lines (SPP, c) and natural regeneration lines (NatRegen, d), both considered restored.
Figure 2.2 Camera trap photos of the five target mammal species. We used camera traps to assess responses to restoration for wolves (*Canis lupus*, a), black bears (*Ursus americanus*, b), white-tailed deer (*Odocoileus virginianus*, c), moose (*Alces alces*, d), and woodland caribou (*Rangifer tarandus*, e).
2.3 Methods

2.3.1 Analytical overview

In this study, I used a landscape-scale manipulated experiment to test hypotheses about species’ responses to restoration. I assessed seismic line treatment effects on mammal line use within a zero-inflated generalized linear mixed modelling (GLMM) framework, using camera trap data from a 30 month period between November 2015 and April 2018. I modelled detection data as a function of treatment as well as other predictor variables hypothesized to affect species’ line use. The inclusion of additional predictors served the dual purpose of explaining residual variance in the data, as well as assessing treatment effect relative to other influential factors. I used AIC model selection to compare among candidate models and identify the most parsimonious model that best fit the data (Burnham & Anderson, 2002). I then used the fully parameterized model to compare treatment effect sizes against additional predictor variables (Table 2.1, see below for model details).

2.3.2 Response variable and random effects

We deployed all camera stations along seismic lines; therefore I considered detection events to be evidence of seismic line use. I summed detection events by month for each species to obtain a count metric sensitive enough to identify seasonal differences in use, yet aggregated enough to reduce the number of zeroes in the dataset. The dataset consisted of 1800 observations, each being a monthly count of species detections at one camera site (60 cameras x 30 months). As our response variable was species detections, observations were repeated across months at each site, and thus were not independent. I therefore included a random intercept of site, thus accounting for non-independence of monthly detections at the same site. I also included a random intercept of month because we sampled the same month (i.e. month of the year) up to
three times across the multi-year survey, and we considered that seasonal weather patterns reduced independence among these observations. For example, observations in January of each year may be similar due to their occurrence in mid-winter. I included the full 30-month sampling period for caribou, white-tailed deer, moose, and wolves. I only used months between April and October for black bear detections to account for their winter hibernation (Fig.A2.2b).

During the 30-month survey period, camera failures resulted in some inactive camera periods. I accounted for this by including a covariate of the number of active days per month for each camera.

2.3.3 Predictor variables

My primary predictor variable of interest to explain variation in detections per month was the categorical variable ‘seismic line treatment’. We assigned camera stations to one of four replicate categories based on the characterization of segments by the restoration program (Silvacom & Nexen, 2015), with a total of 22 SPP stations, 12 NatRegen, 14 human-use, and 12 control (Fig. 1.1; for photos, see Fig. 2.1). Due to the staggered timing of camera deployments, we only sampled human-use and natural regeneration treatments from November 2016 onwards, while control lines and 12 SPP lines were sampled for the full 30 months. A summary of camera trap data collected and survey effort is included in Appendix 2.

To account for the fact that line use by species may also be influenced by their selection for surrounding habitat characteristics, I used data from the Alberta Vegetation Inventory (AVI; Alberta Vegetation Interpretation Standards, 2005) to derive a habitat variable for the proportion of lowland habitat surrounding each camera site. This metric applied criteria previously used by Fisher and Burton (2018), combining ecosite characterizations and moisture regime into the broader lowland, upland, and non-forest habitat categories. Moisture regime differentiated
forested areas as upland or lowland, while forest type differentiated between these two categories and ‘non-forest’. In general, ‘lowland’ habitat was any area dominated by tree cover with a ‘wet’ moisture regime. I also accounted for seasonal effects on seismic line use by including a covariate for the proportion of ‘snow days’ per month to indicate snow presence. I used Timelapse 2.0 Image Analyzer (Greenberg & Godin, 2015; http://saul.cpsc.ucalgary.ca/timelapse) to record snow presence from daily ‘time-lapse’ images captured at each camera. I considered snow to be present if it covered over 50% of the line surface within the camera’s field of view. Summing snow days for each month, I then divided by the number of days the camera was active that month to account for any periods of inactivity (i.e. camera malfunction).

I also included predictor variables describing characteristics of the seismic lines themselves. I measured vegetation height and line width in the field during the November 2017 field visits (vegetation heights were measured three times within 10m of camera and averaged). Although I obtained vegetation height outside the summer growing season, the measurements were mostly from woody shrubs whose height did not change significantly over the course of the study. I measured linear density using Alberta linear feature data (University of Alberta Linear Feature Map, unpublished data), dividing total length of linear features by the area within which they were situated (measurement scales are described below).

Prior to running analyses, I used variance inflation estimation to assess for collinearity and co-plots and multi-panel scatterplots to graphically check interactions between all predictor variables (Zuur, Ieno, & Elphick, 2010). I also centered and scaled all continuous predictors by subtracting the mean and dividing by two standard deviations (Gelman, 2008). Doing so facilitated within-model comparisons of coefficient estimates, especially when comparing
continuous predictors to categorical (i.e. treatment; Gelman, 2008). As I was interested in the effect of continuous predictors relative to the reference treatment level (control seismic lines), I chose not to center my treatment covariate (Schielzeth, 2010). Reported coefficient estimates therefore represent the effect of each covariate relative to control seismic lines when all other predictors are at a mean value.

2.3.4 Scale analysis

The relationship between spatial scale, landscape variables, and species’ site use depends greatly on the species and landscape in question (Fisher, Anholt, & Volpe, 2011; Levin, 1992). The scale at which landscape variables are measured, such as proportion of lowland habitat and linear density, can significantly influence modelling outcome (McGarigal, Wan, Zeller, Timm, & Cushman, 2016). I therefore modelled species-habitat relationships at multiple spatial scales to determine scales of influence for each species and spatial covariate, using generalized linear models (GLMs) and model selection with Akaike’s Information Criterion to compare across scales (AIC; Fisher, Anholt, & Volpe, 2011; Burnham & Anderson, 2002). I chose scales defined by radii varying from 250-2000m surrounding camera stations, at intervals of 250m, to reflect species’ responses to local habitat characteristics in the vicinity of each camera. For each of my target species, I used univariate models assessing monthly detections as a function of the spatial covariate measured at each of the eight scales, then selected the scale with the lowest delta AIC (ΔAIC) score. In cases where models were within 2 ΔAIC points of one another, I selected the scale with the most model weight (Fig. A3.1).

2.3.5 Modelling approach

To determine the influence of line characteristics on species detections, I modelled camera trap detection data using zero-inflated GLMMs coded in the R statistical package
The GLMM framework allows inferences to be made about non-normal data (e.g. count data that cannot be negative), while also accounting for heterogeneity of variance with random effects (Bolker et al., 2009). I chose *a priori* to use zero-inflated models (a type of mixture model; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Many ecological datasets contain zeros that are both the result of the ecological process and the observation process (Martin et al., 2005). In our camera trap count data, observation-process zeros likely arose from sampling a small subset of possible locations of each highly vagile animal (rather than failing to detect an animal that is present at the site, cf. MacKenzie et al., 2002). Modelling monthly detections as zero-inflated therefore accounted for two separate sources of zeros: those resulting from responses to seismic line treatments and ecological predictors, and those resulting from stochastic processes (Martin et al., 2005; Zuur et al., 2009). I verified this choice with preliminary data exploration, indicating that detection data had higher proportions of zeros than would be expected under distributions in the Poisson family (Zuur & Ieno, 2016).

To identify the most suitable distribution with which to model the response variable, I constructed the full model of all predictor variables using a Poisson and 2 forms of negative binomial distribution, then compared them using AIC (Zuur et al., 2009). The *glmTMB* package allows users to choose between negative binomial distributions (‘Nbinom1’ and ‘Nbinom2’) with variance increasing quadratically or linearly with the mean, providing greater flexibility in modelling count data (Brooks, Kristensen, van Benthen, et al., 2017). For all species, the negative binomial distribution best fit our observed detection data, though the treatment of the variance differed (Table 2.2).
Similarly, I applied this model selection approach to determine the random structure of the data. I tested random intercepts for site and month: a site random effect accounted for dependence of detections occurring at the same station, while month addressed seasonal influences on animal movement (for example, animals may travel less during denning or calving seasons, therefore their use of seismic lines may decrease during spring months). Including both random intercepts vastly decreased AIC values compared to the null model (one without random intercepts) for all five species, indicating more predictive power for the two-random-effect models.

2.3.6 Model selection and effect size estimation

I used model selection based on Akaike Information Criterion (AIC) to assess the relative degree of support among candidate models (Burnham & Anderson, 2002). The null model included only active days, the measure of sampling effort that was also included in all other models. Restoration treatment was included in all other candidate models. Our fully parameterized model included all five additional predictor variables (see Table 2.1). As very little is known about species-habitat associations from this region of the boreal forest, I did not have a priori reasons to include only specific candidate models. I therefore constructed multiple permutations of candidate models using the ‘dredge’ function from the R package MuMin. This function generated candidate models using combinations of five predictor variables while keeping the treatment and active days variable fixed in all candidate models, then performed AIC model selection on the model set (Bartoń, 2009). I considered predictors contained in all models that ranked within 2 ΔAIC of the top model to be influential covariates for that species (Burnham & Anderson, 2002). I then compared effect sizes of predictor variables using parameter estimates from a fully parameterized model. Model-averaging across candidate models is considered...
inappropriate for estimating effect sizes (Cade, 2015; Grace, 2018). By using the full model, I obtained effect size estimates that account for influences of all predictor variables included in the model set (B. Bolker, unpublished data). This approach determined the best-fit model to each species’ data, while also comparing treatment effect sizes to all covariates of interest and across species.
Table 2.1 Full list of predictor variables used to model monthly species detections. I constructed a candidate model set from all possible combinations of the above predictor variables, while keeping Treatment and Active Days constant in every candidate model. All predictor variables were included in the full model to estimate effect sizes. \(^1\)ABMI = Alberta Biodiversity Monitoring Institute, updated 2012; \(^2\)AVI = Alberta Vegetation Inventory, updated 2016.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Source</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>Silvacom</td>
<td>Seismic line treatment types: Control, Human-Use, Site Preparation and Plant, Natural Regeneration</td>
</tr>
<tr>
<td>Active Days</td>
<td>Camera traps</td>
<td>Number of days camera was active / total days per month</td>
</tr>
<tr>
<td>Snow Presence</td>
<td>Camera traps</td>
<td>Number of days with snow present / total days per month</td>
</tr>
<tr>
<td>Line Width</td>
<td>Field measurements</td>
<td>Width of seismic line at camera site, measured in metres</td>
</tr>
<tr>
<td>Vegetation Height</td>
<td>Field measurements</td>
<td>Height of tallest vegetation type present on the line at camera site, measured in metres</td>
</tr>
<tr>
<td>Line Density</td>
<td>ABMI(^1)</td>
<td>Total length of seismic lines in km / area in km(^2)</td>
</tr>
<tr>
<td>Lowland Habitat</td>
<td>AVI(^2)</td>
<td>Conifer or deciduous canopy cover, moisture = w</td>
</tr>
</tbody>
</table>
2.4 Results

2.4.1 Summary of survey effort and species detections

Total sampling effort over the 30-month study period was 32,371 camera-days, with a median of 513 active days per camera (range = 158 - 886). There were 2,156 independent detection events of mammals recorded, from which I identified 16 mammal species (Fig. A2.1). Of the five target species, white-tailed deer were most frequently detected (n = 589) and caribou were least detected (n = 148; Fig. 2.3a). Wolves, black bears, white-tailed deer, and moose occurred at over 60% of all camera sites, while caribou occurred at 43% (Fig. 2.3b).

2.4.2 Treatment effects on mammal line use

Seismic line restoration with SPP significantly decreased white-tailed deer line use (-1.393±0.479, p = 0.004; Fig. 2.4c), but did not significantly affect line use by predators or moose. In addition, human-use lines significantly increased wolf line use (1.472±0.562, p = 0.009; 2.4a), but did not influence line use by black bears, caribou, or caribou competitors. NatRegen did not have any significant effect on line use by any of the five target species. Overall, mammal line use did not indicate the expected relationship between the seismic line treatments and stages in line regeneration (Fig. 2.4).

2.4.3 Effect of additional landscape factors

Seismic line treatment was the best-supported predictor variable for wolves, whereas line use by all other species was more strongly influenced by landscape context. Lowland habitat had the strongest effect for two species, significantly increasing line use for caribou (2.931±0.643, p > 0.001; Fig. 2.4e) and significantly decreasing line use for white-tailed deer (-1.982±0.402, p > 0.001; Fig. 2.4c). The second most influential factor was snow presence for wolves and caribou (-0.734±0.263, p = 0.005 and -1.414±0.350, p > 0.001, respectively). Black bears and moose
were most strongly influenced by vegetation height, both increasing line use with taller vegetation (0.956±0.374, p = 0.009 and 0.741±0.348, p = 0.033, Fig. 2.4b and d respectively). Line width also had a positive effect on line use by moose, but this effect was not statistically significant (0.704±0.374, p = 0.060). Seismic line density was only a significant predictor variable for white-tailed deer, with line use increasing with line density (0.784±0.351, p = 0.026).

2.4.4 Predictors in the top model set

For all species except black bears, predictor variables with significant effects on line use appeared in the most parsimonious top model from AIC model selection (Table 2.2). The null model had the most support for black bears, indicating that predictor effects were generally weak. However, the null model was closely followed by one including vegetation height, as indicated by the evidence ratio. All predictor variables appeared in the top model set for wolves, though line density, vegetation height and line width only occurred in one model each. The top model for white-tailed deer included lowland habitat and linear density, though vegetation height and snow were included twice in the four next-best models and line width was included once. Moose line use was best explained by a model containing vegetation height and line width in addition to treatment, with the subsequently ranked models keeping the remaining three predictor variables at least once each. Finally, the best-supported model for caribou included snow presence, lowland habitat and linear density. In the subsequent four ranked models, vegetation height appeared twice and line width appeared once.
Figure 2.3 Relative abundance indices for five focal species across 30 months of camera trap surveying in the Algar study area. Total detections (a) is the sum of independent camera trap detections of that species across all sites and months, and proportion of sites with detections (b) is the number of sites that species was detected at across all months relative to total number of sites.
Figure 2.4 Estimated effects of seismic line treatment and other factors on line use by boreal mammals in northeastern Alberta. Parameter estimates from fully-parameterized zero-inflated GLMMs of monthly detections from 60 camera traps sampled Nov. 2015 – 2018 are displayed as mean ± standard error. Predictor variables have been centred and standardized to indicate effect sizes relative to the unrestored control treatment with all other variables held constant at a mean value. ** denotes estimates with p < 0.01, * denotes estimates with p < 0.05.
Table 2.2 Model selection results for models within 2 ΔAIC for five target mammal species. Top models indicate which predictor variables (in addition to restoration treatment and active days) best explained seismic line use for each species. Treat = treatment type, AD = proportion of active days, snow = proportion of snow days, low = lowland habitat, LD = line density, VH = vegetation height, and LW = line width. Values following lowland and line density indicate the buffer radius used to measure these variables. The column Distribution represents the underlying distribution of the response variable, df is the degrees of freedom in the model, ΔAIC indicates the difference in AIC scores from the top model, AICwt is the AIC weight attributed to that model, Cum.Wt is the cumulative model weight, and ER is the evidence ratio (AIC weight of top model/AIC weight of model).

<table>
<thead>
<tr>
<th>Species</th>
<th>Predictor Variables</th>
<th>Distribution</th>
<th>df</th>
<th>ΔAIC</th>
<th>AICwt</th>
<th>Cum.Wt</th>
<th>ER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wolf</td>
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2.5 Discussion

Seismic line treatment at this spatial and temporal scale influences line use for two of the five large mammal species that play a central role in caribou dynamics in northern boreal forests. If linear restoration is to support recovery of threatened caribou populations, it should “remove” the ecological effects of seismic lines by decreasing line use by caribou predators and apparent competitors, and increasing use by caribou. In the three-six year period post-restoration covered by this study, only white-tailed deer responded to seismic line restoration. I did not see evidence that restoration created movement barriers for caribou predators, although wolves did show higher use of lines left open for human access. Caribou themselves used seismic lines in lowland habitat, regardless of restoration treatment. These results suggest that in the short term, seismic line restoration alone does not support caribou conservation on the working landscape. However, they provide a clearer depiction of how large mammals use this landscape, which will inform future adaptive management practices for multiple species.

2.5.1 Site preparation and planting ineffective as short-term functional restoration for predators

Contrary to a key hypothesis motivating linear restoration in caribou habitats, wolves and black bears did not decrease line use with seismic line restoration in the form of site preparation and planting. Although mounding and application of coarse woody debris has been suggested as a barrier to predator movement, providing functional restoration in addition to structural restoration (Bentham & Coupal, 2015; Dabros et al., 2018), our results do not support this assertion. It is possible that this result is specific to this study area. In the Algar restoration program, coarse woody debris could only be applied to lines where it was readily available in the surrounding forest. At many lowland sites, there was insufficient material to reach target
application for movement barriers. One restoration zone received 40% of targeted coarse woody debris volume, while two others received only 16% (OSLI, 2012; Silvacom & Nexen, 2015). Without adequate woody debris, mounding alone may not be an effective inhibitor of predator movement. Mounding and debris may also be ineffective if predators establish game trails on seismic lines and continue to use them following restoration treatments. Finnegan et al. (2018) reported that wolves were influenced by seismic lines even during late stages of natural regeneration, suggesting that they maintain game trails on seismic lines long after vegetation growth makes the rest of the line impassable – in the same way that trails are maintained in intact forest. Additionally, Tigner et al. (2014) showed higher black bear use of revegetated lines relative to the forest interior. In the field, we observed at least one game trail at most sites regardless of treatment. It is possible that mounding, unless applied randomly across the width of the line to disrupt existing trails, could actually enhance existing trails by making them more obvious to animals.

Consistent with previous studies, wolves exhibited increased use of human-use lines in our study (Dickie et al., 2017; Tigner et al., 2014). As accessible travel routes, human-use lines experienced more vehicle traffic than other lines (e.g. snowmobile, all-terrain vehicle), causing soil compaction, altered vegetation structure, and decreased likelihood of natural regeneration (Bentham & Coupal, 2015; Dabros et al., 2018; Pigeon et al., 2016). Compared to other line types, these characteristics ease movement barriers and permit faster, more efficient travel for wolves (Dickie et al., 2017; Finnegan et al., 2018). During the winter, vehicle traffic compacts snow on lines to provide firmer trails, decreasing energetic travel costs for wolves when snow presence on lines otherwise acts as a deterrent (Droghini & Boutin, 2017). Finnegan et al. (2018) also speculated that seismic lines with altered vegetation structure may indirectly attract wolves.
by providing early seral forage for ungulate prey, but my results do not show such an ungulate preference for human-use lines. Although there was an indication that black bears showed a non-significant preference for human-use lines, they also exhibited a positive response to lines with taller vegetation. Bears may prefer these lines for their foraging opportunities, as both unrestored and naturally regenerating anthropogenic disturbances are initially re-vegetated with common bear food sources (Brodeur, Ouellet, Courtois, & Fortin, 2008; Finnegan et al., 2018).

2.5.2 Caribou prefer lowland habitat over restored lines

Although the strategic goal of seismic line restoration is caribou habitat regeneration, caribou did not use SPP lines significantly more than controls in the three years immediately following treatment. This is perhaps not surprising, given the slow regeneration time of native vegetation in this boreal landscape (van Rensen et al., 2015). In their model projections of black spruce regeneration in lowland forest, Silvacom estimated planted trees to reach 1.2 m within 14 years following restoration (a threshold chosen to provide cover for an adult caribou, Silvacom & Nexen, 2015). Provided that regrowth reliably follows this projection (as yet undetermined), seismic line regeneration is not yet sufficient caribou shelter. Further, peatland terrestrial lichens (a primary winter food source for caribou, Bradshaw et al., 1995) can take over 20 years to regenerate after disturbance (Dunford, McLoughlin, Dalerum, & Boutin, 2006). Therefore, regenerating seismic lines may not be selected for available forage, either. Continued monitoring of mammal line use would determine whether vegetative regeneration targets on seismic lines produce significant responses by caribou.

Nevertheless, our results show that caribou do use seismic lines over all, despite previous studies suggesting caribou avoidance of industrial features (Dyer, O’Neill, Wasel, & Boutin, 2001). Caribou use of seismic lines is more strongly influenced by surrounding habitat and
season than line treatment, which corroborates evidence from existing literature. Caribou preference for lowland bogs and fens has been well documented and is a primary motivation for restoration in this habitat (James, Boutin, Hebert, & Rippin, 2004; Latham, Latham, & Boyce, 2011; Stuart-Smith, Bradshaw, Boutin, & Hebert, 1997; Government of Alberta, 2017). The negative effect of snow presence indicates decreased line use by caribou in winter, likely due to the higher energetic cost of moving through snow accumulated on lines (Fancy & White, 1987). In addition, Dyer et al. (2001) reported stronger behavioural avoidance of roads by radio-collared caribou during late winter, which correlated with a higher level of human traffic. This result is consistent with our results, which show human use of seismic lines between November and March, the same period of decreased line use by caribou (Fig. A2.2f).

2.5.3 Decreased white-tailed deer line use with site preparation and planting

My hypothesis that caribou apparent competitors would be deterred by line restoration was supported for white-tailed deer, but not for moose. White-tailed deer were negatively associated with actively restored lines, suggesting that SPP is an effective tool for reducing line use for this range-expanding species (Dawe, Bayne, & Boutin, 2014; Latham, Latham, McCutchen, et al., 2011). Although I did not observe a strong effect of restoration treatment on moose, their positive responses to vegetation height and line width are consistent with studies reporting moose selection for woody shrubs (the most frequently-measured vegetation in our study) and open-canopied habitat patches (Latombe, Fortin, & Parrott, 2014; Wasser, Keim, Taper, & Lele, 2011). Moose are negatively associated with anthropogenic landscape features in general (Fisher & Burton, 2018; Wasser et al., 2011), and my results suggest that this response is similar across treatments at this stage of regeneration.
White-tailed deer expansion into the boreal forest is in part attributed to industrial development (Dawe et al., 2014), as anthropogenic land conversion alters habitat in favour of deer. Deer selection for linear features and cut blocks has been previously documented (Fisher & Burton, 2018; Darlington, 2018; Fisher, Burton, Nolan, et al., 2016), and this relationship is further underscored in this study by the positive association between white-tailed deer and line density in this study. Lee and Boutin (2006) found that unrestored lines retained early seral vegetation long after the initial disturbance, and Finnegan et al. (2017) documented more important forage species for deer and moose on seismic lines relative to interior forest plots. Further, white-tailed deer move faster in wolf-selected areas while still selecting for areas with good foraging opportunities (Darlington, 2018). This avoidance response, combined with movement barriers from mounding, could explain the negative responses of deer to human-use and SPP lines observed in our study. Therefore, active restoration via site preparation and planting may provide structural restoration by returning disturbances to natural vegetation faster (Bentham & Coupal, 2015) as well as provide some functional restoration of habitat by deterring a key caribou competitor. Both of these responses could decrease competitive pressures on caribou over time.

2.5.4 Restoration treatments do not represent stages of restoration

Contrary to my expectation, mammal responses did not suggest that naturally regenerating seismic lines were more “restored” than SPP lines. Silvacom classified natural regeneration lines as having vegetation at least 1.5m in height, therefore defining restoration in structural terms (i.e. with respect to barriers to predator movement and line of sight). This classification did not consider other structural restoration of habitat: although target vegetation heights are achieved, altered abiotic conditions on seismic lines promote an early, disturbance-
tolerant successional state dissimilar to natural vegetation in the surrounding forest (Finnegan et al., 2018). In addition, Dickie et al. (2017) suggested that functional restoration of seismic lines occurs faster than structural restoration. Therefore, mammals may not elicit the same response to this novel vegetation structure as they would to a structurally restored habitat site. In general, most target species displayed negative responses to naturally regenerating lines (though effects were not statistically significant). Although expected for caribou competitors and predators, this response was not expected for caribou. This pattern suggests that species are responding to different forms of restoration, and reinforces the recommendation that both structural and functional restoration need to occur to achieve caribou conservation (Dabros et al., 2018). In future wildlife monitoring studies, habitat restoration should be measured continuously along a gradient that accounts for both vegetation height and composition (Dickie et al., 2017).

2.5.5 Limitations

One key limitation of my study was that we did not include camera stations in undisturbed habitat (‘off-line’). Off-line sites would have sampled species’ space use in the absence of anthropogenic disturbance at the site, thus providing a target threshold with which to compare line use across restoration treatments. However, deploying camera traps in interior forest patches posed a number of logistical challenges. Within the study area, the largest areas without seismic lines are open fens in lowland habitat (Fig 1.1). These sites are difficult to access and could confound results by not adequately sampling habitat heterogeneity. Zones of influence around anthropogenic features also made it difficult to set off-line cameras in higher linear density areas within Algar, as these sites may not accurately demonstrate species’ presence in undisturbed habitat (Dyer et al., 2001; Wilson, 2016). Nevertheless, comparing mammal use of treated seismic lines to use of neighbouring forest patches remains an interest and an area for
future research. In November 2017, we deployed an additional 13 camera traps at off-line sites to address this limitation, but results from that survey fall outside the scope of this thesis.

In addition, my analyses did not include models with interactions between predictor variables. During preliminary analyses with pilot data (detections between 2015 and 2016), I tested an interaction between treatment and lowland habitat, but models with interactions did not converge. Graphical data exploration did not indicate any likely interactions, so I did not pursue this avenue of analysis further. However, interactions between restoration treatments and additional predictor variables may be a promising area for continued research. For example, habitat type may influence vegetative regeneration (natural or restored), thus altering the relationship between restoration treatment and species’ line use (van Rensen et al., 2015). Or, an interaction between snow presence and restoration treatment may best explain species’ line use. Snow accumulation on seismic lines may decrease use of lines as travel corridors, but snow depth could differ across treatments according to motorized vehicle use, canopy cover or line vegetation (Droghini & Boutin, 2017; Storck, Lettenmaier, & Bolton, 2002). More data may be required to overcome model convergence issues, permitting this line of inquiry in the future.

2.5.6 Implications

Site preparation and planting provided few direct benefits to caribou over the short term. However, the greater benefit over the long-term is the restoration of landscape functionality (Shackelford et al., 2013), and deer responses to active restoration may indicate the beginning of this process. By deterring seismic line use by deer, site preparation and planting may re-establish spatial segregation between caribou and a key apparent competitor, thus reducing predation risk for caribou on restored lines over time. Although caribou predators did not show negative responses to restored lines in our study, these may emerge as fewer of their prey species are
found at those sites. We recommend that future studies should continue to monitor mammal responses over a longer period of vegetation regeneration, as well as relate seismic line treatments to animal movement rates and behaviour to assess specific mechanisms behind line use (e.g. Dickie et al., 2017; Finnegan et al., 2018). We also recommend comparisons of our results with those in other areas, such as those undergoing different types of restoration treatments, or having different landscape contexts (e.g. different habitats, levels of disturbance, or abundance of predators and prey). Ultimately, responses to restoration at the behavioural level must also translate into population-scale responses in caribou and their interacting species, thereby inducing changes in community-wide landscape use and re-establishing landscape function.

Differential responses to seismic line types also provides support for an integrated land management (ILM) approach to conservation on a working landscape, as outlined in Alberta’s draft range plan (Government of Alberta, 2017). ILM aims to balance conservation and industry values through strategic land use planning. This may include prioritizing restoration in preferred caribou habitat and areas of high restored line density while also consolidating industry access routes to reduce human influence on the landscape (Government of Alberta, 2017). If different line types are preferred by different species, seismic line treatment could be applied accordingly across a landscape to preserve areas of special concern for caribou. For example, site preparation and planting could be implemented in areas where caribou and white-tailed deer occurrences overlap to decrease apparent competition. If the trends observed in this study hold, this strategy shows potential for re-establishing spatial segregation between caribou, their competitors and predators. However, we call for further research to explore which scale of application would best balance human access, caribou habitat needs and predator movement. Integrated land
management may allow for caribou coexistence alongside predators and competitors, but only if sufficient caribou habitat is available (through restoration or conservation). Finding a balance between industry access and habitat protection should be a priority in future studies. In addition, currently the draft range plan focuses predominantly on linear corridors, as they are the most prevalent feature type. A more comprehensive view should account for the cumulative impact of all anthropogenic disturbances on the landscape (Fisher & Burton, 2018; Neilson & Boutin, 2017), and how strategic habitat restoration might mitigate effects on caribou and the rest of the boreal mammal community.

Our study is an early demonstration of using camera traps to monitor wildlife responses to habitat restoration. This tool provides the unique opportunity to assess community-wide influences of anthropogenic disturbance and associated mitigations (Fisher & Burton, 2018; Steenweg et al., 2017), which should ultimately improve conservation efficacy. Rather than studying single species, or a single predator-prey interaction in isolation, monitoring multiple species considers the broader ecological context within which focal species fit. Multi-species studies are useful for identifying patterns and assessing general effects of landscape change, exposing both direct and indirect relationships between community members (Caravaggi et al., 2017). Not only is this valuable for taking a bigger picture approach to species conservation, but it also sheds light on interspecific relationships that have thus far been overlooked.

2.5.7 Conclusion

The status of the Alberta woodland caribou is dire, with some predicting critical population sizes (fewer than 10 individuals), or extirpations, within the next 20 years if current trends continue (Schneider, Hauer, Adamowicz, & Boutin, 2010). Habitat restoration is a key component of caribou conservation (Environment and Climate Change Canada, 2017), but
wildlife responses need to be monitored to ensure efficacy (Bentham & Coupal, 2015; Pyper et al., 2014). At early stages, large boreal mammals are showing some, but not all of the desired responses to habitat restoration; thus continued monitoring is necessary to see if current trends in mammal responses continue, strengthen and ultimately lead to positive change for caribou populations. Further, camera trap monitoring could be extended to other caribou populations and different landscapes to assess how pervasive observed responses are across Alberta. Boreal habitat regeneration is a long-term goal; therefore, coordinated conservation strategies may need to be applied to sustain herds in the interim. However, restoration of legacy disturbances conserves the boreal ecosystem as a whole, and may provide auxiliary benefits to numerous at-risk species. Through mitigation of persistent land transformation and active landscape planning, healthy and sustainable ecosystems may be able to coexist alongside conscientious human development on the boreal landscape.
Chapter 3: Exploring spatiotemporal relationships as evidence of interspecific interactions between boreal predators in northern Alberta

3.1 Introduction

3.1.1 Interspecific interactions in a human world

Interspecific interactions are an integral aspect of ecosystem function, as they influence both population dynamics of interacting species and community-level responses to change (MacMahon et al., 1978). Classic ecology theory describes two broad types of interactions: facilitation – in which one species benefits from another (Bertness & Callaway, 1994; Bruno, Stachowicz, & Bertness, 2003) – or competition – in which one species dominates another (Alley, 1982; Schoener, 1974). Although consequences for interacting species vary, both facilitation and competition can influence resource availability (Bruno et al., 2003; Wiens, 1993) and abiotic conditions (Stachowicz, 2001; Tilman, 1994). In these ways, interspecific interactions help determine the circumstances under which species survive and persist, thus serving a critical function in structuring biological communities (MacMahon et al., 1978). Maintaining these interactions is therefore vital to protecting these communities in an increasingly anthropocentric world (Valiente-Banuet et al., 2015).

As humans continue to shape the planet to meet our resources demands, we induce irreversible changes to the relationships underlying ecological stability (MacDougall, McCann, Gellner, & Turkington, 2013; WWF, 2018). Biodiversity loss, such as declines in apex predator populations, alter top-down processes that keep communities in check (Kuijper et al., 2016; Ripple et al., 2014). Further, human landscape change alters large mammal movement behaviours, decreasing distances travelled and thus potentially reducing the total area within which species interact (Tucker et al., 2018). Anthropic disturbance also creates more favourable environments for generalist species, contributing to widespread invasions that upset
relationships between endemic species (Baskin, 1998). As these ongoing changes affect community composition and species-environment relationships, a key question for ecologists is how interspecific interactions respond to disturbance to influence communities in human-dominated landscapes.

3.1.2 Predator coexistence in the boreal context

In Canada’s boreal forest, anthropogenic landscape change is primarily a consequence of natural resource extraction, forming a heterogeneous working landscape shared between industry and wildlife (Kremen & Merenlander, 2018). Logging alone has an area-footprint of approximately 15 million hectares across the boreal forest, while energy development has created over half a million kilometres of linear corridors stretching across vast expanses of Canada’s north (Pasher et al., 2013). In particular, seismic lines – wide trails cut for seismic exploration of oil reserves – contribute to habitat fragmentation and thus alter landscape connectivity (Pattison et al., 2016). The cumulative effects of these extensive industrial footprints impact the distribution and abundance of a number of boreal mammals, though the strength and nature of influence vary by species (Fisher & Burton, 2018; Toews, Juanes, & Burton, 2018). Changes in individual species can in turn affect interactions among species, leading to broader indirect effects in boreal ecosystems.

In northeastern Alberta, where industrial development has the highest impact (Pickell et al., 2015), the significance of changes to interspecific interactions are best illustrated by effects on predator-prey dynamics related to the conservation of woodland caribou (Rangifer tarandus caribou), a high profile species at risk in Canada (Boutin et al., 2012; Hebblewhite, 2017). Caribou declines are largely blamed on changes in grey wolf (Canis lupus) spatial ecology, as seismic line networks facilitate movement for this apex predator by increasing their speed and
distance travelled across challenging boreal wetland terrain (Dickie et al., 2016). Wolf adaptation to the human-modified landscape has been documented to affect predator-prey dynamics between wolves and caribou by increasing caribou predation rates (James, Boutin, Hebert, & Rippin, 2004; Whittington et al., 2011). Although this interaction creates dire circumstances for an iconic Canadian species, caribou declines are just one example of interspecific interactions changing as a result of anthropogenic disturbance. We know relatively little about how other boreal mammal species use linear networks (but see Tigner et al., 2014; Tigner, Bayne, & Boutin, 2015; Toews et al., 2018). Further, these responses to industrialization of the boreal may indirectly influence interspecific interactions, of which we know less about (Burgar et al., 2018). For a more comprehensive understanding of how landscape change impacts the boreal mammal community, it is thus imperative to investigate how additional community dynamics operate on these working landscapes.

In particular, the interactions between wolves and other predators in industrializing boreal landscapes are poorly known. In addition to wolves, northeastern Alberta is home to a number of large and medium bodied predators. Black bears (*Ursus americanus*), coyotes (*Canis latrans*), and Canada lynx (*Lynx canadensis*) are all commonly detected in the Algar study area (Fig. A2.1). In the last 100 years, coyotes (*Canis latrans*) have expanded their ranges further north and now persist in the boreal forest in part due to increasing human development (Hody & Kays, 2018). Like wolves, evidence suggests that black bears prefer linear corridors for ease of travel (Latham, Latham, & Boyce, 2011; Tigner, Bayne, & Boutin, 2014), and lynx also show an affinity for certain linear features (Fisher & Burton, 2018). Therefore, each of these predators responds individually to living within a working landscape, but we do not know if this in turn influences the interactions between them. Specifically, we do not know if changes to wolf spatial
ecology induce subsequent responses from black bears, coyotes, and lynx. This gap in our knowledge of community dynamics in the boreal forest limits our ability to document, predict, or mitigate consequences of landscape change on boreal mammals.

As the apex predator, wolves may exert top-down influences on non-apex boreal predators that regulates how they use the landscape (Estes et al., 2011). Wolves are commonly regarded as dominant over black bears, coyotes, and lynx in direct confrontation, suggesting that these subordinate predators would seek to avoid encounters with wolves (Palomares & Caro, 1999). Indeed, Fuller & Keith (1981) found that coyotes in northeastern Alberta spatially segregated their home ranges from wolf territories. However, predators also benefit from scavenging subsidies proffered by wolf kills, and may thus have a facilitative interaction with wolves. Such relationships have been well-documented for sympatric coyotes and wolves elsewhere in North America (Atwood & Gese, 2008, 2010; Paquet, 1992), and proposed for black bears based on their scavenging behaviours (Allen, Elbroch, Wilmers, & Wittmer, 2014; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003). In addition, some mesocarnivores may indirectly profit from wolves via suppression of competitors, as demonstrated for red foxes (*Vulpes vulpes*; Levi & Wilmers, 2012; Sivy, Pozzanghera, Colson, Mumma, & Prugh, 2018) and suggested for lynx (Ripple, Wirsing, Beschta, & Buskirk, 2011).

Outside of top-down apex predator effects, black bears, coyotes, and lynx may experience horizontal influences from intraguild competition, or bottom-up influences from predation opportunities. Although there is little evidence in the literature of intraguild competition between black bears and other subordinate predators, competition between coyotes and lynx has been insinuated in areas of human disturbance (Bayne, Boutin, & Moses, 2008) and may influence habitat selection (Murray et al., 1994). Further, all three subordinate predators
may respond to predator-prey interactions. Black bears are opportunistic predators whose diet mainly consists of vegetation, but they have also been known to hunt boreal ungulates (Brodeur et al., 2008; Linnell, Aanes, & Andersen, 1995). Both coyotes and lynx in northern Alberta hunt small mammals such as red squirrels (*Tamiasciurus hudsonicus*) and snowshoe hare (*Lepus americanus*), and coyotes have also been known to hunt white-tailed deer (Latham et al., 2013; O’Donoghue et al., 2001). Of all types of interspecific interactions, none are necessarily mutually exclusive, and may happen simultaneously within the same systems, including across separate spatial or temporal scales (Karanth et al., 2017; Sivy, Pozzanghera, Grace, & Prugh, 2017).

Due to the complexity of studying interspecific interactions, classic research of interspecific interactions commonly involves experimental manipulations in laboratory settings, using plant communities or invertebrate species (Bertness & Callaway, 1994; Goldberg & Barton, 2011). For large mammal species ranging across entire landscapes, interspecific interactions are difficult to quantify in the field without extensive survey effort. Nevertheless, in lieu of direct observations of interactions, they can be inferred using spatiotemporal relationships of species occurrences (Cusack et al., 2016; Karanth et al., 2017; Swanson, Arnold, Kosmala, Forester, & Packer, 2016). An important caveat to this work is that correlation is not equivalent to causality – spatiotemporal segregation or overlap does not directly indicate interspecific interactions. However, examining these associations reveals whether patterns in predator occurrences are consistent with those predicted from interspecific interactions, thus providing motivation for further inquiry into process behind the observations.
3.2 Objectives and Hypotheses

In this chapter, I investigated how boreal predators interact on a working landscape by assessing spatiotemporal associations. To do so, I examined predator occurrences within a network of linear anthropogenic features, looking at how predators use linear features relative to each other as evidence of the interspecific interactions governing predator use of these modified landscapes. I focused on interactions between predators, especially those between apex predators – wolves – and subordinate predators – black bears, coyotes, and lynx. However, for a comparative assessment of interspecific interactions, I also included interactions between mesocarnivores (coyotes and lynx), as well as predator-prey interactions for all three non-apex predators.

I focused on black bears, coyotes, and lynx because little is currently known about how boreal predators coexist, particularly how these three predators are affected by apex predator spatial ecology in human-modified landscapes. I hypothesized that if black bears, lynx, and coyotes experience top-down pressures from apex predators, their occurrences should either segregate from or overlap with occurrences of wolves. Alternatively, other interspecific interactions may be stronger influences on predator occurrences. Predators should overlap with their prey (Keim, DeWitt, & Lele, 2011; Theuerkauf, 2009) or segregate from their intraguild competitors with whom they share resources (Guillaumet, Bowman, Thornton, & Murray, 2015; O’Donoghue et al., 2001). To test these hypotheses, I also tested whether black bear, coyote, and lynx occurrences are influenced by prey occurrences, as well as whether coyotes and lynx exhibit spatiotemporal relationships with one another (Table 3.1). I found little supporting evidence in the literature for interactions between black bears and other non-apex predators, therefore I excluded these interactions from my analyses.
Three major co-occurrence patterns may arise from interspecific interactions: spatial segregation, spatial overlap with temporal segregation, or spatiotemporal overlap (Cusack et al., 2016; Karanth et al., 2017). For interactions between predators, I assumed spatial segregation of occurrences was indicative of a response to competition, and that spatial overlap was indicative of facilitation. However, interspecific interactions can occur over temporal scales as well (Fahrig, 1992; Frey et al., 2017), and spatial overlap alone is not strong evidence for facilitation. Therefore, to address multiple potential scales of interspecific interactions over the course of my sampling period, I examined predator co-occurrences at the spatial-only scale (i.e. entire 30-month survey) and at two finer spatiotemporal scales (weekly and daily). I assumed that overlap at finer spatiotemporal scales – where species co-occur in a given location within a given occasion length – suggested intentional proximity between two species, and thus was evidence of a facilitative interaction (Cusack et al., 2016; Swanson et al., 2016). Further, I suggested that the spatiotemporal scale at which an interaction manifested was indicative of the strength of interaction. I predicted that spatial segregation was indicative of strong competition (Fuller & Keith, 1981), whereas spatial overlap alone indicated weak or indirect interactions. I hypothesized that spatiotemporal segregation at fine temporal scales indicated weak competition, or avoidance of direct conflict, and that fine spatiotemporal overlap indicated strong facilitation without fear of direct conflict (Swanson et al., 2016). Finally I predicted that patterns occurring at coarse spatiotemporal scales would be consistent with a combination of both facilitation and competition, where the direction of response indicated the stronger interaction (Atwood & Gese, 2008, 2010).

In addition, I hypothesized that the strength of interspecific interactions may vary with anthropogenic disturbance and season. Both influences alter predator space use, which in turn
could affect interspecific relationships (Pozzanghera, Sivy, Lindberg & Prugh, 2016; Smith, Thomas, Levi, Wang, & Wilmers, 2018; Fraser, 2018). To address this, I further compared the effects of interspecific interactions on predator occurrences with the effects of season and anthropogenic disturbance, allowing for interactions between the two (Table 3.1).

3.3 Methods

3.3.1 Analytical overview

To examine the effects of interspecific interactions on boreal predators, I used camera trap data from the Algar study area to assess occurrences of black bears, coyotes, and lynx as a function of hypothesized interspecific interactions. We deployed camera traps along seismic lines; therefore all species’ occurrences indicate species’ presence on a seismic line. I used the full 30-month survey period between November 2015 and April 2018 for coyotes and lynx, and the two summer periods between April–October 2016 and 2017 for black bears. At each spatiotemporal scale, and for each species, I conducted a two-step analysis in which I first estimated relationships between predators and their habitat (specifically, proportions of major forest types). I then controlled for these habitat relationships and tested the strength and direction of the hypothesized interspecific interactions (Table 3.1). I conducted all statistical analyses using the R package glmmTMB (Brooks, Kristensen, & Benthem, 2017).

3.3.2 Three scales of analysis

3.3.2.1 Spatial relationships in species occurrences

To examine spatial relationships, I tested the degree to which spatial variation in relative abundance of a given species across the entire survey was explained by the abundance of potentially interacting species, using number of detections (events at least 30 minutes apart) per site as the response variable. I included each camera’s survey effort (number of days active) as a
predictor variable, thus accounting for the effect of camera inactivity on detections. This explanatory variable was the only fixed effect in the null model and excluded from comparisons of effect size. I modelled detections in a generalized linear model (GLM) framework using a negative binomial distribution for over-dispersed count variables (Bolker, 2009).

3.3.2.2 Fine and coarse spatiotemporal scales of occurrence

To test whether species co-occurring in space were also co-occurring in time, I examined co-occurrences at two temporal scales. At the finest temporal scale, I recorded the presence (1) or absence (0) of a species’ at a given site within a single day, producing a binary occurrence metric for each camera trap day. Although methods exist for finer scale temporal niche partitioning, these analyses require large amounts of detection data (Frey et al., 2017; Swanson et al., 2016; Wang, Allen, & Wilmers, 2015). The northern boreal forests are characterized by relatively low productivity, which translates into lower mammalian abundances and thus lower detection rates. Given such data limitations, I determined that a daily occasion length was therefore the finest temporal scale at which we could detect ecologically significant relationships. However, a single day occasion length results in low detection probabilities, leading to zero-inflated occurrence data (Rovero & Zimmerman, 2016). I therefore also measured occurrence at the coarser temporal scale of a week to assess whether results were consistent across scales. Predators have the ability to indirectly communicate over extended temporal periods through scent marking (Paquet, 1991a; Peters & Mech, 1975), therefore co-occurrences within a week of each other could also indicate a meaningful interaction. For both spatiotemporal scales of influence, I modelled occurrences using binomial generalized linear mixed effects models (GLMMs; Cusack et al., 2016). I included a random effect of site to account for repeated sampling by each camera station across multiple occasions. To account for
camera inactive periods, I omitted inactive days from the daily occurrence analysis and included a predictor variable for camera activity (proportion of active days per week) in the weekly occurrence analysis.

3.3.3 Modelling approach

For all three spatiotemporal scales of analysis, I analyzed data using a two-step process: habitat modelling followed by co-occurrence modelling (Cusack et al., 2016; Fraser, 2018). Dividing the analysis into two steps served the dual purposes of testing species’ interactions against null models that already included predator-habitat relationships and determining the best spatial scales to measure habitat variables. In this way, I control for the effect of habitat when modelling effects of species’ co-occurrences, thus reducing residual variance.

3.3.3.1 Habitat modelling and scale analysis

In the first step of the modelling process, I assessed the influence of both habitat and scale on predator occurrences by conducting a multi-variate scale analysis. Ecological processes can occur at multiple scales (Bowyer & Kie, 2006; Fisher et al., 2011; Levin, 1992), and though the mechanism linking spatial pattern and ecological process can often be difficult to determine, spatial scale of measurement can have significant consequences for the perceived species-environment relationship (Fahrig, 1992; McGarigal et al., 2016). To account for scale effects, I compared multivariate habitat models at multiple spatial scales, using AIC model selection to determine the optimal scale of influence (Fisher et al., 2011; Fig. A4.1a).

Each habitat model consisted of six variables describing forest cover types predicted to have an effect on predator occurrence (Poole, Wakelyn, & Nicklen, 1996; Latham, Latham, Boyce, & Boutin, 2013; Tigner, Bayne, & Boutin, 2014). To create each variable, I combined dominant tree species and moisture regime to create five predictors describing proportions of
forest types in the Algar area (Table 3.1; Fisher & Burton, 2018). Additionally, I included a covariate for the proportion of open forest as a measure of forest density (Murray, Boutin, & O’Donoghue, 1994). For the scale analysis, I chose to measure forest cover variables across a range of scales between 250-2000m surrounding camera stations, at intervals of 250m, to reflect species’ responses to habitat characteristics at local and broader scales. This resulted in eight models, consisting of six habitat variables measured at eight spatial scales. Next, I compared these models using AIC model selection and included the scale and significant habitat variables of the best-supported (lowest ΔAIC) model in the subsequent stage of modelling co-occurrences (Fig. A4.1a and Fig. A4.2). I extracted all spatial variables using the R packages rgeos and rgdal (Bivand & Rundel, 2018; Bivand, Keitt, & Rowlingson, 2018).

### 3.3.3.2 Co-detection modelling

In the second step of the modelling process, I investigated whether hypothesized species interactions had effects on predator occurrences that were in addition to the effects of habitat (Fraser, 2018). To do this, I created a model set for each of the interactions hypothesized to influence black bears, coyotes and lynx: top-down influences from wolves, bottom-up influences from prey species, or horizontal influences of lynx and coyotes on each other. I excluded models assessing interspecific interactions between black bears and coyotes or lynx because I found no supporting evidence for these interactions in the literature (Table 3.2). To assess influences of prey, I included a variable aggregating detections of all prey species for each of the target predators (Table 3.1). As I further predicted that the strength of interspecific interactions could be influenced by season and level of anthropogenic disturbances, I also include additive and interaction models with variables for snow presence and linear density (Table 3.2). Linear features are the most prevalent anthropogenic disturbance within the study area; therefore I
considered the effects of other anthropogenic features to be negligible. I tested all co-occurrence models against three null models: one with only habitat variables, one with snow presence and habitat, and one with linear density and habitat (considered null models because I am only interested in the additive or interactive effects of these variables, not in their effects alone). Because black bears are inactive in the winter, I only included season in model sets for lynx and coyotes. At the spatial scale, I excluded season from the analysis for all species because the response variable aggregated detections across the entire survey period.

I assessed snow presence from daily ‘time-lapse’ images, using the camera trapping software Timelapse 2.0 Image Analyzer (Greenberg & Godin, 2015; http://saul.cpsc.ucalgary.ca/timelapse). Snow was measured as a binary variable at the daily scale and a proportion at the weekly scale (i.e. mean number of days on which snow was present, Table 3.1). I considered snow to be present if it covered over 50% of the line surface within the camera’s field of view. As with forest cover variables, I conducted a scale analysis to obtain appropriate scales of measurement for linear density for each species (Fig. A4.1b). I used data exploration techniques prior to modelling to assess predictor variables for outliers, collinearities, and heterogeneity of variance (Zuur et al., 2010). I also scaled all non-binary variables by subtracting the mean and dividing by two standard deviations, thus improving model convergence and interpretation (Gelman, 2008).

3.3.4 Model interpretation

Following co-occurrence modelling, I compared candidate models using AIC model selection to determine whether interspecific interactions influenced predator occurrences at each of the three spatiotemporal scales. I considered all models within 2ΔAIC of the top-ranked model as having explanatory power over the data (Burnham & Anderson, 2002), and consequently
examined variables in these models for their influence on predator occurrence. I assessed statistically significant parameter estimates as measures of effect size and strength. Where models from competing model sets had less than 2ΔAIC, I assessed both species’ occurrence predictor variables for their effects and used the higher ranked model for the effects of additional variables (Table 3.2). Finally, I validated all top models by graphically examining residual variance for deviance from predicted values, using the R package DHARMa (Hartig, 2018).
Table 3.2: Full list of predictor variables used to model occurrence patterns of black bears, lynx, and coyotes. For each species, I included all habitat variables in the first step of the modelling process, and retained significant habitat variables (p < 0.05) to create a null model for the second step. I measured forest cover variables from the Alberta Vegetation Inventory (Alberta Vegetation Interpretation Standards, 2005), and linear feature data from the Alberta Biodiversity Monitoring Institute (ABMI, unpublished). I used camera trap data to extract all species occurrence and snow variables. Species variables with modelling scale, as spatiotemporal scale affected occasion length and thus occurrence aggregation.

<table>
<thead>
<tr>
<th>Predictor Variable</th>
<th>Step of modelling process</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>pOpen</td>
<td>1</td>
<td>Proportion of forest with &lt;50% density surrounding camera stations</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Proportion of forest with black spruce (Picea mariana), white spruce (Picea glauca), balsam fir (Abies balsamea), or jack pine (Pinus banksiana) as a dominant tree species and a dry or mesic moisture regime</td>
</tr>
<tr>
<td>UpCon</td>
<td>1</td>
<td>Proportion of forest with black spruce (Picea mariana), white spruce (Picea glauca), balsam fir (Abies balsamea), or jack pine (Pinus banksiana) as a dominant tree species and a wet or aquatic moisture regime</td>
</tr>
<tr>
<td>LowCon</td>
<td>1</td>
<td>Proportion of forest with trembling aspen (Populus tremuloides), balsam poplar (Populus balsamifera), or paper birch (Betula papyrifera) as a dominant tree species and a dry or mesic moisture regime</td>
</tr>
<tr>
<td>UpDecid</td>
<td>1</td>
<td>Proportion of forest with trembling aspen (Populus tremuloides), balsam poplar (Populus balsamifera), or paper birch (Betula papyrifera) as a dominant tree species and a wet or aquatic moisture regime</td>
</tr>
<tr>
<td>LowDecid</td>
<td>1</td>
<td>Proportion of forest with trembling aspen (Populus tremuloides), balsam poplar (Populus balsamifera), or paper birch (Betula papyrifera) as a dominant tree species and a dry or mesic moisture regime</td>
</tr>
<tr>
<td>Tamarack</td>
<td>1</td>
<td>Proportion of forest with Tamarack (Larix laricina) as a dominant tree species</td>
</tr>
<tr>
<td>Wolf</td>
<td>2</td>
<td>Binary presence (1)/ absence (0) of wolves per site per day or week; number of detections of wolves per site</td>
</tr>
<tr>
<td>Lynx</td>
<td>2</td>
<td>Binary presence (1)/ absence (0) of lynx per site per day or week; number of detections of lynx per site</td>
</tr>
<tr>
<td>Coyote</td>
<td>2</td>
<td>Binary presence (1)/ absence (0) of coyotes per site per day or week; number of detections of coyotes per site</td>
</tr>
<tr>
<td>Prey</td>
<td>2</td>
<td>Binary presence (1)/ absence (0) of prey species(^1) per site per day or week; number of detections of prey per site.</td>
</tr>
<tr>
<td>LD</td>
<td>2</td>
<td>Linear density measured as total length of linear features divided by a given area surrounding camera stations</td>
</tr>
<tr>
<td>Snow</td>
<td>2</td>
<td>Binary presence (1)/ absence (0) of snow per site per day, or number of snow days/ total days in a weekly sampling period. We marked snow as ‘present’ in daily time-lapse images if it covered 50% of the seismic line surface within the camera’s field of view</td>
</tr>
</tbody>
</table>

\(^1\) Prey species consisted of snowshoe hare (Lepus americanus) and red squirrel (Tamiasciurus hudsonicus) for lynx; hare, squirrel, and white-tailed deer (Odocoileus virginianus) for coyotes; and deer, moose (Alces alces), and caribou (Rangifer tarandus) for black bears (Latham et al., 2013; Zager & Beecham, 2006; Linnell, Aanes, & Andersen, 1995; O’Donoghue et al., 2001)
Table 3.2: Candidate model sets to test the relative effect of interspecific interactions on predator occurrences. Models were negative binomial GLMs at the spatial scale, and binomial GLMMs at the two spatiotemporal scales. Each model set corresponds to a hypothesized interspecific interaction. I tested models with a co-occurring species as a covariate against three null models describing environmental effects. Candidate model sets for mesocarnivores (coyote and lynx) are identical, with mesocarnivore 1 describing the responding predator and mesocarnivore 2 describing the co-occurring intraguild competitor (ex. when mesocarnivore 1 is coyote, mesocarnivore 2 is lynx and vice versa).

<table>
<thead>
<tr>
<th>Species</th>
<th>Hypothesis - Predator occurrence best explained by:</th>
<th>Predictor variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Habitat</td>
<td>Significant forest cover variables from step 1</td>
</tr>
<tr>
<td></td>
<td>Anthropogenic features</td>
<td>Linear density (LD) + Habitat</td>
</tr>
<tr>
<td></td>
<td>Seasonality</td>
<td>Snow + Habitat</td>
</tr>
<tr>
<td>Mesocarnivore 1</td>
<td>Apex predator</td>
<td>Wolf + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wolf + Snow + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wolf * Snow + Habitat</td>
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<tr>
<td></td>
<td></td>
<td>Wolf + LD + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wolf * LD + Habitat</td>
</tr>
<tr>
<td></td>
<td>Intraguild competition</td>
<td>Mesocarnivore2 + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesocarnivore2 + Snow + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesocarnivore2 * Snow + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesocarnivore2 + LD + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesocarnivore2 * LD + Habitat</td>
</tr>
<tr>
<td></td>
<td>Predation opportunities</td>
<td>Prey + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prey + Snow + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prey * Snow + Habitat</td>
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<tr>
<td></td>
<td></td>
<td>Prey + LD + Habitat</td>
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<tr>
<td></td>
<td></td>
<td>Prey * LD + Habitat</td>
</tr>
<tr>
<td>Black bear</td>
<td>Habitat</td>
<td>Significant forest cover variables from step 1</td>
</tr>
<tr>
<td></td>
<td>Apex predator</td>
<td>Wolf + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wolf + LD + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wolf * LD + Habitat</td>
</tr>
<tr>
<td></td>
<td>Predation opportunities</td>
<td>Prey + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prey + LD + Habitat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prey * LD + Habitat</td>
</tr>
</tbody>
</table>
3.4 Results

Of the focal boreal predator species, black bears and wolves were detected most frequently (n = 360 and n = 334, respectively), coyotes were detected at intermediate levels (n = 154), and lynx were detected least frequently (n = 73, Table 3.3). Camera traps sampled black bear occurrences for a total of 13,984 camera-days during their active season, whereas lynx and coyotes were sampled for 32,395 camera-days year-round. At the daily spatiotemporal scale, both coyotes and lynx experienced very low co-occurrences with interacting species (n = 1 and 2), and lynx experienced low co-occurrences with their prey at the weekly scale as well (n = 2; Table 3.3).

3.4.1 Interspecific interactions affect occurrences of all three predators

Modelling results indicated that species interactions were significant predictors of all three predators’ occurrences. After accounting for habitat and anthropogenic effects, wolves had a positive association with all three target predator species on at least one spatiotemporal scale. This effect was most consistently seen for black bears, which significantly co-occurred with wolves even at the daily scale (0.803 ± 0.297, p < 0.01, Fig. 3.1). Coyotes co-occurred with wolves at the weekly scale (0.855 ± 0.348, p = 0.014), but not at the spatial or daily scales (Fig. 3.1). Lynx, on the other hand, only co-occurred with wolves at the spatial scale (0.484 ± 0.212, p = 0.022), not on finer spatiotemporal scales (Fig. 3.1). Although models including interactions between wolf and linear density and wolf and season were included among top-ranked models for all three species on at least one scale, none of these interactions were significant (Table 3.4).

Lynx occurrences increased with those of their prey at both the spatial and weekly-occurrence scale, but the main effect of prey was only significant at the spatial scale (0.822 ± 0.365, p = 0.024). However, when both prey and linear density increased, lynx occurrences
decreased at both scales (-1.204 ± 0.432, p < 0.01 at the spatial scale and -3.327 ± 1.469, p = 0.023 at the weekly scale; Fig. 3.1). Prey was among the variables included in the top-ranked models for coyotes at the spatial scale, but the estimated effect was not statistically significant. Black bears were not affected by prey occurrences at any scale (Table 3.4).

Interactions between mesocarnivores were not strong predictors for either coyotes or lynx. For coyotes, lynx models were included among top-ranked models at all scales, but neither main effects nor season and linear density interactions were significant predictors. The same was true for lynx, although coyote occurrences only helped explain lynx occurrences at the daily scale (Table 3.4). In both top-ranked models for coyotes and lynx at the daily scale, standard errors around the estimates for interacting species were over three orders of magnitude larger than the estimates (-15.730 ± 4199.856 for the top coyote model, -15.763 ± 5023.058 for the top lynx model), and patterns in the model residuals indicated model misspecification. I therefore removed these models from all subsequent analyses.

3.4.2 Predator occurrences affected by anthropogenic disturbance, but not season

All three predators responded to linear density on at least two scales, but the direction and scale of influence differed across species. Black bear occurrences decreased with linear density at both the weekly and the daily scale (-0.737 ± 0.305, p = 0.016 and -0.720 ± 0.322, p = 0.026, respectively; Fig. 3.1). Conversely, both coyote and lynx occurrences increased with linear density at the spatial and weekly scales (2.517 ± 0.438, p < 0.01 and 2.210 ± 0.455, p < 0.01 for coyotes; 0.832 ± 0.0.315, p < 0.01 and 0.993 ± 0.363, p <0.01 for lynx; Fig. 3.1). The optimal spatial scale of measurement for linear density was comparable for all three species (1500m for black bears and coyotes, 1750m for lynx), and remained constant at all three spatiotemporal
scales of analysis (Fig. A4.1b). Season helped explain coyote and lynx occurrences at the daily scale, but did not significantly affect either species as a main or interaction effect (Table 3.3).

3.4.3 Habitat: fewer occurrences with open forest

Excluding effects of interspecific interactions, all three predators significantly decreased occurrences as the proportion of open forest increased on all three spatiotemporal scales of analysis (Fig. A4.2). This significant habitat relationship was retained at all spatiotemporal scales with the inclusion of species’ interactions for black bears and lynx, and at the weekly and daily scales for coyotes (Fig. 3.1). Additionally, lynx occurrences increased with proportions of lowland and upland coniferous forest at all three scales prior to adding interspecific interactions. After inclusion, lynx retained the positive relationship with lowland coniferous forest at all scales and the relationship with upland coniferous forest at the weekly scale (Fig. A4.2c). Optimal spatial scales of measurement for habitat were lowest for black bears (250m) and highest for coyotes and lynx (1750m and 1500m, respectively). As with spatial scales for linear density, optimal scales for each species remained constant across all spatiotemporal scales of analysis.
Table 3.3: Total co-occurrences of predator species across three spatiotemporal scales of analysis. Each value represents the total number of times both species were present at the same site and – for weekly and daily scales – within the same occasion. Rows represent response variables and columns represent predictor variables. The total occurrences of wolves is given both within the summer-only sampling period for black bears (13 984 site-days) and the full sampling period for coyotes and lynx (32 395 site-days). Cells are marked with a dash where no interactions were hypothesized or tested.

<table>
<thead>
<tr>
<th>Spatiotemporal scale</th>
<th>Wolf</th>
<th>Prey</th>
<th>Black bear</th>
<th>Lynx</th>
<th>Coyote</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black bear</td>
<td>15</td>
<td>16</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lynx</td>
<td>2</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Coyote</td>
<td>2</td>
<td>8</td>
<td>-</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>179/295</td>
<td>-</td>
<td>315</td>
<td>71</td>
<td>131</td>
</tr>
<tr>
<td>Week</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black bear</td>
<td>33</td>
<td>55</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lynx</td>
<td>5</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Coyote</td>
<td>15</td>
<td>22</td>
<td>-</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>124/224</td>
<td>-</td>
<td>226</td>
<td>67</td>
<td>106</td>
</tr>
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<td>Spatial</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Black bear</td>
<td>38</td>
<td>43</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lynx</td>
<td>23</td>
<td>18</td>
<td>-</td>
<td>-</td>
<td>17</td>
</tr>
<tr>
<td>Coyote</td>
<td>21</td>
<td>18</td>
<td>-</td>
<td>-</td>
<td>17</td>
</tr>
<tr>
<td>Total occupied sites</td>
<td>46</td>
<td>-</td>
<td>44</td>
<td>27</td>
<td>23</td>
</tr>
<tr>
<td>Total detections</td>
<td>334</td>
<td>-</td>
<td>360</td>
<td>73</td>
<td>154</td>
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Table 3.4 Model selection tables of models of top-ranked models for black bears, coyotes, and lynx. For each species, top-ranked models are shown for each of the three spatiotemporal scales of analysis. Top-ranked models were those within 2ΔAIC of the highest-weighted model. The column df is the degrees of freedom in the model, ΔAIC indicates the difference in AIC scores from the top model, and AICwt is the AIC weight attributed to that model. Cum.Wt is the cumulative model weight, and ER is the evidence ratio (AIC weight of top model/AIC weight of model).

<table>
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<tr>
<th>Species</th>
<th>Scale</th>
<th>Predictor Variables</th>
<th>df</th>
<th>ΔAIC</th>
<th>AICwt</th>
<th>Cum.Wt</th>
<th>ER</th>
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<td>Day</td>
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<td>0.510</td>
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<tr>
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<td>0.534</td>
<td>0.534</td>
<td></td>
</tr>
<tr>
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<td></td>
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<td>7</td>
<td>1.24</td>
<td>0.287</td>
<td>0.821</td>
<td></td>
</tr>
<tr>
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<td>0.569</td>
<td>0.569</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Wolf + LD + pOpen + UpCon</td>
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<td>1.24</td>
<td>0.196</td>
<td>0.779</td>
<td>1.900</td>
</tr>
<tr>
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<td>Day</td>
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<td>6</td>
<td>0.00</td>
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<td>Season + pOpen</td>
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<td>1.24</td>
<td>0.196</td>
<td>0.779</td>
<td>1.900</td>
</tr>
<tr>
<td></td>
<td>Week</td>
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<td>0.255</td>
<td>0.255</td>
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<td>0.200</td>
<td>0.200</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Season + pOpen + LowCon + UpCon</td>
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<td>0.193</td>
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<td>0.34</td>
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<td>1.186</td>
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<tr>
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<td>0.601</td>
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<td></td>
<td></td>
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<td>0.345</td>
<td>0.700</td>
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</table>
Figure 3.1 Effects of interspecific interactions and environmental features on predator occurrences. Effect sizes are shown as parameter estimates (mean ± standard error) from negative binomial GLMs (spatial level) and binomial GLMMs (weekly and daily levels) of black bear, coyote and lynx occurrences at three levels of analysis. Estimates are shown for every parameter occurring within the top-ranked models. Where parameters occurred in more than one model, I used the estimate from the top-ranked model of each model set. I omitted models with interactions at the daily level for coyotes and lynx because they resulted in large (10^3) standard errors around estimates. Instead, second-ranked models at the daily level are shown for coyotes and lynx. Estimates have not been back-transformed and therefore values are not directly interpretable in terms of predator occurrences.
3.5 Discussion

Industrial development has transformed the boreal forest into a novel landscape without a naturally-occurring equivalent (Pickell et al., 2015), setting a new stage on which boreal predators coexist. On the stage examined in our study, black bears, coyotes and lynx all exhibited positive relationships with wolves, suggesting that wolf spatial ecology may be a significant determinant of space use by subordinate predators in working landscapes (Fig. 3.1). These positive associations are consistent with facilitative interactions in which black bears, coyotes, and lynx all benefit from co-occurring with wolves. These spatiotemporal correlations among predators have potential implications for managing multi-predator communities on working landscapes, and additional studies to identify mechanisms underlying interspecific interactions – and their repercussions – will inform efforts to maintain healthy ecological interactions amidst human landscape change.

3.5.1 Facilitative interactions between wolves, black bears and coyotes

While the direct and indirect effects of wolves on many other species have been widely studied, my study provides new insights into fine scale spatiotemporal relationships between wolves and black bears (Fig. 3.1). Both species occur at high densities in the boreal forest (Burgar et al., 2018), and both prefer to use industrial linear features for easy travel, making them likely candidates for strong interspecific interactions in industrializing landscapes (Latham et al., 2011a; Latham et al., 2011b). Although anecdotal evidence describes aggressive interactions between individual wolves and bears (Palomares & Caro, 1999; Rogers & Mech, 1981), I propose that spatiotemporal overlap at the daily scale is indicative of a facilitative interaction between the two large predators. Black bears were more likely to occur at a site even within a day of wolf occurrences, mirroring the spatiotemporal patterns seen between species
scavenging from lion kills in African mammal communities (Cusack et al., 2016; Swanson et al., 2016). Black bears are adept scavengers, and may benefit considerably from carrion subsidies left by wolves (Allen et al., 2014; Wilmers et al., 2003). Further, differences in wolf and black bear niches should mitigate competitive pressures between them, making competition an unlikely cause for the positive relationship. Black bears are primarily opportunistic predators that select habitat for vegetative foraging resources, rather than predation opportunities (Latham et al., 2011b; Mosnier, Ouellet, & Courtois, 2008), which would decrease niche overlap between black bears and wolves. Nevertheless, facilitation does not exclude the possibility of competition; it is possible, for example, that black bears benefit from scavenging kills but compete with wolves when in direct conflict (e.g. Palomares & Caro, 1999; Swanson et al., 2016). Additionally, interspecific interactions occur at scales much finer than those assessed in this study. Further research should explore time elapsed between predator occurrences or analyze patterns in occurrences (i.e. which species occurs first) to observe these relationships at a higher resolution (Schliep, Gelfand, Clark, & Kays, 2018; Swanson et al., 2016).

I further propose that the positive association between coyotes and wolves at coarse spatiotemporal scales is also a result of facilitation (Fig. 3.1). Coyote-wolf interactions have been extensively studied elsewhere in North America; in some cases, these depicted similar spatiotemporal relationships to those recorded here (Sivy et al., 2017) whereas others observed coyotes following wolf tracks (Paquet, 1991b) and scavenging wolf kills (Atwood & Gese, 2008, 2010; Paquet, 1992). However, as sympatric canid species with considerable niche overlap, coyotes and wolves are also likely to experience strong competition in which wolves frequently kill coyotes (Palomares & Caro, 1999; Paquet, 1991b). Fuller & Keith (1981) predicted that this competition produced the spatial segregation observed in their study, which our findings do not
support. Instead, I suggest that this discrepancy may be due to density-dependence of the wolf-coyote interaction: where coyotes exist in low densities, they segregate themselves from wolves to reduce competition. However, when coyotes exist in high densities, they may be able to reduce competition through behavioral mitigations such as increased group size or fine-scale temporal partitioning, thus increasing the benefits of scavenging (Atwood & Gese, 2008, 2010). Fuller & Keith (1981) previously estimated coyote density in northeastern Alberta to be similar to wolf density at approximately 0.84 coyotes per 100 km$^2$. Coyote density was recently estimated to be 2.64 animals per 100 km$^2$ in an area south of our Algar study area, suggesting increasing coyote numbers (Burgar et al., 2018). However, in this study we had greater wolf detections than coyotes, indicating lower coyote relative abundance. Coyotes in Algar may therefore be unable to mitigate wolf competition with high density, and thus avoiding direct competition but benefitting indirectly via scavenging. This would be consistent with the observed co-occurrence at the weekly scale and lack thereof at the daily scale. However, as I did not observe segregation at the daily scale either, this hypothesis requires further inquiry.

3.5.2 Lynx choose sites with high abundance of wolves and prey

Across the entire study period, lynx were also more commonly detected at sites with more wolf detections. However, contrary to black bears and wolves, lynx did not co-occur with wolves at the weekly or daily scales (Fig. 3.1). This suggests that although lynx share a landscape with wolves, they do not directly benefit from co-occurrence at finer temporal scales. Instead, lynx may indirectly benefit from spatial overlap with wolves. Ripple et al. (2011) speculated that lynx would benefit from indirect linkages with wolves through either 1) suppression of competing coyotes or 2) reduction in ungulates competing for forage with snowshoe hares. However, these hypotheses have been refuted as having little support in the
literature (Hodges, 2012; Squires, Decesare, Hebblewhite, & Berger, 2012), and I did not detect the wolf-coyote spatial segregation that would provide the basis for the first hypothesis.

Alternatively, wolves may suppress competition between mesocarnivores through their facilitation of coyotes, which could decrease resource competition between coyotes and lynx. Sivy et al. (2018) found that carrion subsidies provided by wolves reduced diet overlap between coyotes and red foxes (*Vulpes vulpes*), thus decreasing reliance on a shared resource. Coyotes rely on scavenging more frequently than lynx (O’Donoghue et al., 2001), which could therefore decrease coyote reliance on snowshoe hares and other shared prey. This mechanism would explain the relatively weak relationship observed between lynx and wolves, as well as the lack of strong relationship observed between lynx and coyotes (Fig. 3.1). Assessing interactions between all three predators along a gradient of wolf density would provide additional insight into this hypothesis.

In addition to spatial overlap with wolves, lynx showed strong spatial overlap with their prey – snowshoe hares and red squirrels (*Tamiasciurus hudsonicus*; Fig. 3.1c). Based on relative abundances of the two prey species, this relationship is likely dominated by the close association between lynx and snowshoe hares (Fig. A2.1; Keim et al., 2011; Poole, 2003). However, I observed an unexpected negative interaction between prey occurrences and linear density at both the spatial and weekly scale – suggesting that lynx occurrences decreased with increasing prey abundance when linear density was also high, despite having positive interactions with each separately. At the weekly scale, this interaction could be a spurious result arising from low co-occurrences between lynx and their prey (n = 2; Table 3.3), which discouraged further interpretation at this spatiotemporal scale. Nevertheless, the relationship persisted at the spatial scale of analysis – where lynx abundance overlapped substantially with that of their prey (Table
3.3) – thus providing some support for an interactive effect (Fig. 3.1). Although the coyote-lynx relationship was not significant on its own, this interaction may be a result of a coyote-mediated response to both prey and linear density. At the spatial scale, coyotes also preferred sites with higher linear density and exhibited a weak, non-significant response to prey (Fig. 3.1b), which may have further interfered with lynx associations with prey in areas of high anthropogenic disturbance. In a study of lynx occupancy, Bayne et al. (2008) found that lynx were strongly associated with their prey, but that this relationship broke down in the south of their range with higher densities of roads and coyote presence. Although my study assesses these dynamics at a smaller spatial scale, similar interacting relationships may contribute to the patterns observed here. However, I caution that these are speculative suggestions, and increased survey effort combined with a stronger focus on interacting relationships would clarify these patterns.

3.5.3 Species’ relationships with linear density

The negative effect of linear density on black bears, as well as the positive effect on coyotes and lynx, agree with previous research conducted in northern Alberta (Fisher & Burton, 2018; Toews et al., 2018). However, I found no evidence of interspecific interactions changing as a function of anthropogenic disturbance. This result differs from other studies observing influences of anthropogenic disturbance on interspecific interactions in tropical and semi-urban ecosystems (Karanth et al., 2017; Wang et al., 2015) as well as between other boreal species (Fraser, 2018), all of which found changes in spatiotemporal partitioning with level of disturbance. This could be due to the relatively low level of anthropogenic disturbance in the Algar area compared to other ecosystems of concern, both in Alberta and around the world. Although the Algar system has a gradient of linear density, this is the primary disturbance in the area and is much lower than other landscapes containing linear feature networks (Government of
Alberta, 2017). Further, humans are largely absent from the study area (Fig. A2.2f), so direct human influence on interspecific interactions would be minimal. To better assess the influence of anthropogenic disturbance on interspecific interactions, a similar study could be conducted across a number of landscapes with varying levels and types of landscape change (Fraser, 2018).

3.5.4 Limitations

Fine scale temporal analyses of interspecific interactions often require large sample sizes of detections to reveal patterns in activity and co-occurrence (Frey et al., 2017). In my study, low numbers of occurrences – and consequently, co-occurrences – may have limited my ability to reliably detect effects of interacting species. This would be of particular significance for lynx, which were only detected 73 times in the 30-month survey period, and experienced low co-occurrences at finer spatiotemporal scales (Table 3.3). Although coyotes occurred twice as often as lynx, low detection rates for both species caused model misspecifications at the daily scale of analysis. Therefore, I urge caution when modelling co-occurrences from rare or elusive species at fine spatiotemporal scales. More robust methods to assess interactions for these species could use baited camera traps to increase detection probabilities (Stewart et al., 2016) or increase either spatial or temporal extent of the camera trap survey to increase sampling effort. Further, telemetry studies of interacting species could account for interspecific effects on movement patterns, thereby assessing how individual animals respond to space use by other species on a shared landscape (James et al., 2004).

In addition, a key limitation of this study is that I do not directly measure interspecific interactions affecting boreal predators, but rather infer interactions and their mechanisms from co-occurrence data. Although techniques exist to derive interaction strength and predict mechanisms, such approaches are either non-temporal (Dorresteijn et al., 2015) or require large
amounts of data (Schliep et al., 2018; Swanson et al., 2016). Further, when relationships have been revealed, direct observation is often the best method for determining interaction mechanisms (Atwood & Gese, 2008; Cusack et al., 2016). Whereas I assume that species co-occurrences indicate intentional proximity and thus suggest facilitative interactions, co-occurrences of predators with similar niches may be equally indicative of species competing for a shared resource (Fraser, 2018). To make the distinction between interaction mechanisms, spatiotemporal patterns must be related to the underlying ecological process. Camera traps offer a unique opportunity to do so by enabling direct observation of interactions while simultaneously relating this information to spatiotemporal relationships on a landscape scale (Caravaggi et al., 2017).

3.5.5 Implications

Interspecific interactions connecting wolves to non-apex predators suggest that non-apex predators should respond to fluctuations in wolf density. In the last thirty years, wolf populations in the boreal forest have increased drastically in response to growing numbers of white-tailed deer (Latham, Latham, McCutchen, & Boutin, 2011). This growth in prey numbers may have contributed to similar population booms in other non-apex predators. For example, coyotes have expanded their ranges across North America and Central America, a phenomena that has largely been attributed to apex predator extirpations and creeping anthropogenic development (Hody & Kays, 2018). However, despite healthy wolf populations in the north, coyote populations continue to grow, though in the far north remain restricted to areas of urban development (Cluff, 2006). In regions where coyotes have extended their reach beyond human settlements, facilitative scavenging of wolf kills may expedite coyote expansion by providing food resources at the frontiers of their range (Paquet, 1991b, 1992). Although little information is available for
black bear population trends, recent density estimates also suggest growing populations in recent years (Government of Alberta, 2016), providing motivation for research linking population growth between predator species.

In response to growing wolf populations, and out of concern of high predation rates on woodland caribou, the government of Alberta implements annual wolf reduction programs within some caribou herds at extreme risk of extirpation (Government of Alberta, 2017; Hervieux, Hebblewhite, Stepnisky, Bacon, & Boutin, 2014). Although effective in boosting caribou numbers in the short term, wolf removal is controversial and has direct consequences for the interactions structuring the boreal mammal community (Darimont, Paquet, Treves, Artelle, & Chapron, 2018; Sivy et al., 2017). The relationships observed in this study indicate that wolf removal might influence non-apex predators, potentially by reducing facilitative interactions and promoting competition between mesocarnivores. Whereas wolf population growth coincided with growing populations of both coyotes and black bears, wolf removal could have varied effects. Although non-apex predators may benefit from facilitative interactions with wolves, wolf reduction may open up available niche space through mesocarnivore release, allowing non-apex predators to increase their populations further (Ritchie & Johnson, 2009; Sivy et al., 2017).

Further, decreased wolf populations could enhance competitive pressures between mesocarnivores as reduction in carrion supplements increases reliance on shared resources (Sivy et al., 2018). As wolf reduction programs continue in caribou ranges in western Canada, I suggest that research should focus not only on caribou response, but also on responses of other species in the boreal mammal community.

Expanding to the global context, this study supports the increasingly large body of research showcasing community-wide impact of biodiversity loss from top trophic levels (Estes
et al., 2011; Kuijper et al., 2016; Ripple et al., 2014). Despite the incursion of industrial
development onto boreal landscapes, the predator guild of this ecosystem is largely intact,
providing a stark contrast with ecosystems elsewhere in North America as well as around the
world (Ripple et al., 2014). These results demonstrate that relationships of apex predators are
instrumental in governing space use within the predator guild as well as between predators and
prey, emphasizing the top-down influence they have on the entire ecosystem (Estes et al., 2011;
Ford & Goheen, 2015). If conserved, this system could therefore serve as a model with which to
compare others in which apex predators have been extirpated, though consideration should be
given to the unique patterns of anthropogenic landscape change and their impacts on predator
spatial ecology (Pickell et al., 2015).

3.5.6 Conclusions

Interspecific interactions arise from coexisting species partitioning space, time, and life-
sustaining resources on a shared landscape where such resources are limited (Schoener, 1974).
Understanding those interactions enables us to predict how they will respond when perturbed,
empowering us to make informed and proactive management decisions. Here, I show that non-
apex predators exhibit spatiotemporal overlap with an apex predator on a working landscape. I
further suggest that this overlap is consistent with facilitative interactions between the four
boreal predators studied. These species additionally show individual responses to anthropogenic
disturbances, though responses vary and further investigation is necessary to evaluate
consequences for interactions. Results from this study highlight important considerations of the
impact of single-species management decisions, which may unintentionally alter the behaviour
of coexisting species (Burgar et al., 2018). Further, they reinforce the value of conserving apex
predators for their cascading effects throughout the community via interactions linking them
together (Estes et al., 2011). The relationships observed in this study occur in the context of a landscape experiencing ongoing industrial development, offering insight into how species coexist in the face of continuing anthropogenic landscape change. To keep wildlife communities on such landscapes, we must commit to understanding the underlying relationships that allow them to thrive.
Chapter 4: Conserving communities on the working landscape

4.1 Synthesis and conclusions

The rate of anthropogenic change on our planet is quickly outpacing our ability to recognize its consequences, let alone effectively mitigate them (Vitousek et al., 1997). Although we meticulously track biodiversity loss through species extinctions (WWF, 2018), rarely do we appreciate the loss of the ecological interactions that hold communities together (Valiente-Banuet et al., 2015). It is these relationships that allow communities to persist, and in better understanding them, we can implement better conservation solutions to protect not only individual species, but their greater communities as well.

This thesis describes the use of camera traps to assess boreal mammals for their responses to anthropogenic landscape change. By examining two hierarchical levels – mammal behaviours and community interactions – I assessed how the effects of disturbance ripple throughout communities and across ecological hierarchies. I showed that landscape change – even when imposed for conservation – has consequences for numerous mammal species, not just species of conservation concern. These results highlight the value of multi-species monitoring, revealing influences of both disturbance and restoration on abundant generalist species, elusive wide-ranging species, and a high-profile species at risk. Further, they illustrate how species influence one another through their interspecific interactions, which may result in additional community effects of landscape change. This work shows that, at least on the community level, landscape change does trigger responses in biodiversity, which may have consequences for community resilience to disturbance.

In my second chapter, I examined responses to landscape change at a population level by measuring mammal seismic line use following restoration, thereby assessing restoration as a
means of caribou conservation. Three years following implementation, I found that only white-tailed deer decreased their use of restored lines. Although caribou predators were not influenced by restoration, wolves showed higher use of human-use lines, suggesting that the least restored lines provided better movement corridors and revealing a clearer picture of how these species use the working landscape. Caribou preferred seismic lines in lowland habitat regardless of treatment, corroborating the conclusion that this habitat needs to be conserved and restored for the preservation of the species (Government of Alberta, 2017). Although continued monitoring should track mammal responses as restoration progresses, these results suggest that additional conservation measures should be implemented to protect caribou in the short-term. Such measures may take the form of more intensive restoration practices (Pyper et al., 2014), predator exclosures, or wolf removal programs (Hebblewhite, 2017; Hervieux et al., 2014). Each solution comes with its own challenges and controversies, but all of them could trigger unintentional responses throughout the mammal community.

To better understand community level responses, my third chapter focused on interspecific interactions between boreal predators on the working landscape. I found that black bears showed positive associations with wolves even at a fine spatiotemporal scale, and with coyotes at a coarser spatiotemporal scale. Lynx exhibited spatial overlap with both wolves and preferred lynx prey. Further, all three of the predator species that I assessed responded to level of anthropogenic disturbance, but this did not influence interspecific interactions. These results indicate that interspecific interactions are a significant influence on predator use of the working landscape. Therefore, single-species management decisions can strengthen or weaken these interactions, thus unintentionally stressing the mammal community at large. This has particular implications for the impact of wolf management programs imposed for caribou conservation, and
points to community-wide changes to landscape use with the removal of the apex predator 
(Hervieux et al., 2014; Sivy et al., 2017).

4.2 Research strengths and limitations

This research is a long-term, non-invasive survey describing qualitative relationships 
between biodiversity and the landscape at both the population and the community level. Whereas 
responses to disturbance are commonly studied for individual species or particular species pairs, 
camera traps allow the simultaneous study of multiple interacting species, thus allowing 
inferences to be made at multiple ecological levels (Steenweg et al., 2017). Further, this is one of 
the first studies documenting responses to restoration on this industrializing landscape, as well as 
the first to document spatiotemporal relationships between boreal predators. These results 
provide a basis on which to conduct further research on both the efficacy of management 
practices and the relationships governing mammal coexistence on the working landscape.

One limitation of this work is its ability to assess differences in level of disturbance 
through direct comparison with undisturbed landscapes. Although I was able to evaluate effects 
of restored seismic lines relative to non-restored control lines, the study could have been 
improved by a before-after-control-impact (BACI) design, in which mammal responses are 
measured prior to and following restoration treatment. Additionally, to truly assess how 
community interactions respond to landscape change would require analyzing relationships 
across a larger gradient of disturbance, or between landscapes with different levels of 
anthropogenic features (Fraser, 2018). The scale of disturbance across Alberta’s boreal forest 
makes comparisons with ‘undisturbed’ landscapes challenging (Komers & Stanojevic, 2013), but 
conclusions drawn from this research could be supplemented by further study across levels and
types of disturbance. As it is, this work provides a good model of mammal community dynamics on a relatively low-intensity landscape.

Although camera traps allow for multi-species research across hierarchical ecological levels and scales, the design of this study limited our definition of the boreal community. Despite providing a record of numerous species, detections of some species were too low to analyze for meaningful effects (e.g. marten, fisher, red foxes). This design could have been modified to detect elusive mammals by baiting camera stations (Fisher et al., 2013; Stewart et al., 2016); however, adding attractant risked confounding the effect of seismic line treatment. Further, we did not assess bird or amphibious species, thus restricting our study only to mammals. To better assess boreal community responses would require more inclusive sampling of boreal species, which could be conducted both with camera traps and through additional sampling techniques (Burton et al., 2014).

4.3 Applications and future research

Results from this research can be applied to making informed management decisions for the boreal mammal community on the working landscape. In illustrating how large mammals use this landscape, this work informs conservation decisions for species at risk, apex predators, and generalist species alike. The responses to restoration shown here indicate that further action is necessary to conserve caribou while habitat restoration progresses, but also suggests directions for landscape management that allows industry and wildlife to coexist. Additionally, the multi-species responses to change supports a shift towards considering disturbance effects in the context of the community and making management decisions at this level rather than at the level of populations of individual species.
To supplement these findings, future research should focus on the mechanisms behind observed qualitative responses to best understand why the observed patterns of space use occur. For example, movement could be paired with in-depth landscape resistance and connectivity analysis, which would provide further indication of how mammals move across the landscape and how they use different landscape features (Courbin, Fortin, Dussault, & Courtois, 2014). Mechanisms behind responses to landscape features could be explored by associating animal behaviour to site-specific abiotic features, such as vegetation composition and structure (Finnegan et al., 2018) or snow depth (Droghini & Boutin, 2017). Processes and directions of interspecific interactions could also be assessed via recorded video at strategic sites, such as carcasses placed for bait (Caravaggi et al., 2017). Finally, future research should investigate the link between behavioural responses to landscape change (line use) and quantitative responses in populations across the boreal mammal community (Burgar et al., 2018). While studies of ecological resilience require examination of how communities adapt behaviours to disturbance, a true test of persistence reveals how responses translate into population growth or decline, ultimately determining a species’ fate within an anthropogenic landscape.
References


Bolker, B. (2018). Multimodel approaches are not the best way to understand multifactorial systems.


the boreal forest. Écoscience, 15(4), 485–497. https://doi.org/10.2980/15-4-3100


Appendices

Appendix 1: Field data sheet and details

ALGAR WILDLIFE PROJECT: CAMERA STATION DATA COLLECTION SHEET

<table>
<thead>
<tr>
<th>Site ID:</th>
<th>Visit Date: (MM-DD-YYYY)</th>
<th>Deployment Time (24 hr):</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crew:</td>
<td>Treatment Type:</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>☐ Test photos taken?</td>
</tr>
<tr>
<td></td>
<td></td>
<td>☐ Control ☐ Human Use ☐ Nat ☐ Regen ☐ SP+P</td>
</tr>
<tr>
<td>Camera active: Yes ☐ No ☐</td>
<td>Camera replaced: Yes ☐ No ☐</td>
<td>Camera moved: Yes ☐* No ☐</td>
</tr>
<tr>
<td>Camera repositioned: Yes ☐ No ☐</td>
<td>Batteries replaced ☐</td>
<td>SD card replaced ☐</td>
</tr>
</tbody>
</table>

Camera Site Description:
Camera height (cm) ____________
Camera direction (Ex: NW) ____________
Metre stick: Yes ☐ No ☐
*If camera moved, note tree species camera is now attached to, if top of tree was sawed off, nearby landmarks, etc.

Line Segment Conditions:
Line Veg: ☐ Grasses ☐ Sedges ☐ Moss ☐ Lab Tea ☐ Seedlings ☐ Shrubs ☐ Trees
Line veg ave height (m) ____________ Line veg cover (%): ____________
Width of line (m) ____________
Nearest game trail (m) ____________
Number of game trails ____________
Line of sight barrier (both directions): Spongy ☐ Firm ☐
CWD (≥10 cm diameter): Present ☐ Absent ☐ Line
Openness: Closed ☐ Semi-Open ☐ Open ☐

Surrounding Habitat:
Dom Tree Sp.: Dom Shrub Sp.:
Comments:

*Note presence of wildlife (e.g., scat, footprints) and human activity (e.g., litter, tracks).*

<table>
<thead>
<tr>
<th>Field</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site ID</td>
<td>Name of site (e.g., Algar01)</td>
</tr>
<tr>
<td>Visit Date</td>
<td>Date visited site (e.g., 04-19-2017)</td>
</tr>
<tr>
<td>Deployment Time</td>
<td>Time at site (e.g., 13:30)</td>
</tr>
<tr>
<td>Crew</td>
<td>Initials of crew (e.g., JB/ET)</td>
</tr>
<tr>
<td>Test photos taken</td>
<td>Were whiteboard photos taken once camera was set, prior to leaving? Pls include Site ID and Date.</td>
</tr>
<tr>
<td>Treatment Type</td>
<td>Is the site Control, Human Use, Natural Regeneration or Site Prep + Plant</td>
</tr>
<tr>
<td>Camera active</td>
<td>Was the camera still operating/active when the crew arrived at the site?</td>
</tr>
<tr>
<td>Camera replaced</td>
<td>Did the camera need to be replaced? Check if a new camera was deployed.</td>
</tr>
<tr>
<td>Camera moved</td>
<td>Was the camera moved to a new location/tree at the same site? If yes, add info to Camera Site Description section.</td>
</tr>
<tr>
<td>Camera repositioned</td>
<td>Did the camera need to be repositioned? For example, a bear might have slightly displaced, but not damaged, the camera, necessitating the camera to be repositioned on the same tree.</td>
</tr>
<tr>
<td>Batteries replaced</td>
<td>Were fresh batteries put into the camera?</td>
</tr>
<tr>
<td>SD card replaced</td>
<td>Was a new SD card put into the camera?</td>
</tr>
<tr>
<td>Camera height</td>
<td>height (in cm) to base of camera.</td>
</tr>
<tr>
<td>Camera direction</td>
<td>which of the eight directions is the camera facing: N, NE, E, SE, S, SW, W, NW?</td>
</tr>
<tr>
<td>Metre stick</td>
<td>has a metre stick been deployed at the site?</td>
</tr>
<tr>
<td>Distance to camera</td>
<td>If yes to metre stick, distance (in cm) from the base of the camera to the metre stick.</td>
</tr>
<tr>
<td>Angle from camera</td>
<td>If yes to metre stick, angle (in degrees, use a compass) from the base of the camera to the base of the metre stick.</td>
</tr>
<tr>
<td>Line veg</td>
<td>Check if veg type present on the line.</td>
</tr>
<tr>
<td>Seedlings on the line</td>
<td>Does the line contain black spruce or white spruce trees &lt; 1m (i.e., seedlings)?</td>
</tr>
<tr>
<td>Line veg ave height</td>
<td>average height of line vegetation, regardless of type (e.g., 1.4 m).</td>
</tr>
<tr>
<td>Line veg cover</td>
<td>% cover of line vegetation, regardless of type (e.g., 50%).</td>
</tr>
<tr>
<td>Width of line</td>
<td>from the edge of the line, closest to camera, directly across to other edge of line (e.g., 6.5m).</td>
</tr>
<tr>
<td>Ground</td>
<td>check spongy if boot sinks into ground by ≥5 cm, otherwise check firm.</td>
</tr>
<tr>
<td>Nearest game trail</td>
<td>distance (in m) from camera to nearest game trail on line (e.g., 2.5m).</td>
</tr>
<tr>
<td>Mounding</td>
<td>check yes if mounding from SP+P is visible; record height (in cm) from ground to top of mound and depth (in cm) from ground to bottom of trench.</td>
</tr>
<tr>
<td>Number of game trails</td>
<td>number of game trails on line within 10 m from camera (either direction, 20 m total length).</td>
</tr>
<tr>
<td>CWD</td>
<td>check yes if any coarse woody debris with a diameter of at least 10 cm at one end is present on the line, within 10 m of the camera (either direction, 20 m total length)</td>
</tr>
<tr>
<td>Line of sight barrier</td>
<td>distance (in m) to first sight barrier, down length of line; record for both directions. Barrier can be elevation, vegetation, etc. – anything that impedes vision.</td>
</tr>
<tr>
<td>Line openness</td>
<td>a category to denote cover above the line: open is when there is no vegetation cover</td>
</tr>
</tbody>
</table>
above line; *semi-open* refers to a line where vegetation is leaning over the line but does not touch from one edge of the line to the other, a partial cover of the line; while *closed* refers to a line where vegetation from one side of the line touches vegetation on the other side and there is complete cover across the line.

| Dom Tree Sp. | wetland species – balsam poplar, black spruce, tamarack, white/Alaskan birch; upland species – balsam poplar, back spruce, jack pine, lodgepole pine trembling aspen, white spruce |
| Dom Shrub Sp. | wetland species – bog birch, dwarf birch, dwarfed black spruce, ericaceous shrub (bog cranberry, bog-laurel, bog rosemary, leather leaf), Labrador tea, specked alder, willow; upland species – beaked hazelnut, chokecherry, green alder, low-bush cranberry, mountain maple, rose, saskatoon, snowberry. |
| Tree height (camera side) | average height of canopy on side of line with camera, measure three trees and take average (exclude trees towering over canopy). |
| Tree height (opposite camera) | average height of canopy on side of line opposite the camera, measure three trees and take average (exclude trees towering over canopy). |
| Comments | any comments about the site, including presence of wildlife and human activity. |
Appendix 2: Summaries of survey effort and species detections

Table A2.1. Preliminary count data for four periods of camera trap deployment in the Algar study area. *Problem cameras* indicates the number of cameras that malfunctioned during the deployment period and thus had some inactive days during that survey time. *Mean days per station* is the average number of days each camera station was active during the survey period, while *total trap days* is the total number of active days across all stations. *No. images* equals the total images captured during each period, including time-lapse photos and misfires. *Independent detection events* indicates the number of image sequences considered to be a single detection event, i.e. images of a given species captured within 30 minutes of each other.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. stations</td>
<td>24</td>
<td>60</td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td>Problem cameras</td>
<td>0</td>
<td>4</td>
<td>28</td>
<td>20</td>
</tr>
<tr>
<td>Mean days per station</td>
<td>371</td>
<td>160</td>
<td>130</td>
<td>114</td>
</tr>
<tr>
<td>Total trap days*</td>
<td>8911</td>
<td>9025</td>
<td>7779</td>
<td>6816</td>
</tr>
<tr>
<td>No. images</td>
<td>18036</td>
<td>30632</td>
<td>63981</td>
<td>26863</td>
</tr>
<tr>
<td>Independent detection events</td>
<td>1057</td>
<td>479</td>
<td>1247</td>
<td>443</td>
</tr>
<tr>
<td>No. mammal spp. identified</td>
<td>14</td>
<td>13</td>
<td>14</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure A2.1. Total number of independent detection events for mammals captured by all camera traps deployed in the Algar study area from November 2015 to April 2018.
Figure A2.2 Monthly detections of focal species over 30-month camera trap survey in the Algar study area. Plots depict detections per month for wolves (a), black bears (b), white-tailed deer (c), moose (d), caribou, (e) and humans (f). Restoration treatments are differentiated by colour and shape, where orange circles = control, red circles = human-use, green triangles = natural regeneration, and purple triangles = site preparation and planting (note that natural regeneration and human-use sites were added in November 2016). Observations depicting zero detections have been removed for clarity. Vertical jitter has been added to display sites with equal number of detections within the same month.
Appendix 3: Chapter 2 scale analysis for spatial covariates

Figure A3.1 AIC model weights indicate scale of influence for each species. To determine the scale of influence for the five focal species, I constructed univariate GLMs testing species’ monthly detections as a function of lowland habitat (a) and line density (b) calculated at eight different spatial grains. Plots show the AIC weights of candidate models, whereas the model with the highest AIC weight indicates the scale of influence for that predictor variable.
Appendix 4: Chapter 3 scale analysis and habitat modelling

Figure A4.1 AIC model weights indicating scale of influence for habitat features (a) and linear density (b). The scale with the most model weight indicated the scale that best explains occurrences of each predator species, as determined by using AIC model selection to compare identical models measured at different spatial scales.
Figure A4.2 Effects of habitat features on predator occurrences in the habitat modelling step of analysis. Effect sizes are shown as parameter estimates (mean ± standard error) from negative binomial GLMs (spatial level) and binomial GLMMs (weekly and daily levels) of black bear (a), coyote (b) and lynx (c) occurrences at three levels of analysis. Results are shown from habitat variables measured at the optimal spatial scale of influence: 250m for black bears, 1750m for coyotes, and 1500m for lynx. Note that LowDecid is absent for black bears because lowland deciduous forest did not occur within 250m of any camera stations. Significant habitat variables (p < 0.05, annotated by stars) were then included in the second step of the analysis to model effects of interspecific interactions on predators.