A PRIMARY PRODUCTIVITY HYPOTHESIS FOR DISTURBANCE-MEDIATED APPARENT COMPETITION FOR BOREAL CARIBOU IN CANADA

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ABSTRACT

The most widely reported threat to populations of boreal and mountain woodland caribou (*Rangifer tarandus caribou*) involves what has come to be known as disturbance-mediated apparent competition (DMAC). Here, anthropogenic and natural disturbances that increase the abundance of deciduous-browsing cervids (e.g., moose [*Alces alces*] and white-tailed deer [*Odocoileus virginianus*]) are thought to promote predator (especially wolf [*Canis lupus*]) numbers, in turn heightening predation risk to caribou. We know most about the hypothesis of DMAC as it relates to caribou where the species is under threat by industry; i.e., from relatively productive southern boreal and mountain systems where landscapes are highly managed and multiple species of predators and ungulate prey interact with caribou. Yet almost 2/3 of extant boreal caribou range occurs in poorly productive, wildfire-dominated areas where caribou compete with only one ungulate species (moose) in the context of DMAC. In Ch. 2, using data specific to the Saskatchewan Boreal Shield, I tested for evidence of DMAC with data specific to an area of previously known low primary productivity. I found that the successional dynamics after fire of the low-productivity boreal shield did not allow for flushes in deciduous browse, meaning moose density could not increase and resulting in no evidence for DMAC in this system. To test predictions consistent with DMAC, in Ch. 3, I examined the relationship between net primary productivity (NPP) with calf recruitment and adult female survival at a national scale. I accounted for variables influencing DMAC, including metrics of large mammal richness, alternative prey biomass, and predator biomass. While geographic site played an important role, NPP was the most important variable in beta regressions, visually influenced PCA dimensionality in the dataset, and was a primary causal factor for reduced caribou survival and recruitment in Structural Equation Models (SEM). The results indicate that NPP and anthropogenic disturbance act as an impetus for DMAC, where the phenomenon is unlikely to occur in low-productivity areas.

Overall, I postulate that the DMAC phenomenon is dependent on NPP, or energy in the system, where burned areas of low NPP may not create the conditions necessary for DMAC to occur. Understanding what factors influence where DMAC occurs and at what scale will be critical for determining effective conservation strategies for local caribou range-planning and Canada's federal *Recovery Strategy* for boreal caribou.

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LIST OF ABBREVIATIONS

ABMI – Alberta Biodiversity Monitoring Institute

AIC$_c$ – Akaike Information Criterion corrected for small sample size

AKDE – Autocorrelated Kernel Density

ANOVA – Analysis of Variance

CCA – Canonical Correspondence Analysis

CI – Confidence Interval

DCA – Detrended Correspondence Analysis

DMAC – Disturbance Mediated Apparent Competition

KDE – Kernel Density Estimator

MCP – Minimum Convex Polygon

NPP – Net Primary Productivity

PCA – Principal Component Analysis

SBS – Saskatchewan Boreal Shield

SEM – Structural Equation Modelling

UBI – Ungulate Biomass Index

CHAPTER 1: GENERAL INTRODUCTION

1.1 Boreal Woodland Caribou

Boreal woodland caribou (*Rangifer tarandus caribou*, hereafter caribou), located throughout the boreal forest of Canada, are listed on Schedule 1 of the Canada *Species at Risk Act* (SARA) based on population reduction of greater than 30% over the previous three generations (Environment Canada 2012). Threatened and Endangered populations of caribou have been researched and the subject of applied conservation biology for more than 30 years (see Environment Canada 2012, Serrouya et al. 2019). Caribou require large areas of continuous undisturbed old-growth coniferous forest (Environment Canada 2012).

Anthropogenic disturbance and natural fires represent the largest threat to woodland caribou since they disrupt and fragment natural old growth habitat (Sorensen et al. 2008). A study done in Manitoba found that populations of woodland caribou that live near anthropogenic disturbance, especially logging, have decreased home range size and are observed to have increased cortisol levels, likely affecting survival (Ewacha et al. 2017). Of anthropogenic features, linear features such as seismic lines, roads, and pipelines are considered the most detrimental for caribou since they allow predators to move along them, traveling more quickly between areas (James and Stuart-Smith 2000, Latham et al. 2011*a*, Dickie et al. 2017, 2020, Pigeon et al. 2020). Vanlandeghem et al. (2021) modelled that forest management using lower densities of roads and disturbance edges had greater caribou survival when disturbance levels were kept the same, since predation rates were lower with fewer roads.

Another cause for population declines is climate change. There has been evidence of shrubs moving northward as a result of climate change (Sturm et al. 2001, Tape et al. 2006). In addition, apparent competitor white-tailed deer (*Odocoileus virginianus*) are already moving northward into caribou habitat (Latham et al. 2011*b*, Hervieux et al. 2013). The changes in primary productivity as a result of climate change could result in a response from caribou predators and other prey species that share common predators (i.e. alternative prey; Gagné et al. 2016). This will only be exacerbated in the future as the boreal forest retracts, causing increased deciduous browse in the north which provides food for white-tailed deer and moose (*Alces alces*).

1.2 Cultural Importance

Caribou are essential to First Nations and Métis communities for culture, identity, and subsistence (Environment Canada 2012, Mamun and Brook 2016). First Nations traditional knowledge also says that caribou are needed for the balance of nature, where their loss will affect all other wildlife (Environment Canada 2012). Woodland caribou are an important food source and part of the cultural heritage of approximately 300 First Nations communities across Canada (Assembly of First Nations 2007, David Suzuki Foundation and Assembly of First Nations 2013, Mamun and Brook 2016). Factors that contribute to their value include subsistence, enjoyment of the land (as a spiritual and social activity), health and wellness of communities, reciprocity among community members, revitalizing First Nations languages, self-determination, and spirituality (David Suzuki Foundation and Assembly of First Nations 2013).

1.3 Recruitment

Caribou calf recruitment, the number of yearlings that survive to join the adult population (measured as calf:cow ratio), has been shown to be the greatest indicator of population changes (as opposed to adult survival; Bergerud and Elliot 1986, Environment Canada 2011, McCarthy et al. 2011). Calf recruitment has been shown to be negatively affected by disturbance and deciduous forest area (Environment Canada 2011, McCarthy et al. 2011, Leclerc et al. 2014), while no effect was recognized by over-winter snow depth (Larter et al. 2017). Higher recruitment is recorded for years when snow melts sooner in the spring and there is a faster green-up as a result of the Pacific Decadal Oscillation (Hegel et al. 2010*b*). Caribou avoid areas of high road density as well as places where they are likely to encounter wolves (*Canis lupus*) when selecting for calving locations (Mahoney and Virgl 2003, Pinard et al. 2012, Leclerc et al. 2014, Leblond et al. 2016). While some wolf reduction programs resulted in increasing calf survival (Bergerud and Elliot 1986, Hegel et al. 2010*b*, Serrouya et al. 2019), others did not (Valkenburg et al. 2004, Harding et al. 2020).

1.4 Disturbance-Mediated Apparent Competition

While there are many threats to caribou, the most important impact reported for the species has been apparent competition from white-tailed deer and moose as mediated by a predator (principally wolves, as well as possibly cougars [*Felis concolor*], coyotes [*Canis latrans*], black bears [*Ursus americanus*], grizzly bears [*Ursus arctos*], and wolverine [*Gulo gulo*]) but brought about by landscape disturbance (Seip 1992, Festa-Bianchet et al. 2011, Serrouya et al. 2015, DeMars et al. 2019). In the boreal plains it has been shown that landscape disturbance benefits alternative browsing prey in the system (Latham et al. 2011*a*, *b*, Hervieux et al. 2013, Peters et al. 2013). This is a form of apparent competition (Holt 1977), generally termed 'disturbance- or habitat-mediated apparent competition' (hereafter DMAC) and has become increasingly important for caribou conservation throughout Canada (Environment Canada 2012, Hervieux et al. 2013, Serrouya et al. 2015, Environment and Climate Change Canada 2018, DeMars et al. 2019, Serrouya et al. 2019). A similar phenomenon has also been found for competitive species of ants, where anthropogenic disturbance changes habitat succession which regulates competition in the system (Gibb 2011). DMAC is the principal hypothesis upon which I base the investigations of my thesis.

DMAC is based on the premise that disturbance, either anthropogenic or natural, increases the abundance of alternative prey by reducing the age of forests and increasing the amount of deciduous browse (hardwood-dominated stands), thereby increasing the abundance of predators that may be limited by ungulate prey biomass, such as wolves (Seip 1991, Fuller et al. 2003). The link with landscape disturbance is critical, and it is why the pan-Canadian federal *Recovery Strategy* for boreal caribou (Environment Canada 2012), considers total disturbance in setting disturbance thresholds for the promotion of caribou conservation. The purpose for appealing to DMAC in this case is clear, namely because "…habitat alteration (i.e., habitat loss, degradation, and fragmentation) from both anthropogenic and natural sources, and increased predation as a result of habitat alteration have led to local population declines throughout their distribution (Environment Canada 2012;vi)."

While much of the research focus on caribou has been conducted in the south, which strongly informs DMAC-based conservation strategies for caribou, it is within the northern shield and taiga of Canada where the majority of the nation's boreal caribou exist. However, it is in these shield environments that we know the least about caribou ecology. Here, caribou ranges are inhabited by predators including wolves and black bears, and prey species including caribou, moose, beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*), but there is a lack of invasive species such as white-tailed deer and coyotes (*Canis latrans*) that exist in ranges where high levels of anthropogenic disturbance have been documented (Environment Canada 2011, 2012). The predator-alternative prey assemblage changes as one goes from west to east in North America. For example, while the Boreal Shield of Saskatchewan has wolverine and cougars, which are not present further east, it lacks grizzly bears, as well as alternative prey species mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and mountain sheep (*Ovis* spp.), which are present in more westerly populations (Seip 1991, Environment Canada 2011, 2012).

While some studies have begun to doubt that fire plays a role in DMAC (DeMars et al. 2019), Labadie et al. (2021) found that spruce budworm (*Choristoneura fumiferana*) could act as a mediator for apparent competition for caribou. This insect-mediated apparent competition is caused when spruce budworm causes old growth spruce to die off, resulting in a flush of deciduous vegetation leading to a population increase in moose. This (natural) apparent competition found in Québec was exacerbated by salvage logging (Labadie et al. 2021). This means that in areas of high natural disturbance it is unknown whether disturbance can or cannot lead to DMAC for caribou.

1.5 Net Primary Productivity

Net primary productivity (NPP) is measured in the growth rate of plants and is the gross primary production of a plant (total carbon fixation of the plant) minus the respiration of the plant due to metabolism and cell maintenance. This means NPP is the stored biomass of the primary producers in the system. While normalized difference vegetation index (NDVI) has been used as a surrogate of NPP and they are strongly correlated, it is not an accurate measure of plant growth in certain habitat types and NPP is generally considered an updated method compared to NDVI (Phillips et al. 2012, Xu et al. 2012). NDVI is merely a measure of greenness within an area, while NPP is measure of energy (i.e. carbon is in the units of NPP).

NPP varies globally from 30 to 1000 g C/m^2, though boreal habitats rarely exceed 600 g C/m^2 (Scurlock et al. 1999, Running et al. 2000). Increased productivity means increased forage abundance for caribou. However, it is thought that increased predation risk negates the positive effect of increased food abundance for foraging (Leclerc et al. 2014) as caribou are thought to be predation, rather than forage, limited (Hegel et al. 2010*a*, *b*). This begs the question on whether ungulates exhibit top-down control (are limited by predation), or bottom-up control (are limited by the food availability in the system; Bowyer et al. 2005). Other cervids have been shown to be positively affected by increases in productivity. Mule deer survival increases with primary productivity (Sims 2017), while Lukacs et al. (2018) found elk recruitment was most strongly affected by forage productivity (measured in

NDVI). When Saami people raise European reindeer (other subspecies of *Rangifer tarandus*), the calving output is strongly affected by the vegetation productivity fluctuations caused by climatic variation (Reinert 2006). In an agricultural setting, reindeer do best if fed grains, hay, and leaves (Turunen 2014). Heard and Zimmerman (2021), studying mountain caribou in B.C., had increases in population growth in response to a feeding program. Fortin et al. (2017), in their Québec study, found that areas of higher productivity had a positive impact on caribou, which they explained due to the quicker recovery of old-growth forest in these areas. The above evidence would suggest that caribou only select for low productivity areas and area adapted to a lichen-based diet, as a means of avoiding competition and predation.

Primary productivity is also associated with increased animal diversity (Malmstrom 2010). Inferring from this relationship, caribou populations of higher productivity, are more likely to have spatially co-occurring higher predator and alternative prey richness.

1.6 Thesis Objectives

The first goal of my thesis is to test the hypothesis of DMAC as it may occur when evaluated on a local or regional scale, particularly in an area of overall low primary productivity. For chapter 2, I will use data specific to Saskatchewan's Boreal Shield. The area is noted for its short fire-return interval (Parisien et al. 2004), with 55% of the region having been mapped as burned in the past 40 years, while at the same time only 3% of the area occurs within 500 m of industrial and linear features (e.g., roads, transmission lines, settlements, and mines [Environment Canada 2012]). By comparison, percentage area burned (<40 years old) and buffered by industry (500 m) averages 16.7 (*SD* = 15.7, SE = 2.2) and 33.3 (*SD* = 26.6, SE = 3.7) respectively, across all caribou units in Canada (data in Environment Canada 2012). Initiating research on the ecology of caribou of the Saskatchewan Boreal Shield presented an opportunity to test predictions of DMAC in a region little modified by humans where natural processes dominate—the conditions in which boreal caribou evolved. Further, unlike most caribou ranges examined to date, it is likely to be more representative of the 2/3 of extant boreal caribou range for which management objectives based on DMAC are being developed, but for which we do not know how, or even if, DMAC applies to the population dynamics of boreal caribou.

Extrapolating from the analysis in Chapter 2 of my thesis, my second goal was to test the extent to which primary productivity might play a role in DMAC for boreal caribou. Recently, primary productivity was found to have a positive relationship with boreal caribou calf recruitment in Québec, where only moose, wolves, and black bears interact with caribou (Fortin et al. 2017). However, it was found that British Columbia and Alberta caribou populations were negatively associated with range primary productivity (Environment and Climate Change Canada 2017, Serrouya et al. 2021). In chapter 3, I aim to examine the relationship between net primary productivity and caribou calf recruitment across Canada and how it may be influenced by regional environmental factors to account for this discrepancy. I plan to account for variables influencing the relationship with NPP, including regional metrics of large mammal richness, alternative prey richness and density, and predator richness (i.e., food-web composition), all of which I expect to influence the mechanism of DMAC. Specifically, I will test the hypothesis that DMAC is modulated by NPP, with alternative prey and predator biomass in the system being a key component for whether assumptions in DMAC are met.

1.7 Thesis Hypothesis

The hypothesis of DMAC is predicated on the assumption that caribou are negatively affected by disturbance because young seral browse increases alternative prey density, thereby increasing wolf density, which results in more incidental predation of caribou. However, here I predict that this can be modulated by NPP which has a positive effect on caribou recruitment unless high alternative prey and predator densities cause caribou to be too heavily preyed upon.

1.8 Chapter Format

In my first data chapter using data (Ch. 2) specific to the Saskatchewan Boreal Shield, my aim is to test for DMAC using data specific to an area of high fire but low anthropogenic disturbance. In chapter 3 my aim is to examine the relationship between net primary productivity with calf recruitment and adult female survival at a national scale. NPP was found to positively influence caribou in Québec (Fortin et al. 2017) but Environment and Climate Change Canada (2017) and Serrouya et al. (2021) found a negative relationship in the western provinces. In reproducing and modeling these same data, I plan to account for variables influencing this discrepancy, including metrics of large mammal diversity. Specifically, I will test the hypothesis that DMAC is modulated by NPP, with alternative prey and predator richness in the system being a key component for whether predictions of DMAC occur.

Chapter 2 is published in the Journal of Wildlife Management. Included in this thesis is the extended analysis conducted as well as the relevant appendices for this chapter.

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CHAPTER 2: DISTURBANCE-MEDIATED APPARENT COMPETITION DECOUPLES IN A NORTHERN BOREAL CARIBOU RANGE

This data chapter, focusing on wolves as apparent competitors for caribou within the Saskatchewan boreal shield, is published in the Journal of Wildlife Management. Included in the following pages is the extended analysis conducted as well as the relevant appendices for this chapter. Changes from the published manuscript include additions to the introduction and discussion to help fit this chapter within the overall thesis. All images and text are adapted with permission from The Wildlife Society and Wiley Companies.

Neufeld, B. T., C. Superbie, R. J. Greuel, T. Perry, P. A. Tomchuk, D. Fortin, and P. D. McLoughlin. 2021. Disturbance-Mediated Apparent Competition Decouples in Northern Boreal Caribou Range. *Journal of Wildlife Management* 85: 254-270.

2.0 Abstract:

The most widely reported threat to boreal and mountain populations of woodland caribou (*Rangifer tarandus caribou*; caribou) involves habitat- or disturbance-mediated apparent competition (DMAC). With DMAC, natural and anthropogenic disturbances that increase the abundance of deciduous-browsing cervids (e.g., moose [*Alces alces*], deer [*Odocoileus* spp.]) are thought to promote predator (especially wolf [*Canis lupus*]) numbers, which heightens predation risk to caribou. We know most about the effects of DMAC on caribou where the species is under threat by anthropogenic activities in relatively productive southern boreal and mountain systems. Yet, >60% of extant boreal caribou range in North America consists of northern shield and taiga ecoregions of low productivity where caribou may compete with only 1 ungulate species (moose) in the context of DMAC. In this environment, we know very little of how DMAC acts as a limiting factor to caribou. In Saskatchewan, Canada, from 2014–2018, using a combination of vegetation sampling, aerial surveys, and telemetry data (n = 38 wolves), I searched for evidence of DMAC (trends in data consistent with the hypothesis) in an 87,193-km^2 section of the Western Boreal Shield, a poorly productive but natural region (0.18% of land cover classed as an anthropogenic feature) with a historically high fire-return interval (47% of stands aged <40 years). Despite the high levels of disturbance, moose density was relatively low (47 moose/1,000 km^2), likely because of the scarcity of deciduous or mixed-wood stands and low abundance of deciduous browse in the young conifer stands that dominated the landscape. In contrast, boreal caribou density was relatively high for the species (37 caribou/1,000 km^2). Wolf density (3.1 wolves/1,000 km^2) and pack sizes ($\bar{x}$ = 4.0 wolves/pack) were low and resident (established) territories were large ($\bar{x}$ = 4,360 km^2; 100% minimum convex polygon). The low density of wolves mirrored the low (standardized) ungulate biomass index (UBI; moose + boreal caribou) of the study area (0.36 UBI/km^2). I conclude that wolf and hence caribou populations were not responding in accordance with the outcomes generally predicted by DMAC in my study area because the requisite strong, positive response to fire of deciduous-browse and alternative-prey abundance was lacking. As a limiting factor to caribou, DMAC is likely modulated at a macroecological scale by factors such as net primary productivity, a corollary to the general hypothesis that I highlight here (i.e., “primary productivity hypothesis” of DMAC). I caution against managing for caribou based on the presumption of DMAC where the mechanism does not apply, which may include much of boreal caribou range in the north.

Keywords: boreal caribou, Canadian Shield, disturbance-mediated apparent competition (DMAC), moose, net primary productivity, Saskatchewan, ungulate biomass, white-tailed deer, wolves.

2.1 Introduction:

Boreal and mountain populations of woodland caribou (*Rangifer tarandus caribou*, caribou) are listed on Schedule 1 of the Canada Species at Risk Act (SARA). The most important limiting factor for the species has been apparent competition—exacerbated by landscape disturbance—from deer (*Odocoileus* spp.) and moose (*Alces alces*) as mediated by predators, principally wolves (*Canis lupus*) in addition to cougars (*Felis concolor*), coyotes (*Canis latrans*), American black bears (*Ursus americanus*), grizzly bears (*Ursus* arctos), and wolverines (*Gulo gulo*). Thus far, apparent competition in this context has been largely studied at the southern front of range retraction for caribou. For example, in the Boreal Plains and Rocky Mountains of Alberta and British Columbia, Canada, landscape disturbance plays an important role in the strength of suspected or observed apparent competition between caribou and alternative browsing prey, where the latter benefits from disturbance (Latham et al. 2011*a,b*, Peters et al. 2013, Hervieux et al. 2014; Serrouya et al. 2019). This form of apparent competition (Holt 1977), termed ‘disturbance-mediated apparent competition’ (hereafter DMAC, also see DeMars et al. 2019), has been important for drafting caribou management plans throughout Canada (Environment Canada 2012, Hervieux et al. 2013, Serrouya et al. 2015, 2019*b*, Environment and Climate Change Canada 2017, DeMars et al. 2019).

With respect to caribou, DMAC is perhaps best explained as a corollary to the spatial separation hypothesis of Bergerud et al. (1984), whereby the species uses habitat selection as an anti-predator tactic by avoiding areas more amenable to alternative ungulate prey (James et al. 2004). At a landscape scale caribou select for areas of relatively low productivity (e.g., bogs and fens, high elevations, old growth conifer forests) that cannot support high densities of deciduous-browsing cervids such as moose and deer (Bergerud and Page 1987, Seip 1992). Predators such as wolves are numerically supported by total ungulate biomass (Todd K. Fuller et al. 2003); hence, by avoiding habitat supportive of other ungulates, caribou minimize exposure to predation. At higher orders of habitat selection (Johnson 1980) adaptations to a lichen-based diet by caribou, especially in winter, is also thought to reflect the selective use of non-deciduous landscapes (Thomas et al. 1994, Thompson et al. 2015). DMAC relates to the spatial separation hypothesis by invoking landscape disturbance in altering the spatial structure of habitat upon which the latter is based. Specifically, disturbances in or adjacent to caribou habitat act to reduce the seral age of forests, including forest logging or clearing but also natural disturbance, especially wildfire.

Direct (including experimental) evidence for the role of wolves in DMAC between alternative ungulate prey and boreal caribou comes primarily from Alberta (e.g., Latham et al. 2011*a*,*b*, Hervieux et al. 2014, DeMars and Boutin 2018, Mumma et al. 2018) and British Columbia for mountain caribou (e.g., Wittmer et al. 2005, Serrouya et al. 2017, 2019). These relationships are the principal reason why the pan-Canadian federal Recovery Strategy for boreal caribou (Environment Canada 2012), as mandated by SARA, takes into account anthropogenic and natural disturbance in setting landscape-level disturbance objectives for the promotion of caribou conservation (Environment Canada 2012: vi).

Although much of the research focus on caribou has been conducted in the western and southern extents of caribou range, which now strongly informs DMAC-based conservation strategies for the species across the continent, it is within the northern shield and taiga regions of Canada where most extant populations of boreal caribou occur. This area covers approximately 62.5% of extant boreal caribou range (1.5 million km^2) classed as the northern reaches of the Western and Eastern Canadian Shield and southern Taiga ecozones (Fig. 2.1). The area is typically farther north than most commercial forestry, oil, and gas operations. In this area, moose are often the only alternative ungulate prey available to predators and there are few (if any) deer. These forests are characterized by generally low net primary productivity (e.g., <0.3 kg carbon/m^2/year; Lui et al. 2002) and linear features (anthropogenic corridors) occur at relatively low levels; hence, wildfires remain the dominant agent of disturbance (Fig. 2.1; comparative natural vs. anthropogenic disturbance rates presented in Environment Canada 2012). Major caribou predators in these regions are wolves and black bears, and alternative mammalian prey species are relatively few, including moose, beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*), and small mammals. Notably, there is also a general lack of invasive species, such as white-tailed deer (*O. virginianus*) and coyotes (*Canis latrans*) in the north, species now common in southern caribou ranges (Environment Canada 2011, 2012).

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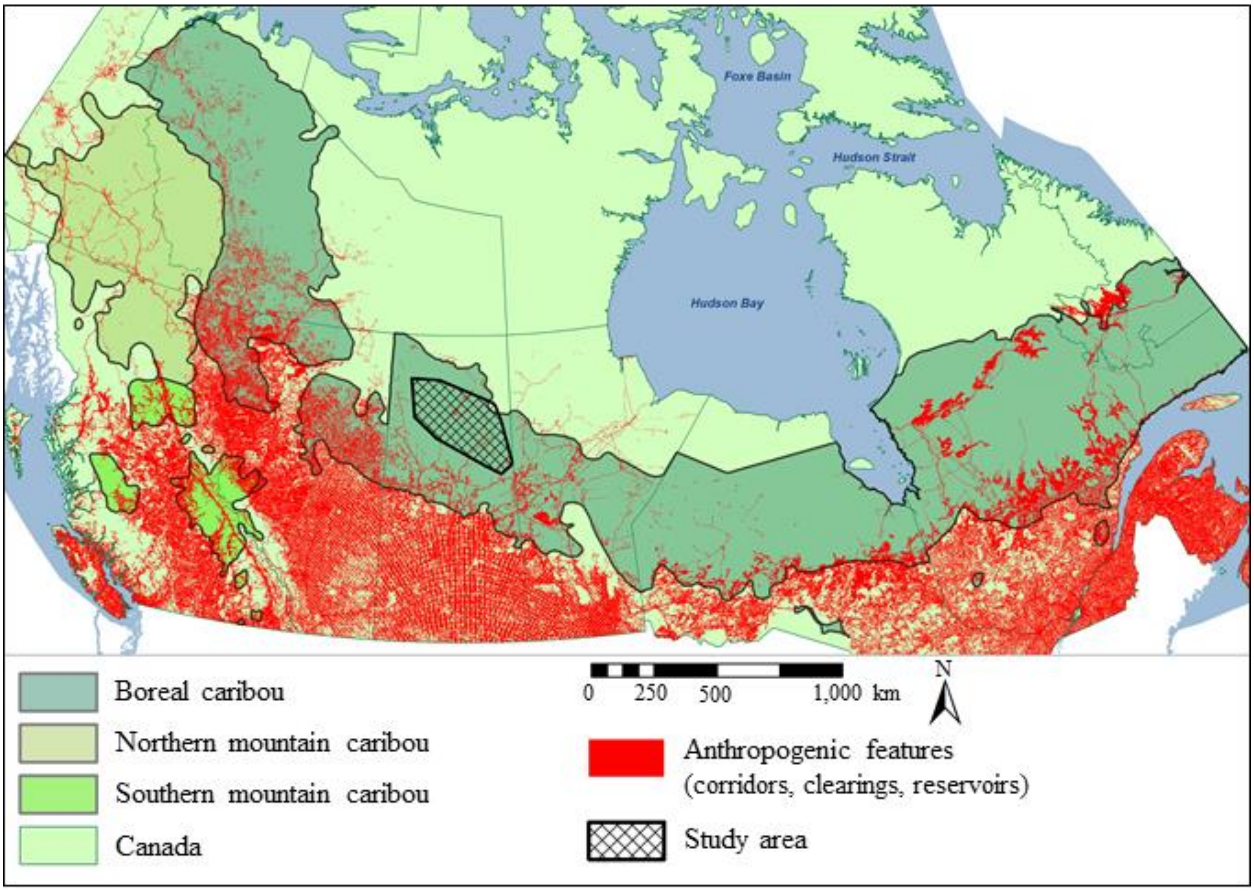

Figure 2.1. Study area in northern Saskatchewan, Canada, in relation to the distribution of populations (Boreal, Northern Mountain, and Southern Mountain) of non-migratory woodland caribou and the existing footprint of anthropogenic disturbance. Caribou distribution maps are from Environment Canada (2007). I obtained anthropogenic disturbances from the 2009 shapefiles Cumulative Anthropogenic Access, Western Canada, Cumulative Anthropogenic Access, Central Canada, and Cumulative Anthropogenic Access, Western Canada (Global Forest Watch, https://databasin.org/datasets/55ec942d370d49fb824bb662d66dfe32, accessed 22 Jan 2019).

The above characterizes the Saskatchewan Boreal Shield (SBS; Fig. 2.2), a 187,000-km^2 area noted for its naturally short fire-return interval (Parisien et al. 2004), 55% of which has been mapped as burned in the past 40 years and only 3% of the area occurs within 500 m of any industrial or linear feature (e.g., roads, transmission lines, settlements, and mines [Environment Canada 2012]). In comparison, across all (area-independent) caribou units in Canada, the percentage of area burned (<40 yrs old) and affected by industry (footprint buffered by 500 m) averages 16.7% (*SD* = 15.7, *SE* = 2.2) and 33.3% (*SD* = 26.6, *SE* = 3.7), respectively (Environment Canada 2012). Initiating research on the ecology of caribou of the

SBS presented an opportunity to test a series of predictions of DMAC within the environment and predator-prey assemblages that are likely similar to the conditions in which the local caribou population is adapted.

The response of predators to disturbance is indirect in the context of DMAC but depends on a direct link between landscape disturbance and alternative ungulate-prey density or biomass. For this bottom-up cascade to initiate after fire, I expected that post-fire habitat in the study area would firstly present quantitative benefits in forage availability to moose. By proxy, I anticipated this would improve coverage of deciduous species known to be of value for moose browse, especially in winter. In North America, moose tend to be specialists with respect to browse, where willows (*Salix* spp.) make up 40–99% of their diet (Dungan and Wright 2005, Poole and Stuart-Smith 2005, Shipley 2010), while other deciduous species, like young aspen (*Populus* spp.), birch (*Betula* spp.), and, among conifers, young firs (e.g., *Abies* spp.) are commonly browsed (Crête and Courtois 1997, Shipley 2010). Forests disturbed by human activity (Lavsund 2003, Peters et al. 2013) or wildfire (MacCracken and Viereck 1990, Loranger et al. 1991, Maier et al. 2005), with which early stage browse species are often associated, are therefore considered to be (relatively) good moose habitat (but see DeMars et al. 2019, a recent paper I espouse in the Discussion). I quantified percent of deciduous stands on the landscape and relative amount of moose-browse within plots, and from these data made inferences regarding the potential for fire to generate a bottom-up response for moose of relevance to the hypothesis of DMAC in the Saskatchewan Boreal Shield (SBS).

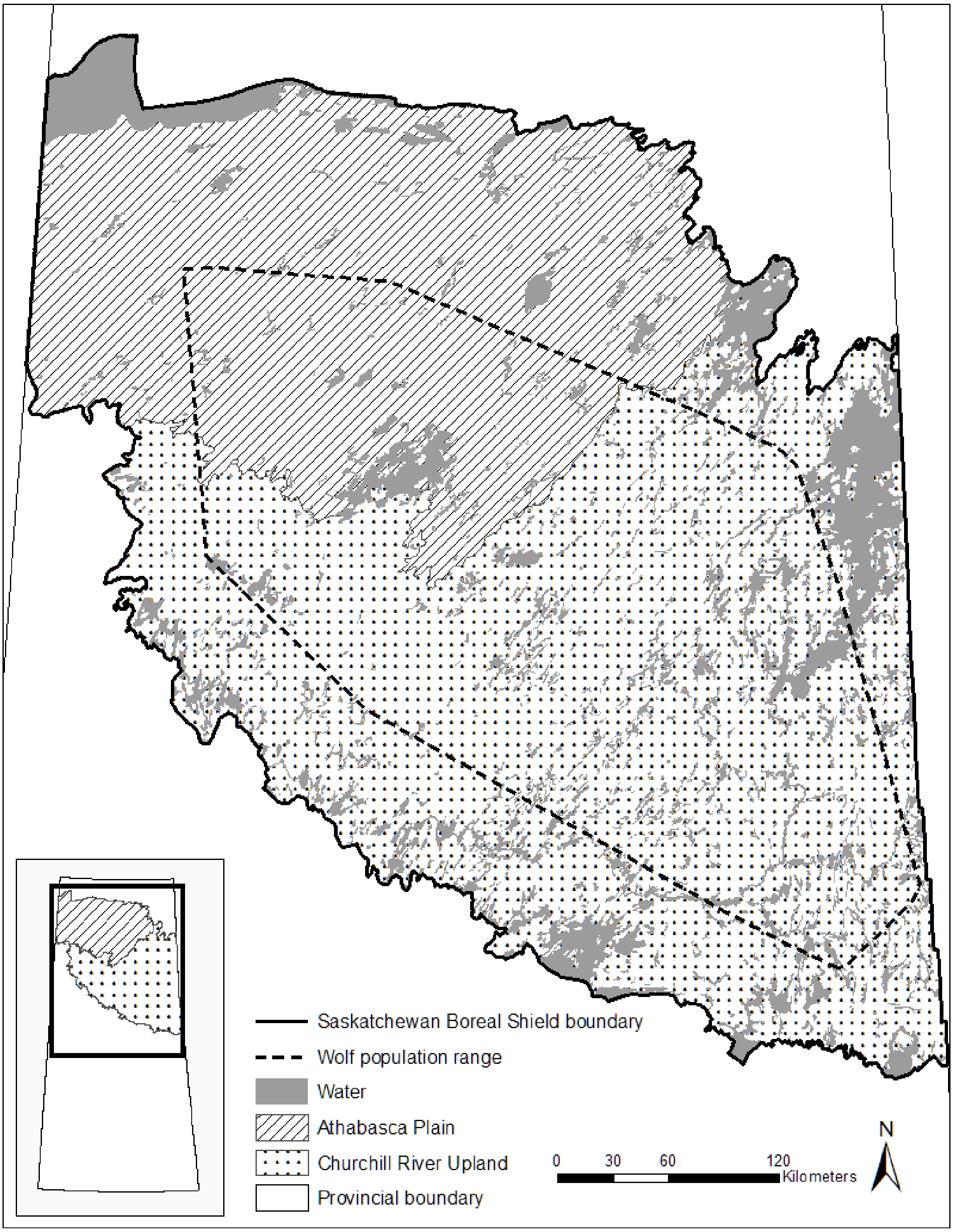

Figure 2.2. Study area defined by the multiannual composite range (minimum convex polygon) of global positioning system-collared wolves in the Saskatchewan Boreal Shield (SBS), Canada, 2014–2016. Water is represented in dark grey. The Athabasca Plain and Churchill River Upland ecoregions of the SBS ecozone are lined and dotted, respectively.

The next predicted response under DMAC is a quantitative increase in moose abundance in response to fire to which populations of predators, and in this specific case, wolves, would also increase in number. While I lacked the data necessary to conduct a direct study of this cascade link (e.g., longitudinal data and moose telemetry tracking data in my study area), I did have access to a series of 16 standardized aerial surveys specific to estimating densities (per 1,000 km^2) of moose and caribou (since 2009), and 1 survey specific to that of wolves (Appendices B, C). Based principally on the high levels of fire disturbance in the SBS, at the outset I predicted that if DMAC was of biological significance to caribou, moose and consequently wolf populations would occur at densities that could negatively affect caribou persistence.

It is now generally held that caribou populations are likely to be suppressed in environments supporting densities of ≥6.5 wolves/1,000 km^2 (A T Bergerud and Elliot 1986, Bergerud 1988, 1996). At <6.5 wolves/1,000 km^2, and certainly at <5.0 wolves/1,000 km^2, caribou populations are expected to grow if limited solely by natural predation by wolves in either a multi- or single-prey system (Bergerud 1988), noting here that the deterministic models upon which these statements have been based implicitly assume that caribou recruitment and mortality rates are also free of other density-dependent constraints including food limitation (i.e., modelled populations are well-below food carrying capacity). While defining these density thresholds was subjective, and notwithstanding the limitations of aerial survey data, I expected that in the highly burned SBS moose densities of >70 moose/1,000 km^2, which predicts a wolf density of 5.0 wolves/1,000 km^2 (applying the wolf-moose numerical response equation of Messier 1994), would minimally satisfy a DMAC-response cautionary to boreal caribou demography.

Furthermore, as wolves are often considered to be obligate-ungulate predators, ungulate biomass is widely accepted (and predictively modelled) to be positively related to wolf density at a macroecological scale (Keith 1983, Fuller 1989, Fuller et al. 2003, Cariappa et al. 2011, Kuzyk and Hatter 2014). Hence, combined with estimated caribou density in this system, in accordance with DMAC I also expected an ungulate biomass index (UBI) comprised predominantly of moose of at least 0.95 UBI/km^2 (computed on a per km^2 basis using standardized moose and caribou body-size equivalents following Keith [1983], Fuller et al. [2003], and Kuzyk and Hatter [2014]). This value would predict a wolf density of 5.0 wolves/1,000 km^2 following the refined (quadratic) UBI-wolf density equation of Kuzyk and Hatter (2014). I also expected my direct estimation of wolf density by winter aerial survey in the center of the study area to approximate or exceed this density if DMAC between moose and caribou was to be of significance in suppressing caribou population growth.

For wolves, a numerical response to increasing ungulate prey generally precipitates a decrease in territory size (Fuller et al. 2003). Indeed, territories of wolves can be used as a proxy for both wolf and prey density, where wolves in areas of high prey density have smaller home ranges (Messier 1994). Where moose is the primary prey, territory size appears to be inversely related to wolf habitat quality, which can be determined based on projected wolf use, probability of moose occupancy, and proportion of preferred land cover classes (Kittle et al. 2015). I predicted wolf territory sizes of resident (established) wolves to be within 1 standard deviation (*SD*) of the average observed for packs where the predominant prey is moose, assuming that under DMAC wolves will be switched on to moose rather than other prey (including caribou) in the system (in the sense of predator-switching; Messier 1994). Fuller et al. (2003) presented a range of wolf territory sizes of 250–1,645 km^2 ($n = 12$) in this context (excluding data from Isle Royale due to areal constraints) averaging 873 ± 506 km^2 ($\bar{x} \pm SD$), but noting that these values were also associated with a relatively high UBI/km^2 (2.69 ± 1.9 UBI/km^2) with no UBI <1.0/km^2.

If wolves had numerically responded to a disturbance-driven increase in alternative ungulate prey (moose) density, I expected pack sizes to reflect wolf strategies of hunting moose rather than smaller prey, including caribou, beaver, and hares. Wolf pack sizes can differ depending on the prey species consumed, and the largest packs are found where large-bodied ungulates are the principal source of prey. For example, MacNulty et al. (2014) showed that in Yellowstone National Park, capture success of elk (*Cervus canadensis*) did not improve beyond pack sizes of 6 wolves, but for wolves hunting bison (*Bison bison*) capture success did not asymptote until there were at least 9 to 13 wolves per pack, with the largest packs in North America occurring where wolves specialize on hunting this species (e.g., Carbyn et al. [1993] observed an average pack size of 9.1 wolves and up to 42 wolves/pack in Wood Buffalo National Park, Canada). In Minnesota, where wolf packs specialized on differing prey, packs that focused on deer averaged 5.1 wolves/pack compared to 8.2 wolves/pack for moose specialists (Barber-Meyer et al. 2016). Even in areas supporting high densities of wolves, if smaller species are the primary prey source, pack sizes can be quite small. For example, in Fuller's (1989) study of wolves in northeast Minnesota, where deer and beaver were the primary and secondary prey respectively, pack sizes averaged 4.9 wolves. Fuller et al. (2003) presented pack sizes averaging 6.9 ± 2.3 wolves ($\bar{x}$ ± *SD*) for 13 study areas across North America where moose were classed as the primary prey (including data from Isle Royale, 'all years'; mean pack size was 7.0 ± 2.4 wolves excluding these data). Territory size and pack sizes may therefore not correlate (Kittle et al. 2015), but if wolves in the study area were relying primarily on moose as a preferred prey, I expected wolves to have an average pack size within 1 *SD* of what has been observed for other moose-hunting wolf packs (Fuller et al. 2003).

In this study, I proposed to determine the likely strength of DMAC in the context of a disturbance-moose-wolf-caribou trophic cascade to limit boreal caribou populations in a wildfire-dominated, northern Canadian Shield ecosystem. I used a combination of vegetation sampling, ungulate and wolf density surveys, and locations of global positioning system (GPS)-collared wolves in the SBS (Figs. 2.2, 2.3) to test predictions of the role of DMAC on caribou ecology in the system. I aimed to determine the relative abundance of moose browse in recently burned versus older stands; to compare moose and caribou densities and determine corresponding ungulate biomass in the study area; to determine how wolves were distributed in the SBS both in terms of density and territory size; and to document pack sizes to make inferences regarding likely predation strategies of wolves in the system. The response of predators to disturbance is indirect in the context of DMAC but depends on a direct link between landscape disturbance and alternative ungulate-prey density or biomass. For this bottom-up cascade to initiate after fire, I expected that post-fire habitat in the study area would firstly present quantitative benefits in forage availability to moose (younger stands would contain more abundant moose browse). As this is the first study to document DMAC in such a region, I anticipated that my results would be of relevance to the relatively unstudied northern shield and taiga regions of Canada, where the largest populations of boreal caribou remain.

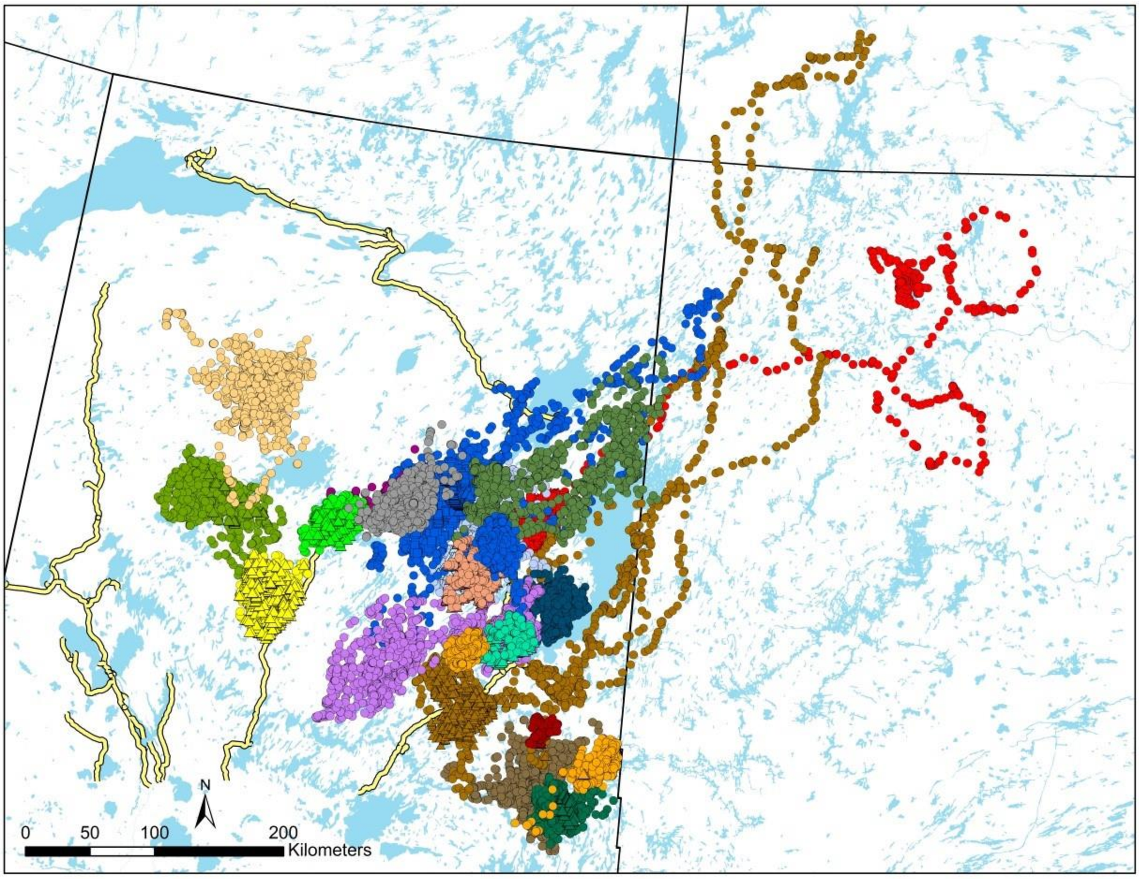

Figure 2.3. Global positioning system (GPS) location data obtained from 37 wolves (21 packs, 1 solitary wolf) ranging from northern Saskatchewan, Manitoba, and southern Nunavut, Canada, collected March 2014–2016. Circles, squares, and triangles represent GPS locations of individual wolves and symbol color indicates pack membership. Yellow lines are roads in the study area within Saskatchewan.

2.2 Study Area:

My study area included an 87,193-km^2 section of the 187,000-km^2 SBS, extending roughly from 55.0^o to 61.0^o N and −96.9^o to −108.6^o W (Figs. 2.1, 2.2). I defined this study area primarily from the movements of telemetry-tracked wolves from 2014 to 2016, which mostly overlaps with species tracked as part of a larger study of animal ecology in the system (including caribou and black bears; McLoughlin et al. 2019). Moose, boreal caribou, American black bear, wolf, lynx (*Lynx canadensis*), wolverine, beaver, and snowshoe hare were present in the study area, and cougar and white-tailed deer have been observed on rare occasions. Migratory barren-ground caribou (*R. t. groenlandicus*) of the Qamanirjuaq range were also present, during mid-winter, along the northern border of the study area. Recent mapping data (Stewart 2016, Greuel 2018, Hart et al. 2019, McLoughlin et al. 2019) collapsed 27 Forest Ecosite Classifications (FECs) for the province of Saskatchewan, Canada (Jiricka et al. 2002, M S McLaughlan et al. 2010), into 13 biophysical (terrestrial) land cover classes determined *a priori* to be meaningful to caribou and moose ecology (Stewart 2016; Appendix A). The study area largely consisted of young stands (aged ≤40 yrs) dominated by jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) at 36.9% and 5.0% terrestrial coverage, respectively, followed by mature stands aged >40 years with canopies dominated by these same species at 22.3% and 8.5% coverage, respectively. Black spruce-dominated bogs composed of trees >40 years (11.0%) and lowland bogs and fens with low tree cover (i.e., open muskeg; 9.1%) were also common vegetation associations. Despite the relatively young age of the forest, mixed-wood and hardwood-dominated stands of aspen (*Populus* spp.) and white birch (*B. papyrifera*) occurred at 7.0% coverage. Rare white spruce (*Picea glauca*)-dominated forest and sand dunes made up the remaining land cover classes.

Elevation ranged from 278–644 m, with higher elevations observed in the western half of the study area. The study area contained 2 ecoregions: Churchill River Upland, which contains exposed Precambrian Canadian Shield bedrock, and the Athabasca Plain, which is more homogeneous and composed of sandstone (Acton et al. 1998). The temperate continental climate of the area is also relatively dry. Total yearly precipitation was 482.5 mm, with 318.1 mm of rainfall and 164.4 cm of snowfall (Environment Canada 2015). Mean monthly temperature ranged from −22.3°C to 14.7°C, with a mean yearly temperature of −2.3°C (data from 1981–2010 at Key Lake, near the center of the study area; Environment Canada 2015).

Hart et al. (2019) reported the forest of the region to be resilient to fire, particularly with respect to jack pine stands, and that self-replacement was the most common postfire trajectory. The fire cycle is approximately 100 years (Parisien et al. 2004), but Environment Canada (2012) mapped 55% of the entire SBS as being burned in the last 40 years (based on 2010 data). When the study commenced, fire disturbance in the study area was similarly high (47.0% being burned in the last 40 years; McLoughlin et al. 2019). In comparison, total human disturbance (e.g., footprints of mine sites, communities, roads, trails, transmission lines) was low (0.18% of the study area), with anthropogenic linear features (cleared corridors) of all types occurring at 0.11 km of lines/km^2 (McLoughlin et al. 2019).

2.3 Methods:

2.3.1 Vegetation and Moose-Browse Availability:

The Johnson Plant Ecology Lab sampled the study area in summers 2014, 2015, and 2016 at 312 stratified random sites (n = 92, 114, 106 sites in each year, respectively). Stratification of the sampled plots was based on time since fire (Parisien et al. 2004) and dominant tree species. Each site consisted of a 10 × 10-m plot containing a 2 × 2-m subplot to estimate tree densities and vegetation composition. They determined vegetation community composition in the 4-m^2 subplots by estimating Braun-Blanquet cover classes for general ground cover, and lichen, moss, and vascular plant species. They also measured forest attributes at each plot, including soil characteristics, canopy cover, and collected tree disks and cores to determine stand age (range = 1–241 yr). Using these characteristics, they determined the ecosite type following the Saskatchewan FEC system (Jiricka et al. 2002, McLaughlan et al. 2010). Details of methods regarding site selection and stand aging are presented in Greuel (2018) and Hart et al. (2019).

The Johnson Plant Ecology Lab designated canopy dominance based on FEC type (coniferous BS3 through BS10, mixed conifer-deciduous BS13, BS14, and BS15; McLaughlan et al. 2010). Plots that they designated as coniferous were dominated by jack pine or black spruce and were further separated into stands of young (<10 yr; n = 57), intermediate (10–40 yr; *n* = 65), and mature ages (>40 yr; *n* = 79) to distinguish between recently disturbed, disturbed, and undisturbed habitat for range-planning purposes for boreal caribou (Environment Canada 2012). Plots designated as mixed coniferous-deciduous were those dominated by deciduous species, also divisible into young (*n* = 9), intermediate (*n* = 28), and mature (*n* = 8) stands using the same age breaks.

In assessing moose-browse availability, I first tested for the relative presence or absence of relevant browse species among stand types and forest age. For this purpose, I considered the occurrence of the species in at least the subplot or in the main plot as presence. Based on Shipley (2010), I limited my analysis to willows, small (<1.3 m) trembling aspen trees, and small (<1.3 m) birches. I tested for differences in frequency of each species in each stand type using 2-tailed *Z*-tests for proportion data (R version 3.2.5, www.r-project.org, accessed 1 Jun 2018). I also conducted multivariate analyses on the data, first transforming the data by adding a constant (0.01; to avoid including zero as a response) and then running a detrended correspondence analysis (DCA) to test whether the data were linear or unimodal, followed by a canonical correspondence analysis (CCA) to test for cover of moose-browse species across stand type and forest age using package vegan in R version 2.5-4 (Oksanen et al. 2019). Cover class of suitable moose-browse species in the subplot were the dependent variables and stand age (as a continuous variable) and type (coniferous or mixed wood) were environmental variables. My goal was to determine whether there were differences in availability of moose browse as a result of disturbance for the 2 main classes of conifer-dominated and mixed-wood forest types. I ran an analysis of variance (ANOVA) with 1,000 permutations on the results of the CCA to determine significance. If evidence of DMAC was present in SBS, I expected that post-fire habitat in the study area would present quantitative benefits in forage availability to moose. I anticipated this would improve coverage of deciduous species known to be of value for moose browse.

2.3.2 Animal Densities:

I estimated moose and caribou densities based on the arithmetic means obtained from 16 winter aerial surveys conducted by collaborating partners and the University of Saskatchewan in the study area from 2009–2014 (Appendix B). These survey blocks ranged in size from 320–2,285 km^2 and relied on a 100% coverage of parallel and immediately adjacent transects at 400-m strip width, or, for larger areas, a 40% area coverage using the same 400-m strip width. In all cases pilots flew helicopters at 50–150 m above ground level and at air speeds ranging from 70–100 km/hour; 3 recorders accompanied the pilot. When they observed animals, the pilot made complete turns to provide additional time for age and sex classification and an accurate count of the number of animals observed. Observers determined sex and age of moose and caribou using combinations of the presence or absence of antlers, antler scars, vulval patch, and nose color. They recorded all animal observations using hand-held GPS units and maps. These counts were minimum counts of species abundance. I conducted a sightability test using the survey method in 2015, which indicated that identification of caribou (n = 49) from the air was likely biased low because only 7 of 11 collared caribou inside the survey area bounds within the past 24 hours (from GPS telemetry locations) were observed (Appendix B). Because I had no data to model sightability of moose relative to caribou, I did not model imperfect detection in survey data in my analyses.

In addition to these aerial surveys, in February 2017, the Alberta Biodiversity Monitoring Institute (ABMI) conducted a wolf-specific density survey in the study area following methods specific to a search-image dedicated to estimating wolf density (Appendix C).

Based principally on the high levels of fire disturbance in the SBS, at the outset I predicted that if DMAC was of biological significance to caribou, moose and consequently wolf populations would occur at densities believed to be cautionary to caribou persistence.

Caribou populations are likely to be suppressed in environments supporting densities of ≥6.5 wolves/1,000 km^2 (Bergerud and Elliot 1986, Bergerud 1988, 1996). At <6.5 wolves/1,000 km^2, and certainly at <5.0 wolves/1,000 km^2, caribou populations below carrying capacity are expected to grow if limited principally by natural predation by wolves in either a multi- or single-prey system (Bergerud 1988). Although estimating these wolf-density thresholds for SBS was subjective, and notwithstanding the limitations of aerial survey data, I expected that in the highly burned SBS moose densities of >70 moose/1,000 km^2, which predicts a wolf density of 5.0 wolves/1,000 km^2 (applying the wolf-moose numerical response equation of Messier 1994), would be the minimum threshold to satisfy a DMAC-expected response to boreal caribou demography. I also expected my direct estimation of wolf density by winter aerial survey in the center of the study area to approximate or exceed this density if DMAC between moose and caribou was to be of significance in suppressing caribou population growth.

2.3.3 Ungulate Biomass Index and Predicting Wolf Density:

Following the same scoring as Keith (1983), Fuller et al. (2003), and Kuzyk and Hatter (2014), I calculated the ungulate biomass index (UBI/km^2) for the study area from the average minimum moose + boreal caribou densities I acquired from aerial survey data (moose/1,000 km^2 × 6 + caribou/1,000 km^2 × 2 = UBI/km^2). I specifically excluded biomass that may have been seasonally present from wintering barren-ground caribou and other prey (e.g., beaver). Assuming (initially) that moose were the preferred prey for wolves, I used the numerical response equation presented in Messier (1994) to predict wolf from moose density ($y = [3.36x]/[0.46 + x]$, where y = moose killed/wolf/100 days and x = moose/km^2), which I compared with the linear equation in Fuller et al. (2003) designed to predict wolf density based on UBI/km^2 ($y = 3.5 + 3.27x$, where y = wolves/1,000 km^2 and x = UBI/km^2). I further predicted wolf density based on the quadratic equation of Kuzyk and Hatter (2014), which was recently refined from the Fuller et al. (2003) model to include a zero-intercept ($y = 5.40x - 0.166x^2$, where y = wolves/1,000 km^2 and x = UBI/km^2), which could be important at low-ungulate UBI (Cariappa et al. 2011). I estimated 95% confidence intervals around estimates of ungulate biomass and wolf density using non-parametric bootstrapping with 50,000 iterations in Program R.

For predictions supporting the hypothesis of DMAC, I expected a UBI composed predominantly of moose of >0.95 UBI/km^2. This value would predict a wolf density of 5.0 wolves/1,000 km^2 following the refined (quadratic) UBI-wolf density equation of Kuzyk and Hatter (2014).

2.3.4 Wolf Captures, Territories, and Pack Sizes:

Between March 2014 and May 2016, the McLoughlin Population Ecology Lab tracked 37 wolves (15 males, 19 females, 3 unrecorded sex) representing 22 packs in the study area using GPS telemetry collars (Lotek Iridium® TrackM 2D; Lotek, Newmarket, ON, Canada). In March 2014, they deployed 25 GPS-collars (10 males, 12 females, 3 unrecorded sex) representing 15 packs. In March 2015, these were supplemented by 12 GPS-collars (5 males, 7 females), 9 of which were distributed between 7 novel packs and 3 were deployed on wolves in packs with a previously collared individual to improve sample sizes following collar malfunction and wolf mortality after the first year of tracking. They captured all wolves and equipped them with collars after physical immobilization (net gun) through the services of Bighorn Helicopters (Cranbrook, British Columbia, Canada) following an animal care protocol approved by the University of Saskatchewan (protocol 20130127), guided by the Canada Council on Animal Care and the University of Saskatchewan Animal Research and Ethics Board, and a permit from the Saskatchewan Ministry of the Environment (permit 14FW037). Capture teams recorded pack size at time of capture.

The GPS-collars were scheduled to record wolf locations every 3 hours and had an average fix-rate success of >94%. I removed all non-fixes, 2-dimensional fixes, and fixes with low horizontal dilution of precision (e.g., >10; Adams et al. 2013) from the dataset (n = 5,051) and used only 3-dimensional fixes or better for estimating territory sizes (n = 94,045). I truncated the resulting GPS data to match the time of collaring and suspected time the collar was dropped or deemed stationary. Following Kusak et al. (2005) and Mattisson et al. (2013), I removed wolves with <9 months of data to obtain accurate estimations of home range size. The remaining 17 wolves generated 61,851 GPS fixes, with 2,045–6,005 locations/wolf ($\bar{x}$ = 3,632, *SD* = 1,214). By visually inspecting wolf movement patterns and following Hinton et al. (2016), I separated collared animals into resident (n = 13, those with a consistent home range) and transient wolves (n = 4, those that were either migratory or dispersing).

I calculated territory sizes of resident wolves on an individual basis. On 2 occasions, they collared a pair of wolves in the same pack in the study, although in both cases 1 individual was classified as transient and therefore did not affect my analysis of mean territory size. Because there are various methods for home range analysis and there is some debate and recent improvement in home range analysis (Fleming et al. 2015, 2018), I provided home range estimations from 4 different methods for comparison. I calculated 100% and 95% minimum convex polygon (MCP), and 95% kernel density estimator (KDE) home ranges in R using the adehabitatHR package, version 0.4.15 (Calenge 2006). I calculated the 95% KDE using the *ad hoc* method for unbroken home ranges (Kie 2013). To account for spatio-temporal auto-correlation in the telemetry data, I also estimated a 95% weighted autocorrelated kernel density (AKDE) home range using the autocorrelated Gaussian reference function bandwidth with debiased area (Fleming et al. 2015, 2018) available in the ctmm (continuous-time movement modeling) package (version 0.5.1) in R (Calabrese et al. 2016). In this method, the optimization of the smoothing bandwidth explicitly accounts for autocorrelation in the data using an autocorrelated movement model. Specifically, I used a fitted Ornstein-Uhlenbeck-F (OUF) motion model characterized by a continuous, correlated velocity motion restricted to a finite home range using initial model parameters obtained from the empirical variogram of the telemetry data, which provides a means of visualizing autocorrelation structure (Fleming et al. 2014).

2.4 Results:

2.4.1 Vegetation and Moose-Browse Availability:

All moose-browse species occurred significantly more frequently in intermediate (10–40-yr-old) mixed conifer-deciduous stands than in intermediate conifer-dominated (jack pine or black spruce) stands (Table 2.1). Small birch occurred more in mature (>40) mixed conifer-deciduous stands than in mature conifer stands (Table 2.1). Aspen was also more common in young mixed wood compared to young conifer stands (Table 2.1). For conifer stands, age only significantly affected willow presence, with young stands having significantly more willows than older stand types and intermediate stands having more willows than mature stands (Table 2.1). In mixed-wood stands, small birches were more common in intermediate than young stands (Table 2.1). All other comparisons were non-significant (Table 2.1). For my multivariate analyses, initial exploration of the vegetation data using DCA found that the data would fit a unimodal better than linear distribution. The first canonical axis of the CCA explained nearly all the variance in stand type (0.974 factor score; 97.4% of the variance) but only explained stand age to a lesser extent (−0.35 factor score; 35% of the variance; Table 2.2), meaning stand type was the main criteria used in the model. The results indicated that small trembling aspen and small white birch occurred with greater cover in mixed wood over conifer stands and willows presented greater cover in conifer stands (Table 2.2). Younger stands had greater cover of small trembling aspen and white birch, whereas older stands had greater cover of willows (Table 2.2), though, as stated above, effect sizes of age were small

(Table 2.2). Results from 1,000 permutations of the ANOVA of axes of the CCA indicated only the first canonical axis was significant (CCA1: χ_1^2 = 0.018, F = 6.571, P = 0.007; CCA2: χ_1^2 = 0.0002, F = 0.063, P = 0.934). I ran an ANOVA with 1,000 permutations for the CCA results (F = 3.317, P = 0.019) and the R^2 of the model was very low (0.027). These results did not meet my criteria for evidence of DMAC, as post fire habitat did not improve coverage of preferred moose browse species.

Table 2.1. Frequency (%) of occurrence of common moose-browse species (willows, small [<1.3 m] trembling aspen, and small [<1.3 m] white birch) of sampled conifer-dominated and mixed-wood (deciduous-conifer) cover types of different ages of the Saskatchewan Boreal Shield, Canada, 2014–2016. Conifer stands (con) had young (Y; <10 yr, $n = 57$), intermediate (I; 10–40 yr, $n = 65$), and mature (M; >40 yr, $n = 79$) age classes. Mixed conifer-deciduous stands (mix) also had young ($n = 9$), intermediate ($n = 28$), and mature ($n = 8$) age classes. I conducted comparisons using 2-tailed Z-tests for proportions (significance as P).

Species	Conifer		*Z*	*P*	Mixed conifer-deciduous		*Z*	*P*	Stand age		*Z*	*P*
Willow	Y	I			Y	I			Y Con	Y Mix		
	54.4	29.2	2.87	0.004**	55.6	75.0	−1.00	0.317	54.4	55.6	−0.06	0.950
	Y	M			Y	M			I Con	I Mix		
	54.4	11.4	5.68	≤0.001***	55.6	37.5	0.71	0.477	29.2	75	−4.54	≤0.001***
	I	M			I	M			M Con	M Mix		
	29.2	11.4	2.65	0.008**	75.0	37.5	1.87	0.062	11.4	37.5	−1.40	0.162
Trembling aspen	Y	I			Y	I			Y Con	Y Mix		
	22.8	16.9	0.81	0.421	77.8	71.4	0.37	0.710	22.8	77.8	−3.49	≤0.001***
	Y	M			Y	M			I Con	I Mix		
	22.8	12.7	1.50	0.133	77.8	50.0	1.16	0.246	16.9	71.4	−5.52	≤0.001***
	I	M			I	M			M Con	M Mix		
	16.9	12.7	0.71	0.478	71.4	50.0	1.03	0.303	12.7	50	−1.94	0.053
White birch	Y	I			Y	I			Y Con	Y Mix		
	24.6	33.8	−1.13	0.260	44.4	82.1	−1.98	0.048*	24.6	44.4	−1.08	0.282
	Y	M			Y	M			I Con	I Mix		
	24.6	24.1	0.07	0.946	44.4	62.5	−0.71	0.477	33.8	82.1	−5.11	≤0.001***
	I	M			I	M			M Con	M Mix		
	33.8	24.1	1.28	0.199	82.1	62.5	1.00	0.319	24.1	62.5	−2.03	0.042*

* $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$.

Table 2.2. Species scores on Axis 1 and 2 of a canonical correspondence analysis (CCA) performed on sampled (n = 312) conifer-dominated and mixed-wood (deciduous-coniferous) stands of different ages (1–241 yrs) of the Saskatchewan Boreal Shield, Canada, 2014–2016. Presented are species scores based on Braun-Blanquet cover types for common moose-browse species (willows, small [<1.3 m] trembling aspen, and small [<1.3 m] white birch), biplot scores for constraining variables, and results of a 1,000-permutation analysis of variance (ANOVA) of axes. Environmental variables included stand types of coniferous and mixed-wood and the continuous variable stand age.

Species scores	CCA Axis 1	CCA Axis 2
Willows	−0.182	0.007
Trembling aspen	0.14846	0.013
White birch	0.034	−0.017
Biplot scores for constraining variables		
Stand age	−0.345	0.939
Stand type: mixed-wood	0.974	0.226

2.4.2 Animal Densities:

From aerial surveys in the study area (Appendix B), I computed an average density of 36.9 caribou/1,000 km^2 (95% CI = 26.7–47.2 caribou/1,000 km^2) and 45.7 moose/1,000 km^2 (37.8–53.6 moose/1,000 km^2; Table B1). The February 2017 wolf survey (Appendix C) observed 3.6 wolves/pack and 3.1 wolves/1,000 km^2 (no CI for this point estimate). Neither the surveyed moose density nor the wolf density met my a priori threshold for evidence of DMAC as a means of suppressing caribou population growth (>70 moose/1,000 km^2, and ≥5.0 wolves/1,000 km^2).

2.4.3 Ungulate Biomass Index and Predicting Wolf Density:

Total moose plus boreal caribou biomass in the study area was 0.36 UBI/km^2 (95% CI = 0.27–0.48 UBI/km^2). Following equations presented in Messier (1994) and based on the observed average moose density, I estimated that wolves in the study area would be encountering and killing moose at a rate of 0.30 moose killed/100 days/wolf (95% CI = 0.22–0.43 moose killed/100 days/wolf), and in numerical terms moose would support a density of

<2.0 wolves/1,000 km^2. The linear equation of Fuller et al. (2003) predicted wolf densities of 4.7 wolves/1,000 km^2 (95% CI = 4.40–5.08 wolves/1,000 km^2), whereas the quadratic equation of Kuzyk and Hatter (2014) predicted a wolf density of 1.9 wolves/km^2 (95% CI = 1.47–2.57 wolves/ km^2). The calculated UBI did not meet the minimum threshold as a means of suppressing caribou population growth ($>$0.95 UBI/km^2).

2.4.4 Wolf GPS Locations, Territories, and Pack Sizes:

I tracked 37 wolves in the study area from March 2014–May 2016. During the monitoring period, 28 of the GPS-collars went offline (76%), 6 wolves were confirmed dead (16%), 1 collar prematurely released (3%), and 2 stationary collars were not investigated (5%). Seventeen (46%) wolf collars lasted ≥1 year on the animal and 2 collars (5%) lasted ≥2 years. Mean territory size of resident wolves was 4,358 km^2 (*SE* = 839 km^2) and 2,865 km^2 (*SE* = 595 km^2) for the 100% and 95% MCP, respectively. Territories averaged 2,687 km^2 (*SE* = 515 km^2) for the 95% KDE and 3,316 km^2 (*SE* = 751 km^2) for the 95% AKDE (Table 2.3). The 100% MCPs of transient wolves ranged from 12,132–87,627 km^2, all 4 of which were larger compared to resident wolves (Table 2.3; Fig. 2.3). Wolf packs (≥2 individuals) with size recorded at capture ($n = 21$) ranged from 2–10 wolves with a mean of 4.00 ± 2.32 wolves/pack ($\bar{x} \pm 1$ *SD*; *SE* = 0.51). The average pack size of wolves in SBS was lower and territory size was much larger than would be expected under the expectations of DMAC as proposed by Fuller et al. (2003).

Table 2.3. Wolf identification (ID), sex, pack size, and home range estimate (km^2) of wolves of the Saskatchewan Boreal Shield (2014–2016) in Canada using the following methods: 100% and 95% minimum convex polygon (MCP), 95% kernel density estimator (KDE), and 95% weighted autocorrelated kernel density (AKDE) home range. Only wolves with ≥9 months of data are included. I include mean, standard deviation, and standard error of home ranges for the 13 resident wolves. I also estimated the mean home range size excluding wolf 140023, given its large area.

ID	Sex	Pack size	100% MCP	95% MCP	95% KDE	95% AKDE
Resident wolves						
140004	F	6	3,194	1,114	953	1,012
140005	F	2	2,158	1,182	1,086	1,120
140007	F	5	7,855	4,372	3,795	6,001
140008	M	2	8,211	6,391	4,866	6,767
140010	M	4	3,507	2,381	2,260	2,336
140017	F	5	2,218	1,390	1,262	1,521
140019	M	5	1,735	1,551	1,688	1,752
140021	M	Unknown	2,011	1,476	1,498	1,717
140023	F	10	11,184	7,111	7,026	9,568
140027	F	3	2,566	2,013	2,540	2,605
140037	F	2	1,841	949	1,098	1,149
140038	F	2	4,213	2,099	2,263	2,234
140039	F	9	5,958	5,220	4,594	5,325
$\bar{x}$			4,358	2,865	2,687	3,316
SD			3,023	2,145	1,857	2,707
SE			839	595	515	751
Transient wolves						
140009	M	6	87,627	59,978	82,729	119,655
140015	F	Unk.	12,132	9,843	8,734	18,844
140018	F	2	17,265	13,071	11,728	22,508
140020	M	6	33,631	22,670	18,269	23,701
Resident wolves excluding 140023						
$\bar{x}$			3,789	2,511	2,325	2,795
SD			2,320	1,801	1,381	2,036

SE	670	520	399	588

2.5 Discussion:

Despite the high fire frequency in the study area, the Saskatchewan Boreal Shield presently supports a relatively low density of moose and, for the species, a relatively high density of boreal caribou. This is the first indication that DMAC, which is predicated on a numerical response of alternative prey and related inverse response by caribou to disturbance (via predation), shows signs of decoupling in the study area. Low densities of alternative prey relative to caribou are not known for any region where DMAC has been suggested as a primary limiting factor to caribou (Latham et al. 2011*a*, *b*, Hervieux et al. 2013, Peters et al. 2013, Serrouya et al. 2019).

Across the entire study area and all years, moose were only slightly more abundant than caribou (Table B1). However, caribou density was 2–3 times greater in comparison to averages reported for most other boreal caribou ranges in Canada (caribou density reported in orther areas ranged 4.3–18.7/1,000 km^2; Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2014). The SBS's high caribou density reinforces the hypothesis of Stewart et al. (2020) that caribou can tolerate natural disturbance. In contrast, the density estimates for moose rival the lowest reported for populations where moose and wolves are sympatric in North America (Messier 1994, n = 33 study areas) and compared well with other northern boreal shield regions including the Pickle Lake and Nakina regions of Ontario (24 and 46 moose/1,000 km^2, respectively; Kittle et al. 2015). Brewster (1988) and Trottier (1994), conducting surveys in a 5,000-km^2 area near Key Lake, in the center of the study area, reported similar low moose (30 moose/1,000 km^2 and 20 moose/1,000 km^2, respectively) and caribou densities (43 caribou/1,000 km^2 and 38 caribou/1,000 km^2, respectively). These older surveys and the SBS-wide survey data are not entirely comparable, however, because spatial extent and methods are not standardized. Yet, the ratio of moose:caribou detection has remained similar over the past 30 years in the Key Lake area; Brewster (1988) and Trottier (1994) averaged a ratio of 0.61 moose:caribou, and from 2011–2014 the ratio averaged 0.68 for the same area (Table B1).

Notwithstanding the limitations of comparing aerial survey data, an important conclusion from the densities observed in the SBS is that the ratio of moose to caribou when compared across the study area is not far from unity (~1.2), with 7 of 13 surveys offering direct comparisons indicating more moose than caribou, 5 of 13 surveys observing more caribou than moose, and 1 survey balancing abundance at 1:1 (Table B1). This contrasts with what has been observed in areas where DMAC is expected to be a major limiting factor for caribou. For example, in northeast Alberta, Latham et al. (2011*b*), using direct line flight paths (Latham et al. 2013), recorded 3.0–4.8 moose/100 km flown (yrs 2005–2007, respectively), 1.8–5.2 deer/100 km, and 0.9–2.3 caribou/100 km. These estimates translate into moose:caribou abundance ratios of 3.3 in 2005 and 2.1 in 2007 and deer:caribou ratios of 2.0 and 2.3, respectively. Because the SBS has no deer, the alternative prey:caribou abundance ratio in the study is clearly lower than expected at least in comparison to what is known from the Boreal Plains of eastern Alberta. This is despite the relatively young age of the forest in the SBS. This is not to say that moose do not benefit from landscape disturbance, only that despite the very high amount of disturbance on the landscape and relatively young forest in the SBS, the limited numbers of moose on the landscape in relation to caribou are wholly unexpected under DMAC. I conclude that moose must be limited more strongly by something other than amount of disturbance, including, possibly, reverse apparent competition with caribou and the successional dynamics of the system. This topic requires further research, although I suspect that this is one reason why, in latitudinal space, a moose-deer-caribou-wolf system gives way eventually to a caribou-wolf system.

The observed decoupling of moose and caribou densities from disturbance is likely related to the poorly productive shield ecosystem of the study area and successional dynamics that favor conifers at all seral stages, resulting in limited production of deciduous browse post-disturbance. With jack pine and black spruce stands predominantly self-replacing and within relatively short periods of time (Hart et al. 2019), the SBS contrasts strongly with the successional dynamics of forests typical of southern, more productive boreal caribou ranges. Indeed, despite the high extent of wildfire in the region, the vegetation-mapping work determined that there was little hardwood or even mixed-wood land cover (7.0% of the landscape) available to browsing species like moose (Stewart 2016, Hart et al. 2019). The sampling of vegetation plots also indicated that common moose-browse species were more likely to occur (presence, absence) and small aspen and birch had more cover (in terms of Braun-Blanquet cover class) in intermediate (10–40 yr old) mixed-wood (deciduous) stands compared to intermediate conifer-dominated stands. Young (<10) conifer-dominated stands had more presence of willows than intermediate and mature conifer stands (Table 2.1); however, older conifer stands had more cover (Table 2.2), meaning fire does not improve available browse of willows. Overall, based on the presence and cover of browse species, the best stand type for moose browse was mixed-wood stands regardless of age, of which there were few on the landscape.

DeMars et al. (2019), working to the west of my study area, principally in Alberta and the northeast Taiga Plains of British Columbia, observed that moose did not select for recently burned (≤40 yr) areas regardless of land cover type. Echoing DeMars et al. (2019), I too question the role of natural disturbance as being a principal factor influencing moose-related DMAC, at least in the absence of other alternative prey such as white-tailed deer or substantive anthropogenic disturbance, both of which were negligible in my study area. Gagné et al. (2016) reported that moose selected for clear-cuts only at low latitudes in their study area in Québec, Canada, where the availability of deciduous vegetation and net primary productivity was higher, suggesting that moose responses to fire, and hence DMAC, may be predicated on the modulating effects of primary productivity. I believe that in the SBS there is a diminished relationship between extent of natural disturbance and how moose respond to it. The weakening of this link in relation to areas where the hypothesis of DMAC (as a limiting factor for boreal caribou) was initially developed appears to be due to macroecological habitat differences including successional dynamics after fire (Hart et al. 2019). In a broad-scale sense, I expect these differences to be underlain by the decline in net primary productivity with increasing latitude in the northern hemisphere (Rosenzweig 1968) and subsequent lack of browse generated for moose after fire (data herein, Gagné et al. 2016). That is, the strength of DMAC in the context of caribou is likely modulated by primary productivity, which I can generally term here as the primary productivity hypothesis of DMAC.

The above conclusion is reinforced by how wolves, the primary predator of boreal caribou, responded to the high levels of natural disturbance in the SBS. Observed densities of wolves were low, mirroring the low density of moose. My wolf-survey estimate of 3.1 wolves/1,000 km^2 was 3–4 times lower than what has been observed in areas with documented DMAC (e.g., 11.0 wolves/1,000 km^2 in west-central Alberta [Kuzyk 2002]; 11.5 wolves/1,000 km^2 for northeast Alberta [Latham et al. 2011*b*]; 25 wolves/1,000 km^2 prior to wolf control in the Little Smoky caribou range of Alberta [Hervieux et al. 2013]). Notably, these areas have much higher densities of ungulate biomass than does the SBS.

In more productive systems like the foothills and boreal plains of Alberta and low-elevation slopes of the Rocky Mountains of British Columbia, where evidence supporting DMAC has been reported, total ungulate biomass was much higher. Moose densities can be as high as 120–250 moose/1,000 km^2 (e.g., Little Smoky, Alberta, pre-wolf removal [unpublished data cited in Kuzyk et al. 2006]). But the alternative-prey guild is also diverse, including populations of elk (*Cervus canadensis*), mule deer (*O. hemionus*), and white-tailed deer. In one caribou range in northeast Alberta, Latham et al. (2011*b*) estimated deer densities as high as 1,700 deer/1,000 km^2, whereas Ranger and Anderson (2012) reported 260 moose and 490 deer/1,000 km^2 for a related portion of caribou range in 2011. Alternative ungulate prey densities in this area (approximating wildlife management unit 516) translate into an ungulate biomass of 2.05 UBI/km^2, even excluding boreal caribou (calculated following equations in Keith 1983, Fuller et al. 2003, Kuzyk and Hatter 2014). In contrast, in the SBS, total moose + boreal caribou biomass may locally be as low as 0.36 UBI/km^2. The latter is lower than any UBI observed in the 32 studies reviewed by Fuller et al. (2003).

Resident wolves of the SBS also exhibited notably large territories (4,358 km^2 100% MCP) compared to wolves living in more productive environments (e.g., 1,087 km^2 100% MCP in northeast Alberta [Latham 2009]; 937 km^2 100% MCP in west-central Alberta [Kuzyk 2002]). Even excluding transient ranges, resident territories were also twice as large (2,687 km^2 95% KDE) as those in other areas of low ungulate biomass (1,395 km^2 95% KDE in Yukon Flats of north-central Alaska; Lake et al. 2013, 2015). The smallest territories for wolves have been noted in areas of exceptionally high ungulate biomass. For example, Fuller (1989), in northeast mainland Minnesota, USA, reported a mean territory size of 116 km^2 where white-tailed deer densities were estimated at 6,200 deer/1,000 km^2 and moose at 20 moose/1,000 km^2, translating into 6.3 UBI/km^2 (following equations in Keith 1983, Fuller et al. 2003, Kuzyk and Hatter 2014). Kittle et al. (2015) observed that wolf territory size was inversely related to wolf habitat quality, measured as projected wolf use, probability of moose occupancy, and proportion of preferred land cover classes. The large territory sizes for resident wolves observed in the SBS is consistent with low overall ungulate biomass.

The largest ranges for wolves occur in tundra and taiga environments, where packs make seasonal movements with migratory barren-ground caribou. For example, 95% MCPs were 63,058 km^2 for males and 44,936 km^2 for females for wolves tracking movements of the Bathurst caribou herd in central Canadian Arctic (Walton et al. 2001), and the 100% MCP was 45,848 km^2 for wolves in northeast Manitoba, Canada (Scurrah 2012). Stephenson and James (1982) and Ballard et al. (1997), working in northwest Alaska, showed that wolves only migrated with the western Arctic caribou herd in years when alternative ungulate prey densities were too low to sustain territories. Several of the transient wolf packs I followed appeared to follow the movements of the Qamanirjuaq (barren-ground) caribou herd (Fig. 2.3), which calves in the Kivalliq region of Nunavut but winters as far south as the northern borders of my study area (Nagy et al. 2011, COSEWIC 2016). On 2 occasions, collared pack males diverged in their patterns; 1 remained within the territory and the other became transient. The adult female of my largest resident home range (wolf 140023, 100% MCP = 11,200 km^2; Table 2.3) was suspected of becoming transient near the end of her tracking history. Such variable behavior might be expected where prey densities needed to support territories are marginal. A similar mix of transient and resident territories was noted by Scurrah (2012) for wolves in boreal shield and taiga ecosystems in Manitoba, which also bordered the range of Qamanirjuaq caribou.

I also found that wolf packs of the SBS were relatively small in size, with approximately 4 wolves/pack. Indeed, Fuller et al. (2003) estimated an average pack size of 6.5 wolves from 11 studies across North America where moose were prey (Kuzyk [2002] and Latham [2009] had averages of 8.2 and 7.8 wolves/ pack, respectively). Small pack size is not unusual for other low-density wolf populations existing in areas with moose densities similar to those in the Boreal Shield of Saskatchewan (Lake et al. 2015). For instance, Kittle et al. (2015, 2017) observed pack sizes averaging 4.5 wolves/pack (*n* = 17) in the Nakina region and 3.8 wolves/pack (*n* = 12) in the Pickle Lake region of northern Ontario's Shield Ecozone (computed from Kittle et al. 2017: appendix S1).

While total ungulate biomass available is significantly and positively related to wolf density in North America, the same is not true for pack size (Fuller et al. 2003). Wolves are not prey specialists, but regularly feed on prey ranging in size from arctic hares and beavers to moose and bison (Fox-Dobbs et al. 2007, Mech 2007, MacNulty et al. 2014, Neufeld 2018).

Hunting tactics and efficiency or risk to wolves are likely to differ considerably depending on the prey species consumed. Therefore, pack sizes may better reflect the primary prey base used by wolves rather than total biomass of ungulates on the landscape. The observed pack sizes here strongly suggest that moose, despite being higher in biomass on the landscape than are boreal caribou, are perhaps not the primary prey of wolves. Instead, it is more likely that smaller prey such as caribou and beaver are more important to the diet of wolves in the Boreal Shield of Saskatchewan.

Boreal woodland caribou are neither listed as a primary nor secondary prey source in Fuller et al.'s (2003) meta-analysis of ungulate biomass relative to wolf densities in North America. In northeast Alberta, Latham et al. (2011*b*) reported that caribou rarely factored into the scat-content of wolves (5%) compared to moose (18.6%), white-tailed deer (40.8%), and beaver (47.9%). But even prior to the observed 17.5× increase in deer densities and widespread landscape disturbance reported in the Latham et al. (2011*b*) study area, when wolves were preying more commonly on moose (64% of scats), beaver (14.7%) and deer (9.4%) still out-ranked caribou (0.5%) as a component of wolf diet.

Where boreal caribou have been studied in the absence of white-tailed deer, diets of wolves can still be biased towards moose (e.g., Tremblay et al. 2001), but this likely depends on the availability of moose and pack size. In Tremblay et al. (2001) ungulate densities occurred at 80 moose/1,000 km^2 compared to 33 boreal caribou/1,000 km^2, while wolf densities of the region were 7.4 wolves per 1,000 km^2. Biomass consumed by these packs ranged from 65.2 to 96.3% moose, while caribou generally factored in as <2% of biomass consumed. However, in the shield and taiga of northern Manitoba, by performing stable-isotope analyses of wolf hair, Moayeri (2013) found that boreal woodland caribou were primary summer prey for wolves in northern ranges of their study area even where rare, while moose were the primary prey farther south, followed by caribou (with beaver also providing important contributions). Some migratory wolves consumed up to half their summer diet from Qamanirjuaq barren-ground caribou (Moayeri 2013), matching with Scurrah's (2012) observations that wolves of the region moved widely between boreal caribou and barren-ground caribou ranges. While I currently do not know the diet of wolves in the Boreal Shield of Saskatchewan, I believe that they are most likely to have diets similar to those observed in northern Manitoba (Moayeri 2013), with caribou and beaver as the two main food sources. Upon considering the literature, the densities at which I observed wolves (3.1/1,000 km^2) and their average pack sizes (4.0 wolves/pack), the moose (47/1,000 km^2) and boreal caribou densities (37/1,000 km^2) documented, and the seasonal presence of Qamanirjuaq caribou in the north, caribou are possibly more important to wolves than are moose. In fact, I would go so far as to argue that in terms of apparent competition, it may be that the caribou in the region may be more detrimental to moose than vice versa. Future research on diet of wolves from archived samples, along with a resource selection function study currently underway, may help me to better frame this hypothesis.

Although DMAC has been shown to be a very likely and strong limiting factor to caribou within the inference space of southern boreal (and mountain) caribou range, all instances of this have thus far been indicated for areas characterized by higher (relative) net primary productivity, as is found in lower elevations and especially in the foothills of the

Rocky Mountains, the boreal plains, and southern boreal shield (e.g., indicated by forests capable of supporting commercial forestry within or in close proximity to caribou habitat); and areas of high biomass of alternative-ungulate prey within or near caribou refugia that include not only moose but other species (especially white-tailed deer) as alternative-ungulate prey for predators. I believe these conditions are jointly influenced, in a general sense, by the amount of energy available within the system to generate the trophic cascade necessary to link predator-caribou-alternative prey dynamics. The SBS deviates from the above, and, on a macroecological scale, so does much of extant boreal caribou range in Canada (i.e., most, if not all, northern boreal shield and taiga populations). Understanding where DMAC does and does not apply to boreal caribou and the extent to which it should factor into how we manage populations (e.g., whether for harvest, disturbance type, or scale of disturbance) is an important topic of future research. We need to develop a better understanding of the extent to which DMAC is influenced by the competitive dynamics of different alternative-prey species (e.g., white-tailed deer vs. moose), the associated ecology of invasive alternative prey and predators in the boreal (deer, coyotes), species richness including numbers of predators available to limit caribou, relationships between net primary productivity and DMAC in the context of climate change, and the nature of the influence of anthropogenic versus natural disturbance on DMAC.

2.6 Management Implications:

Northern caribou ranges, such as the Saskatchewan Boreal Shield, have thus far received very little attention. This is not surprising as most research on woodland (boreal and mountain) caribou occurs in areas of substantive resource extraction and in the context of industrial impacts on caribou population viability. Excepting the longitudinal and fundamental research programs on caribou of Newfoundland (e.g., Schaefer and Mahoney 2013, Mahoney et al. 2016, Schaefer et al. 2016), almost all work on non-migratory woodland caribou occurs in the boreal plains of western Canada, the southern shield region of Québec and Ontario, and with respect to mountain caribou, in heavily developed regions of the Rocky Mountains. Caribou are rarely studied in areas where logging or oil and gas development are not occurring. Yet, it is in the northern boreal shield and taiga where the majority of Canada's boreal caribou exist, both in terms of numbers of individuals and extent of range. This includes approximately 62.5% of extant boreal caribou range (1.5 million km^2) classed as (northern) western and eastern Canadian shield, where moose are the only alternative ungulate prey available in the context of DMAC, forests are characterized by generally low net primary productivity (e.g., <0.3 kg C/m2/year; see Lui et al. 2002), and linear features on the landscape occur at levels similar to that of the Saskatchewan Boreal Shield (i.e., 0.1–0.5 km lines/km2).

The fact that a considerable majority of boreal caribou range in Canada occurs in these low-productivity boreal moose-caribou-wolf systems only highlights how understudied they have thus far remained. At present, our management approach to boreal caribou throughout their Canada-wide range—encompassing roughly 2.4 million km^2—is predicated on the assumption that DMAC is an important consideration for all boreal caribou populations (Environment Canada 2011, 2012, Environment and Climate Change Canada 2017). But the supposition that large-scale wildfire disturbance, resulting in younger forests, can generate the habitat conditions necessary to affect increased abundance of alternative prey, in turn increasing wolf populations and limiting caribou population growth, is inconsistent with what I observed in the SBS. Understanding the validity of DMAC in poorly productive regions, where total ungulate biomass is low regardless of extent of disturbance, will be critical to differentiate management approaches for the conservation of boreal caribou in northern ranges. Managers of boreal caribou populations should be cautious when using presumptions of DMAC in their system where disturbance is primarily natural, and where little is known about the status of caribou populations. I recommend testing assumptions of DMAC in areas of high fire disturbance before management plans are drafted.

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CHAPTER 3: NET PRIMARY PRODUCTIVITY, ANTHROPOGENIC DISTURBANCE, AND SPECIES RICHNESS DETERMINE WHETHER DISTURBANCE-MEDIATED APPARENT COMPETITION OCCURS FOR BOREAL CARIBOU

3.0 Abstract:

Disturbance-mediated apparent competition (DMAC) is the most widely reported threat to populations of boreal and mountain woodland caribou (*Rangifer tarandus caribou*). Disturbances that increase the abundance of deciduous vegetation, and thus deciduous-browsing alternative prey, are thought to promote predator numbers, in turn increasing predation risk to caribou. The DMAC hypothesis has been mostly studied in relatively productive systems where landscapes are highly managed and multiple species of predators and ungulate prey interact with caribou. Yet almost 2/3 of extant boreal caribou range occurs in poorly productive, wildfire-dominated areas where caribou only live alongside moose (*Alces alces*) in the context of DMAC. The relationship between primary productivity and vertebrate species richness is most commonly positive linear or unimodal. Across Canada, the linear relationship is true for ungulates, where higher productivity systems historically had more alternative prey species for caribou to compete with. I tested the hypothesis that DMAC is modulated by net primary productivity (NPP), where alternative prey and predator richness in the system is a key component for whether the assumptions of DMAC occur. Using recruitment (*n* = 40 study areas) and survival (*n* = 34 study areas) data from across Canada, MOD17 1-km resolution NPP maps, disturbance, moose density, and alternative prey and predator richness, I assessed whether NPP drives the phenomenon of DMAC at a national scale. Results of beta regressions show that NPP is the most important predictor for recruitment and survival. NPP was also a crucial part of the of the first principal axis for all models, and NPP was a causal factor for higher predator and anthropogenic disturbance leading to reduced recruitment and survival in the all SEM analyses. This indicates that NPP, or an underlying proxy, can act as an impetus for DMAC, where the phenomenon is unlikely to occur in low-productivity areas. Anthropogenic disturbance, as opposed to fire disturbance, is crucial in the NPP and DMAC equation, likely due to the increased hunting efficiency afforded by man-made linear features. Given that DMAC is a pivotal hypothesis in caribou management, conservation plans for caribou should reflect this so that lower disturbance thresholds are set in areas with more vegetative cover.

Keywords: disturbance-mediated apparent competition (DMAC), disturbance, net primary productivity, species richness, alternative prey, moose density

3.1 Introduction:

Boreal and mountain populations of woodland caribou (*Rangifer tarandus caribou*, hereafter caribou) are listed on Schedule 1 of the Canada *Species at Risk Act* (SARA). Threatened and Endangered populations of the at-risk species have been the subject of intense research and applied conservation biology now for more than 30 years (see Environment Canada 2012, Serrouya et al. 2019). While the threats to caribou are many, the most important impact reported for the species has been apparent competition from white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) as mediated by a predator (principally wolves [*Canis lupus*], as well as possibly cougars [*Felis concolor*], coyotes [*Canis latrans*], black bears [*Ursus americanus*], grizzly bears [*Ursus arctos*], and wolverine [*Gulo gulo*]) but exacerbated by landscape disturbance (Seip 1992, Festa-Bianchet et al. 2011, Serrouya et al. 2015*b*, DeMars et al. 2019, Labadie et al. 2021). The southern front of the range retraction for caribou is where apparent competition has been studied the most in this context.

In places like the boreal plains of Alberta it has been known for some time that landscape disturbance plays a critical role in the strength of suspected or observed apparent competition between caribou and alternative browsing prey in the system where the latter may benefit from disturbance (Latham et al. 2011*a*, *b*, Hervieux et al. 2013, Peters et al. 2013). This form of apparent competition (Holt 1977), termed ‘disturbance-mediated apparent competition’ (DMAC) has become increasingly important in the management and conservation of caribou throughout Canada (Environment Canada 2012, Hervieux et al. 2013, Serrouya et al. 2015*b*, Environment and Climate Change Canada 2018, DeMars et al. 2019, Serrouya et al. 2019).

DMAC is a result to Bergerud et al.’s (1984) ideas regarding how the species might use habitat selection as an anti-predator tactic (often termed the ‘spatial separation hypothesis’ of woodland caribou; see James et al. 2004). This hypothesis suggests that the avoidance of predators is a possible explanation for why, at a landscape scale, caribou select for areas of low productivity that typically do not support browsing ungulates like moose and deer, namely, to avoid their subsequent predators (Bergerud and Page 1987, Seip 1992). At higher orders of selection (Johnson 1980), adaptations to a lichen-based diet by caribou, especially in winter, reflect the selective use of these land cover types and resources therein (Thomas et al. 1994, Thompson et al. 2015).

DMAC relates to the spatial separation hypothesis by invoking landscape disturbance, either as a result of human activity or natural disturbance (especially wildfire), to increase the overall abundance or biomass of alternative prey by reducing the age of forests and increasing the amount of deciduous browse (hardwood-dominated stands), and hence abundance of predators that may be limited by ungulate prey biomass, such as wolves (Seip 1991, Fuller et al. 2003) and cougars (Knopff et al. 2010). These disturbances diminish the effectiveness of habitat selection strategies by which caribou minimize predation through spatial separation. Direct evidence for the role of wolves in DMAC between alternative ungulate prey and caribou comes primarily from the boreal plains of Alberta (e.g., Latham et al. 2011*a,b*, Hervieux et al. 2014) and in British Columbia for mountain caribou (e.g., Wittmer et al. 2005, Serrouya et al. 2017, 2019), which are areas with high anthropogenic disturbance and relatively high densities of apparent competitors, white-tailed deer and moose.

The term recruitment is used to mean the number of yearlings that survive to join the adult population. Caribou calf recruitment is measured by the number of calves that survive to 10 months of age compared to the number of adult females (calf:cow ratio). Calf recruitment has been shown to be negatively affected by disturbance and deciduous forest area (Environment Canada 2011, McCarthy et al. 2011, Leclerc et al. 2014). When selecting for calving locations, caribou avoid high road density areas as well as areas where they are likely to encounter wolves (Mahoney and Virgl 2003, Pinard et al. 2012, Leclerc et al. 2014, Leblond et al. 2016). Wolf reduction programs have had varying results, with some increasing calf survival (Bergerud and Elliot 1986, Hegel et al. 2010*b*, Serrouya et al. 2019) while others did not (Valkenburg et al. 2004, Harding et al. 2020).

While recruitment has been extensively studied, research has so far largely neglected to consider the productivity of the caribou habitat. NPP varies globally from 30 to 1000 g C/m^2, though boreal habitats rarely exceed 600 g C/m^2 (Scurlock et al. 1999, Running et al. 2000). It is thought that increased predation risk negates the positive effect of increased food abundance for foraging vascular plants (Leclerc et al. 2014) as caribou are thought to be predation, rather than forage, limited (Hegel et al. 2010*a*, *b*). However, other cervids have been shown to be positively affected by productivity. Mule deer (*Odocoileus hemionus*) survival is known to increase with primary productivity (Sims 2017), while elk (*Cervus canadensis*) recruitment was most strongly affected by forage productivity (measured in

Normalized Difference Vegetation Index [NDVI], Lukacs et al. 2018). For Saami people's ranching of European reindeer (a different subspecies of caribou), the output is strongly affected by the productivity fluctuations caused by climatic variation (Reinert 2006). When raised for agriculture, reindeer flourish best if fed grains, hay, and leaves (Turunen 2014) while bottom-up strategies have been shown to increase population growth for mountain caribou in British Columbia (Heard and Zimmerman 2021). This suggests that caribou only select for low-productivity and lichen areas as a means of avoiding competition and predation.

Kang et al. (2006) found that fire disturbance in the boreal ecozone results in lowering of NPP. Serrouya et al. (2021), however, used total disturbance in their models and made predictions assuming that disturbance increased productivity, based on evidence from human disturbance increasing productivity (Zhu et al. 2016). I instead predict that fire and anthropogenic disturbance will affect caribou recruitment in substantially different ways. While fire decreases habitat use and lichen availability (Schaefer and Pruitt 1991, Gustine et al 2014, Greuel et al. 2021), there is little evidence that fire disturbance negatively affects caribou in the context of DMAC (Johnson et al. 2020, Stewart et al. 2020, Neufeld et al. 2021) as moose density has been shown to respond to fire disturbance only after 25 to 30 years since burn (Demars et al. 2019, Julianus et al. 2019). Instead, it is likely that anthropogenic disturbance is of greater importance for moose (DeMars et al. 2019). This means that total disturbed area is not a sufficiently precise indicator, but that considerations need to be made regarding disturbance (i.e. linear vs polygonal; James and Stuart-Smith 2000, DeMars and Boutin 2018, DeMars et al. 2019).

Primary productivity is also associated with increased animal diversity (Malmstrom 2010), while its relationship with species richness is dependent on scale, but it is most often unimodal or positive (Waide et al. 1999). In boreal forests, productivity has a negative linear relationship but is unimodal based on succession (Waide et al. 1999). This analysis, however, takes into account plant, fungi, and animal richness, whereas, for vertebrates, terrestrial systems are most commonly positive linear or unimodal for species richness as productivity increases (Waide et al. 1999).

The purpose of this chapter is to follow up on my published chapter 2 (Neufeld et al. 2021) as well as an analysis in the Enhanced Analysis to Support Regional Boreal Caribou (*Rangifer tarandus*) Range Planning and Action Planning (Environment and Climate Change Canada 2017) in which they analyzed data from 49 caribou study areas across Canada. In my published chapter, I showed a decoupling of moose densities and wolf densities from assumptions under the hypothesis of DMAC in an area of high natural disturbance (Neufeld et al. 2021). I also mentioned that my conclusions directed toward formation of the primary productivity hypothesis of DMAC, a corollary of DMAC proper. I believe the difference in the Saskatchewan Boreal Shield is that the low productivity of the system does not allow for alternative prey to exploit disturbance as occurs in the plains or foothills where primary productivity is higher (and hardwood successional stages are more common). To test this, I will be looking at caribou recruitment as a response of net primary productivity (NPP in g C/m^2) for study areas across Canada.

The food web involving caribou is less complex in eastern than western Canada. For the eastern boreal caribou study areas in Québec, moose, wolf, black bear, and caribou are the only large mammals in the boreal forest (Fortin et al. 2017). Therefore, if the moose density is low, wolf density will also be low. The mean fire cycle can be longer than 250 years (Fortin et al. 2017), so early seral species are not abundant, meaning moose stay at low density for relatively long periods of time. Primary productivity in this region does increase deciduous vegetation for moose, negatively affecting caribou, but the forest also reaches mature stages faster, so the period of time where moose and wolf abundance is high remains shorter (Fortin et al. 2017). Overall, high productivity is still positive for caribou in the east.

The food web involving caribou is more complex in western Canada. Predators such as coyotes, cougar, grizzly, and wolverine, and alternative prey white-tailed deer and elk occur sympatrically with boreal caribou in British Columbia and Alberta (Environment Canada 2011, 2012). The shorter fire return in the west also means there is always a higher abundance of deciduous browse (Greene and Johnson 1999). Here, wolves do not rely solely on moose but have an abundance of early-seral favouring alternative prey, such as deer (Latham et al. 2011*b*) and elk (Unsworth et al. 1998), to maintain high densities. Higher productivity in this area does not necessarily mean that the forest reaches and stays mature long, since the fire return is short. Instead, it indicates that more early-seral browse is available, but the forest may be disturbed again before it reaches maturity. Therefore, there is a marked difference in the role of primary productivity in eastern and western regions.

Overall, the purpose of this project is to discover how NPP affects caribou recruitment and survival at a national scale, how this relationship is influenced by differing species diversity and predator and alternative prey densities in different study areas, and how differences in disturbance type can change this relationship. The phenomenon of DMAC says that caribou are negatively affected by disturbance because young seral browse raises alternative prey density, thereby increasing wolf density, which results in more incidental predation of caribou. But I predict this can be modulated by NPP which has a positive effect on recruitment and adult female survival unless high alternative prey and predator densities cause caribou to be too heavily preyed upon. This means that I predict that caribou recruitment is positively affected by NPP, as this bottom-up effect would mean there is greater food availability for adult female caribou. Also, as found in Fortin et al. (2017), higher productivity also means faster regrowth of forests into ideal habitat for caribou.

However, in study areas where the relationship with NPP is negative, I think this is caused by increased large mammal species richness. Increased richness means there are more predators and more alternative prey that help drive the DMAC phenomenon, so a top-down effect occurs that is stronger than the bottom-up effect of increased NPP (top-down control is common among cervids; see Ripple and Beschta 2012). Moose, white-tailed deer, and elk all prefer early seral stage stands (Unsworth et al. 1998, Maier et al. 2005, Latham et al. 2011*b*). Between 10-30 years since disturbance (Maier et al. 2005), moose and other alternative prey should have greater densities than they do in older forest stands. Total disturbance on the landscape also varies between study areas. It is generally higher in Alberta than for any population in Québec (Environment and Climate Change Canada 2017). I predict that NPP will have varied effects for caribou recruitment depending on the alternative prey richness in the system. For example, in Québec, higher NPP helps caribou, probably as predicted in Fortin et al (2017), by decreasing the time it takes for forests to regrow. In Alberta, on the contrary, if two study areas have different NPP, the one with higher NPP will, I predict, also have higher alternative prey biomass and predator biomass than the low NPP population, if disturbance is the same. This means that predation will be much greater in the high-NPP population than the low one. Therefore, in Alberta, top-down control and alternative prey biomass predict caribou recruitment but are a result of NPP in the area (i.e. more productivity means more alternative prey). Overall, I hypothesize that total alternative prey biomass, and consequently total predator biomass, is the main predictor for caribou recruitment; I predict a negative correlation between biomass and recruitment and survival, where more biomass means a negative effect on recruitment and adult female survival.

3.2 Methods:

3.2.1 Data Collection:

I collected Annual NPP from the MOD17A3 NASA Earth Observing System MODIS Land Algorithm (Running and Zhao 2015). The original strategy for validation of the MOD 17 NPP data is available in Running et al. (1999). The data were available in 1 km resolution raster data maps with NPP in units of g C/m^2. Data were available for years 2000 to 2015. I used the long-term average value for each pixel over this period to represent the mean NPP value. This is the updated version of the technique Lui et al. (2002) used to calculate NPP across Canada as referenced in Neufeld et al. (2021). Using cross-validation, MOD17 data has been found to be accurate for calculations of boreal forests (Turner et al. 2003)

For independent variables, I collected predator and ungulate prey species ranges as well as densities for all available species. This included wolf, cougar, black bear, grizzly, wolverine, and coyote for predators and moose, white-tailed deer, mule deer, and elk, and bison (*Bison bison*) for ungulate alternative prey (Table D1 and D2). While we know that beaver and hares are contributing prey of wolves (Fox-Dobbs et al. 2007, Mech 2007, Neufeld 2018), I assumed that they were present in similar abundance in all caribou ranges as these data were not available.

Species distribution data was sent from a variety of sources (Table D1). For species distributions sent by Northwest Territories Environment and Natural Resources, I used rare+ designation to represent presence for distribution mapping, meaning whitetails and coyotes are rare in these study areas when present. For Canada-wide distribution data to supplement what was provided by provincial governments, coyote (Hody and Kays 2018), white-tailed deer distribution (Heffelfinger 2011) were found. Bison distribution was found in COSEWIC (2013) as well as supplemented from data from the ABMI and Fiera Biological Consulting. Designation of caribou study areas and densities from COSEWIC (2014).

For caribou recruitment (calf:cow ratio), survival (female adult survival rate), and study area polygons, I obtained data from Northwest Territories, British Columbia, Saskatchewan, Ontario, and Québec provided through Environment and Climate Change Canada (Table D1).

3.2.2 Data Analysis:

First, I used the cor.test function in R Statistical Software Version 4.0.1 to test the Pearson correlation between my major explanatory variables. This was used to assess collinearity among the explanatory variables. I used a cut-off of 0.7 for variables that were too correlated to be used in the same model (Zuur et al. 2007, Dormann et al. 2013, Akoglu 2018, Schober and Schwarte 2018).

Next, as an exploratory analysis, I used beta regression models on the arithmetic means both recruitment (calf:cow ratio at 10 months of age) and adult female survival (proportion) using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1. The demographic rates within each population were weighted by the number of years of recruitment or survival data. Models were only tested using one explanatory variable per model based on the collinearity results. I used Akaike information criterion corrected for small sample size (AIC_c) to test for which of the variables best explained the response variable.

Next, I ran a principal component analysis (PCA) using the vegan package in R version 2.5-7 (Oksanen et al. 2019) for the 40 study areas which had recruitment data (n = 40) on the variables: NPP (g C/m^2), precent anthropogenic disturbance, precent fire disturbance, predator richness, and prey richness. This was done due to the non-independence of the variables as seen in the correlation tests (Table 3.1). I used a broken-stick method using the vegan package in R version 2.5-7 (Oksanen et al. 2019) to determine which axes could be run as a beta regression for recruitment. This process was repeated for the study areas that have survival data (n = 35), and again adding the moose density variable for study areas with caribou survival and moose density data (n = 30).

Lastly, I used structural equation modeling (SEM) (Grace 2006) to test the main connections found in the exploratory models above, testing validity of models using Akaike information criterion corrected for small sample size (AIC_c). SEM was used to test for indirect influences or pathways the explanatory variables may have on the response variables. Based on Fortin et al. (2017), I predicted that NPP will have a positive effect on all species, including caribou recruitment and survival. The positive influence on caribou comes from higher food availability (non-lichen) and also the faster forest regrowth limiting the abundance of alternative prey as shown in Fortin et al. (2017). Disturbance, especially anthropogenic disturbance, will have a direct negative impact on caribou (McCarthy et al. 2011, Leclerc et al. 2014) while increasing the density of alternative prey and non-obligate predators like bears by increasing deciduous browse (Knopff et al. 2010, Andren et al. 2011, Hervieux et al. 2015, Leblond et al. 2016). Obligate predators will be positively affected by increased prey density, while all predators will have a negative impact on caribou survival and recruitment (Holt 1977, Hervieux et al. 2015).

3.3 Results:

3.3.1 Mapping:

I constructed maps to extract values for the data as well as present information. I made an NPP map which included 40 caribou study areas (Fig. 3.1), and anthropogenic disturbance with those same study areas (Fig. 3.2). For species distributions, I did not display moose, wolf, or black bear distributions because they are sympatric throughout woodland caribou range. I made four maps of predator distributions, including cougar, coyote, grizzly bear, and wolverine (Fig. 3.3), and four for alternative ungulate prey, including white-tailed deer, mule deer, elk, and wood bison (Fig. 3.4).

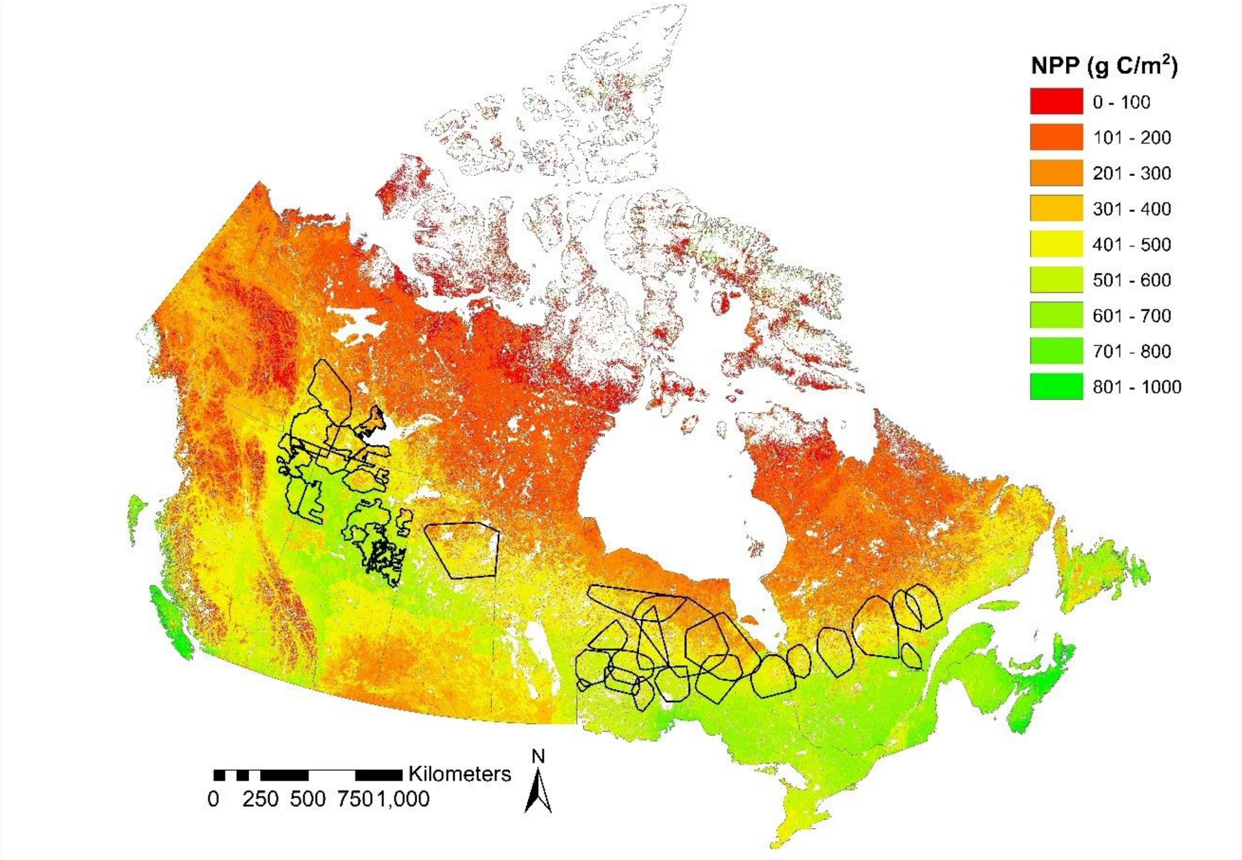

Figure 3.1: Polygons showing forty caribou study areas across Canada, in relation to the gradient of Net Primary Productivity (NPP) in g C/m^2. NPP data was obtained from the MOD17A3 NASA Earth Observing System MODIS Land Algorithm (Running and Zhao 2015) and is the average value from 2000-2015.

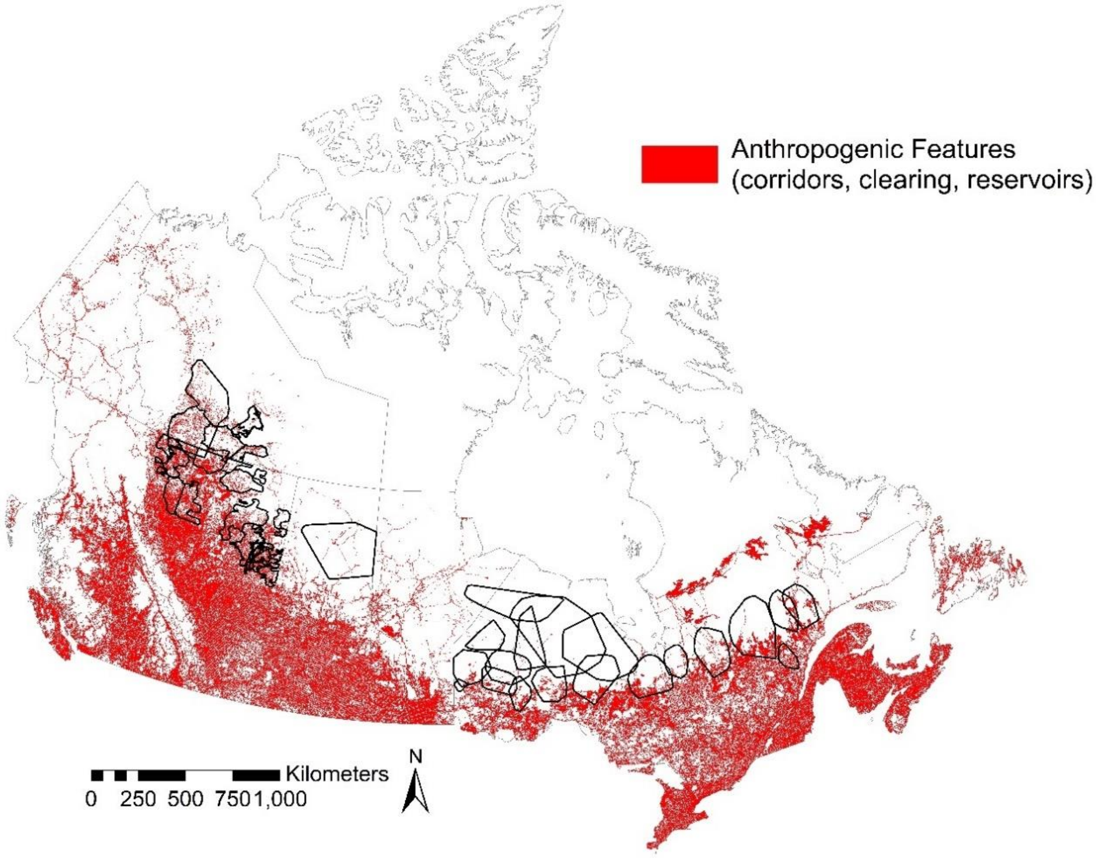

Figure 3.2: Polygons showing forty caribou study areas across Canada, in relation to the existing footprint of anthropogenic disturbance. I obtained anthropogenic disturbances from the 2009 shapefiles Cumulative Anthropogenic Access, Western Canada, Cumulative Anthropogenic Access, Central Canada, and Cumulative Anthropogenic Access, Western Canada (Global Forest Watch, https://databasin.org/galleries/6297fc7da503423a9d50c10e03523cee/, accessed April 22, 2020).

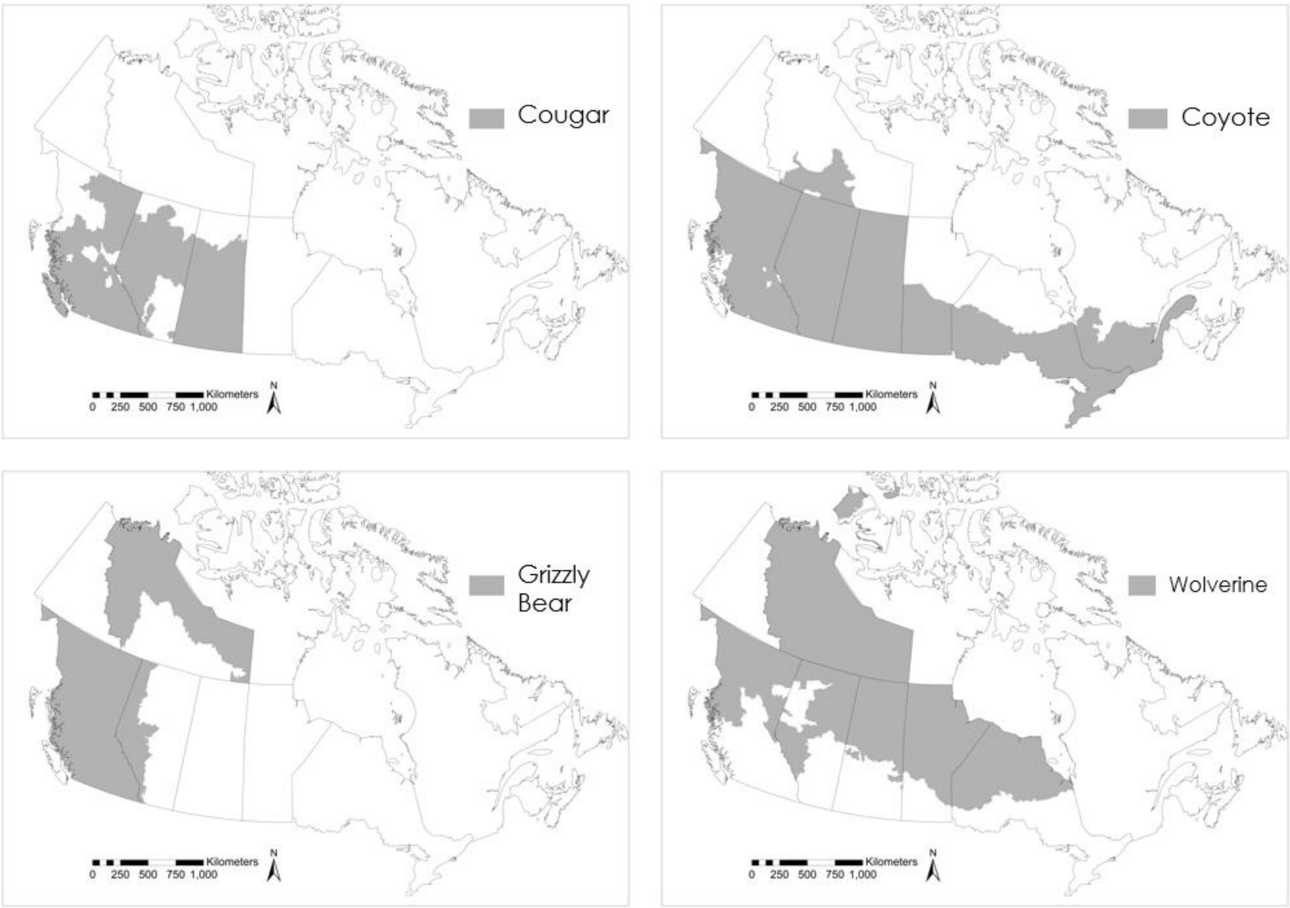

Figure 3.3: Caribou predator distributions across Canada, including cougar, coyote, grizzly bear, and wolverine. Species ranges were provided by each province or territory. See Table D1 for data sources.

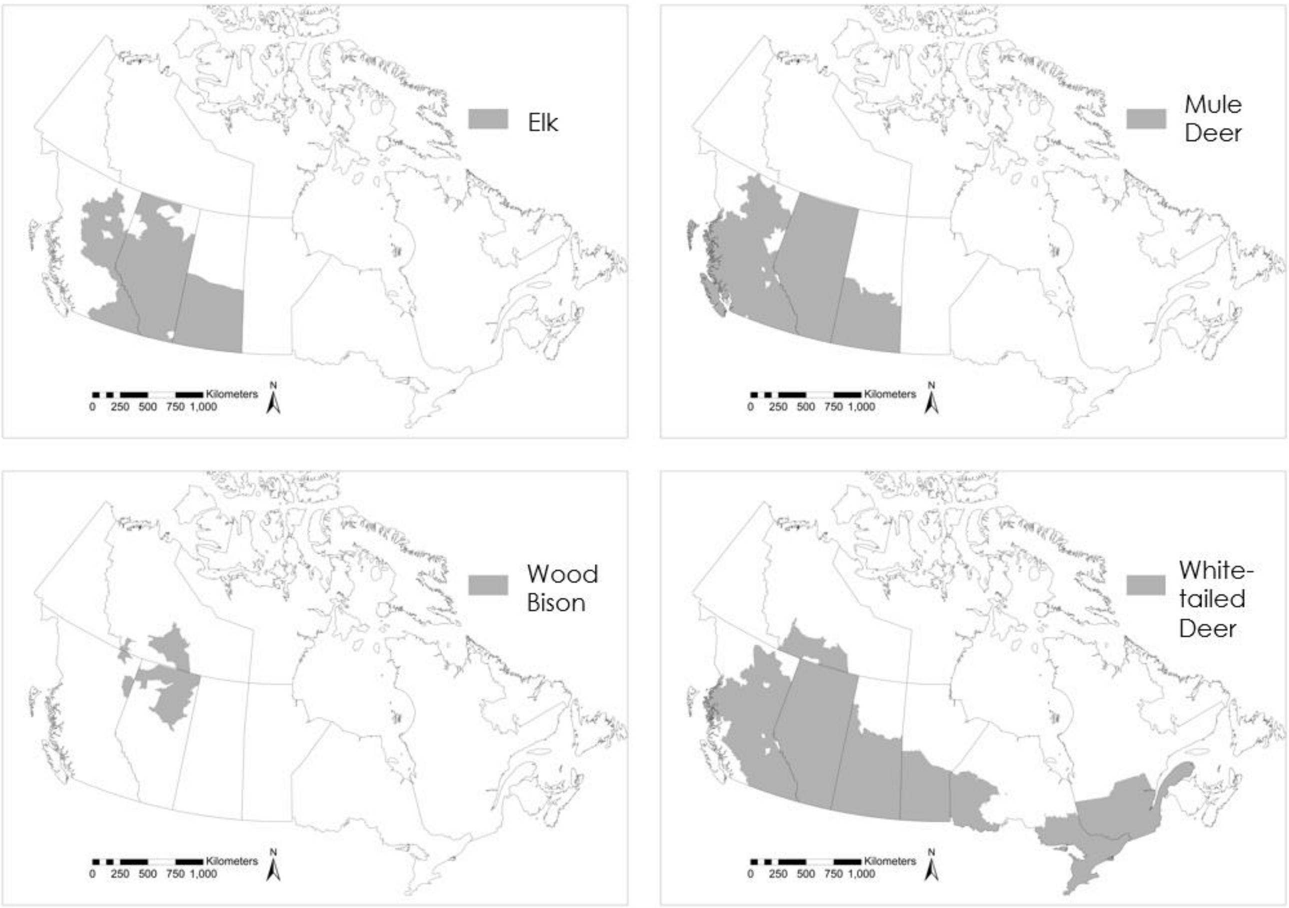

Figure 3.4: Caribou alternative prey distributions across Canada, including elk, mule deer, white-tailed deer, and wood bison. Species ranges were provided for each province or territory. See Table D1 for data sources.

3.3.2 Correlation Matrix:

Most covariates were highly correlated and were unable to be included together in the same regression analysis. The only covariates below the 0.7 threshold for variables too correlated to be used in the same model (Zuur et al. 2007, Dormann et al. 2013, Akoglu 2018, Schober and Schwarte 2018) were fire disturbance with any covariate and moose density with any variable except NPP (Table 3.1).

Table 3.1: Pearson correlation values (with 95% confidence intervals) between explanatory variables obtained using the cor.test function in R Statistical Software Version 4.0.1. Correlation values above our cut-off value of 0.7 (including confidence intervals) are coloured red (Zuur et al. 2007, Dormann et al. 2013, Akoglu 2018, Schober and Schwarte 2018).

	NPP	**Moose Density**	**Fire Disturbance**	**Anthropogenic Disturbance**	**Total Disturbance**	**Predator Richness**	**Prey Richness**
NPP	1	0.569 (0.269-0.769)	-0.048 (-0.396 - 0.311)	0.747 (0.535-0.871)	0.689 (0.443-0.839)	0.597 (0.308-0.785)	0.766 (0.565-0.881)
Moose Density	0.569 (0.269-0.769)	1	-0.101 (-0.439 - 0.263)	0.386 (0.037-0.651)	0.359 (0.005-0.633)	0.435 (0.095-0.684)	0.447 (0.110-0.692)
Fire Disturbance	-0.048 (-0.396 to 0.311)	-0.101 (-0.439 - 0.263)	1	-0.155 (-.483 to 0.211)	0.246 (-0.119 - 0.552)	0.083 (-0.280 - 0.425)	0.131 (-0.234 - 0.464)
Anthropogenic Disturbance	0.747 (0.535-0.871)	0.386 (0.037-0.651)	-0.155 (-.483 - 0.211)	1	0.904 (0.808-0.953)	0.685 (0.437-0.837)	0.714 (0.482-0.853)
Total Disturbance	0.689 (0.443-0.839)	0.359 (0.005-0.633)	0.246 (-0.119 - 0.552)	0.904 (0.808-0.953)	1	0.732 (0.510-0.862)	0.710 (0.475-0.850)
Predator Richness	0.597 (0.308-0.785)	0.435 (0.095-0.684)	0.083 (-0.280 - 0.425)	0.685 (0.437-0.837)	0.732 (0.510-0.862)	1	0.659 (0.398-0.822)
Prey Richness	0.766 (0.565-0.881)	0.447 (0.110-0.692)	0.131 (-0.234 - 0.464)	0.714 (0.482-0.853)	0.710 (0.475-0.850)	0.659 (0.398-0.822)	1

3.3.3 Recruitment:

Beta Regressions:

Only single explanatory variable models were run do to issues of collinearity (Table 3.1). For the 40 study areas with recruitment data, observed variability in recruitment was best explained by NPP (Table 3.2). Of note here is that while fire disturbance was considered very significant, the R^2 was extremely low (0.0003). For the 35 study areas which had moose density and recruitment data, results were similar for all variables, though no relationship was found between moose density and recruitment. Similar results were found for all models so anthropogenic and fire disturbance were used separately instead of combining them for total disturbance for all PCA and SEM models. All models were better than the null model (ΔAIC_c = 161.3).

Table 3.2: Beta regression models relating caribou recruitment (calf:cow ratio of at 10 months of age) to each major explanatory variables using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1. Each explanatory variable was run independently due to issues of collinearity. I weighted study areas by the number of years used to calculate arithmetic means of recruitment models. Models included 40 study areas which had recruitment data.

Model	**Estimate**	**Std. Error**	***P* (*df* = 38)**	**R^2**	**AIC_c**	**ΔAIC_c**
NPP	-0.005	0.0004	***	0.31	-733.9	0.0
Fire Disturbance	-0.008	0.0021	***	0.0003	-582.9	151.1
Anthropogenic Disturbance	-0.012	0.0011	***	0.20	-679.5	54.4
Total Disturbance	-0.0137	0.0012	***	0.15	-681.1	52.8
Predator Richness	-0.267	0.1107	**	0.18	-656.8	77.1
Prey Richness	-0.208	0.0191	***	0.17	-672.4	61. 5

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

NPP as a quadratic function better fit the recruitment data than the linear form (R^2 of 0.3275, Δ AIC_c = -2.94, though only negative term was significant, Fig. 3.5). The relationships for fire disturbance (Fig. 3.6), anthropogenic disturbance (Fig. 3.7), total disturbance (Fig. 3.8), predator richness (Fig. 3.9), and alternative prey richness (Fig. 3.10) all had negative relationships with recruitment (Table 3.2).

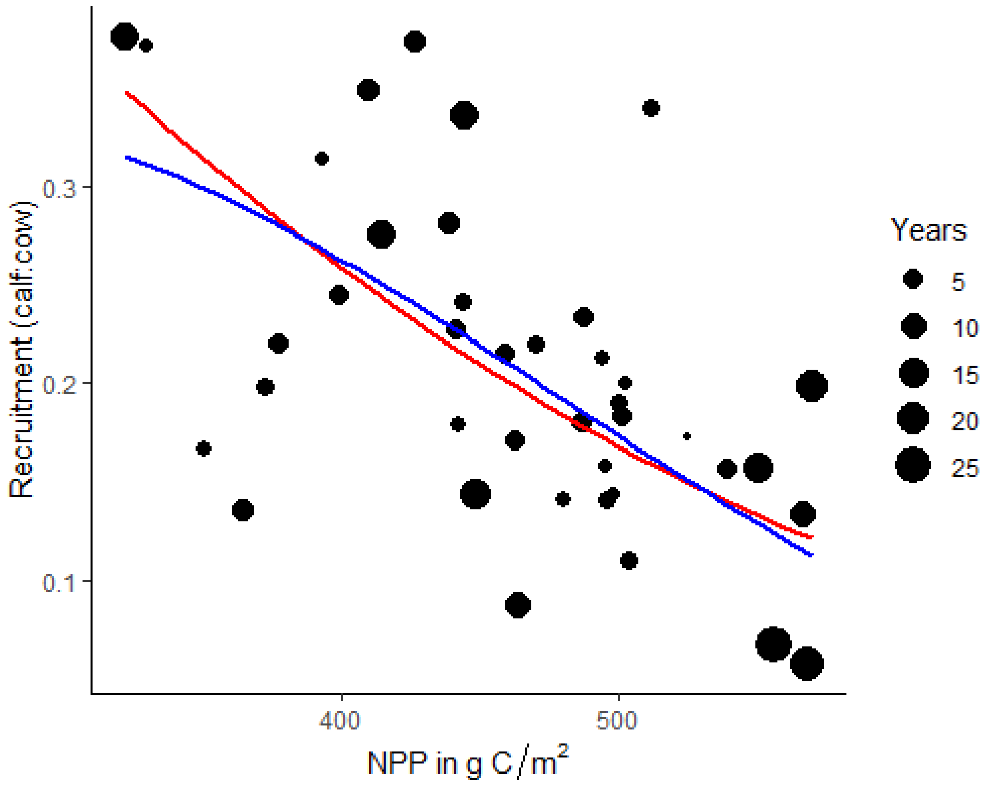

Figure 3.5: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of Net Primary Productivity (NPP) in g C/m^2 for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. Lines represent the various functions tested (red = linear, blue = quadratic).

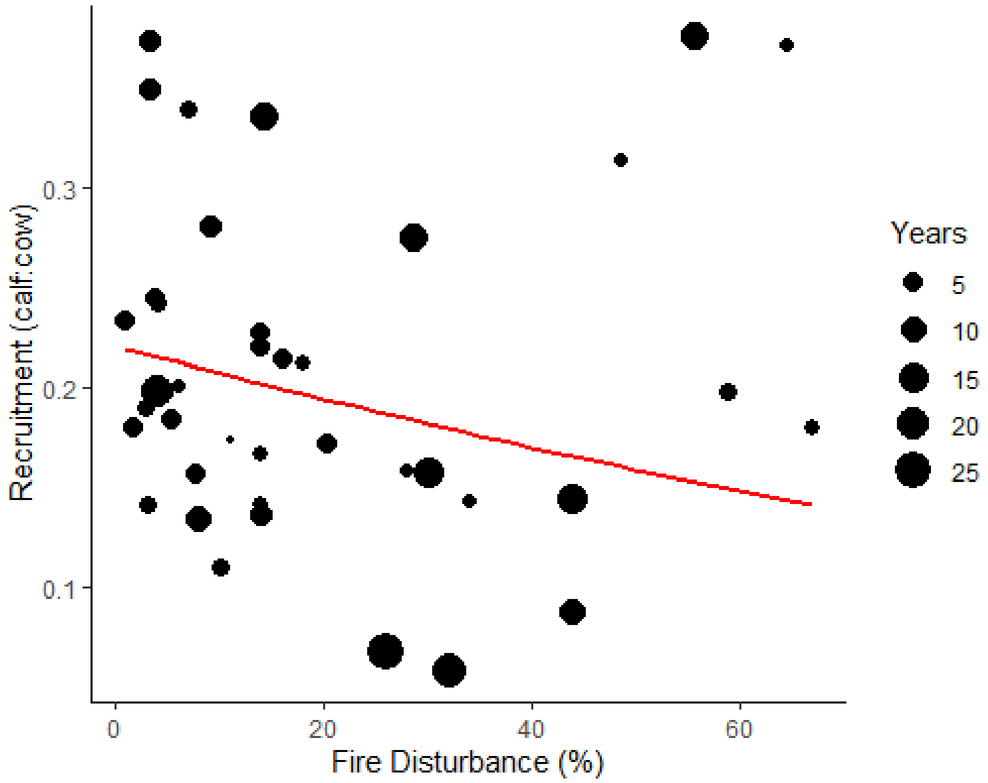

Figure 3.6: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of fire disturbance (%) for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the best regression model.

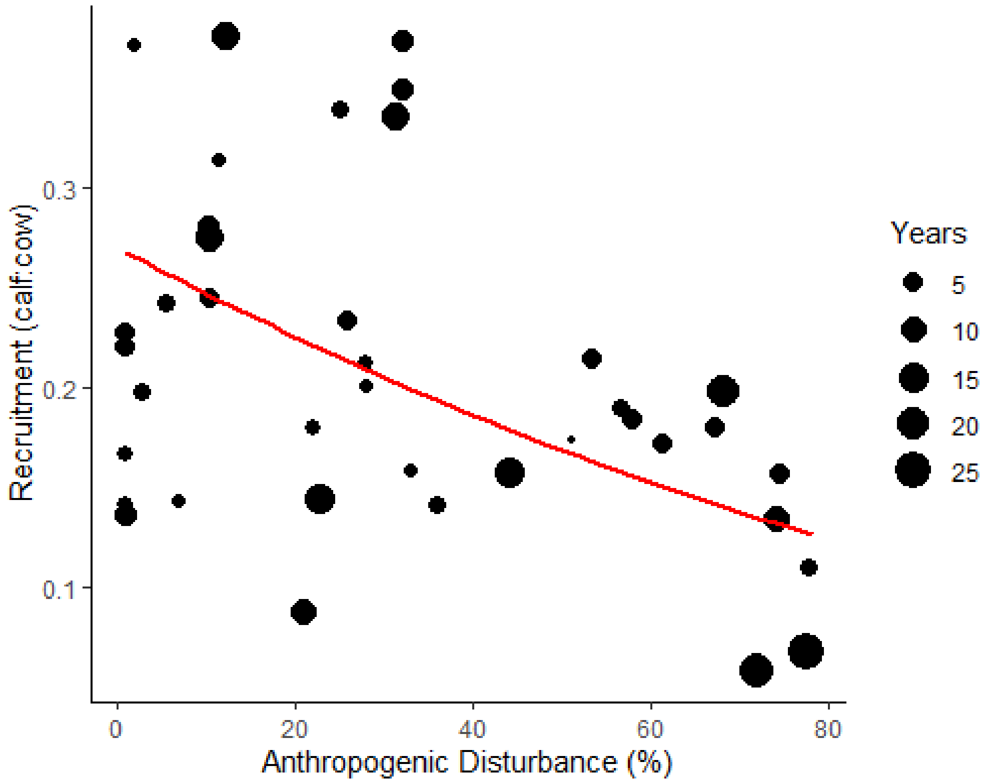

Figure 3.7: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of anthropogenic disturbance (%) for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

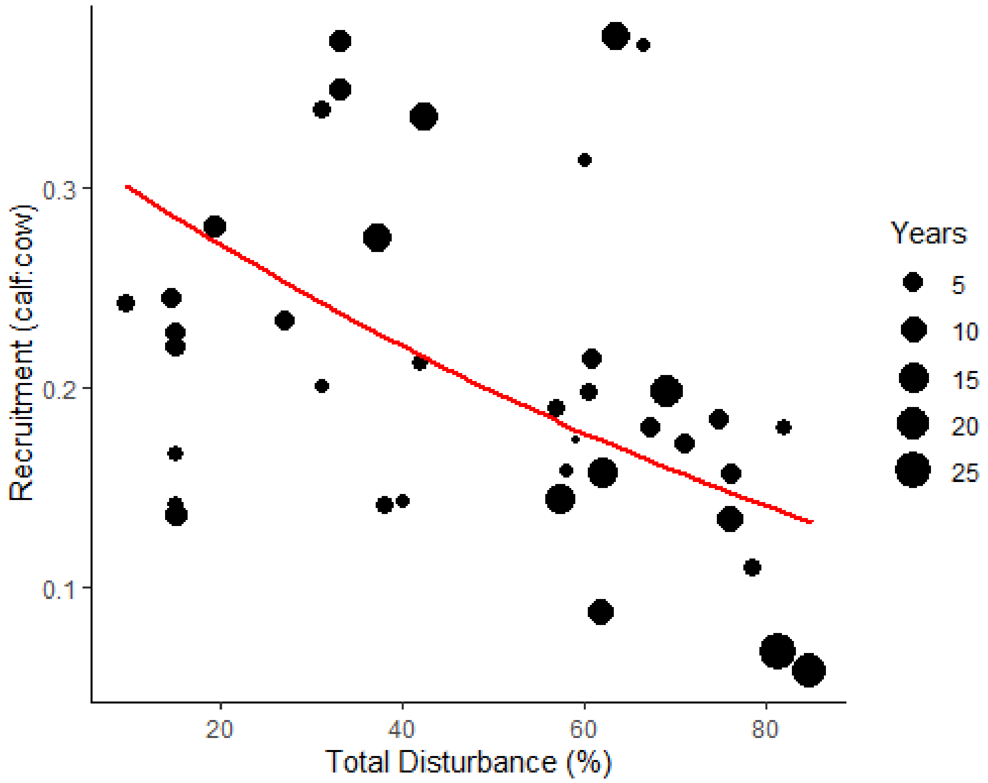

Figure 3.8: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of total disturbance (%) for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

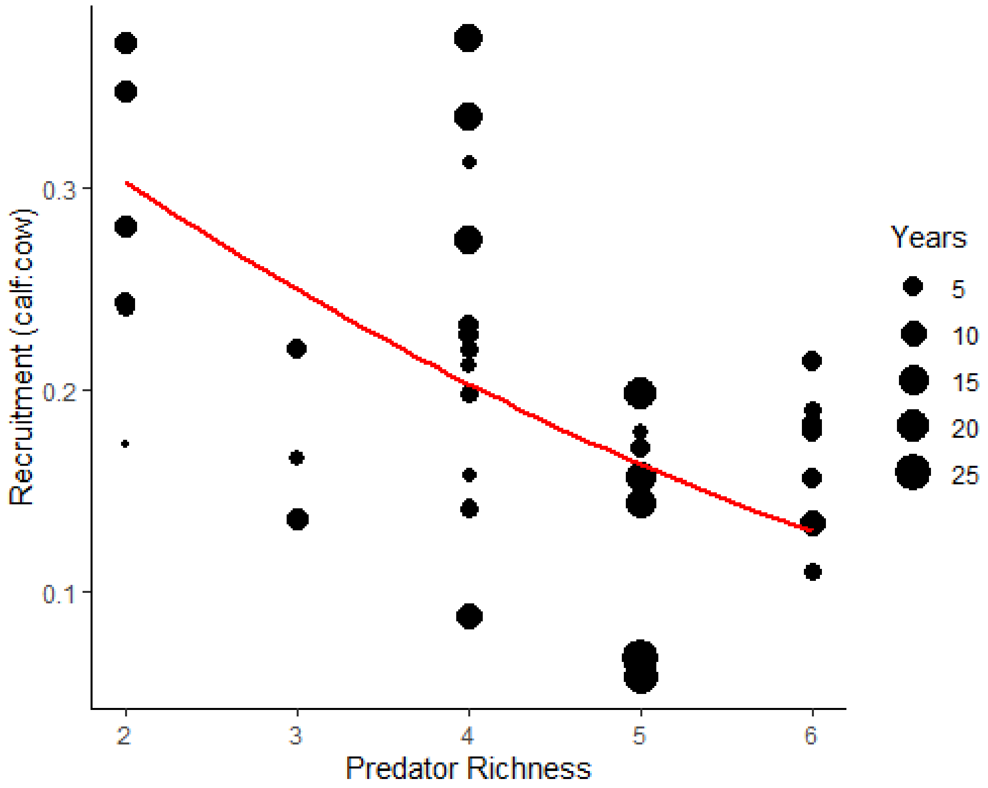

Figure 3.9: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of predator richness (number of species) for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

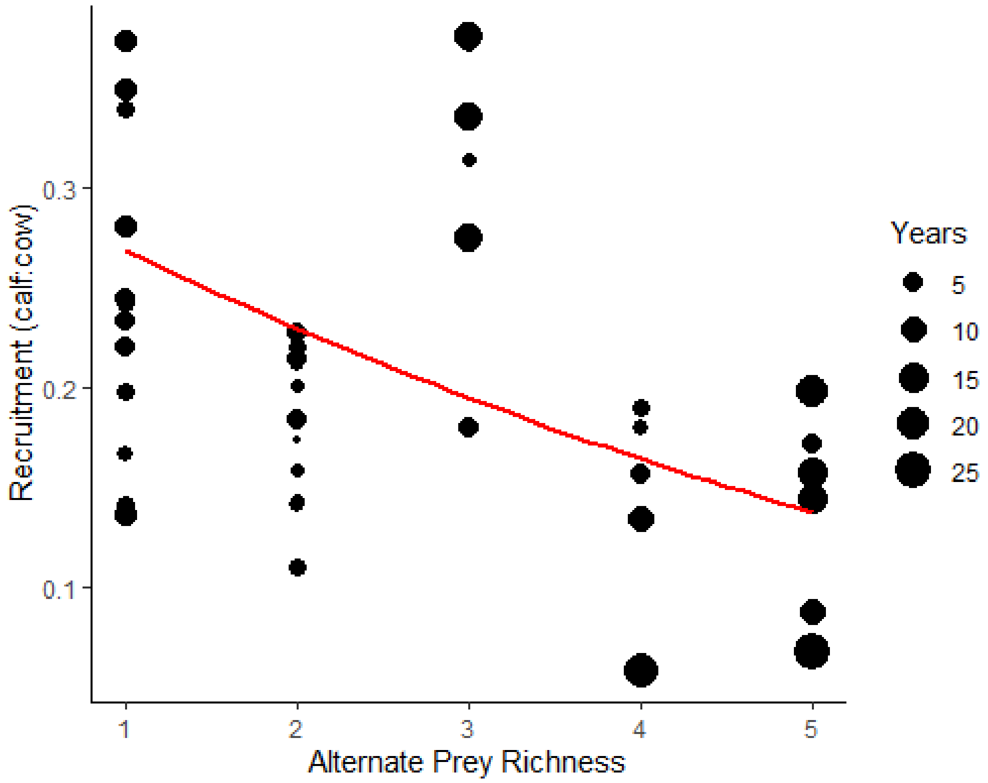

Figure 3.10: Caribou recruitment (calf:cow ratio) at 10 months of age as a function of alternative prey richness (number of species) for 40 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

Principal Component Analysis:

Due to the non-independence of the variables as seen in the correlation tests, a PCA was run using the independent variables (Fig. 3.11, Table 3.3) and the axes scores were used in subsequent regressions. The broken stick model showed that only PC1 and PC2 should be considered for subsequent regressions. The best model when comparing the AIC$_c$ of the first three axes and combinations thereof is represented in Table 3.4. For PC1, all variables had a negative effect except for fire disturbance, which had a weak factor loading (-0.242), which is within the range too close to zero to interpret (+/-0.3, Gentleman et al. 2011). Recruitment also tends to be relatively low in poorly productive but largely burned landscapes where many predators and alternative prey species can be found (PC2).

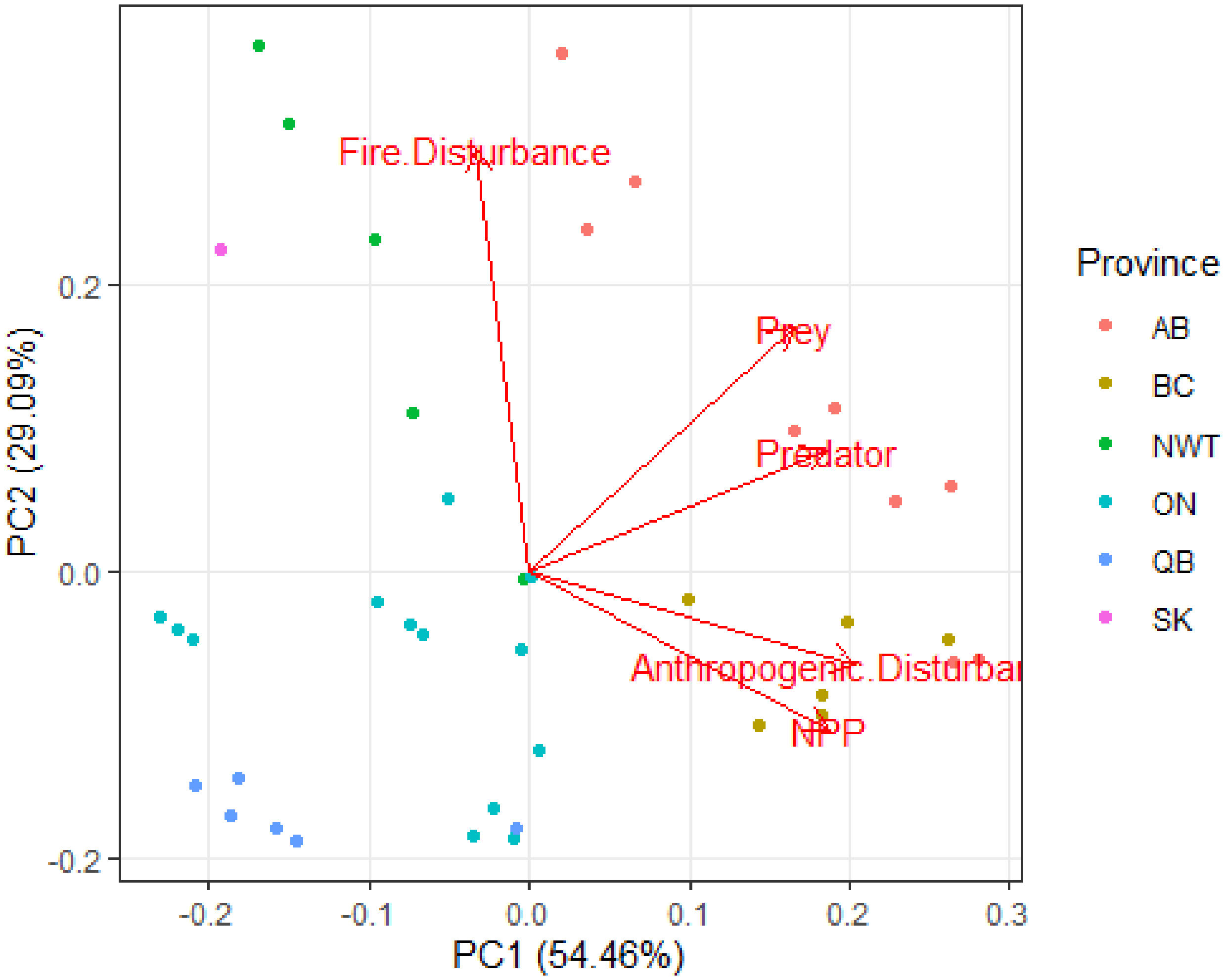

Figure 3.11: Principal component analysis (PCA) of main variables for 40 study areas across Canada with caribou recruitment (calf:cow ratio). Variables include net primary productivity (NPP), anthropogenic disturbance, fire disturbance, predator richness, and prey richness. Population points are included and coloured by province.

Table 3.3: Principal component analysis (PCA) species scores of main variables for 40 study areas across Canada with caribou recruitment (calf:cow ratio).

	PC1	**PC2**
Fire Disturbance	-0.242	1.587
Anthropogenic Disturbance	1.508	-0.354
NPP	1.382	-0.601
Predator Richness	1.371	0.456
Prey Richness	1.218	0.922
Variance Explained	54.46%	29.09%

Table 3.4: Summary of the multiple regression model relating caribou recruitment (calf:cow ration) to scores of each of the first two axes of principal component analysis (PCA). Data is from 40 study areas across Canada with caribou recruitment (calf:cow ratio). Axes scores are from PCA in Figure 3.11 and Table 3.3.

Variable	**Estimate**	**Std. Error**	***P* (*df* = 36)**
Intercept	-1.35	0.03	***
PC1	-0.60	0.04	***
PC2	-0.11	0.05	0.02*

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Structural Equation Modeling:

Figure 3.12 represents the best SEM model. This simplified model had the lowest AIC_c of models that had significant interactions with recruitment (for example, using alternative prey richness in place of predator richness give $\Delta AIC_c = 14.9$), including testing the reverse hypothesis as found in Serrouya et al. (2021) where the arrow is reversed for NPP and disturbance (ΔAICc = 56.3). All arrows except for anthropogenic disturbance~recruitment are significant (Table 3.5).

Table 3.5: Structural equation modeling (SEM) best model. Data is from 40 study areas across Canada with caribou recruitment (calf:cow ratio) data.

Regressions:	**Estimate**	**Std.Err**	***P* (*df* = 2)**
Recruitment ~ Predator Richness	-0.019	0.010	0.049
Recruitment ~ Anthropogenic Disturbance	-0.001	0.000	0.130
Anthropogenic Disturbance ~ NPP	0.293	0.042	***
Predator Richness ~ NPP	0.009	0.003	***

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

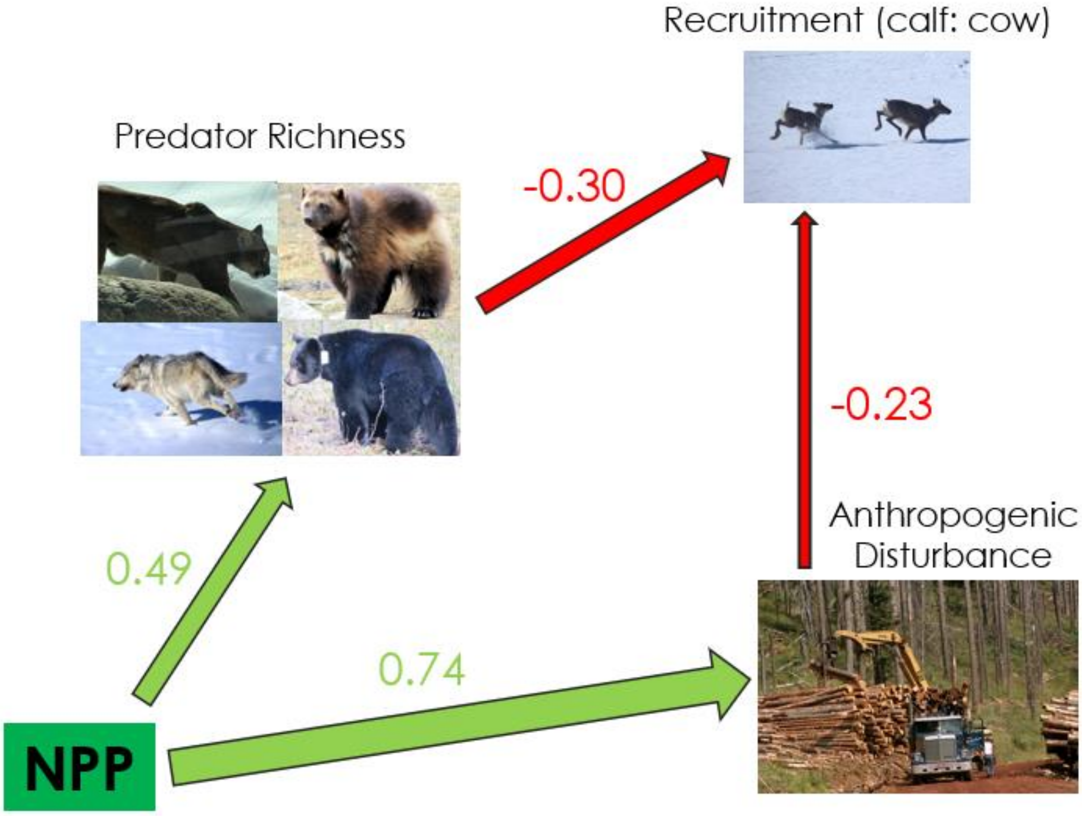

Figure 3.12: Results of structural equation modeling (SEM) for top model for caribou calf recruitment (calf:cow ratio) for 40 study areas that had recruitment data. Boxes represent net primary productivity (NPP), predator richness, anthropogenic disturbance, and calf recruitment. Arrows represent the strength of the relationship.

3.3.4 Survival:

Beta Regressions:

For adult female survival, the best model was NPP (Table 3.5). All variables had significantly negative relationships with survival except for fire disturbance. For NPP, the quadratic model was slightly better than the linear model ($\Delta AIC_c = -1.8$, $R^2 = 0.127$), though did not have any significant coefficients (Fig. 3.13). Anthropogenic disturbance, predator richness, and alternative prey richness were also all significantly negative (Table 3.6, Fig. 3.14 to 3.16).

Table 3.6: Beta regression models relating adult female caribou survival to each major explanatory variables using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1. Each explanatory variable was run independently due to issues of collinearity. I weighted study areas by the number of years used to calculate arithmetic means of survival models. Models included 35 study areas which had survival data.

Model	**Estimate**	**Std. Error**	**P (df = 33)**	**R^2**	**AIC$_c$**	**ΔAIC$_c$**
NPP	-0.0021	0.0003	***	0.121	-973.1	0.0
Fire Disturbance	0.0001	1.0E-03	0.957	0.080	-919.8	53.3
Anthropogenic Disturbance	-0.0034	0.0007	***	0.052	-943.5	29.5
Total Disturbance	-0.0030	0.0008	***	0.002	-933.7	39.4
Predator Richness	-0.0897	0.0143	***	0.036	-958.8	14.2
Prey Richness	-0.0709	0.0109	***	0.035	-959.3	13.8

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

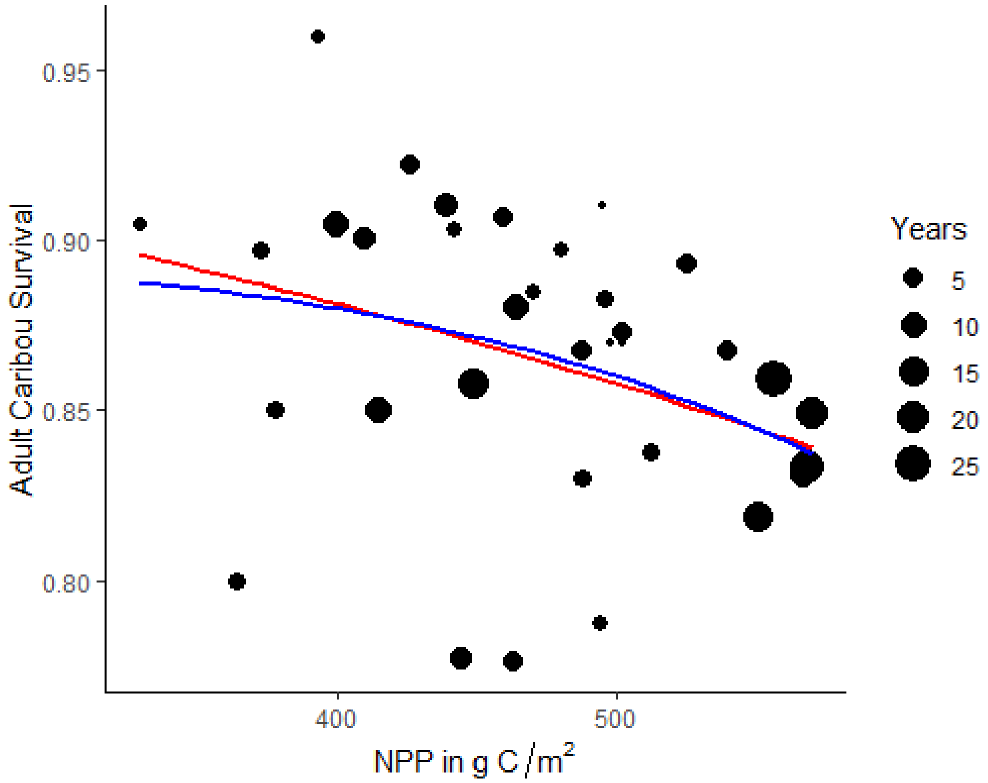

Figure 3.13: Adult caribou survival as a function of Net Primary Productivity (NPP) in g C/m^2 for 34 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. Lines represent the various functions tested (red = linear, blue = quadratic).

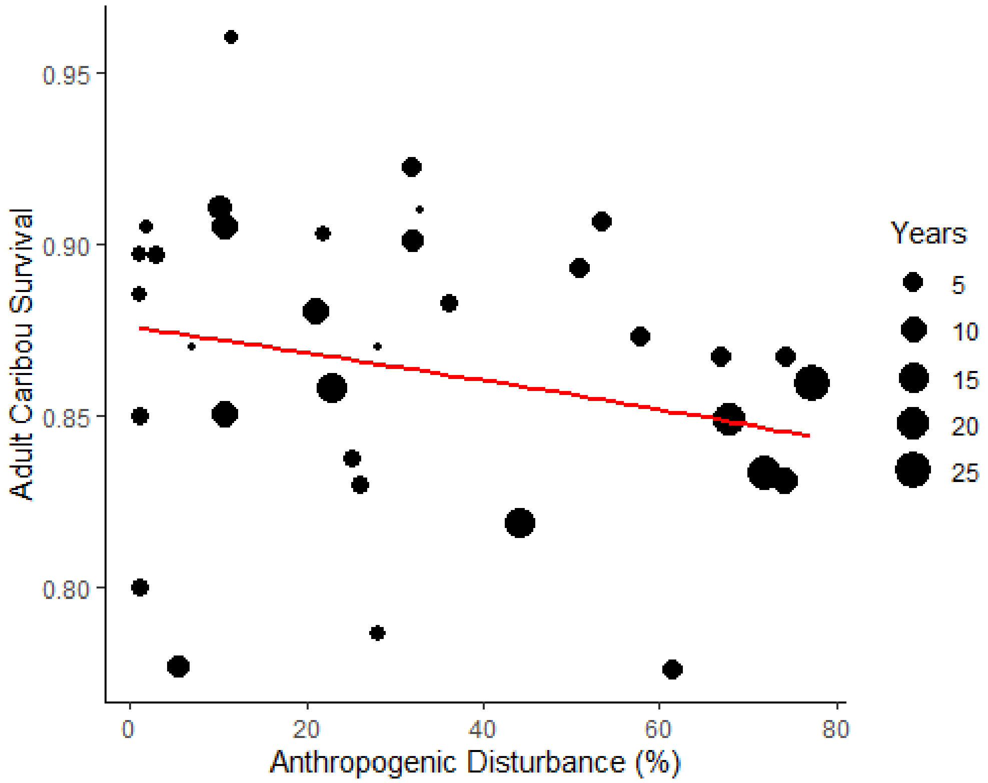

Figure 3.14: Adult caribou survival as a function of anthropogenic disturbance for 34 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

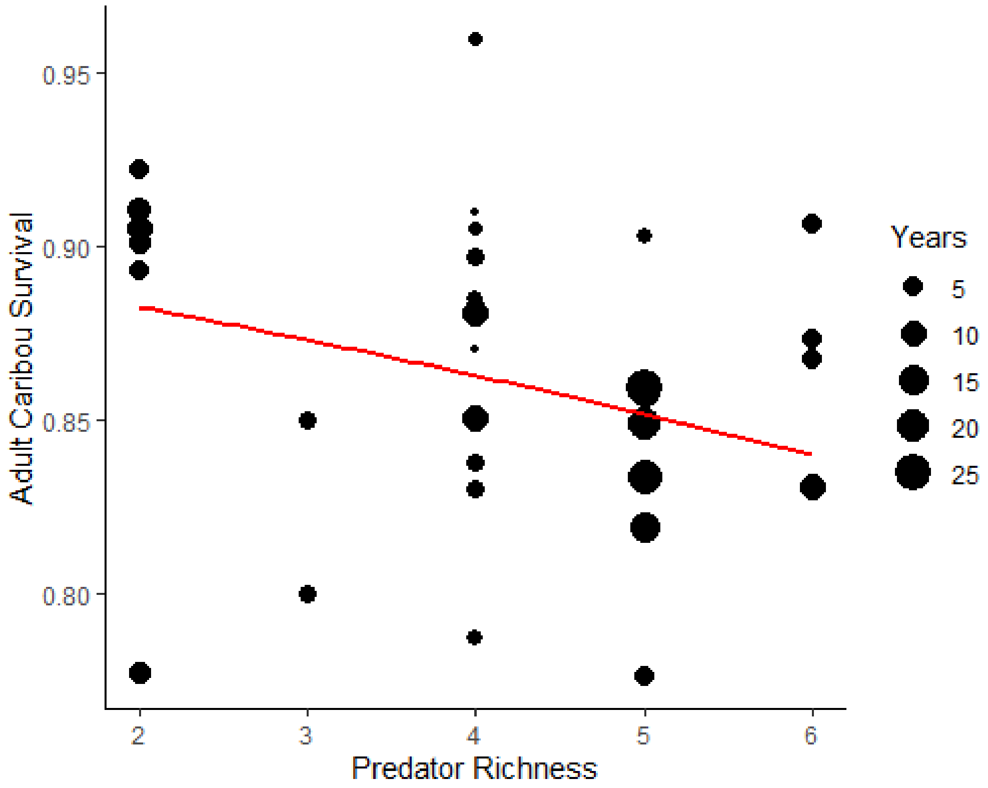

Figure 3.15: Adult caribou survival as a function of predator richness for 34 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

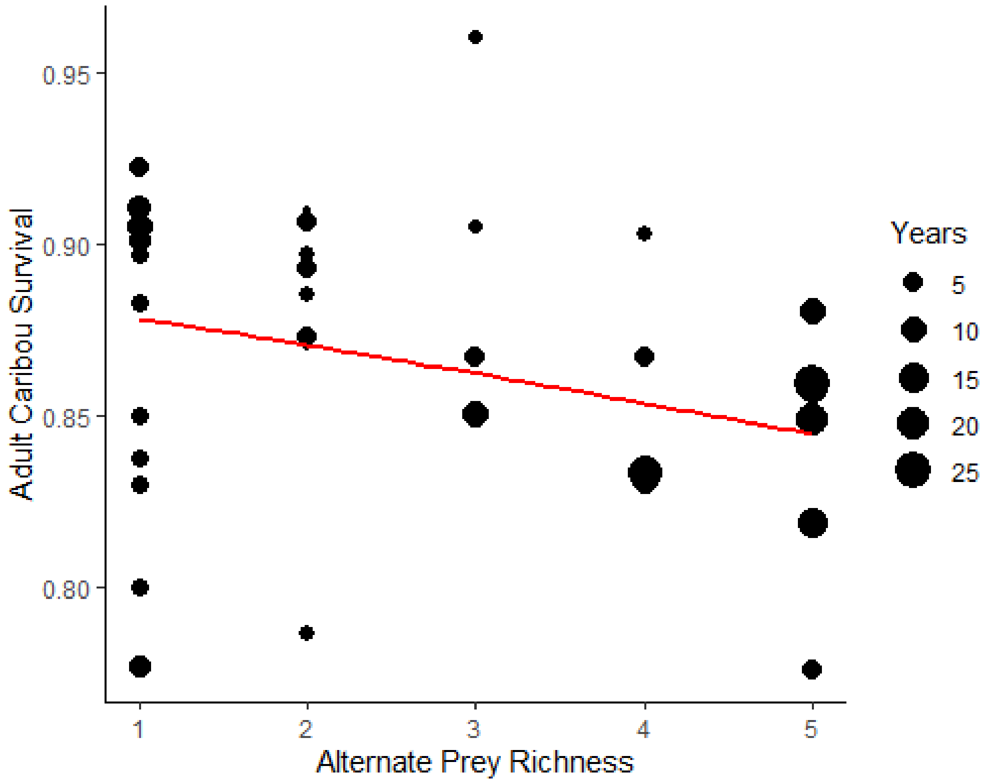

Figure 3.16: Adult caribou survival as a function of alternative prey richness for 34 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. The red line represents the linear model tested.

For the 30 study areas which had survival and moose density data, the best model was still NPP (Table 3.7). All variables, including moose density, had significantly negative relationships with survival except for fire disturbance (Table 3.7). The best moose density model was the survival~log(moose density) ($\Delta AIC_c = 9.34$; Fig. 3.17).

Table 3.7: Beta regression models relating adult female caribou survival to each major explanatory variables using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1. Each explanatory variable was run independently due to issues of collinearity. I weighted study areas by the number of years used to calculate arithmetic means of survival models. Models included 30 study areas which had survival and moose density values.

Model	**Estimate**	**Std. Error**	***P* (*df* = 28)**	**R^2**	**AIC_c**	**ΔAIC_c**
NPP	-0.0022	0.1422	***	0.136	-828.7	0.0
Fire Disturbance	-0.0015	0.0015	0.331	0.090	-773.4	55.3
Anthropogenic Disturbance	-0.0032	0.0007	***	0.030	-789.6	39.0
Total Disturbance	-0.0031	0.0008	***	0.005	-785.8	42.9
Predator Richness	-0.0868	0.0148	***	0.030	-806.5	22.2
Prey Richness	-0.0816	0.0119	***	0.020	-814.6	14.1
Moose Density	-0.0008	0.0001	***	0.158	-804.1	24.6

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

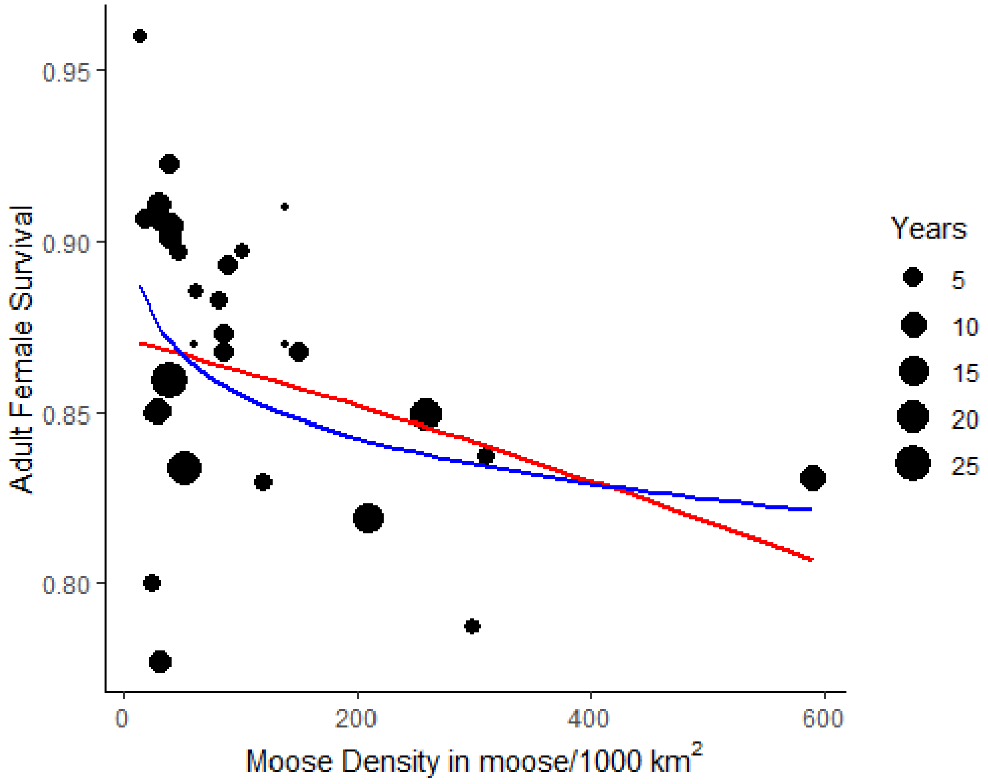

Figure 3.17: Adult caribou survival as a function of moose density per 1000 km^2 for 30 study areas across Canada. Regressions were done using the BETAREG package (Cribari-Neto and Zeileis 2010) in R Version 4.0.1 weighted by number of years of data. Lines represent the various functions tested (red = linear, blue = log(moose density)).

Principal Component Analysis:

Due to the non-independence of the variables as seen in the correlation tests, a PCA was run using the major independent variables (Fig. 3.18, Table 3.8) and the axis scores were used in a subsequent regression. The broken stick model showed that only PC1 and PC2 should be considered for subsequent regressions. For PC1, adult female caribou survival decreased as anthropogenic disturbance, NPP, and predator and alternative prey increased, regardless of fire disturbance (i.e., increase in PC1; Table 3.9). Fire disturbance had weak factor loading (-0.082), which is within the range too close to zero to interpret (+/-0.3, Gentleman et al. 2011). PC2 was not significant in this model (Table 3.9).

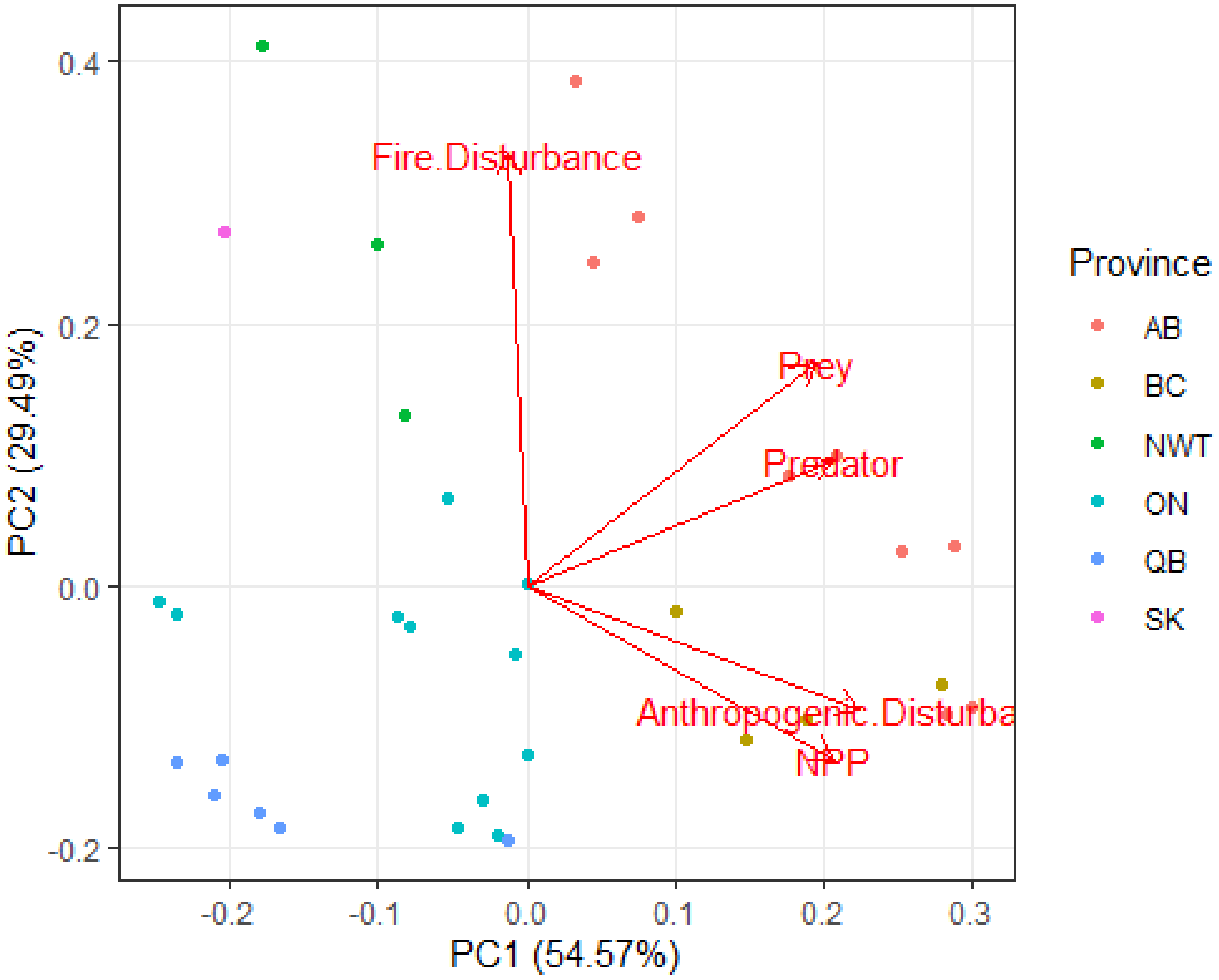

Figure 3.18: Principal component analysis (PCA) of main variables for 35 study areas across Canada with caribou survival. Variables include net primary productivity (NPP),

anthropogenic disturbance, fire disturbance, predator richness, and prey richness. Population points are included and coloured by province.

Table 3.8: Principal component analysis (PCA) species scores of main variables for 35 study areas across Canada with caribou survival.

	PC1	**PC2**
Fire Disturbance	-0.082	1.544
Anthropogenic Disturbance	1.424	-0.440
NPP	1.316	-0.617
Predator Richness	1.309	0.446
Prey Richness	1.237	0.795
Variance Explained	54.57%	29.49%

Table 3.9: Summary of the multiple regression model relating adult female caribou survival to scores the first two axes of the principal component analysis (PCA). Data is from 35 study areas across Canada with caribou survival. Axes scores are from PCA in Figure 3.18 and Table 3.8.

Variable	**Estimate**	**Std. Error**	***P* (*df* = 33)**
Intercept	1.87	0.02	***
PC1	-0.19	0.03	***
PC2	0.01	0.03	0.85

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

I also ran a PCA using the major independent variables for the 30 study areas which had survival and moose density data (Fig. 3.19, Table 3.10) and the axes scores were used in a subsequent regression. The broken stick model showed that only PC1 and PC2 should be considered for subsequent regressions. For PC1, all variables had a negative effect except for fire disturbance, which had an axis score of -0.242, which is within the range too close to zero to interpret (+/-0.3, Gentleman et al. 2011). PC2 was not significant in the model (Table 3.10 and 3.11).

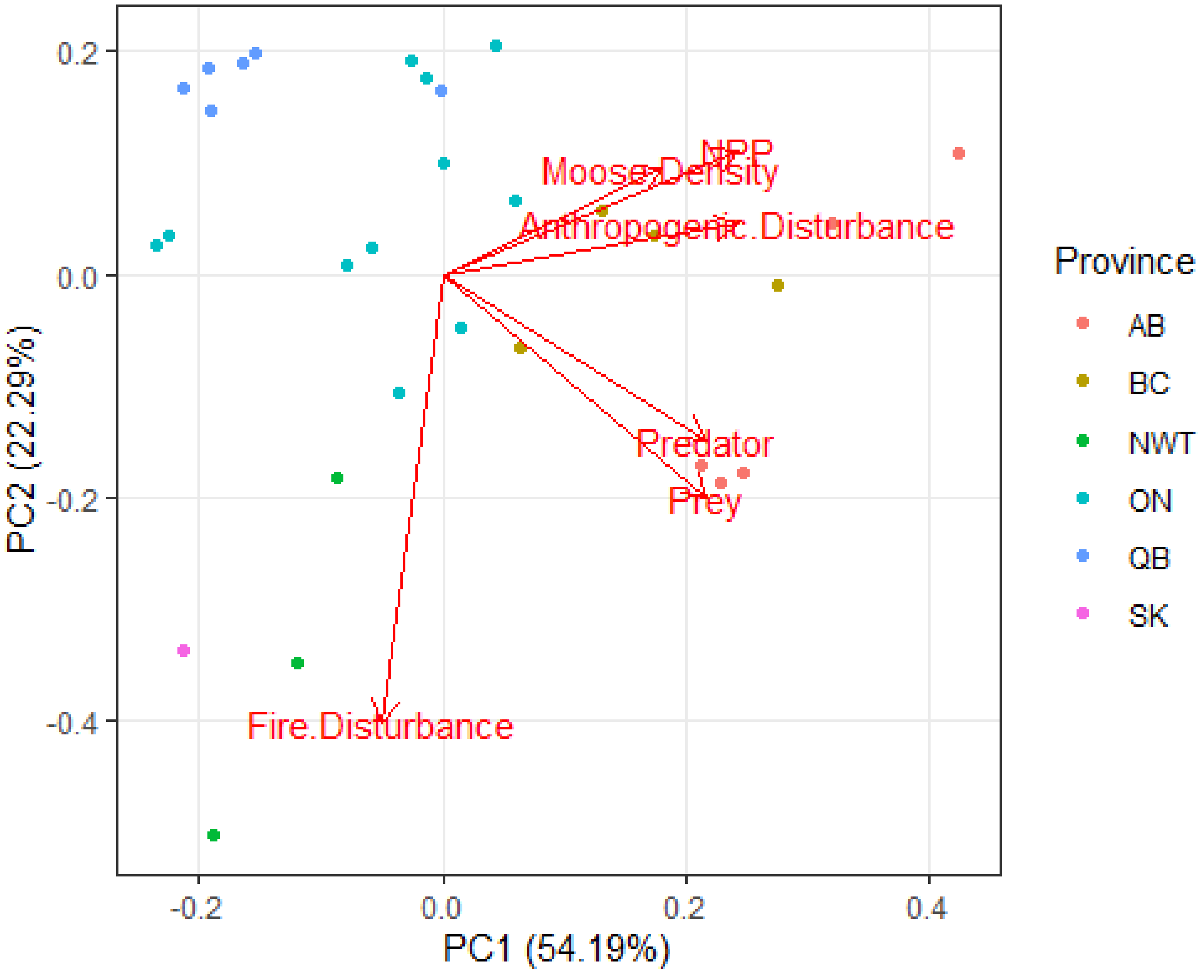

Figure 3.19: Principal component analysis (PCA) of main variables for the 30 study areas across Canada with caribou survival and moose density data. Variables include net primary productivity (NPP), anthropogenic disturbance, fire disturbance, predator richness, prey richness, and moose density. Population points are included and coloured by province.

Table 3.10: Principal component analysis (PCA) species scores of main variables for 30 study areas across Canada with caribou survival and moose density data.

	PC1	**PC2**
Fire Disturbance	-0.269	-1.388
Anthropogenic Disturbance	1.309	0.156
NPP	1.307	0.382
Moose Density	0.965	0.332
Predator Richness	1.161	-0.512
Prey Richness	1.170	-0.687
Variance Explained	54.19%	22.29%

Table 3.11: Summary of the multiple regression model relating adult female caribou survival to scores of first two axes of the principal component analysis (PCA). Data is from 30 study areas across Canada with caribou survival and moose density. Axes scores are from the PCA in Figure 3.19 and Table 3.10.

Variable	**Estimate**	**Std. Error**	***P* (*df* = 27)**
Intercept	1.87	0.02	***
PC1	-0.19	0.03	***
PC2	0.01	0.03	0.73

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Structural Equation Modelling:

Figure 3.20 represents the best SEM model for survival. None of the models using 34 study areas of survival data had significant interactions with survival. This simplified model, using the 30 study areas with survival and moose density data, had the lowest AIC_c, including testing the reverse hypothesis as found in Serrouya et al. (2021) where the arrow is reversed for NPP and disturbance ($\Delta AICc = 61.8$). All arrows except for anthropogenic disturbance~survival are significant (Table 3.12).

Table 3.12: Structural equation modeling (SEM) best model. Data is from 30 study areas across Canada with caribou survival and moose density.

Regressions:	**Estimate**	**Std.Err**	***P* (*df* = 2)**
Survival ~ Moose Density	0.000	0.000	0.027
Survival ~ Anthropogenic Disturbance	0.000	0.000	0.833
Anthropogenic Disturbance ~ NPP	0.304	0.047	***
Moose Density ~ NPP	1.052	0.276	***

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

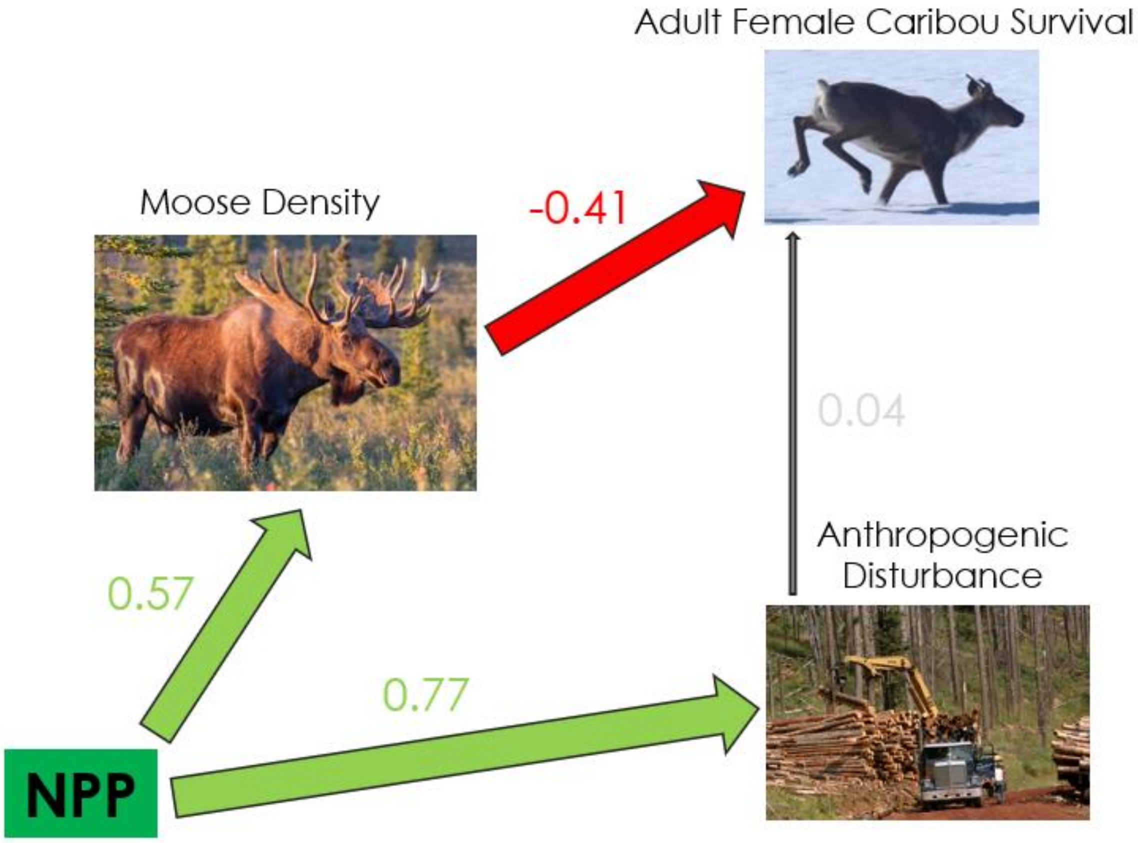

Figure 3.20: Structural equation modeling (SEM) for top model for caribou survival for 30 study areas that had data for survival and moose density. Boxes represent net primary productivity (NPP), moose density, anthropogenic disturbance, and caribou survival. Arrows represent the strength of the relationship.

3.4 Discussion:

Despite my prediction that NPP would have a positive effect on caribou recruitment and survival, there was little evidence for it in my analysis. However, there was evidence to support my hypothesis that DMAC is modulated by NPP, where anthropogenic disturbance and species richness are key determiners if DMAC occurs in a population. Despite the limitations of lacking provinces' data and not having as detailed data as could have been available (Appendix D), I believe this trend would hold true if I had access to all the requisite data. There was only one indication from my analysis that NPP can have a positive effect on caribou. PC2 for the recruitment PCA regression (Fig. 3.11, Table 3.3 and 3.4) had recruitment and NPP have a positive relationship and shows that recruitment tends to be relatively high in productive but unburned landscapes where few predators and alternative prey species can be found. This relationship was non-significant in models with survival (Fig. 3.18 and 3.19, Tables 3.9 to 3.12). Although I did not get any other positive response for recruitment or survival with NPP as expected and as found by Fortin et al. (2017), all of my other results were as expected. All covariates, excluding fire, were highly correlated, meaning areas of high NPP are also most likely to have higher anthropogenic disturbance, higher species richness, and greater moose densities. There is also a trade-off between anthropogenic and fire disturbance; there is only 100 percent of an area to be disturbed meaning there can not be a high amount of both disturbance types within the same area. My results show that NPP is the most important factor for predicting both caribou recruitment and survival and how these relate to DMAC at the national scale.

All the covariates except fire disturbance were highly correlated. This can bee seen in the maps (Fig. 3.1-3.4) as well as the results from the correlation tests (Table 3.1). The areas of highest NPP (Fig. 3.1) correspond with the areas of the highest anthropogenic disturbance (Fig. 3.2). These study areas also, generally, are found in the west where caribou populations have more species richness. Figure 3.3 shows that cougar, grizzly bear, and wolverine are distributed in the west but have a maximum eastern extent. Figure 3.4 shows the same is true for elk, mule deer, and wood bison. Meanwhile, white-tailed deer and coyote have a maximum northern extent (Fig. 3.3 and 3.4, Heffelfinger 2011, Hody and Kays 2018) which seems to correspond with levels of anthropogenic disturbance (Fig. 3.2, Latham et al. 2011*b*, Hody and Kays 2018). Figure 1 from Jensen et al. (2018) for moose density across North America tracks closely with NPP (Fig. 3.1). Moose prefer highly productive forest while plains and low productivity forest have lower densities of moose (Jensen et al. 2018). There is overlapping evidence that shows that these variables are highly correlated and that species richness, NPP, anthropogenic disturbance, and moose density are all positively related.

One explanation as to why the covariates are so correlated could be explained by considering the spatial autocorrelation of the datasets. A series of quick spatial autocorrelation tests using Moran I in the DHARMa package in R (Hartig and Lohse 2021) for variables in comparison to recruitment shows that some of my data does have spatial autocorrelation. Anthropogenic disturbance (P = 0.005), fire disturbance (P = 0.03), and predator richness (P = 0.06) were all significant for distance-based autocorrelation while NPP (P = 0.5), and alternate prey richness (P = 0.09) were not. Earlier exploratory models that I conducted using longitude and latitude showed that the trends I am finding can be explained on a north-south/west-east gradient (i.e. all highly productive ranges were in the northwest like B.C. and Alberta while the lower productivity/disturbance areas were found in the southeast like Ontario and Québec). The spatial autocorrelation inherent in my data means that study areas near each other are more likely to be similar. However, this emphasizes that evidence for DMAC is all found only in geographically related study areas in close proximity, and only in the highly productive B.C. and Alberta study areas (Latham et al. 2011*a*,*b*, Hervieux et al. 2014, Wittmer et al. 2005, Serrouya et al. 2017, 2019, DeMars and Boutin 2018, Mumma et al. 2018).

NPP and anthropogenic disturbance have been shown to be linked, with some research focused on how human impacts have caused increase in productivity (Zhu et al. 2016, Serrouya et al. 2021). However, Serrouya et al. (2021) are working at a different scale than my data, which could explain the different direction of the interaction. ΔEVI (Enhanced Vegetation Index) is also not interchangeable with NPP. The biggest difference is that ΔEVI is still a measure of deciduous greenness (similar to NDVI), while NPP is a measure of energy (which is seen as it has carbon within its units). Here, I instead argue that the direction of this relationship is reversed at the national scale. This was shown both by the increase in AIC_c when SEM models were reversed (Fig. 3.12 and 3.18, Table 3.5 and 3.12), and by the needs of forestry. Low-productivity areas cannot produce the yields necessary for high profits. This can be seen in the SK1 caribou population in Saskatchewan (Hart et al. 2019, Neufeld et al. 2021). Figure 3.21 (adapted from McLoughlin et al. (2019)) and Figure 3 from Hart et al. (2019) show that mature conifer and deciduous stands (Fig. 3.21, images A, C, and G) have small diameter trees and, therefore, low mass despite a span of over 40 years since disturbance. Trees in low-productivity areas take longer to become mature and never reach the size (diameter and height) that they do in higher-productivity areas. Thus, high-productivity areas (i.e. areas with high NPP values), are best suited to maximize forestry profits (Gholz 1982, Garkoti and Singh 1995, Urrutia-Jalabert et al. 2015). Forests grow much quicker in these areas and forest biomass has been found to be directly related to NPP (Gholz 1982, Garkoti and Singh 1995, also see Table 2 in Urrutia-Jalabert et al. 2015 comparing above ground biomass with above ground coarse wood productivity). Since NPP is the difference between gross photosynthesis and respiration, it directly shows the amount of forest growth in terms of vegetation. Higher net productivity areas, then, theoretically have faster forest growth and quicker accumulation of biomass than low productivity areas (Fortin et al. 2017).

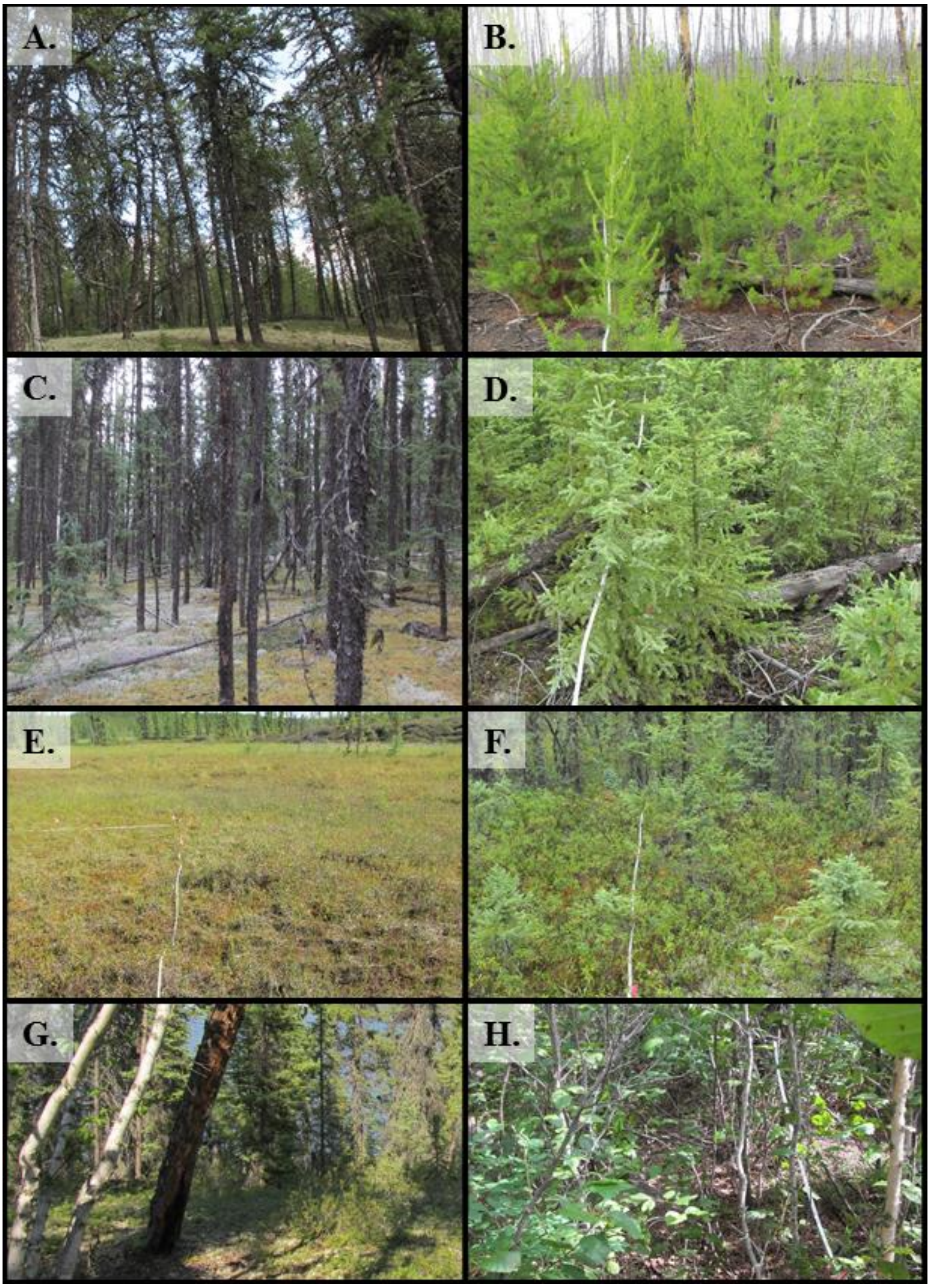

Figure 3.21: Images of the habitat classes for Saskatchewan Boreal Shield. A. Mature (>40 years) jack pine forest; B. Early successional (≤ 40 years) jack pine forest; C. Mature black spruce forest; D. Early successional black spruce forests; E. Open muskeg; F. Black spruce swamp; G. Mixed coniferous-deciduous forests. H. Early successional deciduous forests. Photo credit: Ruth Greuel. Figure adapted from McLoughlin et al. (2019).

Another explanation for the differences in NPP between study areas could be in the forest type. Gower et al. (1997), studying boreal forests in Saskatchewan and Manitoba, found that aboveground NPP is higher in deciduous forests than in coniferous forests. This could explain the productivity gradient moving from boreal plains (BC and AB) to boreal shield (SK, ON, and QB) and while moving northward within each province. Neufeld et al. (2021) found deciduous mixed-wood stands to represent only 7% of the study area in SK1. Coniferous stands were also found to be self-replacing (Hart et al. 2019) instead of going through the deciduous stage (often aspen as a result of asexual regeneration, Johnstone and Chapin 2006) characteristic of boreal plains (Strong 2004). Table 6 in Gower et al. (1997) shows that aspen stands had over double the NPP as black spruce or jack pine stands, while young jack pine stands had less than half of their mature counterparts. Conifer-dominated caribou study areas and areas where successional dynamics favour stand replacement, then, will have generally lower levels of NPP.

NPP has been shown to be positively linked with vertebrate species richness (Waide et al. 1999, Malmstrom 2010). My data show this as well. The high correlation between NPP with predator and alternative prey richness (Table 3.1), as well as species distribution maps (compare Figure 3.1, with Figures 3.3 and 3.4), show that areas of high NPP have both a larger predator guild and more alternative prey for living alongside caribou. Areas of high NPP, then, are at greatest risk of DMAC for caribou. More alternative prey species means a greater biomass of prey in the system. Increases in alternative prey densities, like white-tailed deer (Latham et al. 2011), or total ungulate biomass (Keith 1983, T. K. Fuller et al. 2003, Kuzyk and Hatter 2014) have been shown to increase wolf densities. Greater predator richness means that avoidant strategies that may work against one species may lead caribou to be more at risk of other predators (Leblond et al. 2016). In these highly disturbed high NPP areas, DMAC is exacerbated by the presence of more species because more alternative prey species equals greater ungulate biomass in the system, leading to increased wolf density, while more predator richness causes avoidance strategies to become less effective.

Moose-density covariates were shown to be closely related to NPP (Table 3.1) and PCA analysis had moose density vectors closely related to both NPP and anthropogenic disturbance (Fig. 3.19). Moreover, as previously mentioned, Figure 1 in Jensen et al. (2018) of moose density across North America tracks closely compared to Fig. 3.1 NPP and Fig. 3.2 anthropogenic disturbance. My results show that moose density has a negative effect on caribou survival in all model types (models Fig 3.18, Table 3.7; PCA regression Fig. 3.19, Table 3.10 and 3.11; SEM Fig. 3.20, Table 3.12). The SEM for survival shows that NPP has a positive effect on moose density which in turn negatively impacts caribou survival (Fig. 3.20, Table 3.12). This could be due to the differing forest composition of low- and high-productivity boreal populations. Some research has shown that moose populations do not respond to fire in stands less than 25 to 30 years since fire (Demars et al. 2019, Julianus et al. 2019), while Neufeld et al. (2021) showed that this was likely do the lack of deciduous trees in the forest succession of low productivity boreal shield. High-productivity areas where forest succession favours deciduous species are where moose can have the greatest biomass on the landscape. This is exacerbated by anthropogenic disturbance, which moose are known to respond to (Rempel et al. 1997, Serrouya et al. 2011). These high-productivity, highly human-disturbed areas are where evidence of DMAC is prevalent (Hervieux et al. 2013, Peters et al. 2013, Serrouya et al. 2019).

There is a trade-off between anthropogenic and fire disturbances. Evidence for this is in the correlation matrix (Table 3.1). There is limited space, so when an area has a lot of one disturbance, it cannot also have a lot of the other. This conflict between the timber industry and habitat protection (allowing fire and natural processes) has been occurring for years (Cumming et al. 1994). The high levels of anthropogenic disturbance in the western boreal plains (exceeding 70% in some Alberta and British Columbia study areas, Environment Canada 2011) reduces the area left to burn. Also, while the area may be small, fires are suppressed around industrial features (Danneyrolles et al. 2016).

It is already well documented that anthropogenic disturbance negatively affects caribou (James and Stuart-Smith 2000, Sorensen et al. 2008, Latham et al. 2011*a*, DeMars and Boutin 2018, DeMars et al. 2019). There is a conflict between the forestry industry and caribou habitat. Apps et al. (2001) showed that old growth areas which are favoured by caribou also have high timber value, yet old growth habitat is considered essential for caribou (Environment Canada 2012). My results showed that anthropogenic disturbance was negatively related with both caribou recruitment and survival in all models, though it was non-significant for the SEM models. On the other hand, recent research suggests that fire, while it does limit habitat use (DeMars et al. 2019), does not contribute to a functional response by moose and subsequently does not show evidence of DMAC (DeMars et al. 2019, Johnson et al. 2020, Stewart et al. 2020, Neufeld et al. 2021,). Industrialization of boreal forests has also led to a change in forest composition from mostly coniferous to mostly deciduous (Cumming et al. 1994, Danneyrolles et al. 2016). This is compounded with the fact that linear features are the dominant form of anthropogenic disturbance in the western boreal, which increases hunting efficiency of wolves (James and Stuart-Smith 2000, Latham et al. 2011*a*, Dickie et al. 2017, 2020, Pigeon et al. 2020). Based on this evidence, I would argue that fire disturbance is of much lesser importance than anthropogenic disturbance, especially in the context of DMAC, and that this should be reflected in management plans for caribou.

The results indicate that NPP is critical at the national scale. It was the best model for both recruitment and survival (Tables 3.3 and 3.7). It is an important axis of the PCA regressions (Fig. 3.12, 3.19, 3.20, and Tables 3.4, 3.5, 3.9 to 3.12) and it is the base of the SEM models (Fig. 3.12 and 3.20, Tables 3.6 and 3.13). In Saskatchewan, the long-term NPP for the SK1 area averaged 372 g C/m^2 (Table D2). Other study areas with comparably low NPP include Dehcho North (322 g C/m^2) and Mackenzie (329 g C/m^2), Pine Point/Buffalo Lake (393 g C/m^2), and Hay River Lowlands (415 g C/m^2) in Northwest Territories, Swan (350 g C/m^2), Missisa (364 g C/m^2), and James Bay (378 g C/m^2) in Ontario, and Temiscamie (399 g C/m^2) and Manicouagan Ouest (410 g C/m^2) in Québec (Table D2). All of these study areas also had above-average recruitment (ranging from 0.2 to 0.37 calf:cow ratio), except for the Ontarian study areas Swan and Missisa (which were 0.14 and 0.17 calf:cow ratio respectively). On the other end of the spectrum, the study areas with the highest NPP are Pipmuacan in Québec, Churchill and Nipigon in Ontario, Parker, Snake-Sahteneh, Prophet, and Chinchaga in British Columbia, and Red Earth, East Side Athabasca River, West Side Athabasca River, Chinchaga, and Cold Lake in Alberta (all ranging from 500 to 570 g C/m^2; Table D2). All of these study areas have lower than 0.2 calf:cow ratio (and as low as 0.06 calf:cow ratio), excluding Nipigon in Ontario. All of the highest-productivity areas also had high anthropogenic disturbance (ranging from 51 to 78% disturbed, excluding Churchill and Nipigon which had less than 30%), while the low-productivity study areas never exceeded 12% anthropogenic disturbance on the landscape (Table D2). All of this evidence shows that the primary productivity hypothesis of DMAC, as proposed in Neufeld et al. (2021), stating that only areas of high productivity are capable of supporting the hypothesis of DMAC, is plausible at the national scale.

Based on my results, I hypothesize that DMAC can only occur in areas of high NPP. Anthropogenic disturbance is crucial in the NPP and DMAC equation, possibly due to the increased hunting efficiency of predators, as afforded by linear features (James and Stuart-Smith 2000, Latham et al. 2011*a*, Dickie et al. 2017, 2020, Pigeon et al. 2020). SEM models show that NPP fuels the system. With low NPP, there are small trees and little growth and therefore little incentive for forestry. While Serrouya et al. (2021) found that disturbances were causing increase in productivity (measured as ΔEVI) at the boreal plains scale, I found that differences in NPP influence anthropogenic disturbance and species composition at a national scale (SEM Fig. 3.12 and 3.20, Table 3.5 and 3.12). These changes in directionality are not unheard of as one switches the scale at which tests are performed (Levin 1992). At larger scales we are studying caribou at an evolutionary scale and time becomes the greatest measure. It could be that the adult female survival results are much more important at a national scale than the variability in recruitment. Survival is the most important in the long term and is more important for calculations of lambda for large ungulates (Gaillard et al. 2000). This could mean the survival models are actually more crucial than the recruitment ones as regards the persistence of the species. Meaning moose density and NPP as shown in SEM are important as they both cause a decline in adult female survival (Fig. 3.20, Table 3.12). Adult female lifetime reproductive success, then, is the most important for persistence of the species at this larger scale (Gaillard et al. 2000).

Much like what was found for the SK1 caribou population (Neufeld et al. 2021), DMAC is unlikely to be occurring in all areas of low NPP. Fire disturbance does not have the same effect towards DMAC as anthropogenic disturbance (Johnson et al. 2020, Stewart et al. 2020, Neufeld et al. 2021). High NPP is needed for successional dynamics that favour deciduous species rather than a cycle of self-replacing coniferous stands (Hart et al. 2019). Disturbance in these high NPP areas allows for the invasion of white-tailed deer and coyote as well as increases in moose density (Latham et al. 2011*b*, Hody and Kays 2018, DeMars et al. 2019). Disturbance type, especially linear features, could play a key role in determining why I only have evidence of DMAC in areas where anthropogenic disturbance is dominant. While nearly all areas of high NPP had high levels of anthropogenic disturbance and low caribou recruitment and survival, areas of low NPP had low anthropogenic disturbance and above average recruitment and survival. NPP is an important factor for caribou at the national scale, and my results show that DMAC only occurs in areas of high NPP where anthropogenic disturbance is greater than natural disturbance, where successional dynamics favour deciduous species resulting in a functional response to disturbance from moose, and where there is increased predator and alternative prey richness.

3.5 Conclusions and Management Implications:

The primary goal of this chapter is to test the hypothesis that DMAC is modulated by NPP throughout woodland caribou range. While my results show that DMAC is an important management factor where NPP is high, it is not important where NPP is low. While evidence for DMAC was found at a regional/ecoregion scale, management strategies employing it were applied at a national scale. Not taking into account differing ecotypes that caribou inhabit and making inferences when changing scale (Levin 1992) can lead to the mismanagement of threatened species. Future work needs to find the most important limiting factor for medium- and low-NPP caribou populations.

There is a reason why in space as you move northward into less productive areas, moose no longer have the pressure of apparent competitors with caribou, and moving onto the tundra, caribou do not avoid alternative prey habitat any longer but only avoid wolves (Frame et al. 2008). Further decreases in productivity leave little competition from alternative prey, and eventually caribou are the only ungulates on the landscape. The shift then, where DMAC goes from being important for caribou to where it is not rests on NPP and is limited to where successional dynamics can no longer support moose or invasive white-tailed deer. While this area is likely to move northward as a result of climate change, it is not the primary concern for these low-productivity caribou populations at the moment.

Based on my evidence and the work of recent studies (DeMars et al. 2019, Johnson et al. 2020, Neufeld et al. 2021), I would argue that fire disturbance is of much lesser importance than anthropogenic disturbance, especially in the context of DMAC. Management plans for caribou in the west should reflect this so that lower disturbance thresholds are set for anthropogenic disturbance, especially as it relates to linear features.

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CHAPTER 4: SUMMARY, CONCLUSIONS, AND FUTURE DIRECTIONS

4.1 Boreal Caribou and DMAC

Boreal woodland caribou (*Rangifer tarandus caribou*, hereafter caribou) are Threatened across Canada and face many dangers (Environment Canada 2012). Anthropogenic disturbance and natural fires represent the largest threat to woodland caribou since they disrupt and fragment the old growth habitat that caribou require (Sorensen et al. 2008, Environment Canada 2012). Research suggests that linear features such as seismic lines, roads, and pipelines are considered the most detrimental of anthropogenic features since they allow predators to move quickly between areas (James and Stuart-Smith 2000, Pigeon et al. 2020).

Possibly the greatest threat to caribou is disturbance-mediated apparent competition (DMAC), where landscape disturbance benefits early-seral browsing ungulate alternative prey which in turn positively affecting their predators, whose numerical response to the increase in prey negatively affects caribou (Seip 1992, Fuller et al. 2003, Festa-Bianchet et al. 2011, Serrouya et al. 2015, DeMars et al. 2019). It is at the southern front of the range retraction for caribou, like the boreal plains of Alberta, where DMAC has been studied the most (Latham et al. 2011*a*, *b*, Hervieux et al. 2013, Peters et al. 2013). As a result, DMAC has become increasingly important in the drafting of management plans and conservation actions for caribou throughout Canada (Environment Canada 2012, Hervieux et al. 2013, Serrouya et al. 2015, Environment and Climate Change Canada 2018, DeMars et al. 2019, Serrouya et al. 2019).

Despite that much of the research focus on caribou has been conducted in the south, which strongly informs DMAC-based conservation strategies for caribou, it is within the northern shield and taiga of Canada where the majority of boreal caribou exist. These forests are characterized by generally low net primary productivity (e.g., <0.3 kg C/m^2/year, see Lui et al. 2002), low anthropogenic disturbance, and high fire disturbance. However, it is in these environments that we know the least about caribou ecology. Here, only wolves and black bears (*Ursus americanus*) prey on caribou while moose is the only ungulate alternative prey (Environment Canada 2011, 2012).

Net primary productivity (NPP) varies globally from 30 to 1000 g C/m^2, though boreal habitats rarely exceed 600 g C/m^2 (Scurlock et al. 1999, Running et al. 2000). While higher productivity means increased forage abundance for caribou, it is thought that increased predation risk negates this positive effect (Leclerc et al. 2014) since caribou are thought to be predation, rather than forage, limited (Hegel et al. 2010*a*, *b*). Caribou population growth has been shown to increase in response to a feeding program for mountain caribou in British Columbia (Heard and Zimmerman 2021). However, primary productivity is also associated with increased animal diversity (Malmstrom 2010). Caribou populations of higher productivity, then, are likely to have higher predator and alternative prey richness. This suggests that caribou only select for low productivity and lichen areas as a means of avoiding alternative prey and their predators.

Throughout this thesis, I tested the hypothesis that DMAC is modulated by NPP, with disturbance type, alternative prey richness, and predator richness in the system being keys components for whether assumptions in DMAC are met.

4.2 Decoupling of DMAC in Poorly Productive Saskatchewan Boreal Shield

In Chapter 2, I tested the hypothesis of DMAC in a poorly productive, high natural disturbance caribou population in Saskatchewan’s Boreal Shield. Despite the high fire-return interval in the study area, the Saskatchewan Boreal Shield supports a relatively low density of moose and, for the species, a relatively high density of boreal caribou. This is the first indication that DMAC, which is predicated on a numerical response of alternative prey and related inverse response by caribou to disturbance (via predation), shows signs of decoupling in the study area. Low densities of alternative prey are not known for any region where there is evidence of DMAC (Latham et al. 2011*a*, *b*, Hervieux et al. 2013, Peters et al. 2013, Serrouya et al. 2019).

Although DMAC has been shown to be a very likely and strong limiting factor to caribou within the southern boreal (and mountain) caribou range, all instances of this have thus far been indicated for areas characterized by higher NPP, and high biomass of alternative-ungulate prey, that include not only moose but other species (especially white-tailed deer) as alternative-ungulate prey for predators. I proposed these conditions are influenced by the amount of energy available within the system to generate the trophic cascade necessary to link predator-caribou-alternative prey dynamics. The Saskatchewan Boreal Shield, as does much of the extant boreal caribou range, deviates from these high-productivity populations, in that deciduous browse is rare after fire disturbance.

As a consequence of the findings from Chapter 2, it was necessary to further study where DMAC does and does not apply to boreal caribou and the extent to which it should factor into how we manage populations. I showed that DMAC does not occur in poorly productive regions with low species richness where fire is the chief disturbance agent. I was left to determine how DMAC is influenced by the competitive dynamics of different alternative-prey species such as white-tailed deer compared to moose, the ecology of invasive alternative prey and predators into the boreal, alternative prey and predator species richness, the relationships between NPP and DMAC, and the nature of the influence of anthropogenic versus natural disturbance.

4.3 Net Primary Productivity Hypothesis of DMAC

Following up on Chapter 2, Chapter 3 studied the DMAC hypothesis at a national scale. My conclusions in Chapter 2 directed me towards formulating the primary productivity hypothesis of DMAC. From evidence in the Saskatchewan Boreal Shield, I hypothesized that low productivity systems do not allow for alternative prey to exploit disturbance as they can in the plains or foothills where primary productivity is higher (and hardwood successional stages are more common). In order to test this, I looked at caribou recruitment as a response of NPP (in g C/m^2) at the national scale for study areas across Canada.

I found evidence to support my hypothesis that DMAC is modulated by NPP, where anthropogenic disturbance and species richness are key determiners if DMAC occurs in a population. Based on my results, I hypothesized that DMAC can only occur in areas of high NPP with high anthropogenic disturbance. Anthropogenic disturbance is crucial in the NPP and DMAC equation, possibly due to the increased hunting efficiency afforded by linear features (James and Stuart-Smith 2000, Latham et al. 2011*a*, Dickie et al. 2017, 2020, Pigeon et al. 2020), which are common in areas where DMAC has been found. My models showed that NPP fuels the system. Much like what was found in Chapter 2 (Neufeld et al. 2021), DMAC is unlikely to be occurring in all areas of low NPP. Fire disturbance does not have the same effect towards DMAC as anthropogenic disturbance (Johnson et al. 2020, Stewart et al. 2020, Neufeld et al. 2021). NPP is needed for successional dynamics that favour deciduous species, instead of self-replacing coniferous stands as is common in low productivity areas (Hart et al. 2019). Disturbance in these high NPP areas allows for the invasion of white-tailed deer and coyote as well as increases in moose density (Latham et al. 2011*b*, Hody and Kays 2018, DeMars et al. 2019). While nearly all areas of low NPP had low anthropogenic disturbance and above average recruitment and survival, areas of high NPP had high levels of anthropogenic disturbance and low caribou recruitment. My results showed that NPP is an important factor for caribou at the national scale. DMAC seems to only occur in areas of high NPP where anthropogenic disturbance is greater than natural disturbance, successional dynamics favour deciduous species resulting in a functional response to disturbance from moose, and there is increased predator and alternative prey richness. My results show that NPP is the most important factor for predicting both caribou recruitment and survival and how these relate to DMAC at the national scale.

4.4 Limitations, Management Recommendations, and Future Directions

Future work could include verifying my findings with the complete set of data (including data from Manitoba, yearly division of Alberta data, and more accurate species ranges). All of my analyses were done with the data available and forthcoming. Some species distribution maps provided by provinces were done so with less care than from other legislations and could have a slight effect on the species richness recorded for different populations. Another important factor could be if more study areas had moose density surveys completed in order to further test the effect of increased moose density on caribou demographics, especially adult female survival. However, as I had the majority of caribou study areas (40/58), I believe that my findings will hold as representative for the whole of boreal caribou range. Some other limitations might be in extrapolating the work found in SK1 (Ch. 2) to other low productivity environments. While chapter 3 does support this evidence that DMAC is unlikely to occur, eastern low productivity areas have lower fire disturbance and a lower predator guild compared to SK1.

Low-productivity, northern caribou ranges, such as the Saskatchewan Boreal Shield, have thus far received very little attention. This is not surprising as most research on woodland (boreal and mountain) caribou occurs in areas of high anthropogenic disturbance in the form of resource extraction. Almost all work on non-migratory caribou occurs in the boreal plains of western Canada, the southern shield region of Québec and Ontario, and with respect to mountain caribou, in heavily developed regions of the Rocky Mountains. Caribou are rarely studied in areas where logging or oil and gas development are not occurring. Yet, approximately 2/3 of caribou range is in the northern boreal shield and taiga, where moose are the only alternative ungulate prey available in the context of DMAC, forests are characterized by generally low NPP, and anthropogenic features occur at levels similar to that of the Saskatchewan Boreal Shield.

The fact that a considerable majority of boreal caribou range in Canada occurs in these low-productivity boreal moose-caribou-wolf systems only highlights how understudied they have thus far remained. Currently, the management approach to boreal caribou throughout their Canada-wide range is predicated on the assumption that DMAC is an important consideration for all boreal caribou populations (Environment Canada 2011, 2012). But the supposition that fire disturbance, resulting in younger forests, can generate the habitat conditions necessary to affect increased abundance of alternative prey, in turn increasing wolf populations and limiting caribou population growth, is inconsistent with what I observed in the Saskatchewan Boreal Shield.

My results from Chapter 3 show that DMAC is an important management factor where NPP is high, it is not important where NPP is low. While evidence for DMAC was found at a regional scale, management strategies were applied based upon it at a national scale. Not taking into account differing ecotypes that caribou inhabit and making inferences when changing scale (Levin 1992), can lead to mismanagement of threatened species. Based on my evidence and the work of recent studies (DeMars et al. 2019, Johnson et al. 2020, Stewart et al. 2020, Neufeld et al. 2021), I would argue that fire disturbance is of much lesser importance than anthropogenic disturbance, especially in the context of DMAC. Management plans for caribou should consider that fire disturbance does not act the same as anthropogenic disturbance and that DMAC is unlikely to occur in areas of low productivity. Future work needs to find the most important limiting factor for medium and low NPP caribou populations.

As discussed in chapter 3, at the national scale we are studying caribou at an evolutionary scale. We saw Québec populations positively affected by productivity (Fortin et al. 2017) while eastern populations were negatively affected (Serrouya et al. 2021). While these trends are possible at the local scales, they do not hold true for the national scale. Adult female survival results are much more important at a national scale than the variability in recruitment. Survival is the most important in the long term and is more important for calculations of lambda (Gaillard et al. 2000). Adult female lifetime reproductive success, then, is the most important for persistence of the species at this larger scale (Gaillard et al. 2000). This also explains how the species-rich systems give way to moose-caribou-wolf systems which eventually give way to caribou-wolf systems on the tundra. While nutrition can help adult females (Heard and Zimmerman 2021), caribou, generally, are adapted to live in low productivity environments where other browsing ungulates cannot survive. While climate change is likely to push this area northward, it is in these low productivity environments where, with proper management, caribou will continue to persist as a species.

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5 Appendices:

5.1 Appendix A. Vegetation Mapping:

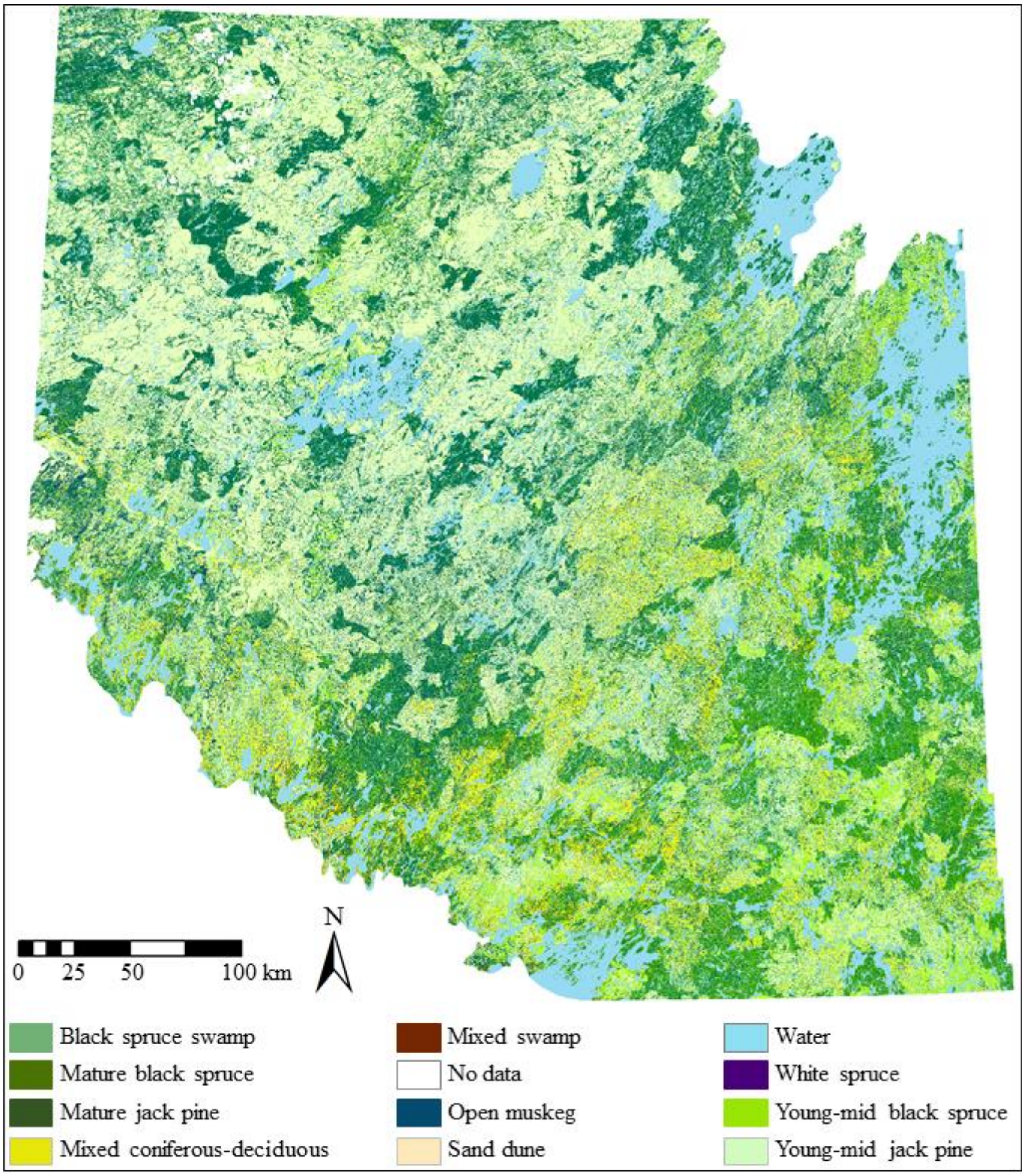

Figure A1. Classified map (187,000 km^2) at 30- × 30-m resolution of various available vegetation associations (classes) used to evaluate habitat selection of female boreal caribou, wolves, and black bears in the Saskatchewan Boreal Shield (reproduced from McLoughlin et al. 2019). Extent of fire in the past 40 years is represented by the age classes of the forest. Young to intermediate (young-mid) black spruce and young-mid jack pine are ≤40 years; all mature classes are >40 years, as are the remaining categories. These classes are not precisely fire classes but rather vegetation associations derived to reflect caribou habitat; however, they generally represent the extent of fire (and young age of stands) across the Saskatchewan Boreal Shield in Canada (2017-2018).

5.2 Appendix B. Ungulate Aerial Surveys:

Of surveys conducted since 2008, 11 of 16 detected boreal (and not barren-ground) caribou in their respective study areas (Table B1). Over all 16 surveys conducted since 2008 (including surveys where no caribou were observed), the average density was 36.9 boreal caribou/1,000 km^2 (95% CI = 26.7–47.2 caribou/1,000 km^2). Thirteen surveys recorded instances of moose when observed (3 surveys did not include counting moose as an objective of their survey). Of the applicable surveys, the average density was 45.7 moose/1,000 km^2 (37.8–53.6 moose/1,000 km^2). Eight caribou surveys reported the ratios of male to female and calf to female in their sample. The average male:female ratio was 0.571 (95% CI = 0.444–0.699) and calf:female was 0.195 (0.158–0.232). The caribou-survey sightability test conducted by the University of Saskatchewan from 17–18 March 2015 indicated that identification of woodland caribou (*n* = 49). There were 4 caribou near the edges of the survey gridlines, however, that had potential to have moved off in the hours between relocations and surveys. Assuming that half of those had as much likelihood as moving onto versus off the survey grid, we computed that the survey we conducted was biased conservatively (in terms of true density) by approximately 22% (i.e., we suspect that my estimate was 22% below the true estimate. We only caution that estimates of density are minimum estimates and population density is likely higher than as reported using the 100% coverage methods (Table B1), assuming that detection probability is approximately constant across all survey

Table B1. Ungulate aerial surveys conducted in the Saskatchewan Boreal Shield in Canada from 2008 to 2015. Most data are summarized by Omnia Environmental Services and presented in McLoughlin et al. (2019).

Study	Survey timing	Survey area (km^2)	Coverage (%)	Search intensity (min flown per km^2)	Species/km^2		Woodland caribou population structure		
					Moose	Caribou	Bulls:Cow	Calf:Cow	Calves as a % of total population
Millennium TRSA 2014	Mar 2014	2,285	40	1.7	0.04	0.005	1.6	0	0
Millennium LSA 2014	Mar 2014	397	100	1.7	0.05	0			
Key Lake 2014 (unpublished)	3–12 Mar 2014	1,616	40	1.7	0.03	0.03			
Key Lake 2013 (unpublished)	13–16 Mar 2013	1,616	40	1.7	0.03	0.06	0.75	0.25	18
Key Lake 2012 (unpublished)	15–17 Mar 2012	1,616	40	1.5	0.05	0.09	0.31	0.13	9
Key Lake 2011 (unpublished)	13–17 Dec 2011	1,616	40	2.0	0.04	0.06	0.714	0.33	12
914	Mar 2011	554				0			
McArthur River 2011 (HAB-TECH 2012)	7–9 Feb 2011	400	100	1.8	0.05	0.04	0.27	0.27	18
914	Feb 2011	554				0.004			
914	Dec 2010	410				0.027			
Cigar Lake 2011 (HAB-TECH 2011)	7–9 Mar 2010	320	100	1.4	0.01	0			
Four Bear 2010 (HAB-TECH 2010a)	5–6 Mar 2010	350	100	1.5	0.08	0			
Key Lake 2010 (HAB-TECH 2010b)	23–24Feb 2009	384	100	1.7	0.02	0.05	0.25	0	0
Virgin River 2009 (HAB-TECH 2009b)	21–24 Mar 2009	376	100	1.8	0.05	0.13	0.32	0.4	20
Courtenay Lake, U of S 2015	17–18 Mar 2015	380	100	1.7	0.024	0.095	0.357	0.18	11.1
Tamarack 2009 (HAB-TECH 2009a)	27–29 Feb 2008	324	100	1.9	0.12	0			

5.3 Appendix C. Alberta Biodiversity Monitoring Institute (ABMI) Wolf Census:

To estimate wolf density, we used data collected by the Alberta Biodiversity Monitoring Institute (ABMI) over 4,500 km^2 in the center of the study area in early 2017. From 25 through 27 February 2017, observers D. Drinnan and G. Watts used a 8GCBC Scout fixed-wing aircraft (American Champion Aircraft Corporation, Rochester, WI, USA) to conduct a wolf-specific density survey following standardized methods to compare with the same team's surveys concurrently being conducted in Alberta, British Columbia, and the Northwest Territories as part of a joint study of wolf-moose-caribou relationships. Tracks were isolated into discrete groups, with group size being estimated when animals branched apart. Flights were staged out of Key Lake Mine and covered a study area of approximately 4,500 km^2 with 3-km transect spacing.

At the time of the ABMI wolf survey, which relies on tracks rather than actual observations of wolves, snow conditions were reported as very good for tracking (significant snowfall event followed-by good weather) and light conditions were fair overall. Although survey flights specifically focused on spotting and following up tracks of wolves (not directly estimating moose or caribou abundance), the team observed 11 moose and 7 boreal caribou incidentally during the survey.

The ABMI team directly sighted 2 wolves on the grid in isolated areas (e.g., not with packs), and 1 wolf was observed to be sick or injured. Based on tracks, 5 packs were identified in the grid area, with an estimate of 18 wolves in total or 3.6 wolves/pack. The team noted that 1 of the 5 packs was on the edge of the survey area that typically would not be included in an ABMI wolf-density estimate; excluding this edge pack, which was estimated at 4 wolves, the density estimate was 14 wolves/4,500 km^2, or 3.1 wolves/1,000 km^2.

5.4 Appendix D. Data and Data Sources

Table D1: Data sources for province, caribou demographics, recruitment years, survival years, disturbance source, species richness source, and moose density source for caribou study areas used in analyses.

Population	**Province**	**Caribou Demographics**	**Recruitment (Years)**	**Survival (Years)**	**Anthropogenic and Fire Disturbance**	**Species Richness**	**Moose Density**
Dehcho North	NWT	Serrouya et al. 2021	2006-2018		Environment Canada 2011, Environment and Climate Change Canada 2017	Northwest Territories Environment and Natural Resources	Serrouya et al. 2021
Dehcho South	NWT		2006-2018				
Hay River Lowlands (South Slave)	NWT		2004-2018	2005-2018	https://open.canada.ca/data/en/dataset/890a5d8d-3dbb-4608-b6ce-3b6d4c3b7dce, accessed 26 February 2021		
Mackenzie (South Slave	NWT		2017-2018	2017-2018			
Pine Point/Buffalo Lake (South Slave)	NWT		2017-2018	2017-2018			
Chinchaga	BC	Ministry of Forests, Lands and Natural Resource Operations, Culling and Cichowski 2017	2013-2018	2014-2018	Johnson et al. 2020	Wildlife Management Units data from the Ministry of Forests, Lands, Natural Resource Operations and Rural Development (https://catalogue.data.gov.bc.ca/dataset/wildlife-management-units accessed January 4, 2019)	Webster and Lavallée 2016, Culling and Chichowski 2017
Calendar	BC		2013-2018	2014-2018			Thiessen 2010, Culling and Chichowski 2017
Maxhamish	BC		2013-2018	2014-2018			Backmeyer 2004, Culling and Chichowski 2017

Prophet	BC		2013-2016				McNay et al. 2013, Culling and Chichowski 2017
Parker	BC		2013-2016				Thiessen 2010, Culling and Chichowski 2017
Snake-Sahteneh	BC		2013-2018	2014-2018			Backmeyer 2004, Culling and Chichowski 2017
Richardson	AB	Hervieux et al. 2013, years ranged from 1994-2012	3 years	3 years	Environment Canada 2011	Alberta Monitoring Institute, Fiera Biological Consulting	
WSAR	AB		18 years	18 years			Ranger and Anderson 2012
Chinchaga	AB		10 years	10 years			Webb and Anderson 2009
Red Earth	AB		15 years	15 years			Ranger and Anderson 2012
Bistcho	AB		5 years	5 years			
Caribou Mountains	AB		17 years	17 years			
Cold Lake	AB		1998-2002, 2004-2019	1999-2019	Environment Canada 2011, Environment and Climate Change Canada 2017		Donker and Maile 2014

ESAR	AB	Hervieux et al. 2013, Serrouya et al. 2021	1995-2019	1995-2019			Webb and Anderson 2009
Yates	AB		2008-2019	2008-2019			
SK1	SK	McLoughlin Population Ecology Laboratory	2015-2018	2015-2018	https://open.canada.ca/data/en/dataset/890a5d8d-3dbb-4608-b6ce-3b6d4c3b7dce, accessed 26 February 2021	Saskatchewan Ministry of Environment	McLoughlin Population Ecology Laboratory
Sydney	ON	Ministry of the Environment, Conservation and Parks	2012-2013	2013	Environment Canada 2011, Environment and Climate Change Canada 2017	Ministry of Natural Resources and Forestry	Ministry of Natural Resources and Forestry 2014*a*
Berens (ON)	ON		2012-2013	2013			MNRF 2014*b*
Churchill	ON		2012-2013	2013			MNRF 2014*c*
Brightsand	ON		2011-2013	2011-2013			MNRF 2014*d*
Nipigon	ON		2010-2013	2010-2013			MNRF 2014*e*
Pagwachuan	ON		2010-2013	2010-2013			MNRF 2014*f*
Kesagami	ON		2010-2013	2010-2013			MNRF 2014*g*
Swan	ON		2009-2012				MNRF 2014*h*
Spirit	ON		2009-2012	2009-2012			
Kinloch	ON		2010-2013	2010-2013			
Ozhiski	ON		2010-2013	2010-2013			
Missisa	ON		2009-2013	2009-2012			
James Bay	ON		2010-2013	2011-2013			
Nottaway	QB	Fortin et al. 2017, Daniel Fortin’s laboratory at the université Laval	2003, 2007, 2009, 2011	2004-2011		White-tailed deer from mffp.gouv.qc.ca	Lefort and Massé 2015
Assinica	QB		2003, 2007, 2009-2015	2004-2012			
Temiscamie	QB		1999-2003, 2007, 2011	1999-2012			
Manicouagan Ouest	QB		1999, 2002-2007	2005-2012			

Manicouagan Est	QB		1999, 2003-2005, 2007, 2009	2007-2012			
Pipmuacan	QB		2012	2004-2009			

Table D2: Data used in analyses for Chapter 2, including study areas with missing data. Sources of data can be found in Table D1.

Prov.	Study Area	Yrs Rec.	Yrs Surv.	Exclusion Reason	Recruit.	Rec. SD	Surv.	Surv. SD	Car. Pop.	Lat.	Long.	Fire Dist. %	Anthro. Dist. %	Total Dist. %	NPP	Moose Density	Predator Richness	Prey Richness
NWT	Dehcho North	13	0	NA	0.3750	0.1925	NA	NA	Unk.	62.546	-121.015	55.7	12.3	63.5	322.34	NA	4	3
	Dehcho South	13	0	NA	0.3356	0.1287	NA	NA	Unk.	60.575	-121.202	14.3	31.3	42.5	444.49	71.6	4	3
	GSA North	1	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	31.1	6.2	35	NA	NA	NA	NA
	GSA South	1	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	41.1	8.5	46.8	NA	NA	NA	NA
	Hay River Lowlands (South Slave)	14	11	NA	0.2746	0.0997	0.8504	0.0745	Unk.	60.723	-118.121	28.8	10.6	37.2	414.77	29	4	3
	Mackenzie (South Slave)	2	2	NA	0.3715	0.0355	0.9050	0.0120	Unk.	61.854	-116.088	64.6	1.8	66.4	329.21	29	4	3
	Pine Point/ Buffalo Lake (South Slave)	2	2	NA	0.3140	0.0480	0.9600	0.0020	Unk.	60.735	-114.409	48.6	11.4	60	392.8	13	4	3
	Fort Liard	NA	NA	No data	NA	NA	0.8553	NA	Unk.	NA	NA	NA	NA	NA	NA	71.6	NA	NA
	Fort Providence Reference	NA	NA	No data	NA	NA	0.8398	NA	Unk.	NA	NA	NA	NA	NA	NA	29	NA	NA
	Fort Providence South FMA	NA	NA	No data	NA	NA	0.8398	NA	Unk.	NA	NA	NA	NA	NA	NA	29	NA	NA
	Fort Resolution FMA	NA	NA	No data	NA	NA	0.9592	NA	Unk.	NA	NA	NA	NA	NA	NA	13	NA	NA
	Fort Resolution Reference	NA	NA	No data	NA	NA	0.9418	NA	Unk.	NA	NA	NA	NA	NA	NA	13	NA	NA

	Fort Providence HRL	NA	NA	No data	NA	NA	0.7602	NA	Unk.	NA	NA	NA	NA	NA	NA	29	NA	NA
	Whati (TASR)	3	NA	Missing data	0.3204	NA	0.9715	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Jean Marie River South	3	NA	Missing data	0.2969	NA	0.9111	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Jean Marie River North	3	NA	Missing data	0.3687	NA	0.9111	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
BC	Chinchaga	6	5	NA	0.1563	0.0562	0.8672	0.0761	483	57.5851	-120.6981	7.7	74.4	76.1	539.45	157	6	4
	Calendar	6	5	NA	0.2143	0.0746	0.9064	0.1242	291	59.7821	-120.8196	16	53.4	60.9	459.65	18	6	2
	Maxhamish	6	5	NA	0.1796	0.0715	0.8672	0.0761	306	59.6325	-122.9306	1.6	67.1	67.4	487.32	87	6	3
	Prophet	4	0	NA	0.1100	0.0711	NA	NA	54	58.3624	-122.6717	10	77.7	78.5	504.15	121	6	2
	Parker	4	0	NA	0.1900	0.1056	NA	NA	25	58.7682	-123.1316	2.8	56.5	56.8	499.9	246	6	4
	Snake-Sahteneh	6	5	NA	0.1831	0.0864	0.8729	0.0517	365	59.0255	-121.5336	5.3	57.9	74.9	501.8	87	6	2
	West Side Fort Nelson	5	5	No data	0.1951	NA	0.7617	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
AB	Richardson	3	3	NA	0.1790	NA	0.9030	NA	150	57.9001	-110.9937	67	22	82	442.41	NA	5	4
	Slave Lake	NA	NA	No data	NA	NA	NA	NA	65	55.0558	-114.3207	37	63	80	553.49	120	5	4
	Nipisi	NA	NA	No data	NA	NA	NA	NA	55	55.8689	-114.7875	6	66	68	588.09	NA	5	4

	WSAR	18	18	NA	0.1980	NA	0.8490	NA	272	56.4993	-113.0795	4	68	69	570.06	260	5	5
	ESAR	25	25	NA	0.0673	0.0378	0.8594	0.0526	150	56.0977	-111.3162	26.1	77.3	81.4	556.47	40	5	5
	Chinchaga	10	10	NA	0.1340	NA	0.8310	NA	250	57.4017	-119.4733	8	74	76	566.71	590	6	4
	Cold Lake Air Weapons Range	22	21	NA	0.0580	0.0474	0.8338	0.0980	150	55.2041	-110.7115	32.1	71.8	84.7	568.11	51	5	4
	Red Earth	15	15	NA	0.1570	NA	0.8190	NA	206	57.5131	-113.9852	30	44	62	550.39	210	5	5
	Bistcho	5	5	NA	0.1710	NA	0.7760	NA	195	59.5784	-118.6375	20.4	61.4	71	463.04	NA	5	5
	Caribou Mountains	17	17	NA	0.1440	NA	0.8580	NA	394	59.1074	-115.2233	44	22.8	57.3	448.38	NA	5	5
	Yates	12	12	NA	0.0879	0.0190	0.8808	0.0664	350	59.6814	-116.6401	43.9	21	61.8	463.7	NA	4	5
	Little Smoky	13	13	Culls throughout	0.1530	NA	0.9010	NA	78	NA	NA	0.2	95	95	NA	NA	NA	NA
SK	SK1	4	4	NA	0.1980	0.0404	0.8970	0.038	3347	57.0214	-104.8334	58.9	2.9	60.3	372.48	45.7	4	1
	Tweedsmuir	3	NA	Missing data	0.2900	NA	0.7871	NA	Unk.	NA	NA	38	32.43	NA	NA	218	NA	NA
	Cold Lake Air Weapons Range	12	12	Missing data	0.1260	NA	0.8660	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	5	4
	Smoothstone-Wapawekka	NA	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	12.7	15.7	25.4	NA	NA	NA	NA

MB	The Bog	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Naosap-Reed	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Owl-Flintstone	3	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Kississing	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	32	18.6	50	NA	NA	NA	NA
	Wheadon	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	27.1	6.9	33.3	NA	NA	NA	NA
	Wabowden	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	12	15.7	26.1	NA	NA	NA	NA
	Charron Lake	2	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	29	0	29.7	NA	NA	NA	NA
	Berens (MB)	1	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Bloodvein	1	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
ON	Sydney	2	1	NA	0.1580	0.0220	0.9100	NA	55	50.8714	-94.65591	28	33	58	494.8	138	4	2
	Berens (ON)	2	1	NA	0.1435	0.0955	0.8700	NA	237	51.7127	-93.84724	34	7	40	497.96	138	4	2
	Churchill	2	1	NA	0.2005	0.0465	0.8700	NA	262	50.9987	-91.74476	6	28	31	502.21	60	4	2
	Brightsand	3	3	NA	0.2120	0.0213	0.7870	0.0125	224	50.323	-90.23886	18	28	42	494.44	300	4	2
	Nipigon	4	4	NA	0.3390	0.0641	0.8375	0.0286	300	50.6377	-87.87915	7	25	31	512.21	310	4	1
	Pagwachuan	5	4	NA	0.2328	0.0842	0.8300	0.1221	164	50.6568	-84.48183	0.9	26	27	487.79	120	4	1
	Kesagami	4	4	NA	0.1410	0.0085	0.8830	0.0415	492	50.1086	-80.51302	3	36	38	495.65	81.6	4	1
	Swan	3	0	NA	0.1660	0.0395	NA	NA	491	54.6171	-90.07915	14	1	15	350.33	4.15	3	1

	Spirit	4	3	NA	0.2200	0.0997	0.8850	0.0896	373	53.0415	-92.40566	14	1	15	469.97	61.2	4	2
	Kinloch	3	3	NA	0.1410	0.0532	0.8970	0.0591	113	51.6103	-90.98696	14	1	15	480.72	102	4	2
	Ozhiski	6	0	NA	0.2270	0.1812	NA	NA	148	52.6557	-89.20904	14	1	15	442.12	61.2	4	2
	Missisa	7	4	NA	0.1360	0.0738	0.8000	0.0682	795	52.9281	-86.71924	14	1	15	364.23	24.4	3	1
	James Bay	5	4	NA	0.2200	0.1299	0.8500	0.0900	177	51.9184	-83.91011	14	1	15	377.84	24.4	3	1
	Pukaskwa/ Coastal	NA	NA	No data	NA	NA	NA	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	NA	NA
QB	Nottaway	4	7	NA	0.2417	0.0712	0.7772	0.3117	308	50.5389	-78.33537	4	5.5	9.5	444.16	30	2	1
	Assinica	8	9	NA	0.2810	0.0744	0.9104	0.0467	580	50.5524	-75.51212	9	10.3	19.3	438.88	30	2	1
	Temiscamie	6	12	NA	0.2438	0.0750	0.9049	0.0530	2200	50.8848	-72.05293	3.9	10.6	14.5	399.23	40	2	1
	Saguenay	3	6	Missing data	0.2500	NA	0.8887	NA	Unk.	NA	NA	NA	NA	NA	NA	NA	2	NA
	Manicouagan Ouest	8	8	NA	0.3490	0.0878	0.9010	0.1396	181	51.151	-69.45177	3.2	32	33	409.82	40	2	1
	Manicouagan Est	7	6	NA	0.3730	0.0827	0.9222	0.0956		51.0918	-68.08959	3.2	32	33	426.2	40	2	1
	Basse Cote-Nord	NA	NA	No data	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	2	NA
	Pipmuacan	1	6	NA	0.1730	NA	0.8930	0.0381	134	49.0449	-70.46848	11.1	51	59	525.4	90	2	2