Influences on Recruitment of Northern Mountain Caribou (*Rangifer tarandus caribou)*

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

In

Wildlife Ecology & Management

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Abstract

Northern mountain caribou (NMC) (*Rangifer tarandus caribou*) face a unique combination of demographic influences among woodland caribou in Canada. To build knowledge of how NMC may respond to these influences, the potential effects of road and fire disturbance, climate (pacific decadal oscillation (PDO)), and harvest of moose (*Alces alces*), wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), and adult NMC on calf recruitment in thirteen NMC populations in the Yukon Territory were explored. Seasonal range maps (annual, winter, and summer) for each population were created using elevational distributions of NMC locations from radio-collared individuals. Elevational use varied by season and population, with some overlap between seasons. Seasonal disturbance values were then assigned for each population. Sensitivity to buffers on roads were tested (0m, 500m, 1000m, 1500m, 2000m, 3000m, 4000m) using boosted regression trees (BRTs). No distinction was found in reduction of model deviance among buffers, therefor 0m and 500m buffer ranges were used for further analysis. The highest road disturbance was found in the Carcross population, with 5.4% of its annual range affected by roads within a 500m buffer. The highest combined disturbance was recorded for the Tatchun population, with 43% of its annual range affected by non-overlapping roads and fire.

Boosted regression trees were further used to parse variables of interest for inclusion in linear mixed models (LMMs). Natural disturbance on annual ranges, road disturbance on summer ranges, average yearly PDO, and moose, grizzly bear and caribou harvest density were all influential variables affecting annual caribou recruitment. Top LMMs did not include an effect of road and fire disturbance on recruitment, but did show moderate positive relationships of both average PDO and moose harvest with recruitment, with no effects from other harvest variables. Higher average PDO values correspond to milder winters and earlier springs, which could lead to higher overwinter calf survival and improved body condition of parturient females, more robust calves, and greater ease in spacing away from predators. Rates of moose harvest were also positively associated with disturbance levels (road access), thus effects on caribou recruitment may be confounded. The ability to address effects of anthropogenic disturbance was severely constrained by the lack of comprehensive mapping of related features throughout the study area. This is a critical need for further investigation of relationships. This study highlights the importance of considering interactive effects between species, and between climate and caribou, when managing NMC populations, and the opportunity for pro-active management of Yukon NMC ranges to avoid potential declines due to human disturbance, as documented for woodland caribou elsewhere.

Acknowledgments

Firstly, I would like to take my supervisor, Fiona Schmiegelow, who first got me delving into the science around caribou. Her wisdom and guidance in this thesis has been invaluable.

Thank you to Troy Hegel for being part of my masters committee and providing invaluable insight into northern mountain caribou dynamics. Your advice was always greatly appreciated and excellent.

Pierre Vernier has provided valuable assistance, advice, and scripts for mapping, shaving a massive amount of work off of disturbance mapping. His help is greatly appreciated.

Thank you to biologists at the Yukon Government for insights and data: Heather Clarke, Carol Foster, Pete Knamiller, Kelsey Russell, Kyle Russell, Gerry Perrier, Marcus Waterreus. Thank you to Nic Larter for providing data for the Redstone and Bonnet Plume, which I unfortunately did not use. Thank you to Don Reid at the Wildlife Conservation Society for providing data and insight.

Without the many funders this would not have been possible, especially my First Nation of Taku River Tlingit. Thank you to many other funders as well: Indspire, The National Indian Brotherhood Trust Fund, Weston Garfield Award, Association for Canadian Universities in Northern Studies, North American Caribou Workshop Award, Yukon Fish and Wildlife Enhancment Trust, University of Alberta.

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Chapter 1: General Introduction

Circumpolar Caribou Status

Caribou are a circumpolar species of importance both socio-culturally and ecologically. Canada is home to four sub-species of caribou: Peary (*Rangifer tarandus pearyi*), barren-ground (*R. t. groenlandicus),* Grant's (*R. t. granti*), and woodland (*R.t. caribou*). Within the woodland caribou sub-species, three ecotypes are recognized: boreal, southern mountain caribou, and northern mountain caribou. Each sub-species and ecotype have unique life histories, including selection and use of habitat. Nevertheless, all are considered vulnerable to anthropogenic disturbances (Boulanger et al. 2012; Hervieux et al. 2013; Johnson et al. 2015).

Caribou have experienced substantial reductions in population size and distribution throughout Canada (Spalding 2000; Vors and Boyce 2009; Festa-Bianchet et al. 2011), and currently face potential extirpation in several regions, including Alberta (Hervieux et al. 2013), central and southern British Columbia (Wittmer et al. 2010; Van Oort et al. 2011; Johnson et al. 2015), and portions of Quebec (Rudolph et al. 2012). A recent assessment of boreal caribou condition throughout Canada identified 33 of 57 ranges unlikely or very unlikely to be self-sustaining, and an additional 7 of 57 to be between not self-sustaining and self-sustaining (Environment Canada 2011). A self-sustaining population is one that is expected to have stable or positive population growth in the short term (≤ 20 years), and able to withstand extreme events and remain viable in the long-term (>50 years) (Environment Canada 2011).

Northern mountain caribou (NMC) are distributed across the Yukon, British Columbia, and the Northwest Territories, with most populations either currently stable or with unknown trends. NMC are also widely harvested, and nearly every population currently experiences regulated bull harvest and/or First Nation subsistence harvest. As such, they present a unique opportunity to develop a knowledge base to pro-actively support sustainable land use and population management, including maintaining harvest opportunities for First Nations. Sustainable harvest is an explicit management goal for both First Nation and territorial governments, an important part of First Nations culture, and a treaty right (Environment Canada 2012; Southern Lakes Wildlife Coordinating Committee 2012). Thirty-three different First Nations have territories that intersect with NMC ranges (Environment Canada 2012).

Drivers of Caribou Population Change

In 2014, northern mountain caribou (NMC) were re-designated as a species of 'special concern' under the Canadian Species at Risk Act (SARA). NMC are designated as special concern due to limited knowledge on population trends, decreases in numbers of southern populations, and increasing industrial development (COSEWIC 2014). There are currently 45 identified NMC populations, comprised of 43,000-48,000 individuals: the trends of 27 populations are unknown, 9 are decreasing, 7 are stable and 2 are thought to be increasing (COSEWIC 2014). Two main parameters used to measure population condition are recruitment rate, the number of calves recruited into the subsequent years' population (commonly expressed relative to the number of adult female caribou in a population), and annual adult female survival rate. Collectively, these can be expressed as population growth rate, or lambda. This study focusses on recruitment, as data on adult female survival rate were not adequate for statistical evaluation of factors affecting population condition in NMC populations. Changes in recruitment rate have been correlated with population growth rates (Harris et al. 2008), and are considered an early indicator of population declines in caribou (Environment Canada 2011). With increasing anthropogenic disturbances and rapidly changing climate regimes throughout NMC distribution, it is imperative to know how NMC recruitment rates respond to natural and anthropogenic disturbances, climate, and hunting pressure.

Environment Canada (2011) found that population condition of the boreal ecotype of woodland caribou, as measured by recruitment, was best explained by total disturbance (anthropogenic and natural) on their population ranges. However, Reid et al. (2013) suggested that this and other models for boreal caribou were not appropriate for NMC, as they did not address the spatial segregation of NMC seasonal ranges and were developed for woodland caribou with different life histories and affected by different climatic conditions. In addition, NMC face hunting pressures that boreal caribou do not. Reid et al. (2013) therefor recommended the development of population models based on the demographic and habitat profiles of NMC.

Anthropogenic Effects on Caribou

Anthropogenic disturbances have been demonstrated to have a strong negative effect on caribou populations. Beyond the direct effect of potential habitat loss, predator-prey dynamics may also be heavily influenced by anthropogenic disturbances. Linear features such as seismic lines and roads may increase predation on calves (Whittington et al. 2011; McKenzie et al. 2012; Dussault et al. 2012; Demars and Boutin 2017), as predators may use anthropogenic features as hunting corridors (McKenzie et al. 2012; Courbin et al. 2014; Ehlers et al. 2014), and travel routes (Tigner et al. 2014), which increases caribou-predator encounter rates. Caribou avoidance of anthropogenic features (Latombe et al. 2014; Avgar et al. 2015) may lead to higher encounter rates with alternate predators such as bears (Leblond et al. 2016). Forest harvesting may also increase predation risk (Losier et al. 2015) and negatively influence recruitment, principally through increased habitat that favours apparent competitors of caribou (McCarthy et al. 2011). This can lead to area abandonment (Boan et al. 2014; Avgar et al. 2015; Hornseth and Rempel 2016). The configuration of disturbances (Galpern and Manseau 2013; Courbin et al. 2014), and the size of disturbances (Nagy 2011; Lesmerises et al. 2013), are also important considerations in their effect on caribou demographics.

Movement barriers created by anthropogenic disturbances can lead to increased energetic costs and potential abandonment of high-quality habitat (Nagy 2011; Beauchesne et al. 2013; Panzacchi et al. 2013; Semeniuk et al. 2014; Beyer et al. 2016). Off-road vehicle use (Seip et al. 2007; Pigeon et al. 2016), and proximity to anthropogenic disturbances (Florkiewicz et al. 2007; Nagy et al. 2011; Polfus et al. 2011; Beguin et al. 2013; Beauchesne et al. 2014; Johnson et al. 2015; Hornseth and Rempel 2016) can also lead to abandonment of otherwise high-quality habitat.

Natural Disturbance Effects on Caribou

Natural disturbance by wildfire can have strong effects on caribou populations. Fire may lead to loss of habitat through reduced forage (Beguin et al. 2013; Robinson et al. 2012; Hornseth and Rempel 2016). Fire can also increase apparent competitor habitat, such as for elk and moose (Robinson et al. 2012). Numerical response of apparent competitors leads to higher selection of theses habitats by wolves, resulting in higher encounter rates with caribou (Robinson et al. 2012). Hence, to avoid apparent competitors, higher predation rates, and reduced forage, caribou avoid burned areas (Robinson et al. 2012; Hornseth and Rempel et al. 2016).

Fire can lead to area abandonment for decades due to forage loss and increased predation risk. Studies in northern systems have found that lichen biomass, a key caribou winter forage requirement, does not recover until approximately 50-60 years after a fire, and younger burns were avoided by most caribou before that time (Thomas and Armbruster 1998; Joly et al. 2007; Joly et al. 2010; Collins et al. 2011; Russell and Johnson 2019). Peak lichen biomass was found approximately 180 years after a fire (Thomas and Armbruster 1998; Collins et al. 2011).

Climate Effects on Predation and Survival

Fluctuating climate is an important contributor to variability in caribou recruitment (Hegel et al. 2010; Bastille-Rousseau et al. 2016). Hegel et al. (2010) found that an increasing April pacific decadal oscillation (PDO) trend (leading to earlier springs) had varying effects on caribou recruitment depending on predation pressure, as inferred through presence or absence of wolf control. If there was no wolf control, recruitment was positively correlated with increasing April PDO, as parturient females may be able to disperse earlier to high elevations to avoid predation (Hegel et al. 2010). With wolf control, recruitment demonstrated a weak negative relationship with increasing April PDO, possibly due to rapid green-up reducing the availability of highly nutritious food during calf growth, and predation not being a factor (Hegel et al. 2010); an effect seen to influence moose recruitment as well (Brown 2011).

Warmer climates may also reduce the availability of frozen lakes and rivers, increasing the energetic costs of migrations (Leblond et al. 2016), and reducing the availability of potential predator escape terrains, mineral licks, and feeding areas on muskrat pushups (Polfus et al. 2014). All these effects could influence calf survival if parturient female body condition is significantly affected.

Harvest Effects on Caribou

An assessment of three populations of boreal caribou in the James Bay region of northern Quebec found that the additive effect of subsistence harvest to other population pressures resulted in a finding of not self-sustaining for all populations (Rudolph et al. 2012). The authors recommended a halt to subsistence harvesting to stabilize these boreal caribou populations, although a subsequent study on the same populations by Rudolph et al. (2017) found that subsistence harvest showed minor effects on probability of caribou persistence on the landscape, with the majority of effect due to cumulative natural and anthropogenic disturbances. While licensed harvesting of NMC in the Yukon is restricted to bulls only, it is important to consider the effects of hunting on NMC. Subsistence harvest of caribou occurs in nearly all NMC ranges, but it is not possible to evaluate effects due to lack of data on harvest composition and rates.

Harvest of apparent competitors and predators can also influence caribou populations. Serrouya et al. (2017) outlined the effects of increased moose hunting on a mountain caribou range. From 2003 to 2014, liberal moose hunting policies led to a 71% reduction in moose numbers (Serrouya et al. 2017), which was believed to be more in line with historic moose population levels. The liberal hunting policies ultimately led to increased adult female caribou survival and halted caribou declines, due to declines in wolf numbers in-line with declining moose numbers (Serrouya et al. 2017).

Similarly, direct wolf control has been found to have substantial effects on caribou populations in the Yukon (Hayes et al. 2003), and Alberta (Hervieux et al. 2014). Within the Yukon's Aishihik herd, when wolf populations were reduced to 20% of their pre-removal levels, caribou recruitment increased from 15 calves per 100 cows to 42 calves per 100 cows (Hayes et al. 2003). In Alberta, wolf control removed 45% of mid-winter wolf populations each year which stabilized the Little Smoky herd by increasing the mean population growth rate by 4.6% through increasing recruitment from a mean of 0.12 calves per cows to 0.19 calves per cows (Hervieux et al. 2014). Given that reductions in wolf numbers through targeted control efforts can have substantial effects on caribou numbers, less aggressive wolf harvest could have similar, smaller effects on caribou numbers.

Objectives

This thesis has 2 major objectives:

1. To characterize conditions over time on northern mountain caribou ranges, including: anthropogenic and natural disturbances, harvest pressure, and climate.
2. To use annual recruitment to evaluate the effects of range conditions on northern mountain caribou demographic response.

Hypotheses

To evaluate the effects of range conditions on NMC recruitment, I developed an impact hypothesis diagram (IHD) structured around three categories of hypotheses, related to direct disturbance, landscape disturbance, and climate. Each category focuses on a different aspect of how caribou adult female survival and calf recruitment may be influenced by associated factors.

Figure 1 illustrates three major pathways by which direct disturbances, landscape disturbances and climate may influence caribou recruitment. Direct disturbances include human recreation and caribou harvest, which can have immediate effects on caribou, though other forms of harvest (predator and apparent competitor harvest) may have lagged effects on recruitment. Landscape disturbances include anthropogenic and natural disturbances that may have long-term effects on the landscape that affect caribou population dynamics. Climate has medium-term effects on caribou recruitment through its effects on caribou predator-prey dynamics. How each pathway ties into hypotheses is discussed below.

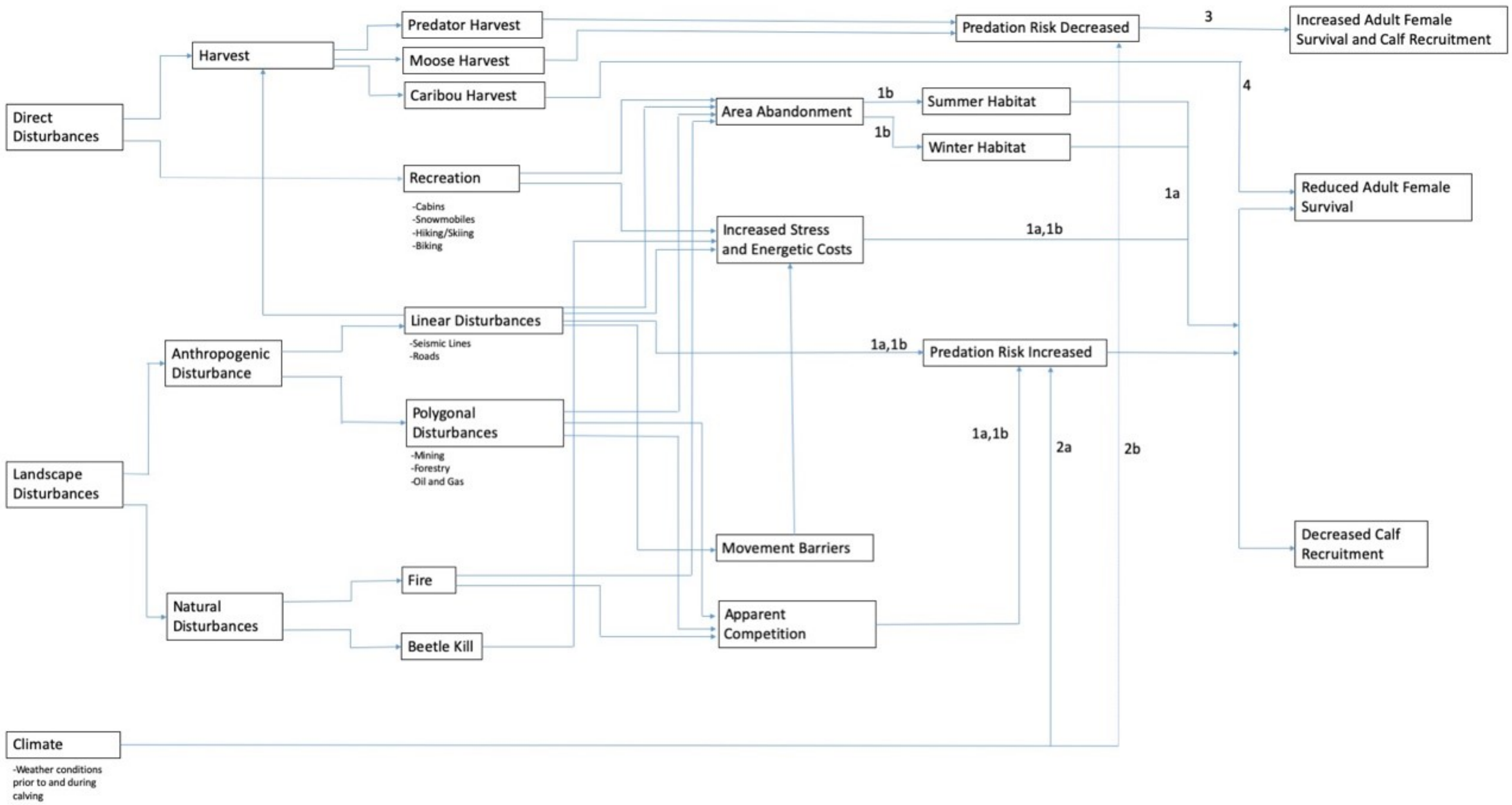


Figure 1 - Impact Hypothesis Diagram for Disturbance Effects on Caribou Landscape Disturbance Hypothesis

H_1*: *Increasing road, fire, or combined disturbance on NMC annual or seasonal range will contribute to decreased recruitment.

As discussed previously, major pathways (Figure 1, pathway 1a,1b) that both anthropogenic and natural disturbances affect recruitment through increasing apparent competition and area abandonment. Anthropogenic features also lead to: increased predator efficiency, and increased travel and energy costs, and reduced connectivity for caribou. In NMC systems effects of both natural and anthropogenic disturbances may vary by season, as winter and summer ranges are often located in distinct elevational and biophysical habitats.

Climate Hypothesis

H_2*: *April PDO, May PDO, average PDO or PDO prior to birth (winter) will be related to recruitment, where positive PDO will correlate with increasing recruitment and negative PDO with decreasing recruitment.

As seen in Figure 1 (pathway 2 a,b), climate may have varying effects on predation risk. In warmer winters and earlier springs, as measured by positive pacific decadal oscillation (PDO), there will be more forage access, and less snow (or faster snow melts), which will allow for easier spacing from predators and increased forage for young. In colder winters, as measured by negative PDO, the opposite effects on predation and forage access for young will occur.

Direct Disturbances Hypotheses

H_3*: *Alternate prey or predator harvest will lead to increasing recruitment.

H_4*: *Regulated NMC harvest will have neutral effects on recruitment.

Alternate prey harvest (moose harvest) is expected to decrease predator density over time and lead to lower predation on caribou calves (Figure 1 pathway 3), through similar mechanisms, predator harvest and trapping could lead to increased recruitment.

It is expected that regulated caribou harvest should have neutral effects on adult female caribou survival and calf recruitment, as seen in Figure 1 (pathway 3a). Regulated harvest is limited to bull caribou, and most subsistence harvest should be bull harvest only, though First

Nations are able to harvest any caribou on their traditional territories in the Yukon. If there is harvest of females, it could lead to elevated recruitment rates, as females are taken but calves remain, resulting in a potentially misleading indicator.

Thesis Structure

Chapter 2 of this thesis describes methods used to develop seasonal ranges for each NMC population, and the quantification of disturbance on NMC ranges with available recruitment data as well as the. The objective of this chapter is to delineate annual and seasonal NMC ranges for all populations with multi-annual recruitment data, and quantify disturbance on each of these ranges.

Chapter 3 presents the underlying rationale, methods applied and results associated with analysis of the effects of disturbance, harvest, and climate on NMC calf recruitment, and discusses these in relation to previous research and the particular context of the study region. This chapter is written in manuscript format.

Chapter 4 synthesizes the outcomes of Chapters 2 and 3 and offers overarching conclusions and potential next steps for research.

Chapter 2: Delineating seasonal ranges for northern mountain caribou and mapping disturbance

Northern mountain caribou (NMC) are known for seasonal migrations between winter and summer ranges (Hatler 1986; Gustine and Parker 2008; Hegel and Russell 2013). NMC migration is primarily based on elevation, with relatively quick movements into the high alpine in the summer for calving (Oosenburg and Theberge 1980), then a more gradual movement to lower elevations for the winter (Gullickson and Manseau 2000). Many populations winter in valleys, while some may remain in lower elevation alpine / sub-alpine areas (Kuzyk et al. 1999). Seasonal migrations for NMC are an important predator avoidance strategy (Bergerud et al. 1984). Seasonal migrations to high elevations can also have the added benefit of decreasing insect harassment and heat exhaustion during summer months (Jandt 1998).

It is widely understood that NMC require seasonal migrations to maintain population viability (Environment Canada 2012). As such, any research on NMC must consider this vital life process. Here, I focus on the elevation aspect of how NMC use the landscape and how that varies from winter to summer. Extensive work has been conducted on how caribou populations located in mountainous areas use elevation as a method of habitat selection. Two studies in Northern BC found strong shifts in elevation depending on the time of year (Chihowski 1989; Gustine and Parker 2008). Similar studies on small populations of caribou in the central mountains of Alaska have found seasonal elevation migrations (Jandt 1998; Horne et al. 2014). Work by Johnson et al. (2004) found elevation and slope were the most effective variables predicting caribou occurrence in the Wolverine herd of northern British Columbia.

Although most work on seasonal ranges has involved resource selection functions (RSF), my objective was not to determine habitat use per se, but to evaluate how populations react to habitat changes over time, a spatio-temporal question. Strong selection for elevation is evident in RSF models for mountain caribou (Jones et al. 2007). Indeed, a 2018 science review of central mountain caribou in BC used an elevation boundary combined with telemetry points to create seasonal ranges for the Scott and South Narraway herds (Price 2018). Methods outlined by Price (2018) also included vegetation, slope and aspect as selection coefficients in RSF models. Two non-migratory mountain herds in Central Alaska also show selection for elevation in association with seasonal ranges (Horne et al. 2014).

Differing stressors on either winter or summer range can also lead to different population effects. Disturbances on lower elevation habitats can lead to increased apparent competition (Brown 2011; Anderson et al. 2018). Disturbances on summer high elevation habitat can lead to increased harvest pressure from humans as areas become more accessible, which correlates with all-terrain vehicle use (Pigeon et al. 2016), and possibly also increasing stress during calving periods. Depending on the season, NMC may also react differently to disturbances. Polfus (2011) found NMC avoided anthropogenic disturbances such as towns (9km – winter, 3km – summer), camps (1.5km summer, limited in winter if activity low), mines (2km summer, limited in winter if activity low) at greater or lesser distances depending on the time of year, most likely due to activity level associated with those disturbances. Seasonal range considerations are an important aspect of NMC response that previous models of caribou response to disturbance have not considered (Reid et al. 2013), and a consideration this study hopes to address.

The two categories of disturbances quantified in this chapter broadly fall into natural (fire) and anthropogenic (as measured by linear density and areal disturbance of roads). Natural disturbance is widely understood to affect caribou populations by increasing apparent competition through increases in early seral habitat (Brown 2011; Anderson et al. 2018), and by avoidance of burned habitat by caribou (Joly et al. 2010; Polfus et al. 2011; Robinson et al. 2012; Rickbeil et al. 2017). Linear disturbances may lead to multiple effects on caribou through altering predator behavior (Wittington et al. 2011; Dickie et al. 2017), decreasing connectivity between seasonal ranges (Beguin et al. 2013; Beyer et al. 2016), and reducing caribou survival (Demars and Boutin 2018). The effects of roads can, however, vary depending on presence or absence of calves, where females with calves strongly avoid roads and those without may not (Viejou et al. 2017).

The objective of this chapter is to present the methods and results used to establish seasonal ranges and disturbance levels for NMC study populations, in order to support quantification of their effects in subsequent analyses presented in Chapter 3.

Methods

Population ranges defined and updated in 2018 by the Yukon Government (Environment Yukon, 2018) were used as a basis for this work (Figure 1). The creation of new annual and seasonal ranges based on available telemetry data was explored using minimum convex polygons and kernel density estimates, but there was too much overlap between resulting seasonal ranges to offer substantial spatial separation between winter and summer ranges, largely due to the mountainous terrain of many herds. For example, individuals may migrate from valley bottoms to alpine areas that are not spatially distinct enough to create adequate separation between seasonal ranges using minimum convex polygons or kernel densities. Hence, the life history of NMC was used to delineate ranges by differing use of elevation between seasons.

Caribou Location Data

A mix of very high frequency (VHF) and global positioning system (GPS) collars data were used to identify seasonal ranges. GPS data were used over VHF data, when available, to improve mapping resolution. Table 1 and 2 report the VHF and GPS data used for creation of seasonal maps. Some points were censored if they lay significantly outside herd range boundaries, as delineated by the Government of Yukon. The herds studied were: Aishihik, Carcross, Chisana, Clear Creek, Ethel Lake, Finlayson, Hart River, Ibex, Klaza, Kluane, South Nahanni, Tatchun, and Wolf Lake.

Points were then divided into either winter or summer categories, based on dates determined from several sources (internal Yukon Government data; Florkiewicz 2007; McNay et al. 2008; Hegel 2012; Francis and Nishi 2015). Summer range was defined as June 01 to September 30, and winter range as December 01 to March 31, in each year. Migratory months were excluded to limit elevational overlap between winter and summer, though some range was still categorized as both winter and summer range.

Some bias could enter into the Finlayson delineations, as only three animals were used to determine elevational cut-offs. Similarly, the Clear Creek delineations were informed by only one year of summer data and two years of winter data. VHF data generally had more total animal years compared to GPS data, but fewer animal locations. Where GPS and VHF data were both available for a herd, only GPS data were used to determine seasonal elevational cut-offs.

Determining Seasonal Ranges

GPS/VHF data were intersected with the Canadian digital elevation model (CDEM) (NRCan 2014) (~20m resolution) to determine where each caribou VHF/GPS location fell on an elevational scale. All GIS work was completed with ArcGIS 10.5.1

The 90th quantile for winter elevational distribution and 10th quantile for summer elevational distribution were identified for winter and summer NMC caribou ranges, to further help limit elevational overlap between seasons, while acknowledging that some areas are important in both winter and summer. R (R Version 3.5.2, www.r-project.org, accessed 10 Nov 2018) and Rstudio (RStudio Version 1.1.463, www.rstudio.com, accessed 10 Nov 2018) were used for all analyses. The rule set was as follows:

If CDEM elevation (m asl) $\geq 10^{th}{}_{\text{quantile summer elevational distribution}}$ = summer range,

If CDEM elevation (m asl) $\leq 90^{th}{}_{\text{quantile winter elevational distribution}}$ = winter range.

For example, if the 90th quantile for winter elevation distribution was 1300m asl, any value below would be considered winter range. Similarly, if the 10th quantile for summer was 1400m asl, any value above would be considered summer range.

Once the 90th and 10th quantiles were determined for each herd of interest, summer and winter maps were created using CDEM and Yukon Government herd ranges. The CDEM map was partitioned by elevation into summer and winter values within each herd range.

Disturbance Datasets

Three main disturbance datasets were used to determine levels of disturbance on annual, winter and summer NMC ranges.

For the period from 1985 to 2015, an automatically generated LandSat based dataset was used that identifies if a 30m pixel has been burnt or harvested in each year (Guindon et al. 2018). The Guindon et al. (2018) dataset was used rather than a fire history dataset to also account for forest harvest and to allow for standardization across provincial and territorial boundaries, if additional caribou ranges were included in the analysis. Other datasets were investigated such as

Global Forest Watch's disturbance dataset (Hansen et al. 2013), but it did not cover as wide a range of years as the Guindon et al. (2018) dataset.

For forest fires before 1985, the fire history datasets available from provincial, territorial or state agencies were used, which span from the mid 1940s to the present day. Before the 1990's, these fire histories are often fire perimeters and do not take into account unburnt areas within caribou ranges (BC Data Catalogue 2018; NWT Geomatics 2018; Yukon Geomatics 2018). Fires were included as far back as data were available and treated as base natural disturbance from the start of recruitment years (1982), as lichen recovery times can be as long as 50-60 years (Joly and Klein 2010; Russell and Johnson 2019).

For the roads layer, the CanVec 2017 at 1:50,000 map scale or 25m resolution was used (NRCan 2019). This was the most up to date and validated roads dataset available in Canada at the time, and the one Geomatics Yukon was adopting. Validation of the dataset back to 1985 using Google Earth imagery determined that all roads listed on the CanVec dataset were on the landscape at that time within the Yukon. Therefore, roads were used as a base layer of human disturbance starting in 1982, as this was the first year of available recruitment data, within the Yukon. This layer did not change over the years of study, though forest harvest as measured by Guindon et al. (2018) was added to overall anthropogenic disturbance, yet ultimately lead to changes in disturbance <0.0001% of total herd ranges. The limited additions from forest harvest as measured by Guindon et al. (2018) could be due to lack of any major forestry in the Yukon, and misclassification error from the Guidon et al. (2018) process.

Determining Disturbances

Removal of Large Lakes

Large lakes were removed from the Aishihik, Carcross, Ethel Lake, Finlayson, Ibex, Kluane and Wolf Lake ranges, following Reid et al. (2013), and (Ferguson and Elkie 2005), who assert that caribou do not use large lakes in the winter. Similar methodology to Reid et al. (2013) was used where lakes greater than 2km wide at its widest point were excluded from caribou range. A cursory examination of GPS and VHF data indicated agreement with Reid et al. (2013). Although there was some use of large lake edges, this was minimal compared to the availability of large lakes. No lakes overlapped with summer range, thus their exclusion affected only winter and annual range area estimates.

Natural Disturbance

Natural disturbances, such as fire, were calculated up to 1985 using territorial and provincial polygons from government sources (BC Data Catalogue 2018; NWT Geomatics 2018; Yukon Geomatics 2018). Post-1985, the CANLAD 2017 dataset (Guindon et al. 2018) was used to quantify natural disturbances. Cumulative disturbance for each year was determined for summer, winter, and annual ranges, including fires up to 60 years old to determine disturbance levels (Joly et al. 2003; Joly and Klein 2010)

Buffering

Varying levels of caribou avoidance of linear features have been found in previous work (Polfus et al. 2011; Boulanger et al. 2012; Johnson et al. 2015). In the central mountains of British Columbia, caribou avoided roads 1.00 km to 1.75km, depending on the season and sub-population (Johnson et al. 2015). In the Atlin NMC herd range of Northern British Columbia, Polfus et al. (2011) found that caribou avoided low use roads by 1km and high use roads by 2km. Barren-ground caribou have been found to avoid roads at least 10 times greater than mountain caribou, with the Porcupine Caribou Herd showing main road avoidance responses from 18.5km to 30km (Johnson and Russell 2014), and the Bathurst herd showing avoidance responses from 11km to 14km (Boulanger et al. 2012). Even semi-domesticated reindeer in Finland show a 1.5km avoidance of roads (Anttonen et al. 2011).

Road Disturbances - Anthropogenic

Roads from the CANLAD 2017 data were buffered by 0m (linear density), 500m, 1000m, 1500m, 2000m, 3000m, 4000m to quantify anthropogenic disturbance for exploratory purposes. The amount of road disturbance on the entire range (annual), summer range or winter range was then recorded. Some fire in CANLAD 2017 was classified as human harvest (due to lack of access in remote locations), and there was no way to otherwise determine the disturbance type, as all forest loss not classified into fires was classified as forest harvest. Forest harvest was included from CANLAD in disturbance totals but is a negligible source of disturbance (<0.0001%) in all NMC herd ranges based on visual inspection of the CANLAD dataset. Due to error in classification of forest harvest which was most certainly fire, forest harvest was not buffered. Road disturbances were recorded as cumulative to each year.

Combined Non-overlapping Disturbance

For each buffer range, the amount of non-overlapping road and fire disturbance was calculated. The resultant combined disturbance measures were recorded as cumulative to each year.

Other Sources of Disturbance Mapping

To method of quantifying road disturbance applied here was compared to Canadian Intact Forest Landscape maps generated for 2000 and 2013 (Lee et al. 2006; Smith and Cheng 2016). These maps consider all detected anthropogenic disturbances at 30 m resolution and buffer these by 500m to obtain the amount of forest that is disturbed, but the mapping is restricted to two intervals. The amount of disturbance for all herds and seasons using the different methods were compared to each other to determine their relationship.

Results

The caribou herd with the highest winter elevational cut-off was Aishihik, at 1598m asl (Table 3) ,while the lowest winter elevational cut-off was Tatchun at 1060m asl. The mean winter elevational cut-off was 1347 m asl. The lowest elevation used for summer was Tatchun at 925m asl, while the highest elevation used for summer was Clear Creek, at 1313m asl. The mean summer elevational cut-off was 1180m asl. The highest max elevation used was South Nahanni at 2416m asl while the lowest max elevation used was Ethel Lake at 1740m asl. The mean max elevation used was 2047m asl.

Generally, there was good agreement between caribou locations and maps created using seasonal elevational cut-offs and digital elevational models (DEMs). Examples are discussed below that highlight some bias and discrepancies.

Clear Creek was the herd with the least data (as measured by number of years) that informed the seasonal elevational cutoffs. Clear Creek also had the least overlap between winter and summer seasonal elevational use. The 90th quantile in summer and winter elevational use overlapped for all other herds except this one (Figure 2) which led to some Clear Creek herd range not being considered in either winter or summer.

Clear Creek seasonal range maps for winter (Figure 2) showed less agreement with winter caribou locations[1], yet those locations still fell within winter range. Clear Creek had only a single year of data from 30 collared animals available for summer, and two years available for winter (Table 1). A small section of total herd range is included in neither winter or summer range (Figure 3).

The Klaza herd is known to remain at high elevations year-round (Kuzyk et al. 1999). Elevational cut-offs from this study agreed with this known biology of the herd. There was, however, a great deal of overlap between winter and summer elevational cut-offs, with the 10th quantile for summer being located well within the winter elevational density plot and vice versa for the 90th quantile for winter (Figure 4). Correspondingly, there is a great deal of overlap between winter and summer range maps, with little range not considered winter habitat (Figure 5).

The Ibex herd is also known to remain in higher elevational habitats for much of the year (Kuzyk et al. 1999). As such, much like the Klaza herd, there is substantial overlap between winter and summer elevational density plots of Ibex elevational use (Figure 6). Of note, this herd's seasonal ranges were created using VHF collar information and thus the maps do not have the definition of those created using GPS collar information, due to the limited number of caribou locations available (Figure 7).

Herd Range Size Change Due to Lakes

Seven herds were affected by the removal of large lakes; on average, this led to a decrease of 1.67% in the herd range area, with larger decreases in winter range and no effects on summer range due to no overlap of large lakes on summer range (Table 4). The herd with the greatest loss of range was Carcross, located in the Southern Lakes area of the Yukon, with 4.34% loss of winter range and 3.51% loss of annual herd range. The herd least affected was the Finlayson, with 0.13% loss of winter range and 0.09% loss of annual herd range.

[1]Data sharing agreement signed with Environment Yukon prohibits sharing individual locations of caribou.

Disturbance levels

Figure 8 illustrates the average cumulative natural disturbance on seasonal ranges for each NMC herd. Tatchun had the highest cumulative natural disturbance on summer, winter, and annual ranges, at 32.9%, 51.8% and 40.7%, respectively. The lowest amount of natural disturbance was recorded on the Chisana herd, which saw 0%, 0.25%, and 0.13% natural disturbance on summer, winter, and annual ranges, respectively. The average cumulative natural disturbance for all NMC herds was 4.53%, 11.4%, and 8.67% for summer, winter and annual range natural disturbance, respectively.

Figure 9 highlights the amount of linear road disturbance on each range. Only three ranges have appreciable amount of road disturbance, with Carcross being the highest by far, and Tatchun and Finlayson having the next greatest linear road disturbance. Most road disturbance is located on winter or annual range, with very little on summer range.

The range with the most fires over the timeframe of the study (1982 – 2015) was Ethel Lake, which experienced a ~20% increase in disturbance on its' range. Clear Creek, Kluane, Klaza, and Tatchun experienced the next greatest disturbance increases at ~10% each. Disturbance by fire over the course of the study was minimal in all other ranges, with <5% change.

The most cumulative (anthropogenic + natural) disturbance on summer ranges at 500m buffering of roads was on Tatchun at 35.2% and Ethel Lake at 16.1%, accounted for mainly by natural disturbance, with roads accounting for <1% of disturbances. When roads were buffered at 4000m, Carcross summer range has 11.8% anthropogenic disturbance, Klaza 5.23%, Hart River 3.90%, Finlayson 2.29% and the rest <2% disturbance. Chisana and Ibex had no recorded roads on their ranges and thus were only analyzed for natural disturbances.

Winter ranges experienced more road disturbance overall at 500m buffering, with Carcross having 6.60% and Tatchun 3.68% of range disturbed; all other herds had <2% disturbance by roads. When roads were buffered by 4000m, Carcross winter range was 31.4% disturbed by roads, Tatchun by 23.2%, and Finlayson by 12.6%. Hart River was 7.20% disturbed with winter roads buffered by 4000m, with Aishihik, Clear Creek, Klaza, and Wolf Lake road disturbance on winter range varying from 4.27% - 6.19%. Ethel Lake and South Nahanni were 2.02% and 1.00%, respectively, for winter road disturbance at 4000m buffer.

Figure 10 summarizes the amount of disturbance attributed to either roads, buffered at 500m or 4000m, and to natural disturbances; this is presented to give an idea of how disturbance rates change as buffers increase. From this comparison we see that most disturbance can be attributed to natural disturbances, with only one herd having appreciably more disturbance due to roads at the 4000m buffer range. Hart River has more disturbances attributed to roads at 4000m but the amount of disturbance overall is still at low levels.

Figure 11 shows the average combined disturbance (natural + roads) with roads buffered by 500m. Carcross and Tatchun herd ranges experienced an increase in annual disturbance of 6.60% and 2.32%, respectively, when roads were added to natural disturbance. All other herds experienced a <1.28% increase in annual range disturbance when roads buffered at 500m were added to natural disturbance levels.

Figure 12 shows a comparison of disturbance values in this project to automatically generated datasets. A general relationship between the proportions of disturbance used here and those recorded through Canadian Intact Forest Landscape (CIFL) maps (Smith and Cheng 2016) was found. CIFL mapping tends to capture more disturbance than the method used here, though Chisana disturbance levels had to be removed due to CIFL mapping constraints. CIFL does not map disturbance outside of Canadian borders and thus any herd range outside of Canada was considered disturbed. There were also significant sections of alpine or non-treed areas that were classified as disturbance (and were not disturbed upon investigation in Google Earth) which had to be corrected in the CIFL dataset.

Discussion

All herds show distinction between seasonal ranges, with a clear shift in the use of elevation from summer to winter months. Clear Creek was the only herd showing no overlap between seasonal ranges, but was also the herd with the fewest years of collar data. Hence, the lack of seasonal range overlap could be due to an inadequate representation of the herds range. Rasiulis et al. (2012) report that 2 years of monitoring data would capture only 38% of a caribou’s range. All other herds show overlap in the use of elevation from winter to summer, with those herds that are known to winter in alpine areas (Kuyzk et al. 1999) showing the most overlap between winter and summer ranges.

Generally, the findings of elevational distinctiveness in seasonal ranges agrees with other studies of NMC (Oosenburg and Theberge 1980; Bergerud et al. 1984; Gustine and Parker 2008; Hegel and Russel 2013). Culling et al. (2005) note after a multi-year study on the Graham herd in Northern British Columbia that all range above 1240m should be protected based on elevation use during vulnerable calving times. An observational study found that Redstone Range caribou pellets were found at higher elevations during July and August (Quayle and Kershaw 1996).

The disturbance levels found in this study are much lower than those found in more southern populations of caribou in Canada. A low human population, very limited commercial forest harvesting and consequently lower road creation when compared to other jurisdictions, contributes to low disturbance levels on Yukon NMC ranges. Disturbance levels can reach >80% in southern caribou populations, with most attributed to industrial disturbance (Sorenson et al. 2008; Environment Canada 2011). In the Yukon, the highest disturbance was 43.03% in the Tatchun range, with 2.32% attributed to roads when buffered at 500m. Overall, for Yukon NMC ranges, the majority of disturbance was from natural causes. The Carcross herd was the only herd with appreciable levels of road disturbance, with 5.37% of its annual range directly affected by roads when a 500m buffer was applied.

Florkiewicz et al (2007) found higher levels of overall anthropogenic disturbance in the Carcross winter range but included additional anthropogenic features, such as rural residences, trails, recreation sites, inactive mines, inactive railroads, and various other polygonal disturbance, in their estimates. When considering comparable disturbances from Florkiewicz et al. (2007), this study found 6.60% of the Carcross winter range disturbed by roads, while Florkiewicz et al. (2007) found 7.46% disturbed by transportation features. Though Atlin was not included in this analysis, it shows similar high anthropogenic disturbance levels to Carcross, due to placer mining activity. Polfus et al. (2011) found 7.95% of winter habitat in Atlin herd was impacted by human disturbance. Including all types of human disturbance in those ranges with regionally high levels of human settlement and activity could roughly double the amount of disturbance captured. For example, Francis and Nishi (2015) found 15% of the Carcross herd's annual range was affected by anthropogenic disturbances, with disturbance mapping followed similar procedures to Florkiewicz et al. (2007). Moreover, comparing the linear density of roads on the Klaza population to those from high resolution maps from Environment Yukon (2016) found that only 7.53% of linear features were captured by the roads layer used here, due to a proliferation of activity associated with mineral exploration and development in the area.

Other methods of disturbance mapping were investigated, such as surveyed land parcels, mining claims, and trail maps. Further investigation of each of these methods through google earth imagery found over-estimation of some disturbances, as registered titled land and claims did not necessarily translate into disturbance (i.e. they could be undeveloped). As well, comprehensive mapping of trails was not available across all herd ranges. It was also impossible to time-stamp any disturbance levels estimated through other methods, while the road layer used here was in-place at the start of the available recruitment data. Since much of this analysis focused on the inter-annual variability of factors affecting recruitment, temporally matched estimates of disturbance were important. Major roads were found to be reliably on the land to the earliest year of recruitment. One further consideration was the hope to extend disturbance mapping into areas outside the Yukon's borders, and using datasets such as Canvec road maps allows for a national standard that works in both British Columbia and the Yukon.

Limitations

Seasonal ranges may not have been as defined as well as they could be using elevation alone, as slope is an often-used variable included in NMC seasonal resource selection functions (Gustine and Parker 2008). Underfitting seasonal range selection processes could lead to either increased bias or variation in consideration of seasonal ranges. Another limitation is that up to 30% of the fires from 1985-2015 could have been misclassified with respect to year (Guindon et al. 2018), a problem with using automatically generated datasets. The misclassification of fire years could lead to greater error in fitting annual models in subsequent analyses, and partial misrepresentation of natural disturbance in this chapter. Snow conditions during the year can change seasonal range use. In low snow years, higher elevations may be used (Culling et al. 2005), which may lead to less definition between winter and summer ranges. Some anthropogenic disturbances were not included (e.g., mining, oil and gas, recreation, and trails), due to limitations in the availability of data and inconsistencies in mapping. As there is no comprehensive mapping of historic disturbances in the Yukon, disturbance maps would have to be created for each herd individually, which was beyond the scope of this study. As a result, the low resolution of disturbance mapping used here underestimates disturbances, although the correlation of other human activities with roads may contribute to reasonable proportional representation in many ranges. Environment Yukon (2016) aimed to map all forms of suspected and known anthropogenic linear disturbance ranging from 1.5m to ~20m resolution in areas of interest (which covers one herd range completely and seven herd ranges from partial to very partially), but this could lead to potential bias as areas of interest are most likely already highly disturbed.

Tables

Table 1. Global positioning system (GPS) collar data used in determining seasonal ranges for northern mountain caribou. Populations were located in the Yukon Territory, Canada, with data collected from 1999 to 2018. Data were combined with digital elevation maps to delineate seasonal ranges based on elevation. Dates for summer locations ranged from June 01 to September 30, and from December 01 to March 31 for winter locations.

GPS						
Population	**Season**	**Total animals collared**	**Total animal locations**	**Total animal years**	**Min year**	**Max year**
Carcross	Winter	26	78395	72	1999	2012
Carcross	Summer	22	72031	44	2000	2012
Clear Creek	Winter	30	1608	56	2017	2018
Clear Creek	Summer	30	2241	30	2017	2017
Finlayson	Winter	3	4950	21	2004	2011
Finlayson	Summer	3	4675	17	2005	2011
Hart River	Winter	43	8322	101	2015	2018
Hart River	Summer	41	11003	85	2015	2017
Klaza	Winter	44	35003	143	2012	2017
Klaza	Summer	38	27466	93	2012	2016
Kluane	Winter	12	13561	45	2014	2018
Kluane	Summer	12	16342	33	2014	2017
Nahanni	Winter	31	14903	108	1998	2013
Nahanni	Summer	29	33754	66	1999	2012

Table 2. Very high frequency (VHF) collar data used in determining seasonal ranges for northern mountain caribou. Populations were located in the Yukon Territory, Canada, with data collected from 1983 to 2009. Data were combined with digital elevation maps to delineate seasonal ranges based on elevation. Dates for summer locations ranged from June 01 to September 30, and from December 01 to March 31 for winter locations.

VHF						
Population	**Season**	**Total animals collared**	**Total animal locations**	**Total animal years**	**Min year**	**Max year**
Aishihik	Summer	91*	462	307	1991	2002
Aishihik	Winter	91*	616	424	1991	2003
Chisana	Summer	332*	3539	1261	1988	2009
Chisana	Winter	332*	1712	1002	1991	2008
Ethel Lake	Summer	12	71	36	1989	1993
Ethel Lake	Winter	12	71	36	1989	1993
Ibex	Summer	17	46	36	1983	2006
Ibex	Winter	21	138	72	1984	2005
Tatchun	Summer	22	83	56	1992	2001
Tatchun	Winter	24	103	69	1992	2001
Wolf Lake	Summer	72	391	235	1984	1999
Wolf Lake	Winter	73	495	293	1985	2000

*(Hegel and Russell 2013)

Table 3. Elevational cutoffs in metres above sea level (asl) used in creation of seasonal ranges for northern Mountain Caribou in Yukon, Canada, as determined by both GPS and VHF collar location data. Summer cutoffs correspond to where 90% of caribou locations fell on a distribution of elevational use from June 01 to September 30, whereas winter cutoffs are where 90% of caribou locations fell on a distribution of elevational use from December 01 to March 31. The max elevation corresponds to the highest point of caribou elevational use in either GPS or VHF collar data. Collar data ranges from 1998 to 2018 for GPS collars and 1983 to 2009 for VHF collars.

Population	Summer cutoff (m asl)	Winter cutoff (m asl)	Max elevation (m asl)
Aishihik	1259	1598	2046
Carcross	1106	1388	2076
Chisana	1251	1513	2298
Clear Creek	1313	1223	1944
Ethel Lake	1078	1125	1740
Finlayson	1297	1325	2147
Hart River	1269	1282	2102
Ibex	1253	1577	1928
Klaza	1088	1351	1956
Kluane	1177	1386	2127
South Nahanni	1144	1449	2416
Tatchun	925	1060	1873
Wolf Lake	1177	1235	1956

Table 4. The effect of removing large lakes from the annual and winter ranges of northern mountain caribou (NMC) study populations, Yukon Territory, 1982-2015. Summer range is not included because no large lakes overlapped with summer range for NMC. Only those populations with lakes large enough to affect winter or annual range are included.

Population	Season	Range Area (km^2)	Change in Range Area Due to Lake Removal
Aishihik	Winter	8471	-1.88%
Aishihik	Annual	9944	-1.60%
Carcross	Winter	12101	-4.34%
Carcross	Annual	14969	-3.51%
Ethel Lake	Winter	2607	-2.77%
Ethel Lake	Annual	4029	-1.79%
Finlayson	Winter	13317	-0.13%
Finlayson	Annual	19426	-0.09%
Ibex	Winter	1827	-1.52%
Ibex	Annual	2517	-1.10%
Kluane	Winter	5593	-1.41%
Kluane	Annual	7951	-0.99%
Wolf Lake	Winter	10218	-1.46%
Wolf Lake	Annual	19181	-0.78%
		Average	-1.67%

Figures

Figure 1. The 13 populations of northern mountain caribou included in this study: Hart River, Clear Creek, Ethel Lake, Chisana, Kluane, Klaza, Aishihik, Tatchun, Finlayson, Nahanni, Ibex, Carcross, and Wolf Lake. Study populations are mainly located in the Yukon Territory, Canada but cross into Alaska, Northwest Territories, and British Columbia. Fall classification surveys used in this study took place from 1982-2015.

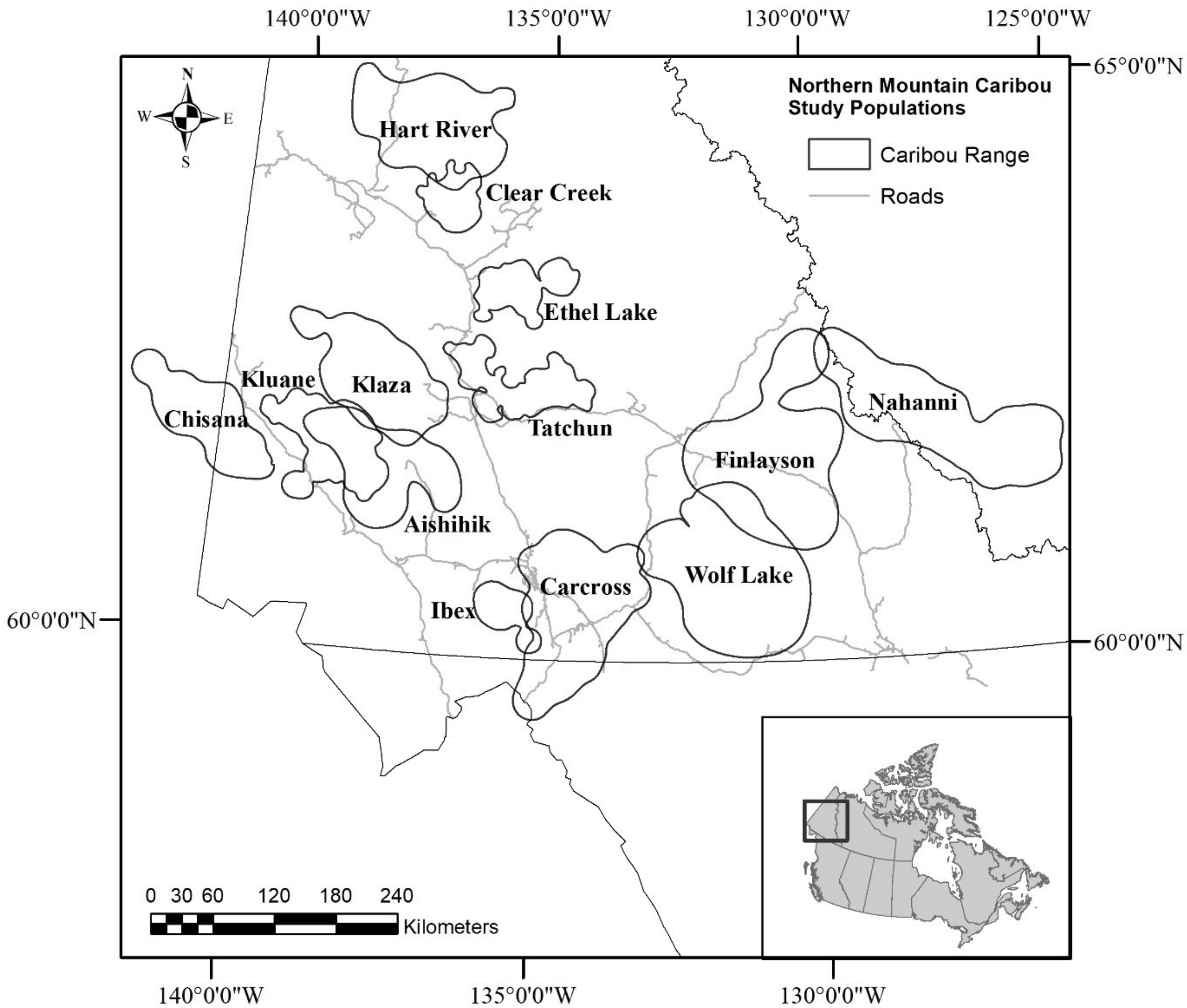


Figure 2. Elevational use of Clear Creek caribou in summer (June 01 to September 30) and winter (December 01 to March 31). Number of GPS collar years of data used ranged from 30 in summer to 56 in winter, from 2017-2018. Vertical lines on the graph correspond to 90th quantiles for winter and 10th quantiles for summer, which were the determining points for summer or winter elevational cut-offs in seasonal range creation.

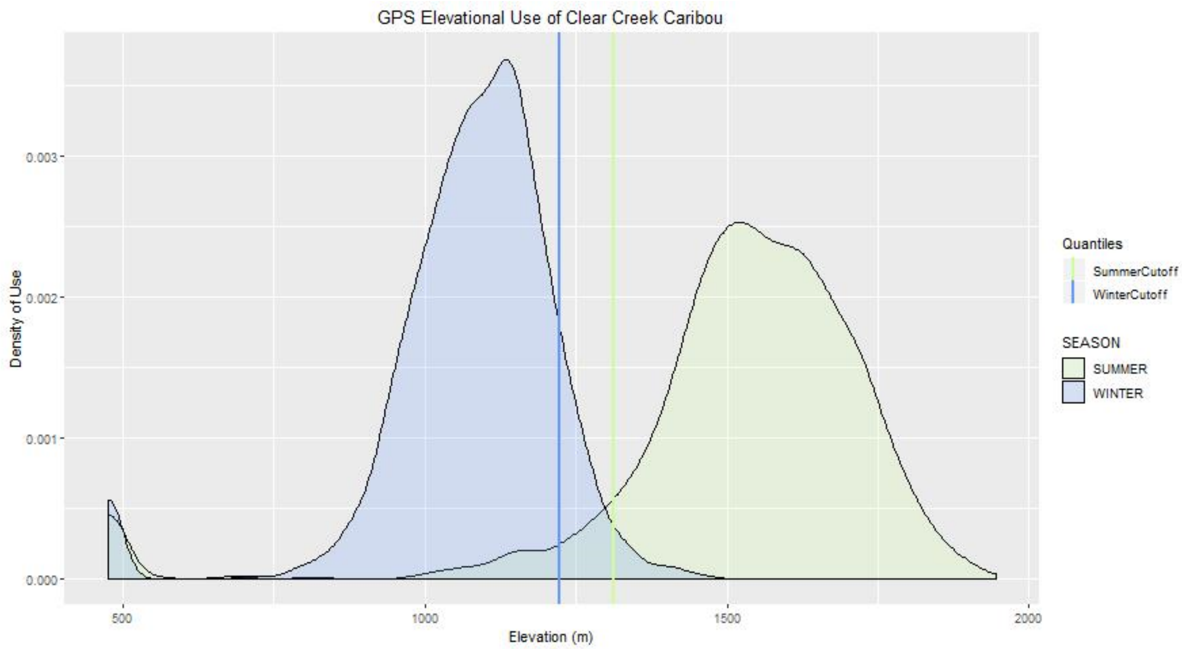


Figure 3. Winter and summer ranges created for the Clear Creek herd using distribution of elevational use from GPS collar data. The maps correspond to where 90% of caribou elevation use fell within either summer (June 01 to September 30) or winter (December 01 to March 31) timeframes.

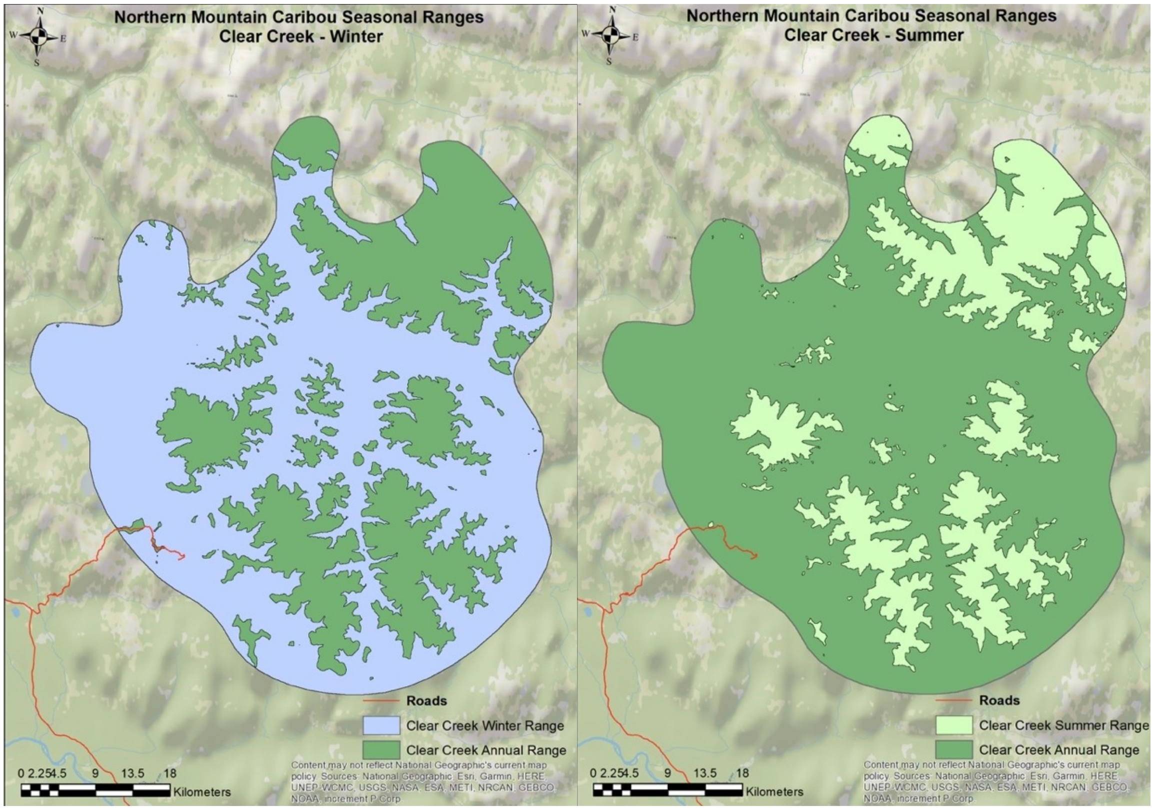


Figure 4. Elevational use of Klaza caribou in summer (June 01 to September 30) and winter (December 01 to March 31). Number of GPS collar years of data used ranged from 93 in summer to 143 in winter, from 2012-2017. Vertical lines on the graph correspond to 90th quantiles for winter and 10th quantiles for summer, which were the determining points for summer or winter elevational cut-offs in seasonal range creation

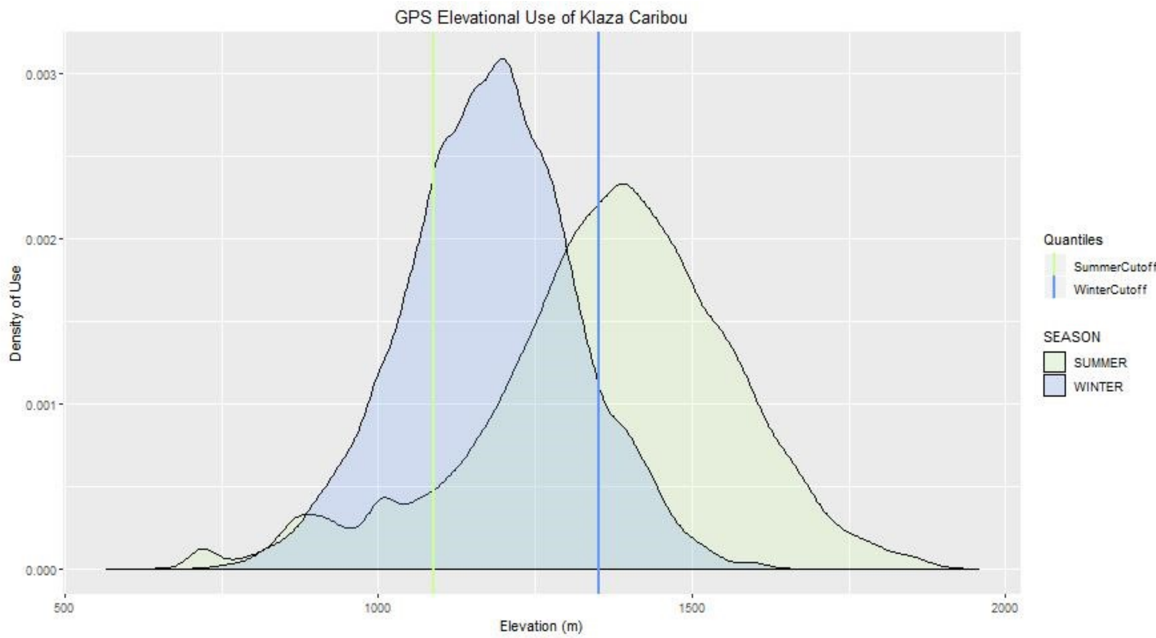


Figure 5. Winter and summer ranges created for the Klaza herd using density of elevational use from GPS collar data. The maps correspond to where 90% of caribou elevation use fell within either summer (June 01 to September 30) or winter (December 01 to March 31) timeframes.

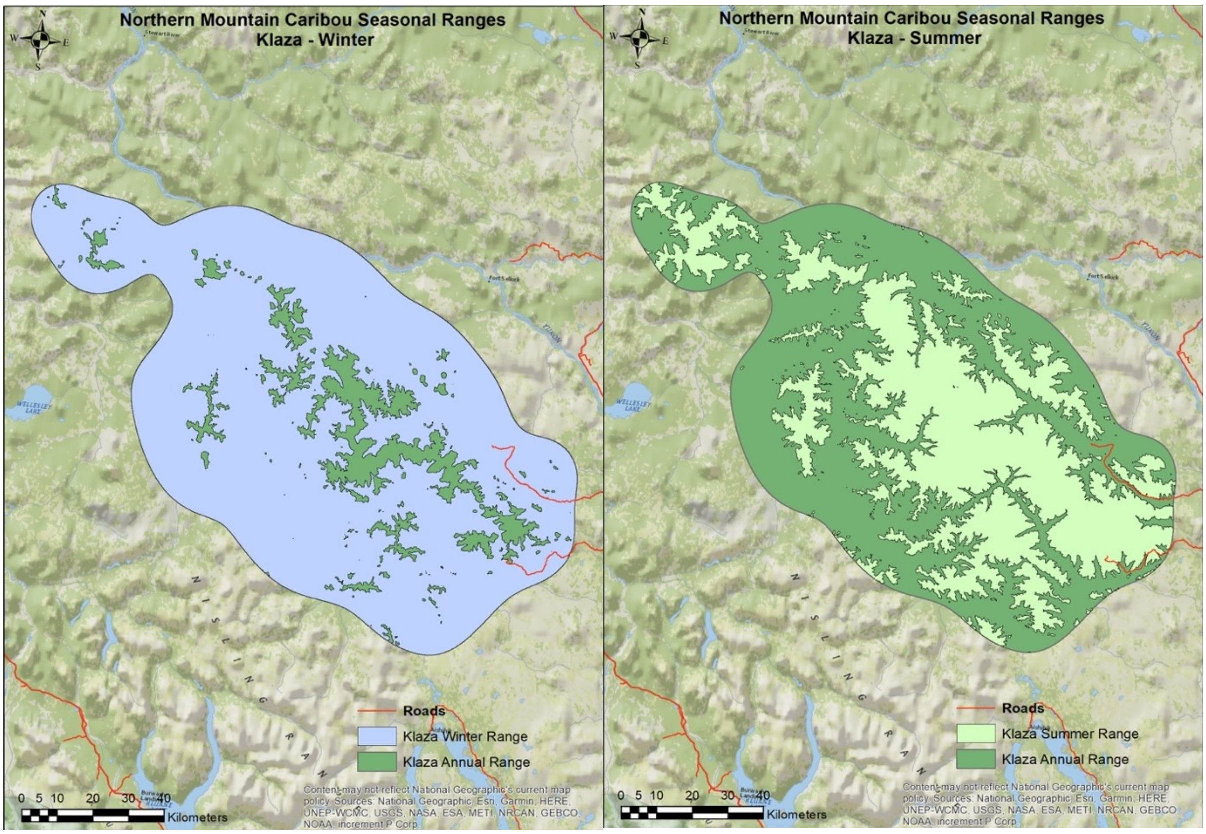


Figure 6. Elevational use of Ibex caribou in summer (June 01 to September 30) and winter (December 01 to March 31). Number of VHF collar years of data used ranged from 36 in summer to 72 in winter, from 1983-2006. Vertical lines on the graph correspond to 90th quantiles for winter and 10th quantiles for summer, which were the determining points for summer or winter elevational cut-offs in seasonal range creation

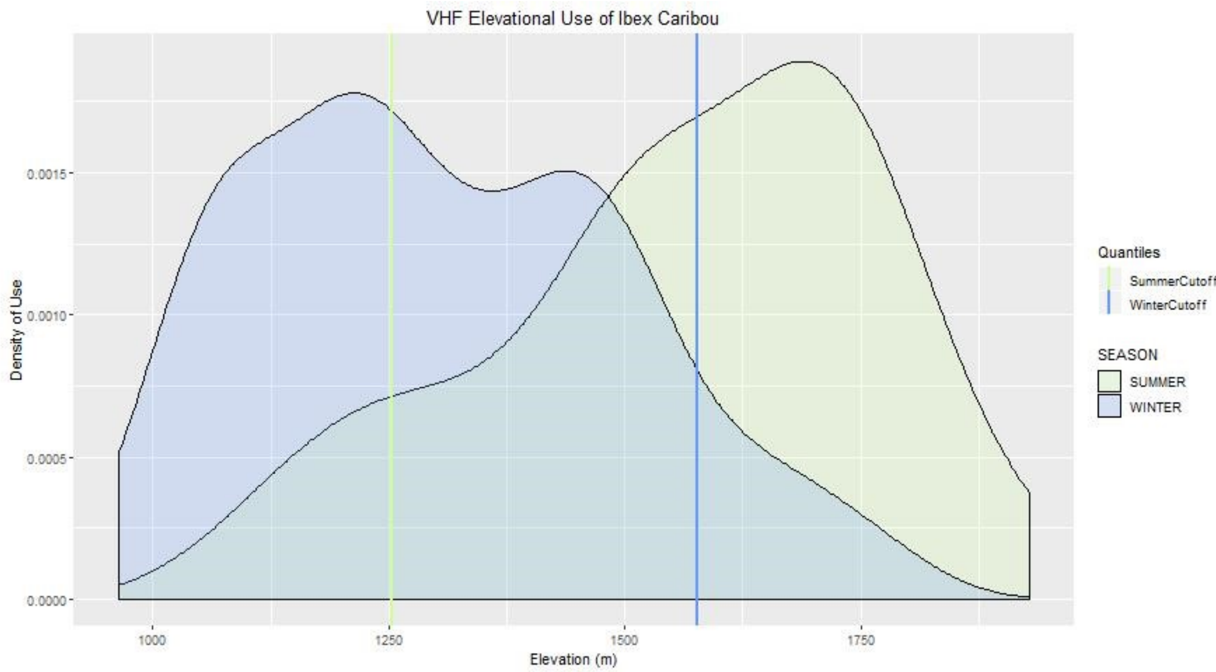


Figure 7. Winter and summer ranges created for the Ibex herd using density of elevational use from VHF collar data. The maps correspond to where 90% of caribou elevation use fell within either summer (June 01 to September 30) or winter (December 01 to March 31) timeframes.

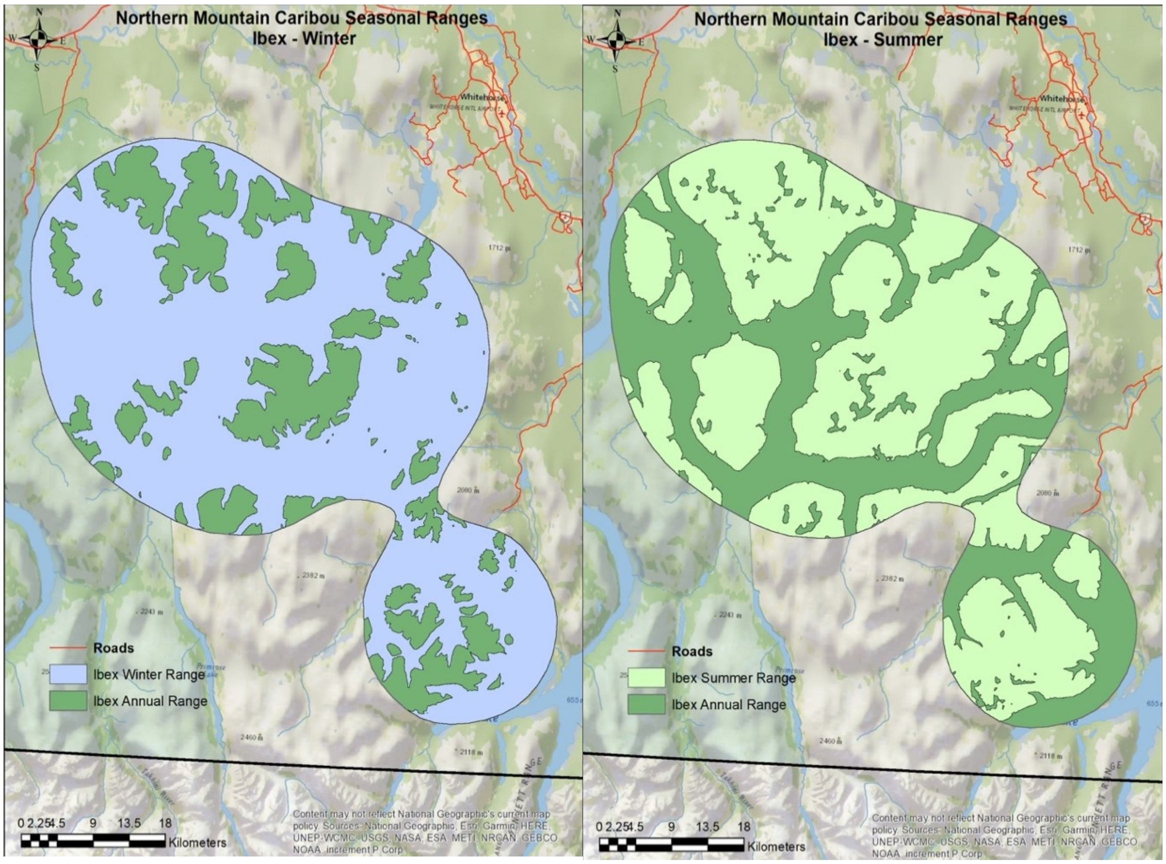


Figure 8. The average cumulative natural disturbance on summer, winter and annual ranges of NMC study populations. The average of cumulative natural disturbance from the years 1982 – 2015 is presented here.

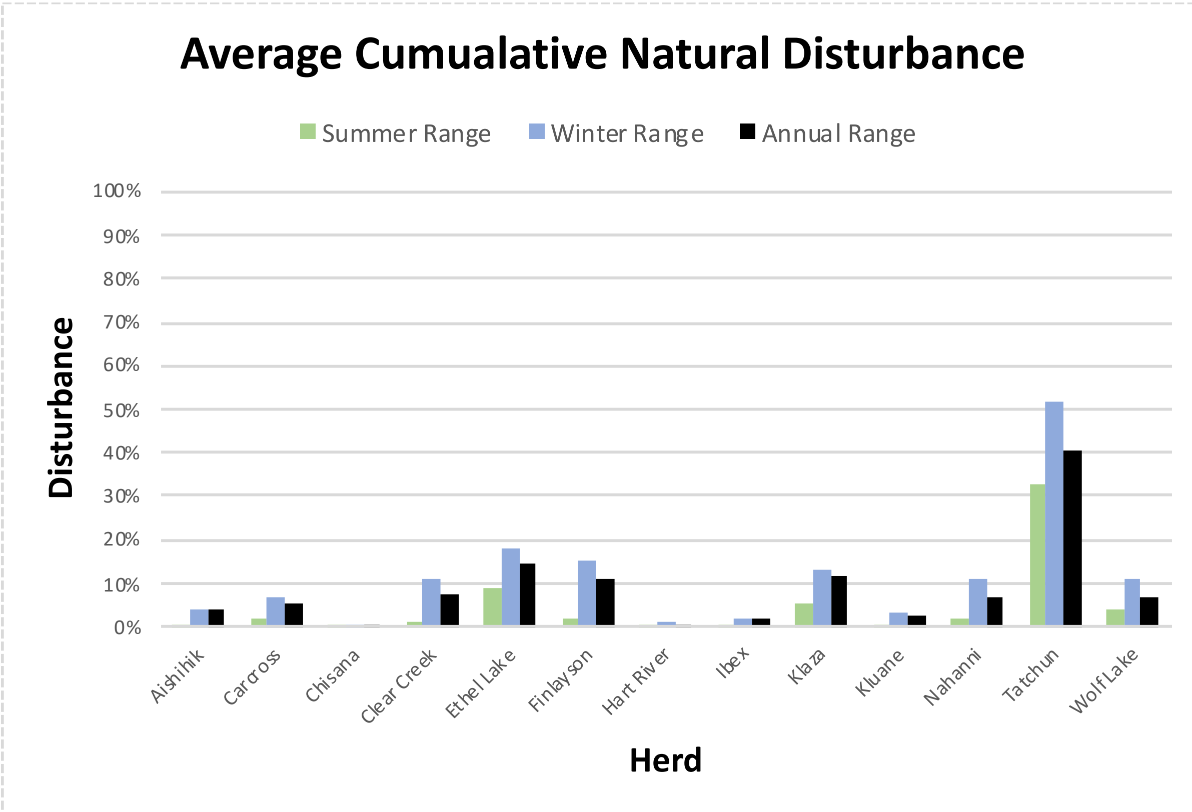


Figure 9. The road disturbance on summer, winter, and annual ranges of northern mountain caribou (NMC) using CANVEC roads layers from Natural Resources Canada (Lee et al. 2006; Smith and Cheng 2016). Linear disturbance is calculated as the density of roads on a NMCs range (km/km^2). Roads are measured by

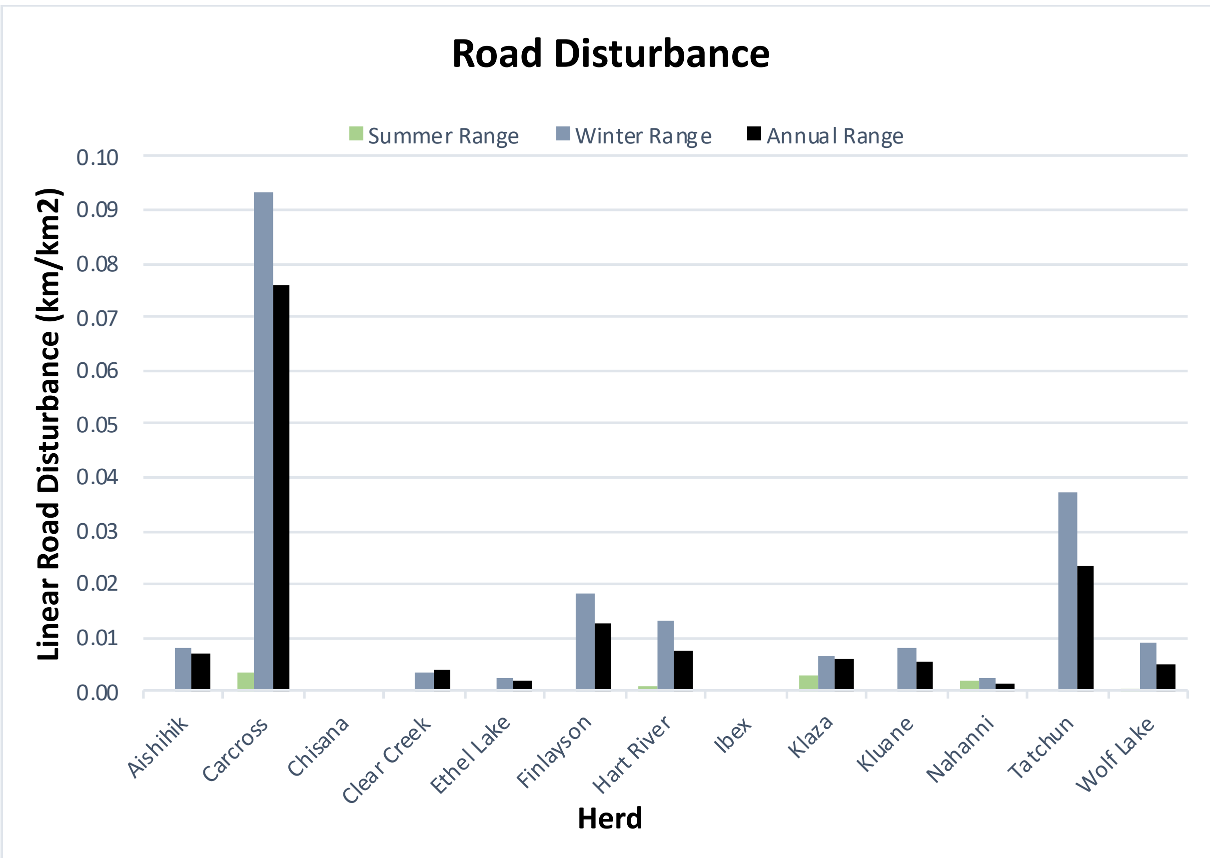


Figure 10. Comparison of road disturbance buffered at 500m and 4000m versus disturbance attributed to natural disturbance on ranges of study populations of northern mountain caribou. Disturbance is measured as the average over the years of 1982-2015, the dates of this study.

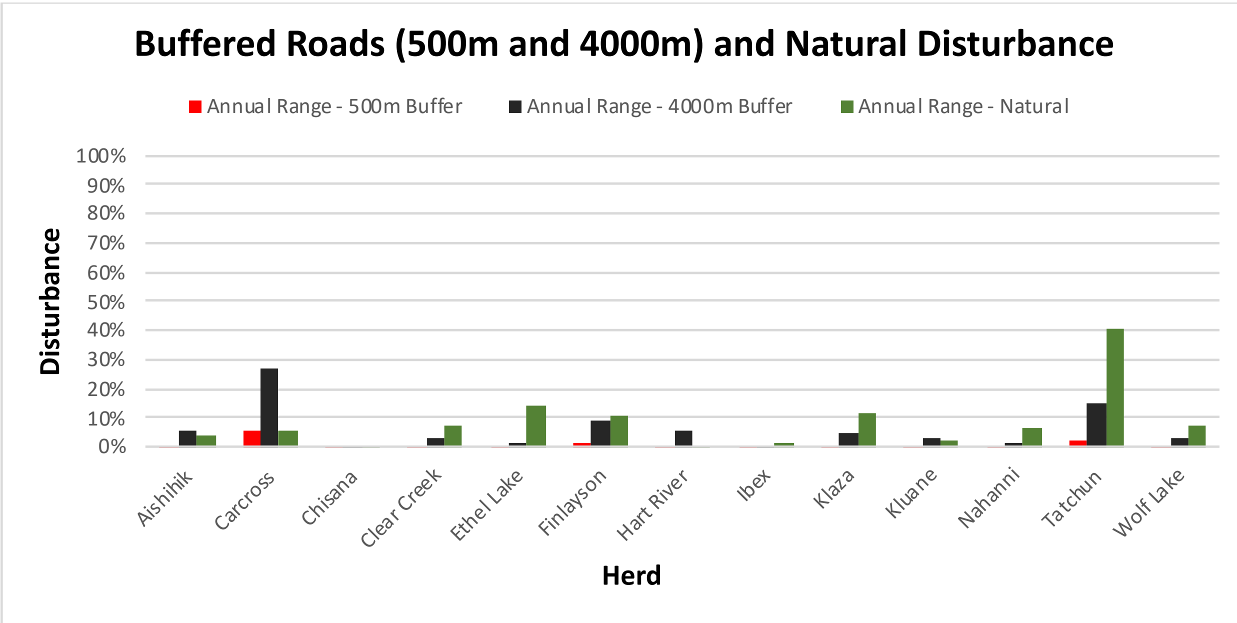


Figure 11. Average combined (natural + road) disturbance, with roads buffered at 500m. Average disturbance levels on summer, winter and annual ranges of northern mountain caribou study populations are presented. The averages are measured over the years 1982-2015, the study dates.

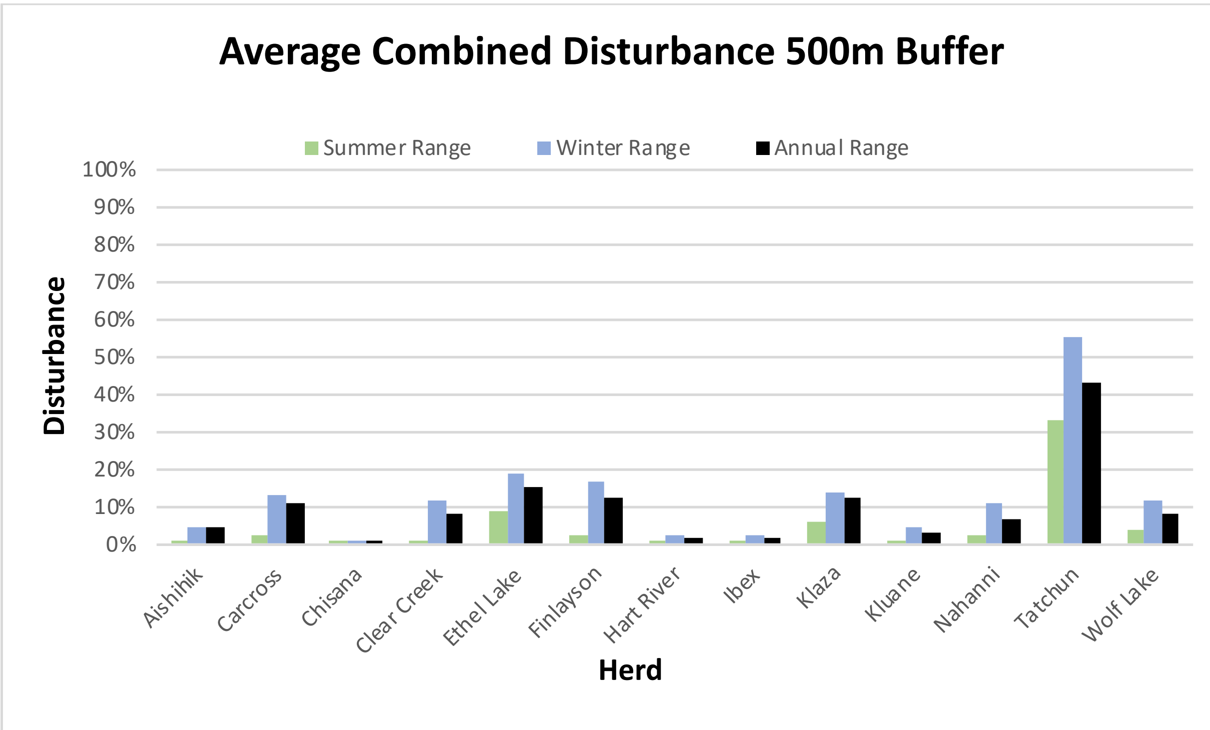
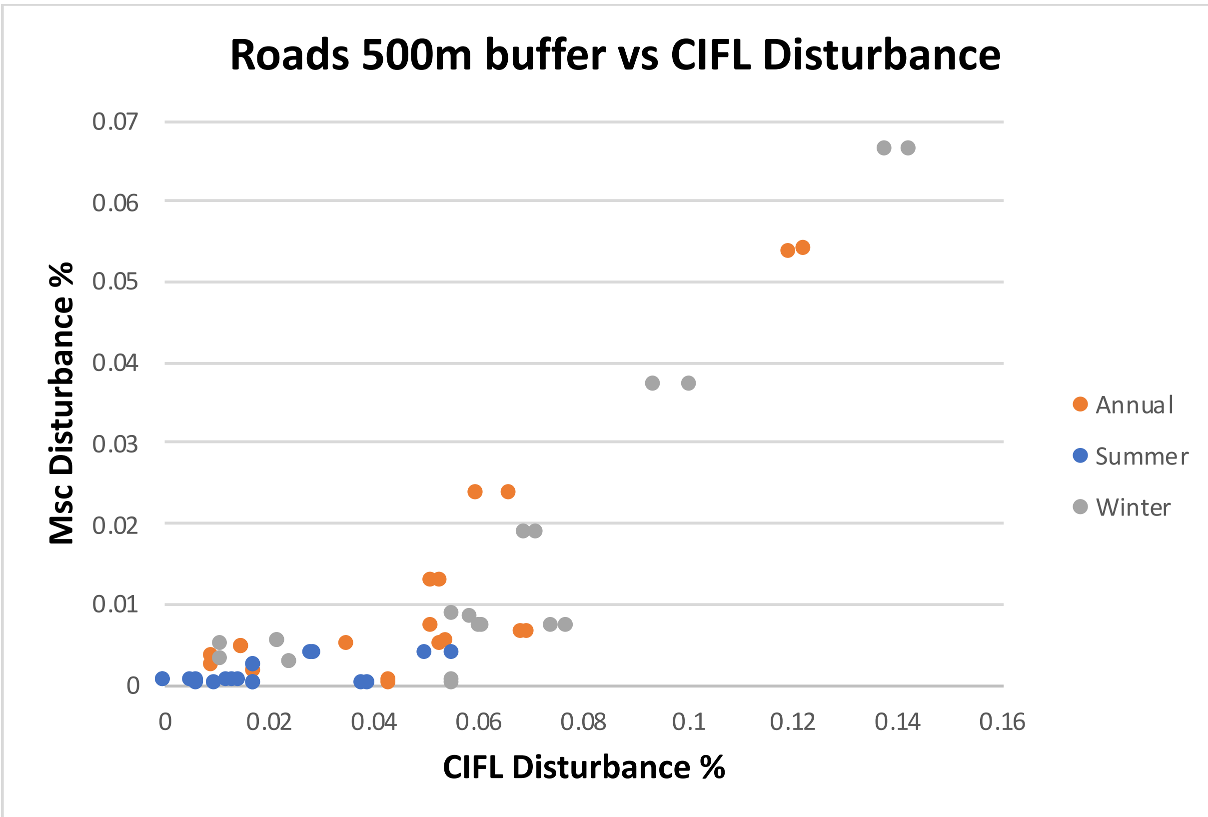


Figure 12 – Comparison of disturbance values used in this study (roads buffered by 500m) to Canadian Intact Forest Landscape (CIFL) 2000, and 2013 disturbance values for 13 northern mountain caribou herds in Yukon Territory, Canada. Chisana was removed due to CIFL mapping constraints. Disturbance is measured as percent of a caribou's herd range disturbed.



Chapter 3: Evaluating the effects of climate, disturbance, and harvest on northern mountain caribou in Yukon, Canada

Throughout Canada and many regions of the world, caribou (*Rangifer tarandus*) are in decline (Vors and Boyce 2009; Festa-Bianchet et al. 2011). Due to large-scale disturbance from industrial activity and infrastructure, 10 of 14 Albertan boreal woodland caribou herds are in serious decline (Sorensen et al. 2008; Hervieux et al. 2013). Similar studies on southern mountain caribou in British Columbia (BC) have found all 10 populations heading towards local extinction (Wittmer et al. 2010). Environment Canada (2011) found disturbance-based recruitment models were able to predict sustainability for 24 boreal caribou populations across Canada; however, these models were found to be inadequate for northern mountain caribou (NMC) populations (Reid et al. 2013). Further investigation of what drives recruitment in NMC was deemed necessary to understand population sustainability in these northern systems.

Apparent competition is strongly tied to population declines in woodland caribou, where forest alteration leads to increases in early seral stands and subsequent increases in moose (*Alces alces*) populations (Brown 2011; Anderson et al. 2018). Caribou are widely affected by seral stage variation in their range; this can be the best predictor of adult female survival (Wittmer et al. 2005), and negatively affect calf recruitment (McCarthy et al. 2011). Caribou also make movement based (Avgar et al. 2015) and habitat based (Hornseth and Rempel 2016) decisions that support the apparent competitor hypothesis, by avoiding habitats associated with both high moose and high wolf abundance. Several other mechanisms can also lead to negative effects on caribou populations.

A decrease over two decades of 52% of high-quality habitat due to industrial development in central mountain herds of caribou in BC strongly correlated with population declines (Johnson et al. 2015). In Newfoundland, every 20 km^2 of disturbance on core calving habitat led to a decline in recruitment by 1 as measured by number of calves per 100 cows (McCarthy et al. 2011). Habitat disturbance is also associated with lower fidelity to seasonal ranges, leading to lowered adult female survival rates (Courtois et al. 2007), possibly through the use of less suitable seasonal habitat (MacNearney et al. 2016). In BC, there is evidence that disturbances in high value high-elevation habitat can lead to disproportionate negative effects on caribou populations (Price 2018).

Roads and other linear features on the landscape may have many impacts on caribou populations. Linear features can lead to loss of landscape connectivity (Beguin et al. 2013; Beyer et al. 2016; Wilson et al. 2016), and contribute to genetic differentiation in mountain caribou (Gubili et al. 2017). Maintaining landscape connectivity may be more important than creation of protected areas in maintaining home-range size and viability of caribou (Muhly et al. 2015). Linear features may also increase predator selection of calving areas, with decreased habitat use and lower calf survival of caribou closer to linear features than those farther away (Demars and Boutin 2017). Wolf (*Canis lupus*)-caribou encounter rates increase near linear features (Whittington et al. 2011), possibly due to increased predator search efficiency, as linear features allow wolves to move 'faster and farther' through landscapes in search of prey (Dickie et al. 2017). Due to the complex nature of linear features effects on caribou, avoidance of these features by substantial distances (1 – 1.75 km) is a common finding in disturbance studies on caribou (Polfus et al. 2011; Johnson et al. 2015). The effect of roads, and their avoidance, may also depend on the season (Polfus et al. 2011) or the presence of calves (Viejou et al. 2018).

Fire is a major source of disturbance on many caribou ranges in North America. Fire has cascading effects on caribou, the most direct being loss of habitat (Robinson et al. 2012; Beguin et al. 2013; Hornseth and Rempel 2016). Fire may also increase cover types preferred by apparent competitors, with corresponding greater selection by predators, and higher caribou-predator encounter rates (Robinson et al. 2012). There is, however, some evidence that in less productive northern systems, fire does not lead to dramatic increases in apparent competitors and their habitat (McLoughlin et al. 2019). Fire-disturbed areas can be avoided by caribou for up to 50-60 years (Joly et al. 2010; Collins et al. 2011; Russell and Johnson 2019), with lichen, a critical food source for caribou, taking up to 180 years to reach peak biomass post-fire in southwest Alaska's taiga on the winter range of Nelchina population as measured during a 2002 survey (Collins et al. 2011). Each of these effects of fire could influence caribou recruitment rates.

In addition to natural and anthropogenic disturbance, climatic conditions may also influence caribou populations. Hegel et al. (2010a) found variance in calf recruitment of NMC was best explained by variation in winter climate prior to birth, as measured by pacific decadal oscillation (PDO). In Northern Europe and Alaska, severe winters can lead to poorer body condition (Weladji and Holand 2003) and lower calf survival (Adams et al. 1995; Albon et al. 2017) of semi-domesticated reindeer, Alaskan mountain caribou, and wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Predation may also be mediated by winter severity. In a study of boreal caribou in Quebec, warmer temperatures increased black bear (*Ursus americanus*) predation in a declining population (Bastille-Rousseau et al. 2016). Along with winter weather, earlier springs allow NMC to employ their predator avoidance strategies by spacing out into alpine areas whereas late springs lead to more efficient predator searching, as NMC are unable to spread out (Bergerud et al. 1984; Bergerud and Elliot 1986). Spring climate also modifies predation rates, for example: when there was no wolf control on the Finlayson's population range and there was earlier springs, as measured by April-PDO, recruitment was higher due to more effective spacing away from predators, whereas when wolves were removed (controlled), earlier springs affected recruitment negatively to a small degree, possibly due to mis-match between green-up and calving (Hegel et al. 2010b). In late winter, caribou natality rates may be affected by increased snow-fall (Adams and Dale 1998a), which may also affect the timing of parturition (Adams and Dale 1998b). Overall, climate is a significant source of influence on caribou populations, with projections of climate change in Ontario predicting a potential complete loss of suitable caribou habitat (Masood et al. 2017).

Average PDO captures the amalgamation of weather patterns throughout the year that may affect caribou, and thus may express the mean effects of various mechanisms on caribou recruitment dynamics. In contrast to other measures of PDO, use of average annual PDO aims to find the average influence of spring, birthing, and winter prior to birth effects on caribou recruitment.

NMC recruitment rates and survival are significantly affected by predation, with wolves being the dominate predator (Bergerud and Elliot 1986; Gauthier and Theberge 1986; Hayes et al. 2003). Wolf densities strongly affect caribou recruitment rates, with Bergerud and Elliot (1986) suggesting that when wolf densities are >6.5/1000km^2, caribou recruitment is too low to maintain numbers. Along with wolves, grizzly bears (*Ursus arctos*) can be a major predator in mountain systems (Adams et al. 1995; Boertje et al. 2017), and they choose habitat similar to caribou during the summer calving months (Milakovic et al. 2012). Grizzly bears have fast kill rates, taking on average 40 minutes to consume a caribou calf (Brockman et al. 2017). In eastern Canada, black bears have been found to be a major predator of caribou calves (Dussault et al 2012; Leblond et al. 2016a), and often active hunters of calves (Rayl et al. 2018).

Human harvest of caribou and moose have also been shown to have effects on caribou populations. In Southern BC, liberalized hunting policies on moose led to population stabilization of caribou, with concurrent decreases in wolf numbers (Serrouya et al. 2017). In Quebec, subsistence harvest of three boreal caribou populations led to predictions that these populations were not self-sustaining under current conditions, though the ultimate cause of population declines was landscape change due to industrial disturbance (Rudolph et al. 2012). In NMC ranges, there is historical evidence that high human harvest during the first four decades of the 20th century, due to poorly regulated harvest and ease of harvesting caribou, contributed to population declines (Spalding 2000).

Seasonal migrations between winter and summer habitats are a vital and well-studied life history strategy for NMC (Hatler 1986; Gustine and Parker 2008; Hegel and Russell 2013), and a requirement to maintain viable populations (Environment Canada 2012). NMC seasonal migrations to higher elevation summer habitats allow parturient females to space away from their predators, lowering their overall densities on the landscape and decreasing predator search efficiencies (Bergerud et al. 1984). Migrations into alpine areas may also decrease insect harassment and heat exhaustion during the summer (Jandt 1998). Most NMC populations winter in valley bottoms in late-stage forests, while the Aishihik, Klaza, Kluane, and Chisana populations are known to undertake smaller movements to low-elevation alpine or sub-alpine areas (Kuyzk et al. 1999). Consideration of seasonal range use is important when evaluating the effects of disturbance and other factors on NMC (Reid et al. 2013).

The objective of this study is to explore potential population drivers in NMC populations, through evaluating the influences of climate, harvest, and disturbance variables on recruitment in Yukon NMC populations. Although adult female survival is an essential component of caribou population dynamics (DeCesare et al. 2012; Serrouya et al. 2017), available NMC adult female survival data were insufficient for statistical analysis. Previous work has shown a strong relationship between boreal caribou recruitment and anthropogenic and natural disturbances

(Sorensen et al. 2008; Environment Canada 2011; Rudolph et al. 2017). However, due to the different life histories, habitat requirements, and harvest pressures on NMC, recruitment models appropriate to NMC must be created (Reid et al. 2013). The major hypotheses evaluated here are as follows:

H_1: Increasing road, fire, or combined disturbance on NMC annual or seasonal range will contribute to decreased recruitment.

H_2: April PDO, May PDO, average PDO or PDO prior to birth (winter) will be related to recruitment, where positive PDO will correlate with increasing recruitment and negative PDO with decreasing recruitment.

H_3: Alternate prey or predator harvest will lead to increasing recruitment.

H_4: Regulated NMC harvest will have neutral effects on recruitment.

Study area

This study was largely located in the central and southern Yukon (Figure 1), with three herd ranges extending into either Alaska, the Northwest Territories, or British Columbia. All study herds fell within the Boreal Cordillera Ecozone (Smith et al. 2004). Mean annual temperature in this ecozone ranges from 9.5C to 11.5C in summer and -13C to -23C in winter (Smith et al. 2004). Precipitation ranges from <300mm in rain shrouded valleys of the Yukon Pacific coast mountains to 1000mm in high elevations of the eastern Yukon mountain ranges (Smith et al. 2004). The boreal forest regions are composed of white spruce (*Picea glauca*) and black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta*), alpine fir (*Abies lasiocarpa*), balsam popular (*Populus balsamifera*), trembling aspen (*Populus tremuloidas*), and paper birch (*Betula papyrifera*) (Smith et al. 2004). High elevation areas are mainly composed of sedge-dominated plateaus where lichen rock-fields are common (Polfus et al. 2011). Elevations range from 32m ($mean_{min}$ = 519m) asl to 4105m ($mean_{max}$ = 2444m) asl for study populations, the $mean_{total}$ elevation was 1210m asl.

The study populations included here belong to the northern mountain designatable unit of woodland caribou, as recognized by the Committee on the Status of Endangered Species in Canada (COSEWIC) (DU 7; COSEWIC 2011), and confirmed by recent genetic analysis (Polfus et al. 2017). Traditional knowledge also agrees with this designation (Polfus et al. 2016). NMC are recognized as a species of special concern through the Canadian Species at Risk Act (Environment Canada 2012). There are 26 northern mountain caribou herds in the Yukon Territory (Hegel and Russel 2013). Human footprint is relatively low throughout the Yukon when compared to the rest of Canada (Guindon et al. 2018). The range of the Carcross herd is the most impacted, with the capital of the Yukon (pop. ~25,000) and 2 smaller communities within its range.

Methods

Data

Recruitment Data

Fall classification surveys conducted from 1982-2015, following standardized procedures (Hegel and Russell 2013), were used to represent recruitment for 13 northern mountain caribou herds included in this study. From late September to mid-October of each year, groups of caribou on alpine plateaus were classified by age and sex to derive a ratio of total number of calves to cows. The number of annual recruitment rates per population ranged from 3 to 34, with an average of 19 surveys per herd (SD = 9.16). Years where active caribou recovery actions such as predator control took place on a populations range were censored from the total dataset (see Supporting Information). As well, harvest data were not available for all years (see below). The total number of caribou recruitment years used for disturbance-climate models was 220, and for disturbance-climate-harvest models was 176.

Disturbance Data

Disturbance variables for each year of study were quantified using road layers buffered at 0m, 500m, 1000m, 1500m, 2000m, 3000m, and 4000m (NRCan 2019), interpreted Landsat imagery from 1985-2015 (Guindon et al. 2018), and government fire records for years preceding 1985 (BC Data Catalogue 2018; NWT Geomatics 2018; Yukon Geomatics 2018). Disturbance variables were further segregated into winter, summer, and total seasonal ranges (as measured by

NMC elevation use: see Supporting Information) to test for differing effects of disturbances on seasonal ranges. All spatial mapping was completed in ArcGIS 10.6 (Environmental Systems Research Institute, Redlands, CA). A comparison between road disturbance values used here and Canadian Intact Forest Landscape (CIFL) maps for 2000 and 2013 was completed, which shows similar relative levels of disturbance captured across herd ranges, although absolute measures of disturbance were much higher using CIFL maps (see Supporting Information).

Climate and Harvest Data

Climate variables were retrieved from the Joint Institute for the Study of the Atmosphere and Ocean (2018), and annual pacific decadal oscillation (PDO) values were quantified, as per Hegel et al. (2010a), Annual statistics on licensed harvest collected by the Yukon Government, and registered to game management sub-zones, were available from 1995-2015 (Milligan 2018). Wolf harvest data were supplemented with trapping data, as trapping can be a significant source of wolf mortality (Webb et al. 2011). Game management zones were intersected with caribou ranges, and harvest numbers truncated by the ratio of overlap. For example, if 50% of a game management zone overlapped with a caribou range, half the animals harvested in that game zone would be included in the estimate of harvest in that caribou range. Harvest densities by species were calculated by dividing the number of individuals harvested per year by the total area of the caribou range the species was harvested in.

Analysis

Boosted Regression Trees - Variable Reduction

A total of 18 variables of interest, and 7 buffer distances on roads, were included in preliminary analyses. Boosted regression trees (BRTs) were used to reduce the number of variables used in further statistical analysis, by evaluating which variables and buffer distances had the most influence on annual recruitment. BRTs were developed as per Elith et al. (2008). Seven different BRT models were created, one for each buffer distance. The BRT models were then compared to one another using 10-fold cross-validation statistics, to determine which buffer range reduced model error the most. If there was no evidence that one model performed better than another, the lowest buffer range was chosen. Once a subset of buffer distance was chosen, variables with >5% influence on recruitment were advanced for further analysis using mixed effects models (e.g., Buston and Elith 2011). Further details of BRT analysis are available in Supporting Information. Time lags of moose harvest effects on recruitment were also tested (t-1 and t-2) but were found to not meet variable influence requirements of >5%, and thus are not further considered here (Supporting information).

Mixed Effects Models

Linear mixed-effects models (LMMs) were used to further evaluate variables of importance from BRT results. All modelling was accomplished through the 'lme4' package in R (R Version 3.5.2, www.r-project.org, accessed 10 Nov 2018), using RStudio (RStudio Version 1.1.463, www.rstudio.com, accessed 10 Nov 2018). All variables were standardized to their z-scores to account for differences in scales between predictor variables. Year and herd were treated as random variables to account for differences in sample sizes between herds and years, and to account for any inter-relationships within herds and/or years. When a variable is treated as a random effect it accounts for a lack of independence among individual samples arising from random samples of an individual sample (herd or year in this case) that is part of a greater population (NMC in this case) (Gillies et al. 2006). Models were separated into two sets in recognition of the availability of relevant data: a disturbance-climate model set from 1982-2015 that contained 220 recruitment years, and a disturbance-climate-harvest model set from 1995-2015 that contained 176 recruitment years. Two measures of model fit were used to compare models among the two sets. The first measure is one of relative model fit, called Akaike's information criteria (AIC) for small sample sizes AICc (Burnham and Anderson 2002). AICc ranks models by parsimony and accuracy of fit. Models with <ΔAICc of 2, and whose fixed effects showed significant results based on visual inspection of confidence intervals, were considered for further inference. The second measure is one of absolute model fit, R^2. Marginal R^2 (R^2_m) is the variance explained by the fixed effects, and conditional R^2(R^2_c) is the variance explained by the fixed and random effects together (Nakagawa and Schielzeth 2013).

Results

Boosted Regression Trees

Boosted regression trees (BRTs) showed no significant difference of buffer distance on model deviance based on 10-fold cross validation statistics, therefore model sets with no buffer and a 500m buffer were chosen for further analysis. Most studies have shown some buffer effect on population responses to disturbance on caribou ranges (Anttonen et al. 2011; Polfus et al. 2011; Fortin et al. 2013), although road density (equivalent to 0m buffer distance) has also been shown as influential (Demars and Boutin 2017). Natural disturbance on annual range was a top performing variable for reducing model deviance (Table 2), accounting for 28.8% of relative influence on recruitment when there was no buffer on roads, and 14.92% with a 500m buffer (Table 2). When roads were buffered by 500m, summer range disturbance became a top performing variable, accounting for 14.62% of relative influence on recruitment. In both model sets, average PDO, and moose, caribou, and grizzly bear annual harvest density were also top performing variables. There is no combined measure of disturbance when road disturbance was not buffered as natural disturbance was measured by % of area disturbed, whereas road density was measured by km of road per km^2. Cumulative disturbance values used in this study are available in supporting information.

Linear Mixed Models

Fixed effects – disturbance-climate model set

All top performing disturbance-climate models had average PDO as a predictor (Table 3); including either natural disturbance or road disturbance only improved AICc marginally (~ΔAICc of 0.68). Although overall model fit increased with inclusion of natural or road disturbance, the fit of fixed effects did not (R^2_m). There were ~10 fewer calves per 100 cows when average PDO was at its' lowest value when compared to the highest values of average PDO (Figure 2). The fixed effects of model numbers 1, 2, 3 (Table 3) did not have a significant influence on the model beyond that of average PDO (model 4) Table 5 displays the model coefficients for the disturbance-climate model set.

Fixed effects – disturbance-climate-harvest model set

Moose harvest and average PDO had positive effects on recruitment as either increased (Figure 3). There was a clear top disturbance-climate-harvest model that included both moose harvest and Average PDO (Table 4). The next best model of moose harvest alone had a ΔAICc of 7.19. The top model also explained the greatest variance due to fixed effects (R^2_m) compared to others, accounting for 20% of the variance in recruitment. The total variance explained by the fixed and random effects (R^2_c) was 35% for the top model. Including average PDO in any model did not increase R^2_c, though including moose harvest did add explanatory power to the model (R^2_m +9%). A model with road disturbance on summer range alone performed marginally worse than a model with random effects alone. Table 6 displays the model coefficients for the disturbance-climate-harvest model set.

Partial Dependence Plots

Partial dependence plots show the marginal effect a predictor has on the response variable when all other values of the boosted regression tree (BRT) model are held at their average effect (Elith et al. 2008). The top performing variables from both BRTs and linear mixed model effects (LMM) are presented here. Moose harvest has a negative effect on the average value of recruitment at approximately <0.00125 moose harvested/km^2, whereas there are generally positive effects on the average value of recruitment when harvest of moose is >0.00225 /km^2, or >2.25 moose/1000 km^2 (Figure 4). Average PDO has mixed effects on recruitment, where negative values of average PDO are associated with lower than average values of recruitment and higher average PDO are associated with higher values of recruitment. Road disturbance on summer range, at 500m buffering, generally had little effect on recruitment, where the proportion of area disturbed varied from 0.00 – 0.36%.

Consideration of seasonal ranges had significant effects on the influence of predictors in BRTs but did not increase LMM model performance. Measurements of summer range disturbance were included in LMMs due to BRT performance, but summer range disturbance was not influential in top performing LMM models. In BRTs, measurements of natural and total disturbance were top performing variables, but in LMMs these variables did not increase model performance and were the poorest performing single variable models. The model of 500m buffered road disturbance on summer range performed slightly worse than the null model of random effects alone in the disturbance-climate-harvest model set.

Discussion

Northern mountain caribou face unique challenges in the Yukon. Harvest pressures not seen in other woodland caribou populations, highly variable climate effects in mountainous, northern terrain, and the potential for significantly increased anthropogenic disturbance, are all key influencers on NMC population demographics. The work presented here explores the current state of NMC demographics as affected by road and natural disturbance, climate, and harvest pressures. Climate and harvest had moderate effects on recruitment, with qualifications discussed below. Disturbance, as measured by fire and roads, did not add to the explanatory power of recruitment models beyond climate and harvest, with significant qualifications discussed below.

Disturbance Hypothesis

Disturbance levels in the Yukon were found to be low, although wide-spread mapping of moderate to fine-scale disturbances was not available, which led to difficulty in generating robust results for the disturbance hypothesis. Overall, there was little support for the disturbance hypothesis at the observed disturbance levels and mapping techniques used, although there was a large difference in how influential disturbance was in BRTs and LMMs. When a 0m buffer was applied to roads (i.e. road disturbance expressed as a density), natural disturbance accounted for approximately three times more influence on deviance reduction than other variables. Summer road disturbance showed vastly different model deviance reduction depending if road disturbance was buffered or not. When no buffer was applied, summer road disturbance has nearly no effect, yet when roads were buffered by 500m, summer range disturbance by roads was the second highest performing variable in reducing model deviance. Winter range disturbance was not a top performing variable. Ultimately, neither road nor natural disturbance had a significant effect on recruitment in LMMs. Moreover, univariate models of each were among the lowest performing models, with some of the highest ΔAICc and lowest R^2_m values. Potential non-linear relationships may have been better captured by BRTs (Elith et al. 2008). It is also possible the range of disturbance values was not large enough to adequately capture effects within LMMs (Feld et al. 2016), particularly in the case of road disturbance. In less productive northern systems there is also evidence that natural disturbance has limited effects on increasing apparent competitor numbers (McLoughlin et al. 2019). However, the comparatively low levels of anthropogenic disturbance measured in this study suggest there is an opportunity to manage caribou in this system before populations declines observed in other caribou systems occur (Vors and Boyce 2009; Johnson et al. 2015).

Natural and anthropogenic disturbance have been shown to have a negative effect on caribou recruitment (Sorenson et al. 2008; Environment Canada 2011; Rudolph et al. 2017).

Overall disturbance varied from near 0% (Chisana) on some caribou ranges to nearly 43.03% (Tatchun: 40.71% of this being natural disturbance) on other caribou ranges. The highest anthropogenic disturbance at 500m buffer was for the Carcross herd, at 5.35% disturbance of annual range. Most herds experienced low disturbance on their ranges; well below management thresholds identified for other caribou designatable units (Sorenson et al. 2008; Environment Canada 2011). Inclusion of data from NMC herds in British Columbia would likely result in a greater range among disturbance data, approaching or exceeding the 35% disturbance threshold identified in boreal caribou work (Environment Canada 2011). Up to nine herds in British Columbia may have recruitment data that could be included in further analysis (Environment Canada 2012).

The data used in this study to quantify disturbance were not limited. When comparing the Canvec roads map layer used in this study to approximate road (linear) density with high resolution (1.5m – ~20m resolution) disturbance mapping available from Yukon Environment (2016) for the Klaza herd, only 7.5% of linear features were captured by the Canvec data. The 2016 mapping identified all linear features on the landscape including: mining trenches, survey/cutlines, all transportation features, suspected anthropogenic features, and utility features. However, these data are only available for areas known to have higher footprints of human disturbance compared to other areas of the Yukon, or areas slated for future development. High resolution mapping was not available for most populations included in this study. As well, inability to reliably time-stamp the date of disturbance precluded interannual analysis of data, which was central to evaluating other variables included in this study. This was a concern in other methods of disturbance mapping investigated (Supporting information). Finally, a comparison and investigation of disturbance values used in this study to Canadian Intact Forest Landscape (CIFL) maps (Smith and Cheng 2016) (Supporting Information) found that CIFL did generally capture more disturbance than mapping methods used here. Yet, a preliminary analysis of effects on recruitment using CIFL data was inconclusive

Climate and Harvest Hypotheses

The only variables that had substantial influence on recruitment in LMMs were moose harvest and average PDO, supporting both the alternate prey and climate hypotheses. When 220 recruitment years informed models (disturbance-climate model set), average PDO was the top performing variable. When 176 recruitment years informed models (disturbance-climate-harvest model set), the inclusion of average PDO into moose harvest models increased model performance significantly. In the disturbance-climate-harvest model set, those models without average PDO explain 7% less R^2_m and have an ΔAICc of ≥ 7.19, showing that the clear top-performing model contained moose harvest and average PDO as explanatory variables. The effect of climate was consistent with predictions and shows similar results to Hegel et al. (2010a). Although average PDO was not tested in Hegel et al.'s (2010a, 2010b) work, it hypothetically incorporates multiple factors that may affect recruitment. Severe winters can lead to poor recruitment (Adams et al. 1995; Albon et al. 2017), and poor springs can lead to increased predation on caribou calves, as they cannot space away from their predators into alpine areas (Bergerud et al. 1984; Hegel et al. 2010b). Negative PDO values are associated with more severe winters and poor springs (Hegel et al. 2010a), and as expected, negative average PDO values were associated with lower recruitment. With rapidly changing climates in the north (IPCC 2014) climate effects could be exacerbated in the future. Novel predators such as coyotes (*Canis latrans*) may become more prevalent, and these have potential to be effective predators on caribou calves (Lewis et al. 2017). Changing climate could also increase the energetic cost to move between habitats in some areas with greater lake cover, due to reductions in ice-cover reducing the likelihood of caribou crossing those lakes (Leblond et al. 2016b).

Both the alternate prey and caribou harvest hypotheses were supported, with moose harvest having the strongest effect on recruitment in LMMs, although the interpretation of this result is unclear. Increasing moose harvest was associated with increasing caribou recruitment; regulated caribou harvest did not affect recruitment. The hypothesized mechanism for the alternate prey effect is that as more moose are harvested, wolf densities decrease due to lack of primary prey, with lower wolf densities linked to greater caribou recruitment in these systems (Bergerud and Elliot 1986; Hayes et al. 2003). Although each annual moose harvest value in this study corresponds with the same year of recruitment, moose harvest levels tended to stay high on certain NMC populations throughout the study period, thus annual values were representative of longer-term patterns. Negative effects of moose harvest on wolf densities has been demonstrated in southern British Columbia (Serrouya et al. 2017). High moose harvest may also lead to higher incidental hunting of wolves in the same areas, limiting predator densities. Moose harvest effects on predator densities could not be evaluated in this study due to lack of number of wolf packs or number of wolves per $1000km^2$ on NMC population ranges. One other possibility is that those caribou populations with high moose harvest have access to, or are forced into, more secure alpine habitat to space away from predators (Seip and Cichowski 1996). The Yukon currently has regulated harvest that is restricted to bulls for both moose and caribou. Subsistence harvest by First Nations on their traditional territories can include bulls, cows, or calves, although most have voluntary measures in place that restricts harvest to bulls. It was not possible to test the effect of subsistence harvest on caribou demographics, as suitable data were not available. However, First Nation peoples have co-existed with caribou on these landscapes for many generations.

In high moose harvest areas there tends to be higher road disturbance (Spearman's rank correlation r=0.86). It is likely that higher harvest takes place where there is greater access for hunters (Pigeon et al. 2016). Generally, higher disturbance is associated with lower caribou population levels (Sorenson et al. 2008; Environment Canada 2011). However, if human disturbance in northern systems leads to more moose harvest, this could lead to an apparent competitor control mechanism, creating secure habitat where there is usually none (Reid et al. 2013). Creation of secure habitat through moose harvest could lead to decoupling of the weather-recruitment relationship (Longshore et al. 2016). Ultimately, moose harvest could be a source of impromptu predator population control, with decades of control required for effective maintenance of caribou populations (Serrouya et al. 2019). More research is required to better understand the mechanisms underlying the apparent relationship between moose harvest and caribou recruitment in this system.

The predator harvest hypothesis was not supported. The fact that wolf harvest and trapping did not have an effect in BRTs was somewhat expected. Wolf control can positively affect caribou populations, at least in the short-term (Hayes et al. 2003; Hervieux et al. 2013); however, wolves are a resilient species that can sustain harvest rates of up to 34% annually without population declines (Webb et al. 2011). As a result, wolf control must be large-scale and widespread to be effective (Boertje et al. 2017), and hunting and trapping alone are unlikely to achieve this. Grizzly bear harvest did have an effect on caribou recruitment based on BRTs, but not LMMs. Grizzlies are a known predator of caribou calves (Reynolds and Garner 1987; Brockman et al. 2017), but the effect of grizzly bear harvest on caribou recruitment may not have been sufficient to stand out in LMMs.

No differences were found when considering seasonally-specific disturbance measures on NMC ranges, most likely due to the low amount of disturbance included overall in models. It is well known that seasonal migrations are an adaptive advantage, and increased fidelity to calving habitat can lead to greater calf survival (Lafontaine et al. 2017). However, fidelity to winter range can lead to lower adult survival, when conditions have been altered by human disturbance (Lafontaine et al. 2017). If NMC are constrained to portions of their winter range due to disturbances, reductions in adult female survival, a metric not tested here, could lead to population declines. Fidelity to summer and calving areas can also become an ecological trap, as even in areas highly impacted by humans, caribou may return to summer or calving locations (Faille et al. 2010). Higher predation risk may also occur when caribou move between seasonal ranges. In managed landscapes, this may be mitigated by limiting the amount of early seral forest next to movement corridors (Johnson et al. 2004). The avoidance of linear disturbances can also vary depending on the time of year (Nagy 2011), where in periods of vulnerability caribou avoid what they perceive as areas with high predation risk, having incorporated responses to them into a 'landscape of fear' (Semeniuk et al. 2014). Caribou may have seasonal importance to wolf diets (Milakovic et al. 2011), with the contribution generally highest in summer and spring. Summer habitat condition (as measured by predation risk, and habitat quantity and quality) was found to predict calf survival more than calving habitat in northern BC caribou herds of the Besa-Prophet area (Gustine et al. 2005).

Limitations

Moose harvest and road disturbance are collinear, which leads to difficult interpretation of results without further study. It is possible that the apparent effects of moose harvest on caribou recruitment are related in some way to increasing anthropogenic effects not considered in this study, rather than being linked to effects on wolf densities, as hypothesized here. There is also an interactive effect of recruitment, climate, and wolf predation (Hegel et al. 2010b) not accounted for in this study, which may be mediated by terrain ruggedness (Bergerud and Page 1986). Unfortunately, the number of herds; in particular, those sampled, is limited, which leads to constraints on the statistical tests that can be used for appropriate inference (Burnham and Anderson 2002). There is also a lack of comprehensive human disturbance mapping on NMC population ranges: the data used here were limited in their detail, and a substantial amount of human disturbance may be missing from some populations. A final limitation is that natural disturbances are potentially over-estimated by the traditional methods of fire mapping used from 1940-1984 in this study, which can over-estimate the within burn area by up ~32% (Kansas et al. 2016). This overestimation could misrepresent the effect of natural disturbance on recruitment.

Management Implications

The results of this study highlight the need for harvest regulations that take into account interactive effects between species. This study also highlights the correlation between harvest rates and access, a consideration that should take place during construction of any new roads in northern systems. Fortin et al. (2013) note that anthropogenic disturbances lead to peak occurrences of caribou 4.25km from a disturbance, due to animals closer to a disturbance moving away, while those farther away staying where they were. This could lead to greater harvest efficiency by both natural predators and humans, and interactive effects between anthropogenic disturbance and harvest. This effect may be exacerbated in northern systems, where lower forest productivity and the potential for increasing disturbance can lead to lower recruitment and adult survival of caribou (Fortin et al. 2017). Climate change is also expected to have increased effects in northern systems (IPCC 2014), which could lead to greater variability in climate-recruitment interactions. Furthermore, there is a need for consistent, comprehensive disturbance mapping on NMC population ranges, to better quantify demographic effects of anthropogenic and natural disturbances on NMC populations. Critical habitat for caribou is related to avoiding predation (Bergerud 2007). In vulnerable northern ecosystems, areas where caribou may avoid predation must be preserved. There currently exists an opportunity for pro-active management of NMC in the Yukon Territory to avoid populations declines due to disturbance observed in other woodland caribou systems.

Tables

Table 1. Variables evaluated in boosted regression tree models, derived from 1982-2015, for 176 - 220 population years of recruitment data for 13 northern mountain caribou herds in the Yukon Territory, Canada. Boosted regression trees (BRTS) containing all 18 variables were created for each road buffer distance (0m, 500m, 1000m, 1500m, 2000m, 3000m, 4000m). Each BRT model was then compared to one another using cross-validation statistics to determine the best fitting BRT model. Density of harvest was measured as (number of individuals of each species harvested/km^2). PDO values were acquired through the Joint Institute for the Study of Atmosphere and Ocean (source) for each year of recruitment data available.

Variable	Description
Disturbance - total range	
Natural	Cumulative fire disturbance up to current recruitment year on herd's total range.
Road	Road disturbance on herd's total range from 1982 onwards.
Combined	Combined cumulative fire and road disturbance on a herd's total range.
Disturbance - summer range	
Natural	Cumulative fire disturbance up to current recruitment year on herd's summer range.
Road	Road disturbance on herd's summer range from 1982 onwards.
Combined	Combined cumulative fire and road disturbance on a herd's summer range.
Disturbance variables- winter range	
Natural	Cumulative fire disturbance up to current recruitment year on herd's winter range.
Road	Road disturbance on herd's winter range from 1982 onwards.
Combined	Combined cumulative fire and road disturbance on a herd's winter range.
Harvest variables - density of harvest	
Moose	Annual moose harvest density on caribou's range.
Caribou	Caribou harvest levels on caribou's range.
Grizzly bear	Grizzly bear harvest levels on caribou's range.
Black bear	Black bear harvest levels on caribou's range.
Wolf	Wolf harvest and trapping levels on caribou's range.

Climate variables - Pacific Decadal Oscillation (PDO)	
Average	Average value of PDO from January to December of the current recruitment year.
Winter Prior to birth	Average PDO from November to April (months prior to birth).
April	PDO value for April of each year.
May	PDO value for May of each year.

Table 2. Relative contributions of predictor variables to reducing deviance of boosted regression tree (BRT) models of northern mountain caribou recruitment. 220 years of recruitment data were used from 13 populations in the Yukon Territory, Canada, 1982-2015. Different buffer ranges on road disturbance were tested (0m, 500m, 1000m, 1500m, 2000m, 3000m, 4000m). Results from models with 0m buffer on road disturbance and 500m buffer on road disturbance are presented as model cross validation statistics showed no significant difference between BRT models.

0m buffer		**500m buffer**	
Variable	**Influence[1] (%)**	**Variable**	**Influence[1] (%)**
Annual range - natural disturbance	28.88	Annual range - natural disturbance	14.92
Summer range - natural disturbance	15.76	Summer range - road disturbance	14.62
Average PDO	9.66	Moose harvest	10.11
Moose harvest	9.17	Summer range - natural disturbance	10.05
Caribou harvest	5.92	Average PDO	8.52
Grizzly harvest	5.35	Annual range - road disturbance	7.05
Winter PDO prior to birth	4.60	Caribou harvest	5.80
April PDO	4.21	Grizzly bear harvest	5.15
Annual range - road disturbance	3.85	April PDO	4.20
Black bear density of harvest	3.43	Winter PDO prior to birth	4.12
Wolf harvest	3.27	Black bear harvest	3.61
Winter range - natural disturbance	2.33	Wolf harvest	3.09
May PDO	1.70	May PDO	2.19
Winter range - road disturbance	1.45	Winter range - road disturbance	1.62
Summer range - road disturbance	0.42	Winter range - combined disturbance	1.48
Winter range - combined disturbance	-	Winter range - natural disturbance	1.35
Annual range - combined disturbance	-	Summer range - combined disturbance	1.34
Summer range - combined disturbance	-	Annual range - combined disturbance	0.79

[1]The amount of times the variable was chosen to reduce BRT model deviance.

Table 3. Disturbance-climate model set with 220 recruitment years from 13 herds, 1995-2015, Yukon Territory. Measures of model fit included: AICc scores, change in AICc (ΔAICc), marginal R^2 (R^2_m), the variance explained by the fixed effects, and conditional R^2 (R^2_c), the variance explained by the fixed and random effects. All predictor variables were standardized, year and herd were included as random effects in all models. The null model includes only the random effects of year and herd. Bolded models are considered for further inference.

Number	Model Variable(s)	AICc	ΔAICc	R^2_m	R^2_c
1	**Roads on summer range, 500m buffer + average PDO**	1666.62	0.00	0.05	0.45
2	**Natural on annual range, 0m buffer + average PDO**	1666.74	0.12	0.05	0.45
3	**Natural on annual range, 500m buffer + average PDO**	1666.74	0.12	0.05	0.45
4	**Average PDO**	1667.30	0.68	0.05	0.44
6	Roads on summer range, 500m buffer	1671.79	5.17	0.00	0.46
7	Natural on summer range, 0m buffer	1671.87	5.24	0.00	0.46
8	Natural on summer range, 500m buffer	1671.87	5.24	0.00	0.46
9	Natural on annual range, 0m buffer	1671.89	5.27	0.00	0.46
10	Natural on annual range, 500m nuffer	1671.89	5.27	0.00	0.46
11	Null	1672.51	5.89	0.00	0.45

Table 4. Disturbance-climate-harvest model set with 176 recruitment years from 13 herds, 1995-2015, Yukon Territory. Several measures of model fit are presented: AICc scores, change in AICc (ΔAICc), marginal R^2 (R^2_m), the variance explained by the fixed effects, and conditional R^2 (R^2_c), the variance explained by the fixed and random effects. All predictor variables were standardized, year and herd were included as random effects in all models. The null model includes only the random effects of year and herd. Bolded models are considered for further inference.

Number	Model Variable(s)	AICc	ΔAICc	R^2_m	R^2_c
1	**Average PDO + moose harvest**	1230.99	0	0.20	0.35
2	Moose harvest	1238.18	7.19	0.13	0.35
3	Natural on annual range, 0m buffer + moose harvest	1238.33	7.34	0.13	0.35
4	Natural on annual range, 500m buffer + moose harvest	1238.33	7.34	0.13	0.35
5	Roads on summer range, 500m buffer + moose harvest	1238.59	7.60	0.13	0.36
6	Natural on annual range, 0m buffer + average PDO	1243.34	12.35	0.11	0.27
7	Natural on annual range, 500m buffer + average PDO	1243.34	12.35	0.11	0.27
8	average PDO	1244.32	13.33	0.09	0.26
9	Roads on summer range, 500m buffer + average PDO	1244.43	13.44	0.09	0.27
10	Grizzly bear harvest	1250.06	19.07	0.03	0.25
11	Caribou harvest	1251.50	20.51	0.02	0.26
13	Natural on annual range, 0m buffer	1252.28	21.29	0.02	0.27
14	Natural on annual range, 500m buffer	1252.28	21.29	0.02	0.27
15	Natural on summer range, 0m buffer	1252.30	21.31	0.01	0.27
16	Natural on summer range, 500m buffer	1252.30	21.31	0.01	0.27
17	Null	1253.18	22.19	0.00	0.26
18	Roads on summer range, 500m buffer	1253.21	22.22	0.00	0.27

Table 5. Disturbance-climate-harvest model set coefficients with 220 recruitment years from 13 herds, 1982-2015, Yukon Territory. Coefficients for variables in each model are listed, along with 95% confidence intervals. All predictor variables were standardized, year and herd were included as random effects in all models. The null model includes only the random effects of year and herd. Bolded models are considered for further inference.

Model Number	Model Variable(s)	Coefficient	CI
1	**Anthropogenic on Summer Range, 500m Buffer**	0.13	-3.10 - 3.35
1	**Average PDO**	2.88	0.43 - 5.33
2	**Natural on Total Range, No Buffer**	-0.21	-3.22 - 2.79
2	**Average PDO**	2.87	0.42 - 5.32
3	**Natural on Total Range, 500m Buffer**	-0.21	-3.22 - 2.79
3	**Average PDO**	2.87	0.42 - 5.32
4	**Average PDO**	2.89	0.44 - 5.35
5	Anthropogenic on Total Range, No Buffer	1.28	-2.17 - 4.72
6	Anthropogenic on Summer Range, 500m Buffer	0.14	-3.11 - 3.38
7	Combined on Summer Range, 4000m Buffer	0.14	-3.00 - 3.27
8	Natural on Summer Range, No Buffer	-0.16	-3.28 - 2.97
9	Natural on Summer Range, 500m Buffer	-0.16	-3.28 - 2.97
10	Natural on Total Range, No Buffer	-0.36	-3.39 - 2.67
11	Natural on Total Range, 500m Buffer	-0.36	-3.39 - 2.67
12	Null	-	-

Table 6. Disturbance-climate-harvest model set coefficients with 176 recruitment years from 13 herds, 1995-2015, Yukon Territory. Coefficients for variables in each model are listed, along with 95% confidence intervals. All predictor variables were standardized, year and herd were included as random effects in all models. The null model includes only the random effects of year and herd. Bolded models are considered for further inference.

Model Number	Model Variable	Coefficient	CI
1	**Average PDO**	2.44	0.87-4.00
1	**Moose Harvest**	3.05	1.51-4.60
2	Moose Harvest	2.24	0.30 - 4.19
3	Natural on Total Range, No Buffer	0.92	- 1.21 - 3.06
3	Moose Harvest	2.18	0.24 - 4.12
4	Natural on Total Range, 500m Buffer	0.92	-1.21 - 3.06
4	Moose Harvest	2.18	0.24 - 4.12
5	Linear on Summer Range, 500m Buffer	0.34	-1.75 - 2.43
5	Moose Harvest	2.4	0.32 - 4.48
6	Natural on Total Range, No Buffer	1.15	-0.86 - 3.15
6	Average PDO	2.69	1.16 - 4.23
7	Natural on Total Range, 500m Buffer	1.15	-0.86 - 3.15
7	Average PDO	2.69	1.16 - 4.23
8	Average PDO	2.66	1.13 - 4.18
9	Linear on Summer Range, 500m Buffer	0.34	-1.75 - 2.43
9	Average PDO	2.65	1.13 - 4.18
10	Grizzly Bear Harvest	1.2	-0.22 - 2.63
11	Caribou Harvest	1.32	-0.17 - 2.81
12	Combined on Summer Range, 4000m Buffer	1.39	-0.64 - 3.41
13	Linear on Total Range, No Buffer	1.4	-0.73 - 3.53
14	Natural on Total Range, No Buffer	1.1	-0.95 - 3.15
15	Natural on Total Range, 500m Buffer	1.1	-0.95 - 3.15
16	Natural on Summer Range, No Buffer	1.09	-1.02 - 3.2
17	Natural on Summer Range, 500m Buffer	1.09	-1.02 - 3.2
18	Null	-	-
19	Linear on Summer Range, 500m Buffer	0.38	-1.74 - 2.5

Figures

Figure 1. The 13 populations of northern mountain caribou included in this study: Hart River, Clear Creek, Ethel Lake, Chisana, Kluane, Klaza, Aishihik, Tatchun, Finlayson, Nahanni, Ibex, Carcross, and Wolf Lake. Study populations are mainly located in the Yukon Territory, Canada but cross into Alaska, Northwest Territories, and British Columbia. Fall classification surveys took place from 1982-2015.

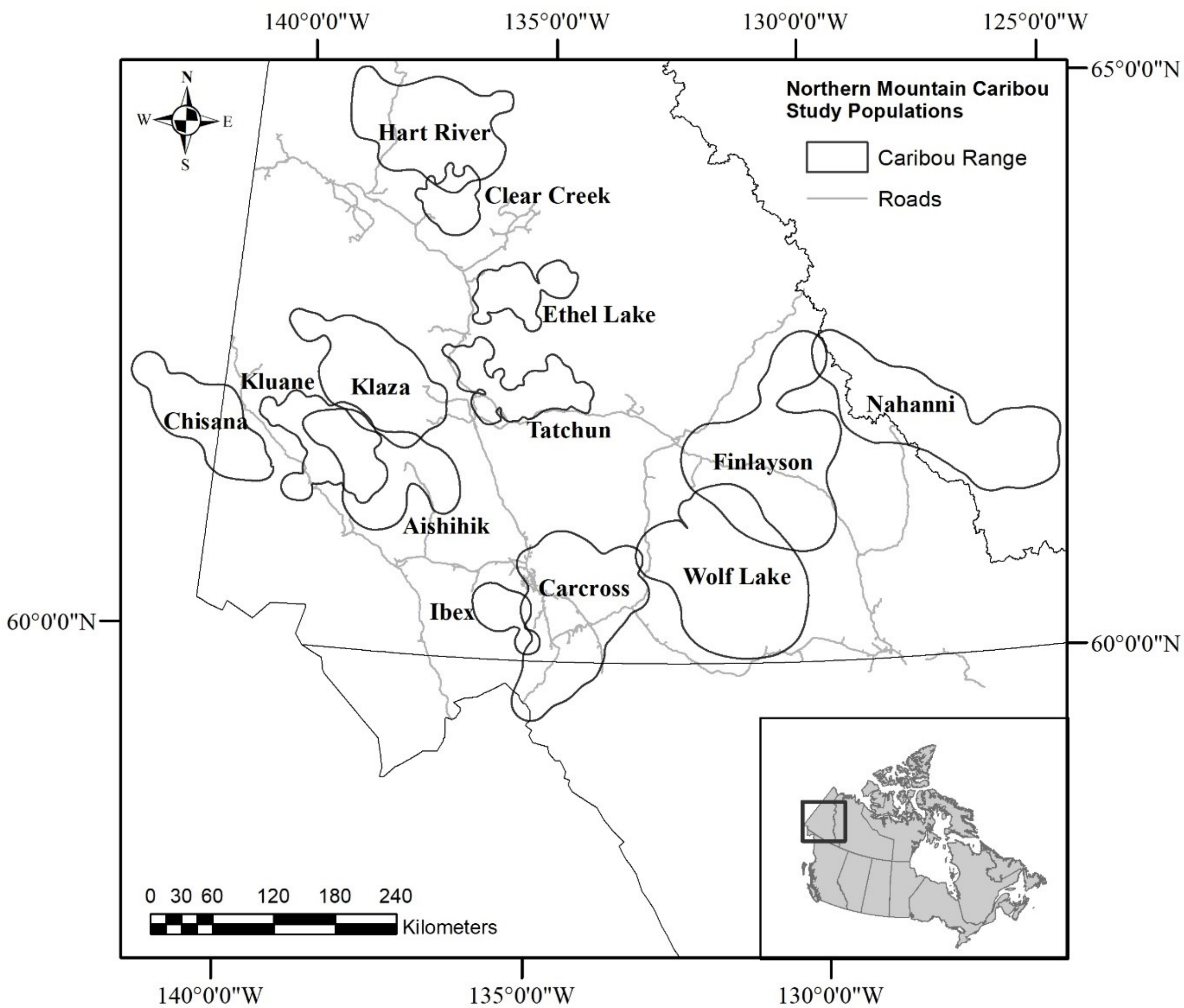


Figure 2. The influence of average pacific decadal oscillation (average PDO) on caribou recruitment in the most parsimonious disturbance-climate model. Recruitment data include 220 population years from 13 northern mountain caribou herds, 1982-2015, Yukon Territory. Shaded areas correspond to 95% confidence intervals. The non-standardized predictor ranges from -1.29 to 1.82 for average PDO. Hash marks on the x-axis are annual values of the variable.

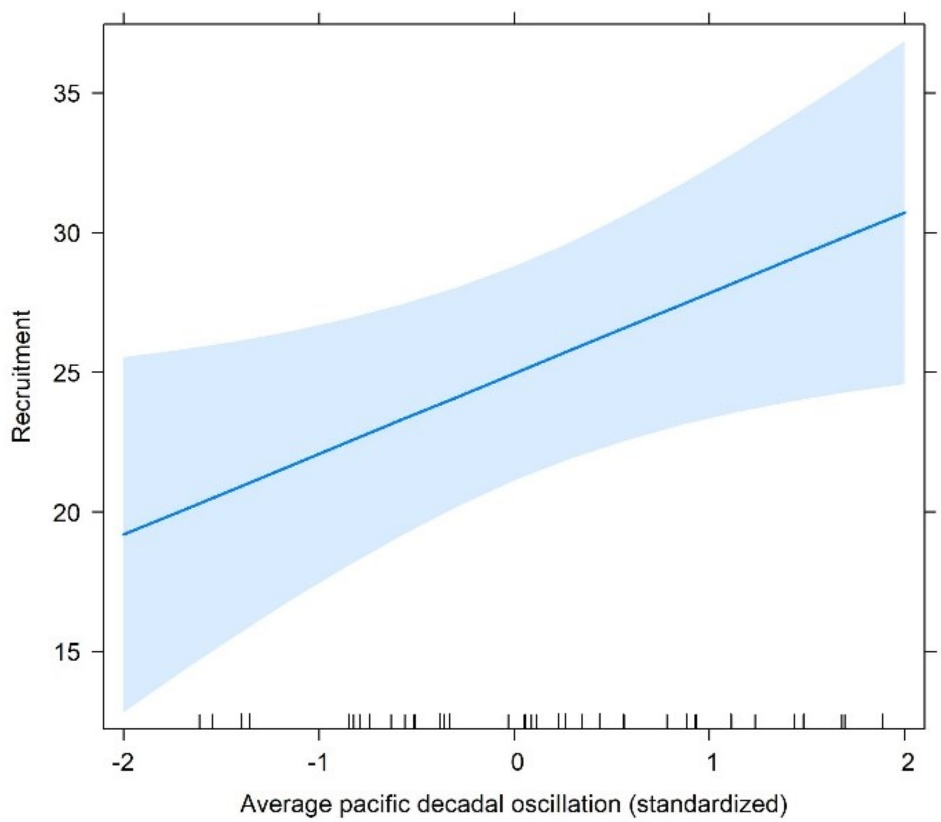


Figure 3. The influence of fixed effects of the top performing disturbance-climate-harvest model with 176 recruitment years. Recruitment data are from 13 herds, 1982-2015, Yukon Territory. Shaded areas correspond to 95% confidence intervals. Non-standardized predictors range from 0.0000 – 0.0039 moose harvested / km² and -1.29 to 1.63 for average pacific decadal oscillation.

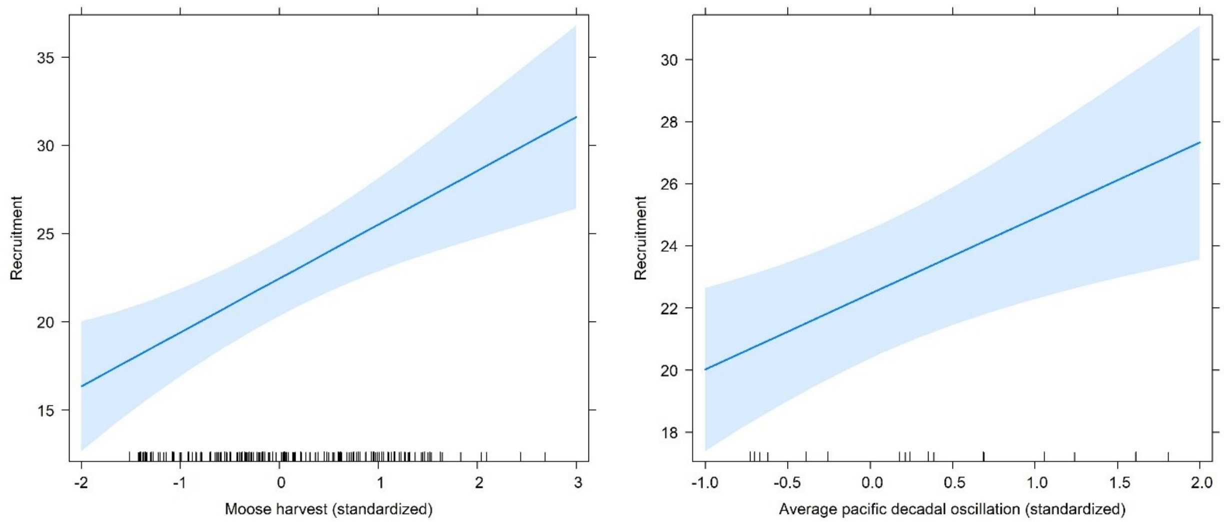
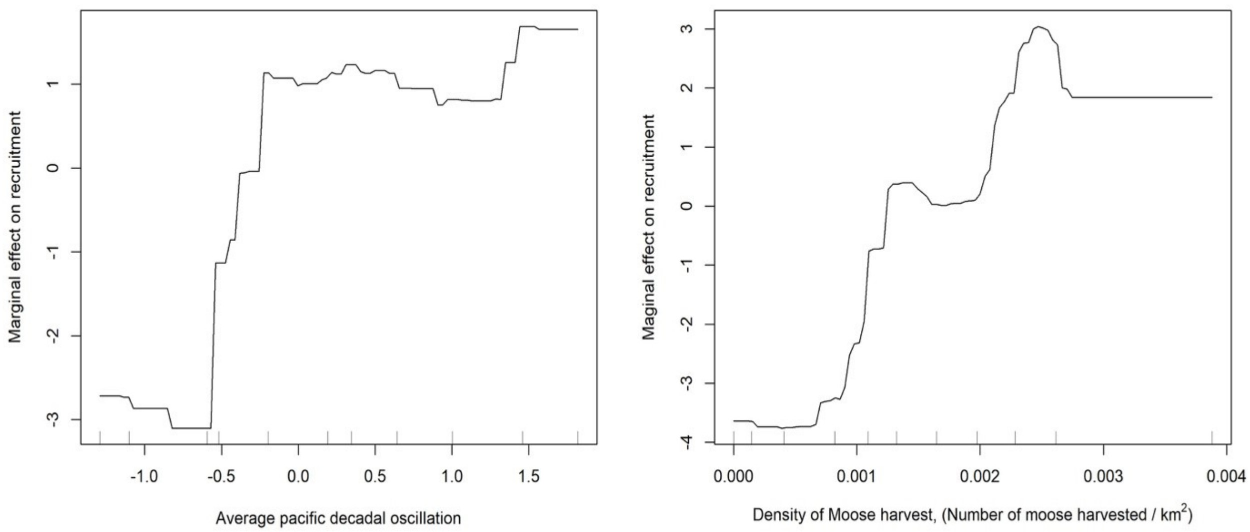


Figure 4. Partial dependence plots for predictors that performed well in both boosted regression trees and linear mixed effects models. Date from 13 northern mountain caribou herds from the Yukon Territory, Canada, with 176 - 220 fall classification surveys completed between 1982-2015, were evaluated. Partial dependence plots are created from boosted regression tree models and show the effect a predictor has on the response after all other predictors are held at their average value.



Chapter 3: Supporting Information

Treatment of Recruitment Data

Removal of some recruitment data was required due to inconsistencies or confounding variables introduced during the long timeframe of collection. Related considerations include:

- From 1983 to 1989 wolves in the Finlayson herd were reduced to 80% of pre-removal levels (Farnell 1998).
- From 1993 to 1997 wolves in the Aishihik herd were either killed or sterilized (Hegel 2010).
- From 1982-1987 wolves were killed and liberalized hunting of grizzly bears took place in the Coast Mountains of the Yukon. These data were not removed as Hayes et al. (1991) concluded there was no effect on the Ibex caribou herd.
- From 2003 to 2006 a captive rearing program took place in the Chisana herd (Hegel 2012).

For wolf control, effects on recruitment were identified by Hegel et al. (2010), with lag effects once treatment ended, as well as adjacent herd effects on Klaza and Kluane herds. Treatment herds had a 5 year lag effect of positive effects on recruitment once wolf removal ended. Adjacent herds took 2 years for positive effects on recruitment to show once treatment began and had no lag effect on recruitment once wolf removal ended on the treatment herd. Where recruitment years were potentially affected by either wolf control or captive rearing, those years were removed from analysis. Ultimately, 32 recruitment-years were removed from 5 herds.

Determining Seasonal Ranges

GPS/VHF data were intersected with the Canadian digital elevation model (CDEM) (NRCan 2014) (~20m resolution) to determine where each caribou VHF/GPS location fell on an elevational scale. All GIS work was completed with ArcGIS 10.5.1

The 90th quantile for winter elevational distribution and 10th quantile for summer elevational distribution were identified for winter and summer NMC caribou ranges, to further help limit elevational overlap between seasons, while acknowledging that some habitat is important in both winter and summer. R (R Version 3.5.2, www.r-project.org, accessed 10 Nov

2018) and Rstudio (RStudio Version 1.1.463, www.rstudio.com, accessed 10 Nov 2018) were used for all analyses. The rule set was as follows:

If CDEM elevation (m asl) ≥ 10^{th} $_{\text{quantile summer elevational distribution}}$ = summer range,

If CDEM elevation (m asl) ≤ 90^{th} $_{\text{quantile winter elevational distribution}}$ = winter range.

For example, if the 90^{th} quantile for winter elevation distribution was 1300m asl, any value below would be considered winter range. Similarly, if the 10^{th} quantile for summer was 1400m asl, any value above would be considered summer range.

Once the 90^{th} and 10^{th} quantiles were determined for each herd of interest, summer and winter maps were created using CDEM and Yukon Government herd ranges. The CDEM map was partitioned by elevation into summer and winter values within each herd range.

The final elevational cutoffs used to create seasonal ranges are presented in table 1, where figure 1 shows the density elevational plots used to create each cutoff value. Figure 2 gives a representation of how final seasonal ranges for winter and summer looked.

Table 1 – Elevational cutoffs in metres above sea level (asl) used in creation of seasonal ranges for northern Mountain Caribou in Yukon, Canada, as determined by both GPS and VHF collar location data. Summer cutoffs correspond to where 90% of caribou locations fell on a distribution of elevational use from June 01 to September 30, whereas winter cutoffs are where 90% of caribou locations fell on a distribution of elevational use from December 01 to March 31. The max elevation corresponds to the highest point of caribou elevational use in either GPS or VHF collar data. Collar data ranges from 1998 to 2018 for GPS collars and 1983 to 2009 for VHF collars.

Population	**Summer cutoff (m asl)**	**Winter cutoff (m asl)**	**Max elevation (m asl)**
Aishihik	1259	1598	2046
Carcross	1106	1388	2076
Chisana	1251	1513	2298
Clear Creek	1313	1223	1944

Ethel Lake	1078	1125	1740
Finlayson	1297	1325	2147
Hart River	1269	1282	2102
Ibex	1253	1577	1928
Klaza	1088	1351	1956
Kluane	1177	1386	2127
South Nahanni	1144	1449	2416
Tatchun	925	1060	1873
Wolf Lake	1177	1235	1956

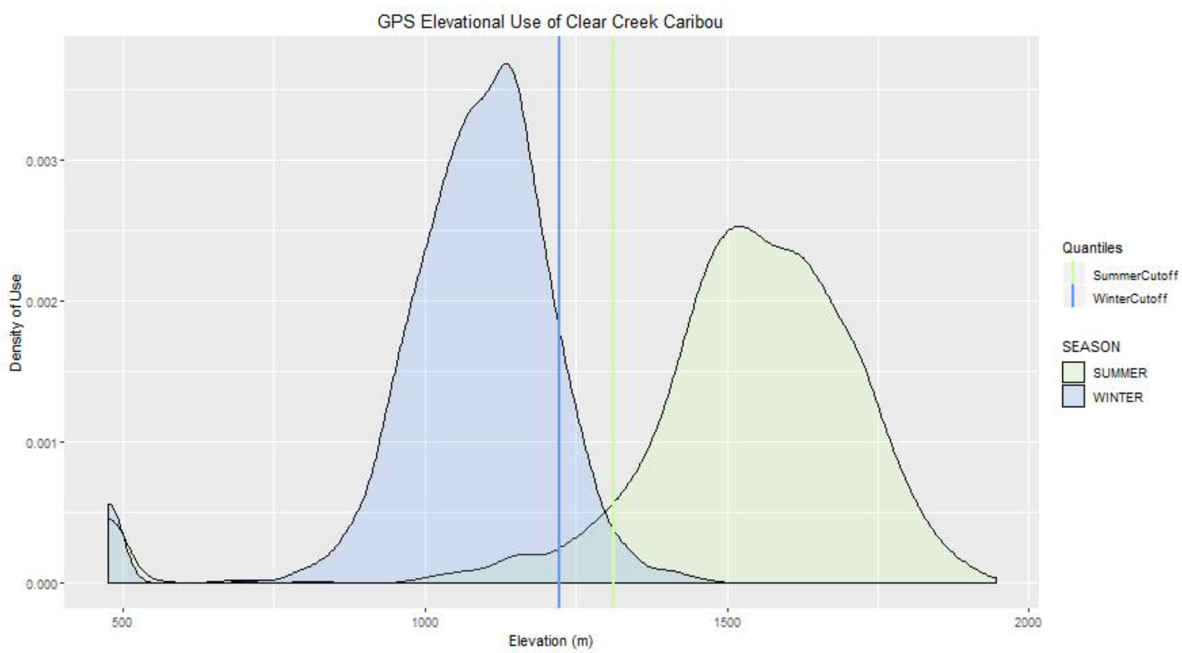


Figure 1 – Elevational use of Clear Creek caribou in summer (June 01 to September 30) and winter (December 01 to March 31). Number of GPS collar years of data used ranged from 30 in summer to 56 in winter, from 2017-2018. Vertical lines on the graph correspond to 90th quantiles for winter and 10th quantiles for summer, which were the determining points for summer or winter elevational cut-offs in seasonal range creation.

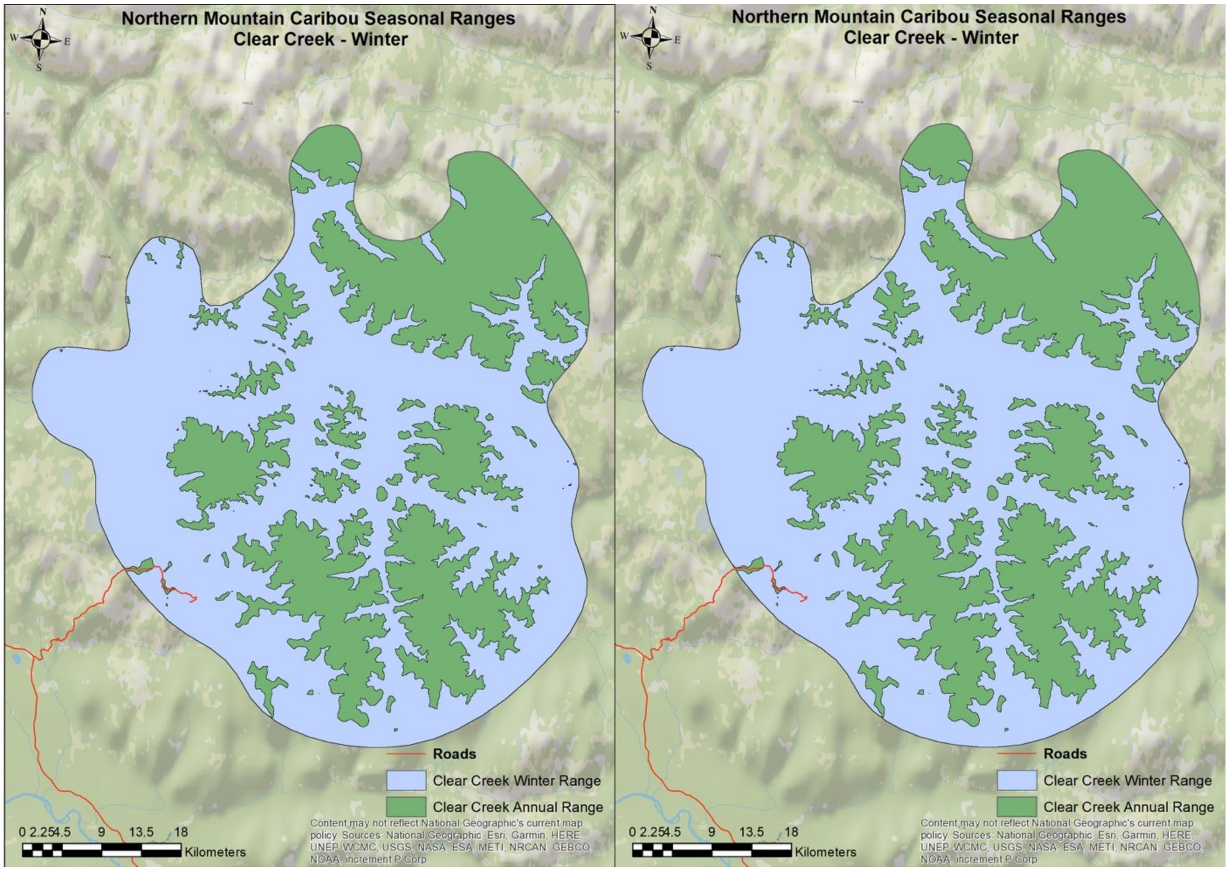


Figure 2 – Winter and summer ranges created for the Clear Creek herd using density of elevational use from GPS collar data. The maps correspond to where 90% of caribou elevation use fell within either summer (June 01 to September 30) or winter (December 01 to March 31) timeframes.

Comparing Disturbance Values

Other methods of disturbance mapping were investigated, such as surveyed land parcels, mining claims, and trail maps. Further investigation of each of these methods through google earth imagery found over-estimation of some disturbances, as registered titled land and claims did not necessarily translate into disturbance (i.e. they could be undeveloped). As well, comprehensive mapping of trails was not available across all herd ranges. It was also impossible to time-stamp any disturbance levels estimated through other methods, while the road layer used here was in-place at the start of the available recruitment data. Since much of this analysis focused on the inter-annual variability of factors affecting recruitment, temporally matched estimates of disturbance were important. Major roads were found to be reliably on the land to the earliest year of recruitment. One further consideration was the hope to extend disturbance mapping into areas outside the Yukon's borders, and using datasets such as Canvec road maps allows for a national standard that works in both British Columbia and the Yukon.

A preliminary comparison of disturbance values in this project to automatically generated datasets was completed (Figure 3). A general relationship between the proportions of disturbance used here and those found through Canadian Intact Forest Landscape (CIFL) maps (Smith and Cheng 2016) was found. Chisana was removed due to CIFL mapping constraints. In further investigation of CIFL data and potential effects on recruitment (to compare mapping techniques used here to CIFL), no conclusive results were found.

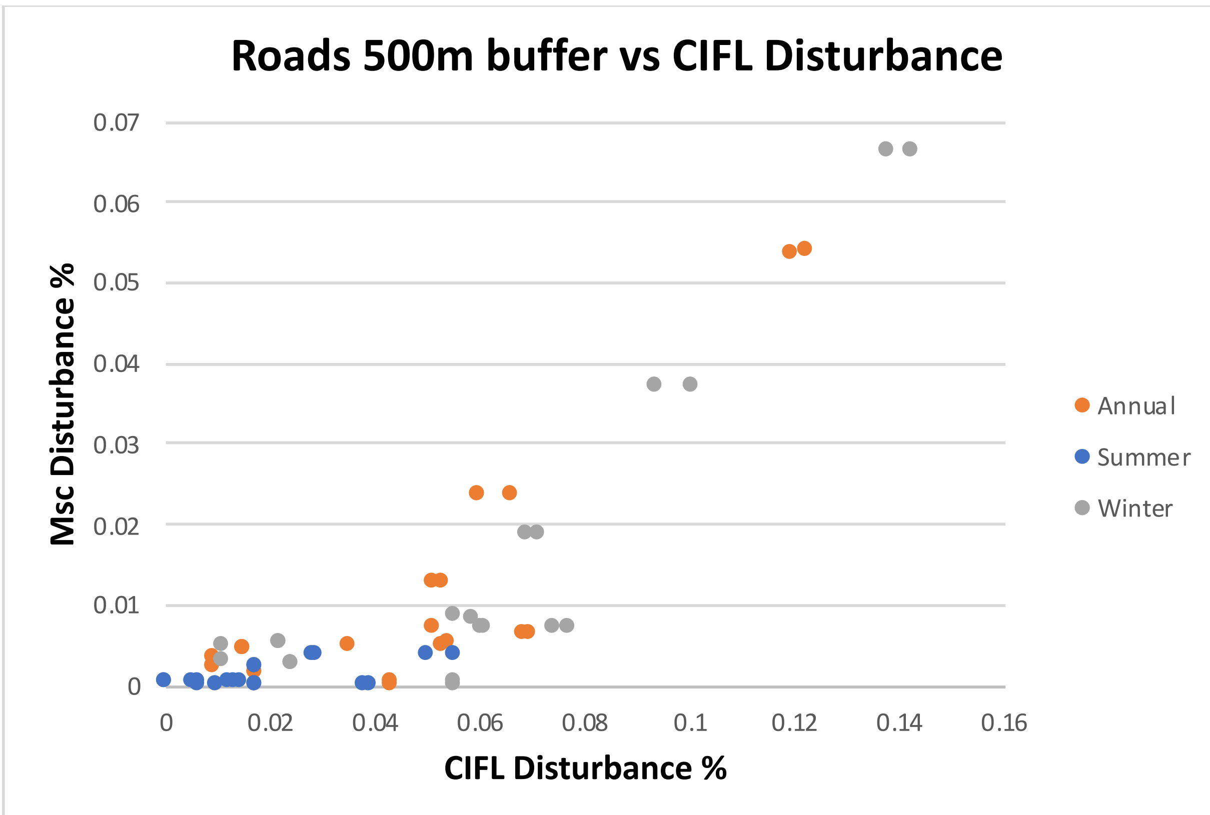


Figure 3 – Comparison of disturbance values used in this study (roads buffered by 500m) to Canadian Intact Forest Landscape (CIFL) 2000, and 2013 disturbance values for 13 northern mountain caribou herds in Yukon Territory, Canada. Chisana was removed due to CIFL mapping constraints. Disturbance is measured as percent of a caribou's herd range disturbed.

Boosted Regression Trees

Methods

BRTs are a machine learning method that combines many small regression trees into one to increase the predictive performance of the model (Elith et al. 2008). Ultimately BRTs reduce model variance and bias, through model averaging and stage-wise fitting, respectively (Elith et al. 2008). BRTs are insensitive to outliers, fit non-linear relationships, account for interaction effects, and do not require the data be transformed (Elith et al. 2008). BRTs have three components that must be set:

- Bag fractions (bf): which adds randomness, helping to reduce prediction error, reduce computation, and decrease model overlearning (De'ath 2007). This is generally set from 0.4-0.75 (De'ath 2007; Elith et al 2008).
- Learning rate (lr): which determines the contribution of each tree to the model (Elith et al. 2008). Generally, smaller lr's decrease predictive error and are set from 0.1 to 0.001 (De'ath 2007).
- Tree complexity (tc): which controls the interaction amount between variables. A TC of 1 would create an additive model, a TC of one would test for first order interactions and so on (De'ath 2007; Elith et al. 2008). Changes in predictive error can indicate what to set this to (De'ath 2007).

To fit BRTs the 'dismo' and 'gbm' packages in R (R Version 3.5.2, www.r-project.org, accessed 10 Nov 2018), using RStudio (RStudio Version 1.1.463, www.rstudio.com, accessed 10 Nov 2018). 10-fold cross-validation was used to fit the optimal number of trees based on the selected setting of the above three components. Elith et al. (2008) recommend fitting BRT models of at least 1000 trees. It should be noted that generally BRTs require 100-150 observations to produce stable and reliable results, with a recommended minimum sample of 50% of the possible range of values the stressor variable can take (Feld et al. 2016).

Final BRTs were fitted with a bf of 0.7, lr of 0.005, and tc of 2 using 10-fold cross validation, as determined by changes in predictive error and to avoid overfitting of models.

Results

There are two main outputs of BRTs. First, summary charts show the contribution of each predicator to explained deviance (Feld et al. 2016), illustrating relative to other variables, how often a variable is chosen to reduce the model deviance (Elith et al. 2008). The second output is comprised of partial dependence plots, which illustrate the dependency of the response variable on one to two variables; the average effect of all other variables in the model are accounted for when the partial dependence plot is created (De'ath 2007; Elith et al. 2008). If predictors are strongly correlated or there are strong interaction effects between variables, partial dependence plots can be an imperfect representation of a predictor variables effect on the response variable (Elith et al. 2008).

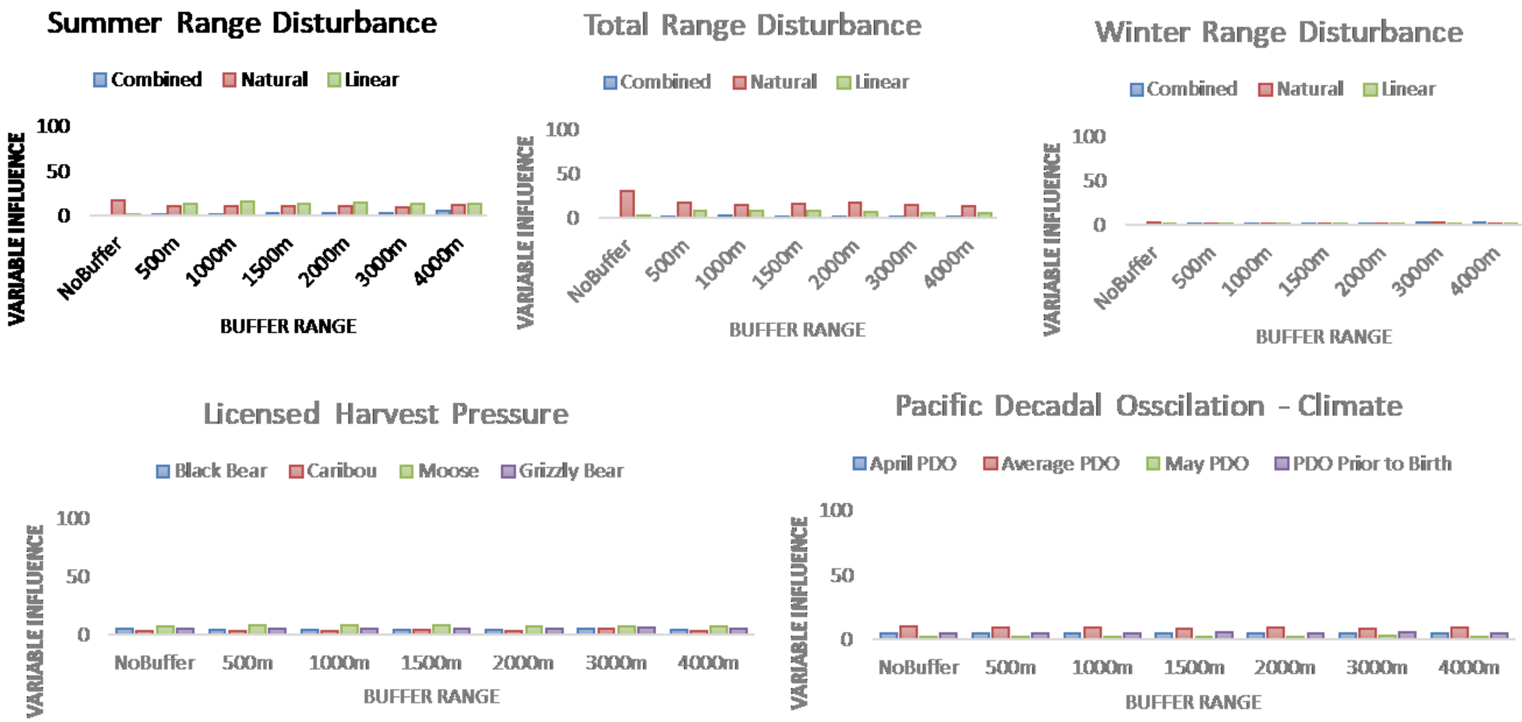


Figure 4 – Variable influence on caribou recruitment from boosted regression tree (BRT) models using different buffer distances of road (linear) disturbance . BRTs containing all 18 variables were created for each road buffer distance (0m, 500m, 1000m, 1500m, 2000m, 3000m, 4000m). Each BRT model was then compared to one another using cross-validation statistics to determine the best fitting BRT model. Recruitment data from 1982-2015 for 13 northern mountain caribou herds in the Yukon Territory, Canada, were used to generate models (total caribou herd years = 220)

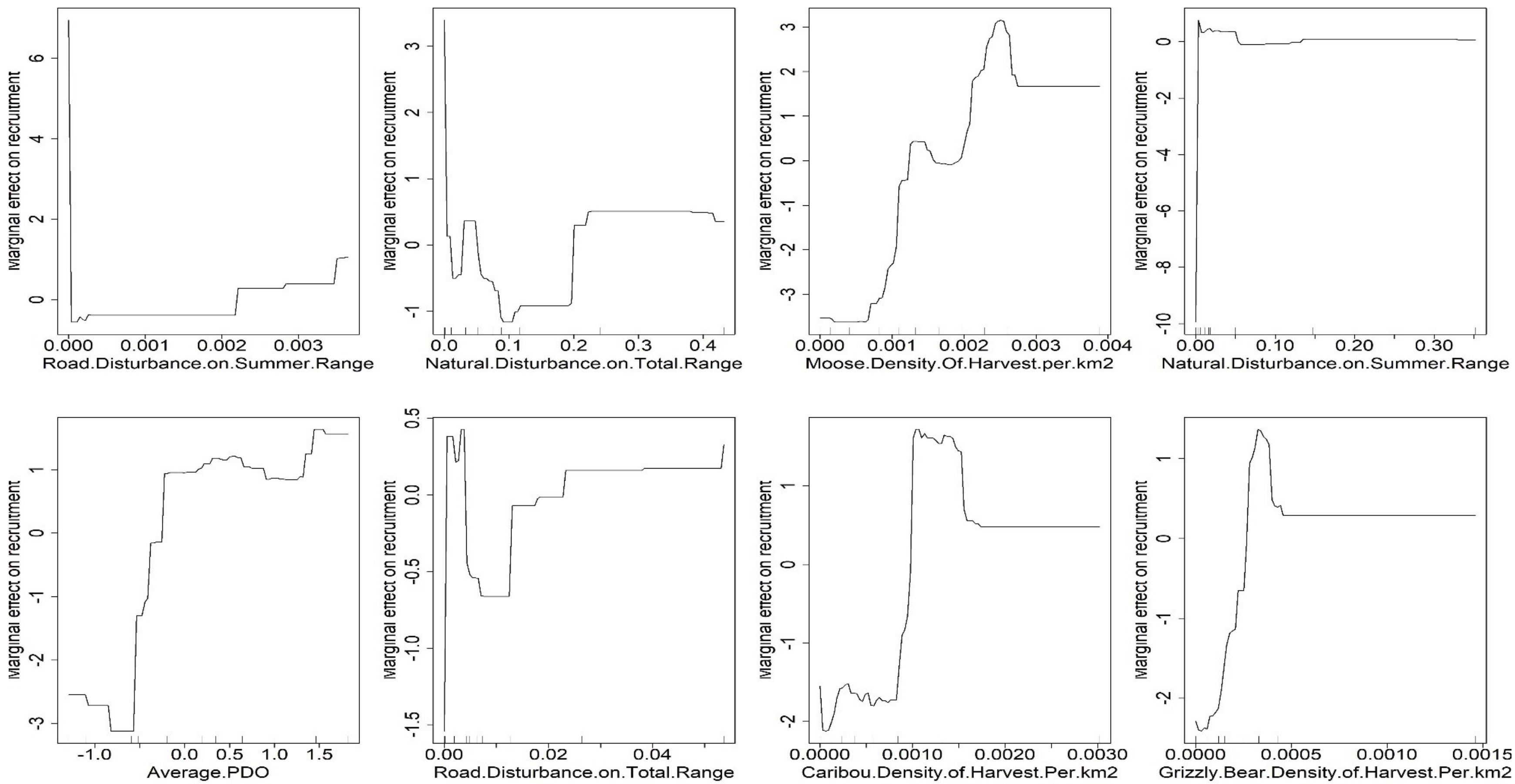


Figure 5 – Partial dependence plots of top 8 influential variables on boosted regression tree models on caribou recruitment. Partial dependence plots show the average influence of a variable on recruitment when all other variables are held at their average influence. 220 years of recruitment years from 1982-2015 for 13 different northern mountain caribou herds in the Yukon Territory, Canada, were used to inform models.

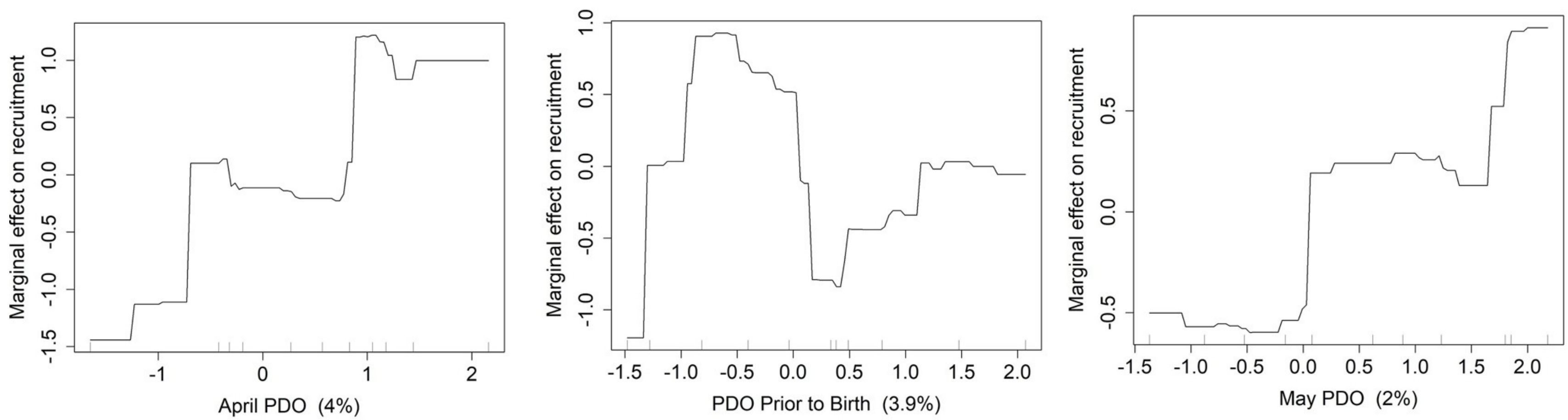


Figure 6 – Partial dependence plots for pacific decadal oscillation (PDO) variables tested in boosted regression trees. Partial dependence plots show the average influence of a variable on recruitment when all other variables are held at their average influence. 220 years of recruitment years from 1982-2015 for 13 different northern mountain caribou herds in the Yukon Territory, Canada, were used to inform models.

Table 2. – Range of disturbance values used to inform boosted regression tree models. Road densities are measured as density of roads on a populations seasonal range. Road and natural disturbance are measured as a percent of disturbed seasonal range across the study period. 220 years of recruitment data determined disturbance measurement timeframes from 1982-2015 for 13 different northern mountain caribou herds in the Yukon Territory, Canada. Summer season ranged from June 01 to September 30, while winter ranged from December 01 to March 31.

0m Buffer				500m Buffer				
Population	**Season**	**Road Density (km/km2)**	**Range of natural disturbance**	**Population**	**Season**	**Range of road disturbance**	**Range of natural disturbance**	**Range of combined disturbance**
Aishihik	Summer	0	0.32% - 0.66%	Aishihik	Summer	0% - 0%	0.32% - 0.66%	0.3% - 0.66%
Aishihik	Winter	0.008	1.13% - 5.19%	Aishihik	Winter	0.8% - 0.8%	1.13% - 5.19%	5.6% - 6.9%
Aishihik	Annual	0.007	1.14% - 5.19%	Aishihik	Annual	0.7% - 0.7%	1.14% - 5.19%	1.8% - 5.9%
Carcross	Summer	0	1.7% - 1.8%	Carcross	Summer	0.4% - 0.4%	1.7% - 1.8%	2.1% - 2.2%
Carcross	Winter	0.1	6.4% - 7%	Carcross	Winter	6.56% - 6.63%	6.4% - 7%	12.5% - 13.2%
Carcross	Annual	0.1	5.2% - 5.7%	Carcross	Annual	5.3% - 5.4%	5.2% - 5.7%	10.1% - 10.7%
Clear Creek	Summer	0	0.3% - 1.3%	Clear Creek	Summer	0% - 0%	0.3% - 1.3%	0.4% - 1.3%
Clear Creek	Winter	0.003	1.9% - 16.5%	Clear Creek	Winter	0.5% - 0.5%	1.9% - 16.5%	2.4% - 17%
Clear Creek	Annual	0.004	1.4% - 11.4%	Clear Creek	Annual	0.4% - 0.4%	1.4% - 11.4%	1.8% - 11.8%
Chisana	Summer		0% - 0%	Chisana	Summer		0% - 0%	
Chisana	Winter		0% - 0.4%	Chisana	Winter		0% - 0.4%	
Chisana	Annual		0% - 0.2%	Chisana	Annual		0% - 0.2%	
Ethel Lake	Summer	0	1.9% - 16.1%	Ethel Lake	Summer	0% - 0%	1.9% - 16.1%	1.9% - 16.1%
Ethel Lake	Winter	0.003	6.5% - 33.2%	Ethel Lake	Winter	0.3% - 0.5%	6.5% - 33.2%	6.8% - 33.7%
Ethel Lake	Annual	0.002	4.8% - 26.4%	Ethel Lake	Annual	0.2% - 0.3%	4.8% - 26.4%	5% - 26.8%
Finlayson	Summer	0	0.4% - 2.4%	Finlayson	Summer	0% - 0%	0.4% - 2.4%	0.4% - 2.4%
Finlayson	Winter	0.019	7.7% - 16.5%	Finlayson	Winter	1.8% - 1.9%	7.7% - 16.5%	9.3% - 18%
Finlayson	Annual	0.013	5.3% - 11.9%	Finlayson	Annual	1.3% - 1.3%	5.3% - 11.9%	6.5% - 12.9%
Hart River	Summer	0.001	0.1% - 0.1%	Hart River	Summer	0.1% - 0.1%	0.1% - 0.1%	0.2% - 0.2%

Hart River	Winter	0.013	0.9% - 1.3%
Hart River	Annual	0.007	0.5% - 0.7%
Ibex	Summer	0	0.2% - 1.2%
Ibex	Winter	0	0.1% - 4.5%
Ibex	Annual	0	0.1% - 3.3%
Klaza	Summer	0.003	2.2% - 8.9%
Klaza	Winter	0.007	6.3% - 20%
Klaza	Annual	0.006	5.5% - 17.9%
Kluane	Summer	0	0.3% - 1.1%
Kluane	Winter	0.008	1.5% - 12.4%
Kluane	Annual	0.006	1% - 8.6%
Nahanni	Summer	0.002	1.6% - 1.9%
Nahanni	Winter	0.002	9.7% - 13.1%
Nahanni	Annual	0.001	6% - 8.1%
Tatchun	Summer	0	24.8% - 35.2%
Tatchun	Winter	0.037	40.6% - 54.7%
Tatchun	Annual	0.024	31.2% - 43.2%
Wolf Lake	Summer	0	3.1% - 4.2%
Wolf Lake	Winter	0.009	10% - 11.6%
Wolf Lake	Annual	0.005	6.4% - 7.7%

Hart River	Winter	1.3% - 1.3%	0.9% - 1.3%	2.2% - 2.6%
Hart River	Annual	0.7% - 0.7%	0.5% - 0.7%	1.3% - 1.5%
Ibex	Summer	0	0.2% - 1.2%	
Ibex	Winter	0	0.1% - 4.5%	
Ibex	Annual	0	0.1% - 3.3%	
Klaza	Summer	0.3% - 0.4%	2.2% - 8.9%	2.5% - 9.2%
Klaza	Winter	0.7% - 0.7%	6.3% - 20%	6.9% - 20.7%
Klaza	Annual	0.6% - 0.6%	5.5% - 17.9%	6.1% - 18.5%
Kluane	Summer	0% - 0%	0.3% - 1.1%	0.3% - 1.1%
Kluane	Winter	0.7% - 0.7%	1.5% - 12.4%	2.1% - 13.2%
Kluane	Annual	0.5% - 0.5%	1% - 8.6%	1.5% - 9.1%
Nahanni	Summer	0.2% - 0.2%	1.6% - 1.9%	1.8% - 2.2%
Nahanni	Winter	0.2% - 0.2%	9.7% - 13.1%	9.9% - 13.3%
Nahanni	Annual	0.1% - 0.2%	6% - 8.1%	6.1% - 8.2%
Tatchun	Summer	0% - 0%	24.8% - 35.2%	24.8% - 35.2%
Tatchun	Winter	3.6% - 3.7%	40.6% - 54.7%	44.2% - 58.1%
Tatchun	Annual	2.3% - 2.3%	31.2% - 43.2%	33.3% - 45.2%
Wolf Lake	Summer	0% - 0%	3.1% - 4.2%	3.1% - 4.2%
Wolf Lake	Winter	0.9% - 0.9%	10% - 11.6%	10.7% - 12.3%
Wolf Lake	Annual	0.5% - 0.5%	6.4% - 7.7%	6.8% - 8%

Table 3 – Range and number of recruitment years used to inform boosted regression tree (BRT) models. BRTs used 220 years of recruitment years from 1982-2015 for 13 different northern mountain caribou herds in the Yukon Territory, Canada.

Population	Year Range	Number of recruitment years
Aishihik	1990 - 2014	15
Carcross	1992 - 2015	22
Chisana	1982 - 2015	24
Clear Creek	1997 - 2014	8
Ethel Lake	1993 - 2015	21
Finlayson	1982 - 2015	22
Hart River	1997 - 2015	3
Ibex	1983 - 2015	30
Klaza	1987 - 2015	13
Kluane	1990 - 2015	23
Nahanni	1995 - 2015	10
Tatchun	1993 - 2015	20
Wolf Lake	1984 - 1999	9

Table 4 – Summary of harvest statistics used in boosted regression trees (BRTs) and linear mixed models (LMMs). Mean, standard deviation, max, min, and number of years of harvest data used is presented. Harvest data ranges from 1995-2015 for 13 different northern mountain caribou herds in the Yukon Territory, Canada.

Harvest Statistics (# Harvested / km^2)

Moose Harvest Stats												
	Aishihik	**Carcross**	**Chisana**	**Clear Creek**	**Ethel Lake**	**Finlayson**	**Ibex**	**Klaza**	**Kluane**	**Nahanni**	**Tatchun**	**Wolf Lake**
Mean	0.00109	0.00253	0.00024	0.00143	0.00187	0.00168	0.00046	0.00077	0.00141	0.00014	0.00241	0.00154
Stdev	0.00028	0.00042	0.00016	0.00081	0.00056	0.00056	0.00056	0.00034	0.00049	0.00004	0.00073	0.00031
Max	0.00165	0.00388	0.00047	0.00290	0.00274	0.00279	0.00195	0.00146	0.00228	0.00022	0.00365	0.00184
Min	0.00062	0.00197	0.00000	0.00054	0.00059	0.00091	0.00000	0.00034	0.00076	0.00010	0.00075	0.00123
# Years	12	19	16	8	19	21	18	9	18	10	19	4

Caribou Harvest Stats												
	Aishihik	**Carcross**	**Chisana**	**Clear Creek**	**Ethel Lake**	**Finlayson**	**Ibex**	**Klaza**	**Kluane**	**Nahanni**	**Tatchun**	**Wolf Lake**
Mean	0.00080	0.00005	0.00000	0.00233	0.00020	0.00057	0.00001	0.00042	0.00017	0.00029	0.00105	0.00080
Stdev	0.00025	0.00015	0.00000	0.00062	0.00027	0.00048	0.00005	0.00032	0.00016	0.00011	0.00043	0.00016
Max	0.00112	0.00065	0.00000	0.00302	0.00100	0.00240	0.00022	0.00110	0.00062	0.00050	0.00167	0.00098
Min	0.00032	0.00000	0.00000	0.00135	0.00000	0.00015	0.00000	0.00013	0.00000	0.00017	0.00043	0.00059

Black Bear Harvest Stats												
	Aishihik	**Carcross**	**Chisana**	**Clear Creek**	**Ethel Lake**	**Finlayson**	**Ibex**	**Klaza**	**Kluane**	**Nahanni**	**Tatchun**	**Wolf Lake**
Mean	0.00007	0.00079	0.00006	0.00015	0.00025	0.00016	0.00033	0.00013	0.00012	0.00000	0.00076	0.00005
Stdev	0.00009	0.00032	0.00011	0.00017	0.00024	0.00015	0.00030	0.00011	0.00021	0.00000	0.00048	0.00001
Max	0.00027	0.00144	0.00037	0.00053	0.00081	0.00062	0.00092	0.00034	0.00086	0.00000	0.00188	0.00007
Min	0.00000	0.00023	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00008	0.00003

Grizzy Bear Harvest Stats

	Aishihik	Carcross	Chisana	Clear Creek	Ethel Lake	Finlayson	Ibex	Klaza	Kluane	Nahanni	Tatchun	Wolf Lake
Mean	0.00033	0.00023	0.00002	0.00019	0.00005	0.00013	0.00038	0.00016	0.00030	0.00005	0.00026	0.00012
Stdev	0.00018	0.00012	0.00003	0.00015	0.00007	0.00008	0.00039	0.00009	0.00017	0.00003	0.00019	0.00008
Max	0.00067	0.00052	0.00007	0.00032	0.00017	0.00036	0.00146	0.00024	0.00071	0.00009	0.00073	0.00023
Min	0.00002	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00001	0.00000	0.00000	0.00005

Wolf Harvest Stats

	Aishihik	Carcross	Chisana	Clear Creek	Ethel Lake	Finlayson	Ibex	Klaza	Kluane	Nahanni	Tatchun	Wolf Lake
Mean	0.00075	0.00091	0.00015	0.00032	0.00157	0.00043	0.00074	0.00044	0.00092	0.00010	0.00103	0.00040
Stdev	0.00047	0.00053	0.00024	0.00060	0.00110	0.00020	0.00082	0.00041	0.00063	0.00007	0.00088	0.00025
Max	0.00131	0.00241	0.00075	0.00179	0.00327	0.00087	0.00354	0.00127	0.00186	0.00023	0.00336	0.00069
Min	0.00000	0.00034	0.00000	0.00000	0.00000	0.00012	0.00000	0.00000	0.00001	0.00001	0.00032	0.00012

Table 5 – Relative contributions of predictor variables to reducing deviance of boosted regression tree (BRT) models of northern mountain caribou recruitment. Moose harvest time lag effects on recruitment were included, matching recruitment rates to moose harvest rates 1 year after harvest (t-1) and two years after harvest (t-2). Results are similar when roads are not buffered. 220 years of recruitment data were used from 13 populations in the Yukon Territory, Canada, 1982-2015.

500m buffer	
Variable	**Influence[1] (%)**
Summer range - road disturbance	14.98
Annual range - natural disturbance	14.66
Moose harvest	10.36
Summer range - natural disturbance	9.58
Average PDO	8.46
Annual range - road disturbance	6.78
Caribou harvest	5.53
Grizzly bear harvest	4.59
Winter PDO prior to birth	4.03
April PDO	3.80
Black bear harvest	3.16
Wolf harvest	2.51
May PDO	2.03
Winter range - combined disturbances	1.56
Moose harvest t-1	**1.56**
Winter range - natural disturbance	1.54
Winter range - road disturbance	1.47
Summer range - combined disturbances	1.43
Moose harvest t-2	**1.37**
Annual range - combined disturbances	0.60

[1]The amount of times the variable was chosen to reduce BRT model deviance.

Chapter 4 – General Conclusions and Recommendations

Distinct seasonal ranges based on elevational distributions were found for NMC in the Yukon Territory. Critical habitat for NMC must take into account elevational considerations, which reflect their method for spacing away from predators (Bergerud et al. 1984; Allison 1998). Mountain ecotypes of caribou may also be highly vulnerable to high elevation disturbances (Price 2018).

The measurements of disturbance used in this study did not correlate consistently with changes in recruitment rates, although results were mixed between different analytical methods. The range of disturbance values for NMC populations included here may not have been sufficient to adequately capture their effects on recruitment (Feld et al. 2016). However, comprehensive human disturbance data were not available, severely limiting the scope of this evaluation. It has also been suggested that natural disturbances may have limited effects on increasing apparent competitor habitat and their numbers in less productive northern systems (McLoughlin et al. 2019). Nevertheless, despite limitations of mapping methods applied here, the majority of study populations had disturbance levels well below management thresholds identified for other caribou designated units (Sorenson et al. 2008; Environment Canada 2011). Extension of this work into NMC populations in British Columbia would encompass a broader range of disturbance values. Up to nine BC NMC populations have appropriate recruitment data available (Environment Canada 2012), but these were not available for the present study. There also exists a critical need for high-resolution human disturbance data throughout NMC, and for adult female survival data; a crucial parameter for evaluating demographic response of caribou to landscape change. Regardless of these study limitations, there exists an opportunity to manage NMC populations in the Yukon pro-actively to prevent population declines associated with anthropogenic disturbances observed in other woodland caribou systems.

Density of moose harvest on NMC population ranges was positively correlated with caribou recruitment. Moose harvest was also correlated with road disturbance, a correlation that was expected as ease of access is associated with use of all-terrain vehicles (Pigeon et al. 2016). These findings point to the importance of considering caribou in a system of effects, and further investigation into the mechanisms underlying moose harvest effects on caribou recruitment is required. Overall, the management of caribou needs to consider not just caribou, but the web of predator-prey and apparent competitor interactions that they are a part of.

Average pacific decadal oscillation (PDO) was also positively correlated with NMC recruitment. As northern latitudes are experiencing faster climate change than other areas of the world (IPCC 2014), the effect climate has on caribou may be exacerbated. Different predators may move into northern ecosystems such as coyotes, who have been shown to be effective predators on caribou calves (Lewis et al. 2017). In Ontario, climate change projections coupled with caribou range requirements lead to projections of potential extirpation from Ontario by 2070 (Masood et al. 2017). When considering NMC, climate must be a key consideration in how they may be affected in the future.

Polfus et al. (2017) emphasize that caribou species should be analyzed in recognition of large-scale eco-evolutionary processes that increase genetic diversity and adaptability of species. Comparisons of how territorial and provincial governments determine the extent of NMC populations were examined in this study, and it was determined that COSEWIC's designatable unit (DU) 7 (COSEWIC 2011) was the most robust method for delineating the extent of NMC ranges. DU 7 also corresponds with naming Dene people have for different caribou types (Polfus et al. 2016). It is recommended that for any further NMC work COSEWIC's DU 7 be used.

Caribou are a harvested species of importance to many First Nations cultures, many with different perspectives on caribou-human relationships (Castro et al. 2016). NMC ranges cross thirty-three different First Nation territories in Canada (Environment Canada 2012), making it imperative that management decisions that involve NMC include First Nations. Many of these communities are actively involved in First Nations-led conservation planning initiatives for caribou, and have valuable knowledge of trends in caribou populations, habitat use and subsistence harvest practices to contribute to their sustainable management.

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