NORTHERN MOUNTAIN CARIBOU (*Rangifer tarandus caribou*) DISTRIBUTIONAL RESPONSE TO HABITAT DISTURBANCE AND ALTERED PREDATOR-PREY DYNAMICS

by

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B.Sc., University of British Columbia, 2014

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

July 2025

Abstract

Woodland caribou (*Rangifer tarandus caribou*) across North America are in decline, largely as a result of habitat change that has altered their relationship with other ungulates and their shared predators, a process known as disturbance mediated apparent competition (DMAC). In British Columbia, Northern Mountain Caribou (NMC) are found at the northern limit of expansive human-footprints. Subpopulations at the southern extent of NMC are threatened by habitat disturbance that has led to population decline and has forced caribou into small and isolated alpine areas. At the northern extent of NMC, caribou freely range in large subpopulations in landscapes with minimal anthropogenic disturbance. The contrast between high- and low-disturbance landscapes offered a unique opportunity to study the predator-prey and distribution dynamics of caribou as they relate to habitat disturbance and DMAC. I used Bayesian stable isotope mixing models to understand the diet of wolf (*Canis lupus*) and grizzly bear (*Ursus arctos horribilis*), the two main predators of caribou and moose (*Alces americanus*), their apparent competitor. There was relatively more moose and less caribou in the diet of sampled wolves in the high-disturbance landscapes. That relationship suggested that caribou subpopulations in that portion of the study area were subject to either numeric or spatial DMAC, and that quantitative measure of predator diet may be a useful index of changes in the relative abundance of moose and caribou over time. I used the same contrast in disturbance among landscapes to investigate the relationship between the distribution of 295 GPS-collared female caribou, disturbance, and DMAC. Seasonal home ranges were smaller and caribou used higher elevation habitats when they were confronted with relatively greater area of habitat disturbance. These two results are consistent with observations for other types of mountain caribou and indicate that habitat disturbance and DMAC contribute to range contraction. In total, my study

suggests that increases in habitat disturbance will lead to continued range contraction for southern subpopulations of NMC and potentially instigate range contraction in the north. Thus, it is critically important to consider ways to reduce habitat disturbance and proactively safeguard intact habitats across the range of NMC.

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Acknowledgment

Dr. Chris Johnson, you are an amazing supervisor. Did you know that alumni from your lab still attended lab meetings long after they graduated! That speaks volumes to the community of young scientists you have helped cultivate that are dedicating to personal growth, support for one another, and joy. All qualities that you lead by example with and for that I deeply appreciate you. Thank you for witnessing my journey as a graduate student. This was a truly special time in my life and I learned so much from you as I leaned on you for more than just science questions, but mentorship in other aspects of life.

Behind every graduate student there is a statistics/R guru. For me, that was Dr. Alex Luscomb. I never did take you up on that beer, but I look forward to sharing an ale with you once this is done and thanks you so much for being there for me, brother!

To the lab – you all are such sweethearts and inspiring young people. Suzanne, your enthusiasm brought us all together. Angus, you're caring nature brought us all closer. Lisa, your leadership kept us all in this. Those were my core, but others were equally supportive and lovely people to call a lab mate and friend.

To the committee – I chose to work with you all for a reason. You all inspire me and I've been a fan of your work for years. There were many "pinch-me moments" working with you all and enjoying the deep level of nerding-out we enjoyed together.

To Zooby, thanks for being my best friend. You were literally at my side the entire time. I will always remember your encouragement as I found myself again during this period of my life.

Alexanne, I did it! There's just not way this would have been such a consistently enjoyable process without your love and support. You know better than anyone how much personal growth I went through. I spent half my time studying caribou, and the other half of my time was spent going inward and studying myself. You encouraged me to stick with it. You live your life with a loving heart. Your love makes such a big difference in the world, especially my world.

Lastly, I want to acknowledge all the project collaborators that made this happen. Lance, Norm, Clements, Richard, Brianna, and the rest of the crew dedicated to caribou stewardship in Tahltan Territory are deeply inspiring. Dorothy Cooley up in Teslin, you are so kind and welcoming. You gave me the confidence to pursue this project knowing I had your support. The folks at the BC Caribou Recovery Program, specifically Bevan Ernst and Kathi Zimmerman, thank you for the support and providing critical funding and analysis that made this project that much better. The folks at the Wildlife Conservation Society of Canada provided funding and mentorship that was instrumental in helping get this project off the ground and keeping me on track. To the funders that awarded me scholarships – the Weston Family Foundation and Habitat Conservation Trust Foundation, thank you, thank you, thank you! I trust my work met the expectations of these prestigious awards. To the guide outfitters and trappers that put up with me wrangling wildlife hair samples – you all really made this project possible and your contributions are not lost on me. Thank you. Thank you everybody who supported me and trusted me to do the best job I could.

Introduction

Background

The biogeography of species is increasingly influenced by land use and climate change. For instance, the distribution of many species of terrestrial mammals is shifting or contracting due to human-caused habitat change and fragmentation (Tucker et al., 2018). Abiotic factors largely driven by human-caused climate change also contribute to range shifts. For example, climate warming is resulting in some species shifting their range to high elevations and at a broader scale, increases in latitude (Chen et al., 2011). Although species distribution varies with abiotic conditions, biotic interactions (such as trophic web interactions) are critically important to understanding distribution dynamics (Boulangeat et al., 2012; Wisz et al., 2013).

Intra- and inter-species interactions such as predation and competition are important determinants of the structuring of plant and animal communities as well as the behaviour, abundance, and distribution of individual species (Pellissier et al., 2010; Yackulic et al., 2014). Moreover, there is mounting evidence that human activities reshape landscapes and the distribution of resources that consequently influence species interactions (Labadie et al., 2023; Potapov et al., 2017; Venter et al., 2016). For example, in British Columbia (BC), black bears (*Ursus americanus*) are thought to limit grizzly bear distribution (*Ursus arctos horribilis*) through exploitive competition mediated by the distribution of food resources (Service et al., 2014). Additionally, landscape partitioning can occur as black bears are more likely to coexist with human activities (Apps et al., 2006; Ciarniello et al., 2009). Thus, accounting for human activities that mediate species interactions can improve predictions about the responses of wildlife to a rapidly changing world.

The introduction of novel species interactions as a result of human-caused landscape change and resulting cascading effects across food webs has the potential to influence the distribution and abundance of wildlife (Potapov et al., 2017; Rosenblatt & Schmitz, 2016; Stoner et al., 2018; Venter et al., 2016). For example, predation can be intensified when a novel species alters the abundance and distribution of predators (Pope et al., 2008; Roemer et al., 2001). The indirect interaction between (at least) two prey species and a shared predator is termed apparent competition (Holt, 1977). Mechanistically, apparent competition relies on a numeric response of a predator to an increase in abundance of the primary prey that regulates an asymmetrical predator-prey dynamic. Given that response, the less productive alternate prey cannot sustain the increased predation from the predator and will decline, possibly to extinction (Holt et al., 1994). There are numerous examples of apparent competition across a range of taxonomic groups (DeCesare et al., 2010).

Ultimately, as predation risk increases from apparent competition, wildlife will distributionally respond often resulting in niche partitioning (Holt, 1984). Whereby apparent competition can mimic the effects of exploitive competition and have similar outcomes. For instance, the competitive exclusion of one prey species by another can lead to extirpation of the less fit prey. However, the spatial arrangement of resources can mediate the degree of overlap among species in natural systems, and act as a stabilizing factor in predator-prey interactions (Hirzel & Le Lay, 2008; Holt, 1984). For example, spatial heterogeneity can create refugia or space unexploited by predators. When apparent competitors spatially separate into unique patches or types of habitats that can reduce the potential for interacting with shared predators (DeCesare et al., 2010). Alternatively, some forms of spatial heterogeneity can enhance the movement or distribution of the prey, potentially increasing spatial overlap with shared predators (i.e., spatial apparent competition, Mumma et al. 2018).

Whereas much effort has been focused on quantifying the effects of apparent competition on population abundance and vital rates, much less is known about the potential for apparent competition to influence the landscape-scale distribution of interacting species. Understanding species interactions is pivotal for conservation in the face of accelerating habitat loss, the consequence of a growing human footprint (Potapov et al., 2017; Venter et al., 2016).

Caribou and apparent competition

All caribou and reindeer belong to the same species (*Rangifer tarandus caribou*) with evolutionary differences that define distinct subspecies. Several contemporary subspecies exist across North America including Grant's (*R.t. granti*), barren-ground (*R.t. groenlandicus*), Peary (*R.t. pearyi*), Dolphin and Union (*R.t. groenlandicus* x *pearyi*), and woodland (*R.t. caribou*) that range across Canada in sub-boreal and boreal forests. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) classified *Rangifer* in Canada into eleven extant Designatable Units (DUs). Those DUs represent morphological, behavioural, and ecological variations across the species' range and allow for unique conservation decisions and protections for each DU (Taylor et al. 2021). There are five DUs of caribou in BC and the Yukon Territory (YT): Barren-Ground (DU3), Boreal (DU6), Northern Mountain (DU7), Central Mountain (DU8), and Southern Mountain (DU9). Taxonomically, the Boreal and Mountain DUs are the same subspecies (*R.t. caribou*) but differ according to ecology and evolutionary origin.

Our focus is on the Northern Mountain DU (hereafter referred to as "NMC") that consists of subpopulations ranging from west-central BC to YT, and through the western Northwest

Territories. A key ecological relationship that distinguishes NMC is their use of forests and plateaus with terrestrial lichens (Cichowski and Haeussler, 2013). During winter, a time when nutritional resources are less diverse for caribou, NMC forage primarily on terrestrial lichens from the *Cladina*, *Cetraria*, and *Cladonia* genera (Cichowski and Haeussler, 2013). Those lichens are generally found in late-seral coniferous forests and alpine habitats, or more generally low-productivity environments.

Woodland caribou persist at relatively low densities in unproductive ecosystems, especially during winter. That distributional pattern allows caribou to spatially separate from other forest ungulates that are more reliant on plant communities that support forage consisting of mostly vascular plants (Serrouya et al., 2021). Spatial separation from predators and sympatric prey is a central tenet to the ecology of mountain caribou, and a key survival strategy (Festa-Bianchet et al., 2011; Seip, 1991).

Climate was likely the primary factor influencing the historic distribution of woodland caribou in western North America (Polfus et al., 2017; Taylor et al., 2021). However, little is known of the influence biotic interactions had on mediating historic population and distribution changes of woodland caribou. Indeed, the historic caribou-wolf (*Canis lupus*) predator-prey dynamic (pre-1900) pre-dates the contemporary population declines and range shifts of NMC (Bergerud & Elliot, 1986; Santomauro et al., 2012). Thus, biotic factors, like predation, may have had less of an effect on the distribution and population dynamics of caribou in the past. It is equally possible that previous to the 20th century, wolf populations were more reliant on caribou, and potentially existed at low density in coexistence with caribou (Bergerud & Elliot, 1986).

Over the past century, woodland caribou have shown continuous range contraction and population decline (Morineau et al., 2023; Santomauro et al., 2012). Although the exact mechanisms are unclear, it is widely accepted that the culmination of land settlement, resource development, excessive human harvest, and increased predation resulted in declines of woodland caribou in the 20th century. Concurrent with those declines, moose (*Alces americanus*) began to increase their range and abundance across western BC (Bergerud & Elliot, 1986; Kay, 1997; Santomauro et al., 2012; Spalding 1990, 2000). The increase in moose provided more prey for wolves and initiated an apparent competition dynamic (Bergerud & Elliot, 1986). Indeed, little empirical information exists on the abundance and distributional changes of both moose and caribou prior to the late 20th century (Santomauro et al., 2012; Spalding, 1990, 2000). Yet there is a clear correlation in caribou population decline as the human footprint increased and moose expanded their range in BC (Bergerud & Elliot, 1986; Santomauro et al., 2012).

The most recent declines in caribou, starting in the late 20th century, are widely assumed to be a result of unsustainable predation by wolves via apparent competition mediated by anthropogenic habitat disturbance (Festa-Bianchet et al., 2011). The loss and fragmentation of old forests has reduced the quality and quantity of habitat for caribou (Cichowski et al., 2022; Ray et al., 2015). In contrast, the creation of early-seral forests has resulted in an increase in density and distribution of moose (Anderson et al., 2018; Darimont et al., 2005) and a positive numerical response of wolves (Serrouya et al., 2017, 2021). Moreover, linear features have created an efficient hunting landscape for wolves (Dickie et al., 2017). This predator-prey dynamic is defined as disturbance mediated apparent competition, hereafter described as "DMAC" (Fortin et al., 2017; Holt, 1977; Neufeld et al., 2021).

Traditionally, DMAC was thought to occur following a habitat related increase in the abundance of dominant apparent competitor and shared predator (i.e., numeric DMAC; Serrouya et al. 2011). Recent evidence suggests that spatial DMAC can occur when disturbance facilitates the distribution of the apparent competitor or shared predator to the demise of the less dominant competitor (Mumma et al., 2018). Spatial and numeric DMAC need not be mutually exclusive or inclusive. Many of the conservation actions for caribou in western Canada are focused on reducing DMAC between caribou, moose, and wolf (e.g., Serrouya et al., 2019).

Research purpose

I explored the predator-prey and distributional dynamics of a threatened species, woodland caribou, in response to anthropogenic disturbance. I used a contrast in habitat disturbance between two study landscapes (i.e., high and low disturbance) to assess change in the diet of predators, wolf and grizzly bear, relative to DMAC. Also, I tested for a relationship between the distribution of caribou, habitat disturbance, and DMAC. Understanding species interactions is important for conservation of species that are threatened by habitat loss from human activities that restructure community dynamics (Potapov et al., 2017; Venter et al., 2016).

As the first research objective, I explored the relationship between predator diet, primarily focussing on consumption of caribou and moose, and habitat disturbance. A change in the predator diet, relative to increasing area of disturbance, would indicate the potential for DMAC. I assumed that moose numbers would increase with habitat disturbance and the fraction of moose in the diet of predators would correspondingly increase. As DMAC progressed, and the abundance of caribou declined across the high-disturbance landscape, predators would have proportionally less caribou in their diet. I expected predator diets to consist of equal proportions of caribou and moose across areas with relatively little habitat disturbance (Merkle et al., 2017). I used an innovative application of stable isotope analysis (SIA) to quantify the diet of wolves and grizzly bears, primary predators of caribou and moose, to test these diet-disturbance relationships across two contrasting disturbance regimes in northcentral and northwestern BC.

As the second research objective, I tested for a relationship between range use, habitat disturbance, and DMAC. Considering the distributional responses of caribou to landscape change, I predicted that the seasonal home ranges for caribou would contract in area as habitat disturbance increased (Wilson et al., 2019). Additionally, caribou would retreat to high-elevation habitats that were spatially disjunct from moose and predators (Bergerud & Page, 1987; MacNearney et al., 2016).

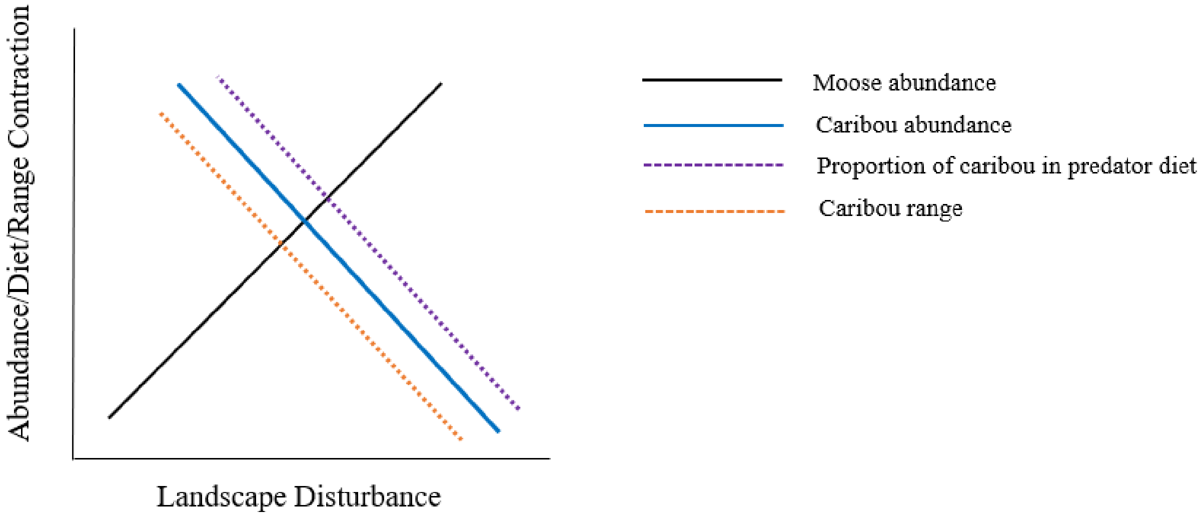

Figure 1 Conceptual illustration of hypothesised relationships between landscape disturbance and the abundance of caribou (*Rangifer tarandus caribou*; solid blue line), moose (*Alces americanus*; solid black line) and the resulting change in the diet of predators (dashed purple line) and contraction of caribou distribution to small isolated ranges at high elevations (orange dashed line).

There is concern that the history of anthropogenic habitat disturbance and decline observed for NMC at their southern range will be the future for NMC in northern BC. If we are to avoid repeating the patterns of decline observed for Southern Mountain Caribou, and associated drastic conservation efforts, then we require a better understanding of the effects of habitat disturbance and DMAC on caribou distribution. I used a space-for-time study design to quantify the spatial and temporal relationship between habitat disturbance, DMAC, and the predator-prey and distribution dynamics of NMC. That relationship may provide insights into the future trajectory of NMC that are currently found across low-disturbance landscapes, but may face habitat loss characteristic of more southern subpopulations.

Indigenous and non-Indigenous governments are attempting to increase the distribution and abundance of some NMC subpopulations in the southern extent of the range, the leading edge of habitat disturbance and population decline. Controversial and expensive conservation actions, such as predator reductions, are now being used as last-ditch efforts to arrest the decline and prevent the extirpation of some subpopulations of NMC (Johnson et al. 2022). Indeed, the politics of caribou recovery are complicated by natural resource extraction, where economic values are often prioritized over the needs of caribou (Palm et al., 2020). Thus, there is concern that the patterns of decline and consequent recovery actions experienced in the southern range of NMC will be the future in the north if projected increases in habitat disturbance occur.

Thesis Structure

My thesis was built around Chapters 2 and 3, the two primary research chapters. I began my thesis with Chapter 1, “Introduction”, that provided an overview of the background ecology and theory that supports the research objectives. In Chapter 1, I included a description of the study area as well the methods and results from the analysis of habitat disturbance that I developed in partnership with the BC Caribou Recovery Program. The results from this analysis are applied in Chapters 2 and 3.

In the second chapter, I presented an analysis of the diet of the two primary predators of caribou and moose. I used Bayesian stable isotope mixing models to quantify the diet of grizzly bears and wolves in two study landscapes with contrasting disturbance footprints (high and low) using hair samples obtained from community-science. I argued that the diet of predators can serve as a cost-effective measure of changes in the abundance of the prey community. I used a combination of predator diet and estimates of ungulate abundance to develop an indirect measure of DMAC for 11 subpopulations of NMC.

For the third chapter, I presented an analysis of the distributional response of caribou to habitat disturbance and DMAC. I compared home range size and elevation use of individual caribou that were exposed to varying degrees of habitat disturbance and DMAC. I argued that range use was a function of the extent of habitat disturbance and altered predator-prey dynamics.

In the conclusion chapter, I synthesized my learnings from the research and knowledge that I gained through this experience.

Study Area

This study took place within the unceded territories of multiple First Nations. The extent of the study area encompasses sub-boreal and boreal landscapes of northwestern and northcentral BC. The study area includes the Fraser Plateau, Bulkley Ranges, Skeena Mountains, Omineca Mountains, Boreal Mountains and Plateaus, and Yukon Southern Lakes ecoregions. At treeline, dwarf birch (*Betula glandulosa*) and willow (*Salex* spp.) transition into boreal and sub-boreal coniferous forests of lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*), white spruce (*P. glauca*), subalpine fir (*Abies lasiocarpa*), tamarack (*Larix laricina*), and deciduous stands of trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). The understory plant community varies by Biogeoclimatic zone and subzone (Pojar et al., 1987) yet can be characterized by a fairly dense covering of lichens, mosses, herbs, and shrubs that vary from site to site.

Wildfire, now mediated by fire suppression, is the primary natural disturbance across the study area. The climate is typified by long, cold winters and short, warm summers (Pojar et al 1987). Four major watersheds dominate the hydrology including the Fraser, Skeena, Stikine, and Yukon Rivers. The topography in this area consists of broad, sinuous valley bottoms, and rugged mountain ranges with extensive high-elevation plateaus. The defining mountain ranges include the Bulkley, Skeena, Omineca, and Cassiar.

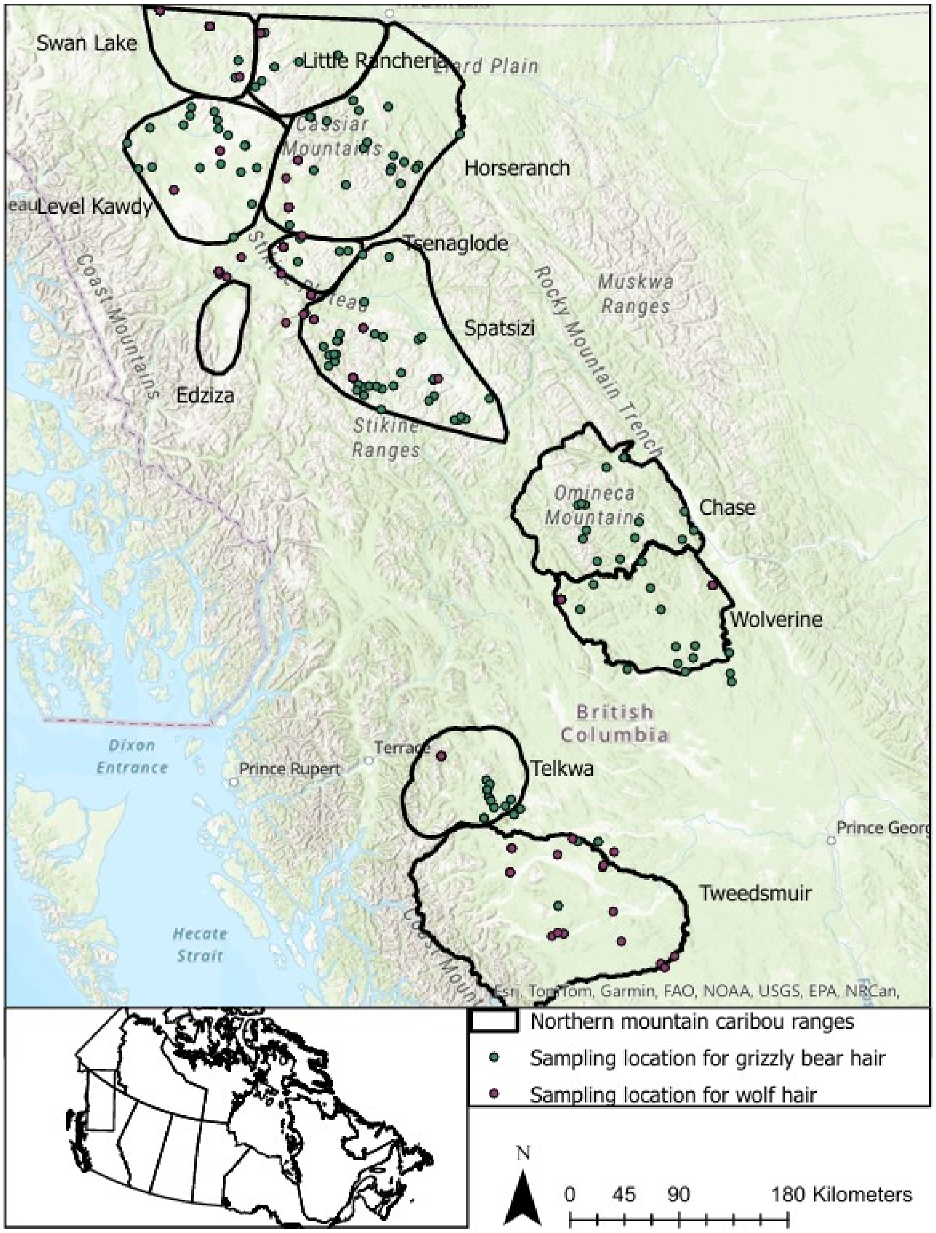

Figure 2 Boundary of study subpopulations of northern mountain caribou (*Rangifer tarandus caribou*) and locations for hair sampling used for stable isotope diet analysis of wolf (*Canis* lupus) and grizzly bear (*Ursus arctos horribilis*) in northcentral and northwestern British Columbia, Canada.

Contrast in landscape condition

I collaborated with the British Columbia Caribou Recovery Program to quantify the area of natural and anthropogenic disturbance across the known range of each subpopulation of NMC. I worked with publicly available spatial data to analyze the disturbance footprint for each of the caribou herds (Appendix A). Disturbance data were assembled in GIS for an analysis area encompassing the eleven focal caribou subpopulations. I mapped disturbance features that occurred in the past 40 years (Fortin et al., 2017; Vors et al., 2007; Wilson et al., 2019). All data were in vector format and were sourced from either DataBC or from BC Cumulative Effects (BCCE) disturbance dataset (2019 Version). I identified two disturbance types: anthropogenic (roads, cutblocks, agriculture, airstrip, dam, mine, pipeline, rail, reservoir, seismic, transmission line, urban, and well) and wildfire. I recognised that the range boundaries for individual populations of caribou were dynamic and open to interpretation and revision. However, I applied the disturbance footprints to the range boundaries that were identified by the BC provincial government at the time of the analysis (2023). I used spatial datasets for each year from 2015–2023.

Data were prepared using a custom python and R script (BC Caribou Recovery Program). The script iterates through each herd selecting, clipping, and exporting intersecting disturbances. Where disturbances overlapped, the following hierarchy was used to assign the dominant type: Roads > Static Disturbance > Most Recent Temporal Disturbance (cutblock, fire). I did not buffer or represent an area adjacent to each disturbance feature, as was applied to other disturbance footprint analyses for woodland caribou (e.g., Environment Canada, 2011).

I limited the quantification of disturbances to elevations < 1200m to account for 1) the disproportionate concentration of human and natural disturbances across forested ecosystems (Cichowski et al., 2022); 2) our assumption that disturbance of productive forested habitats had the greatest influence on the distribution and abundance of caribou, moose, wolves, and grizzly bears (MacNearney et al., 2016); and 3) to limit the extent of alpine (i.e., rock and glacier) that would be incorporated in the total range area that could bias disturbance footprint calculations. The elevation cut-off was the approximate treeline across the study area and represented the point of termination of most forest harvesting operations and associated infrastructure (i.e., roads). Each individual disturbance was represented as total hectares (< 1200m) and percentage of herd range area (< 1200m).

For analyses, I grouped caribou subpopulations into high-disturbance and low-disturbance study landscapes. The division was based on a qualitative assessment of overall disturbance, with high-disturbance ranges having >10% of area disturbed by anthropogenic activities. Caribou in the low-disturbance landscapes included Spatsizi, Tsenaglode, Edziza, Level-Kawdy, Swan Lake, Little Rancheria, and Horseranch. Caribou in the high-disturbance study landscape included Tweedsmuir, Telkwa, Wolverine, and Chase.

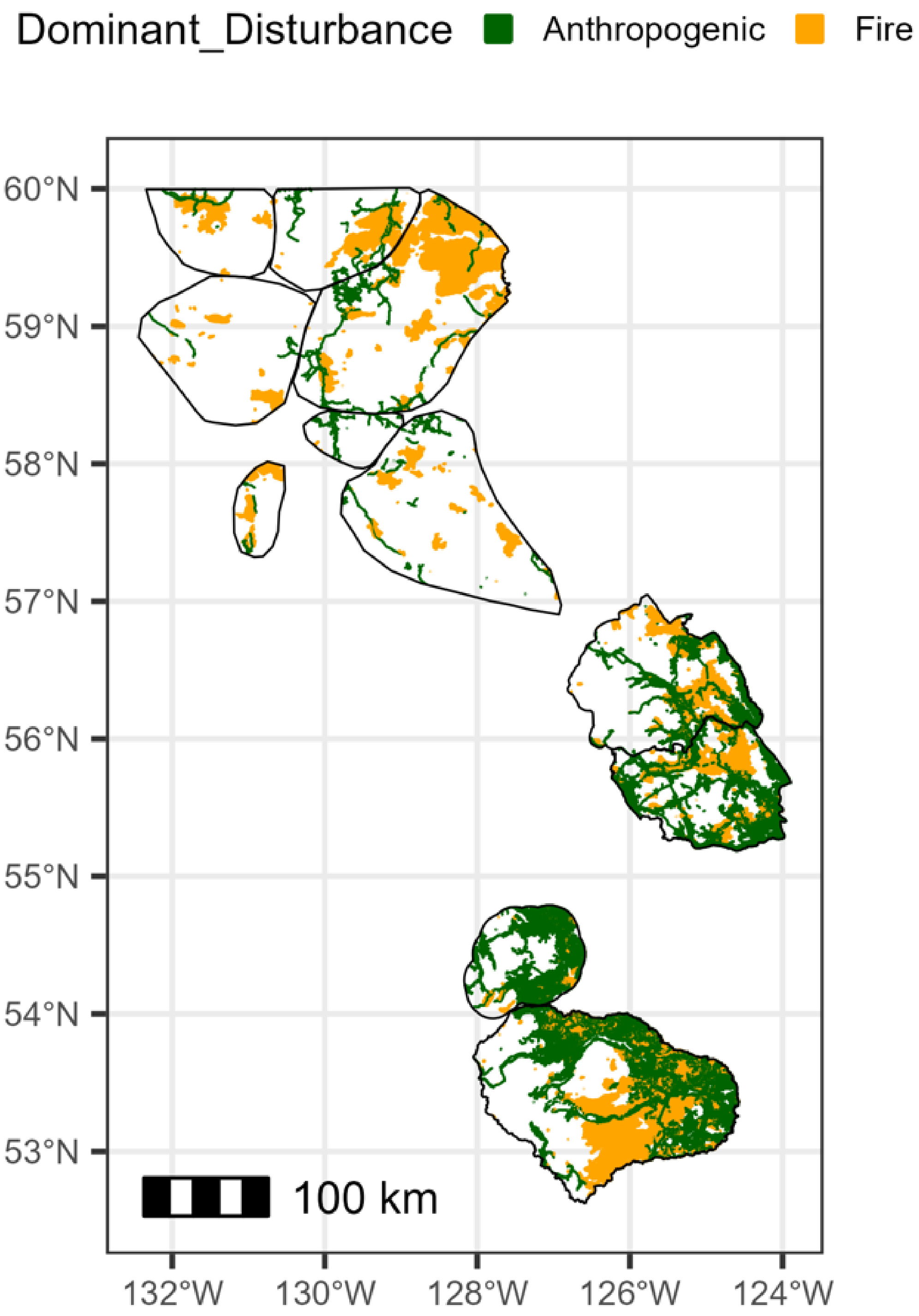

Figure 3 Contrast in low-elevation habitat disturbance for 2023 that was used to compare predator diets and range use of northern mountain caribou (*Rangifer tarandus caribou*) in northcentral and northwestern British Columbia, Canada. Southern subpopulations (Tweedsmuir, Telkwa, Wolverine, and Chase) demonstrated greater area of disturbance.

Table 1 Total low-elevation disturbance footprint (%) in 2023 for four disturbance categories (cutblock, fire, road, static) across 11 subpopulations of northern mountain caribou (*Rangifer tarandus caribou*), in northcentral and northwestern British Columbia, Canada. The sum of cutblock, road, and static was equal to the total anthropogenic dominant disturbance footprint.

Subpopulation	**Cutblock**	**Road**	**Static**	**Anthropogenic**	**Fire**
Telkwa	17	7	4	28	5
Tweedsmuir	8	5	1	14	41
Wolverine	13	6	0	19	27
Chase	9	5	1	15	35
Tseneglode	< 0.01	2	0	2	1
Horseranch	< 0.01	1	0	1	42
Little Rancheria	< 0.01	1	< 0.01	1	27
Spatsizi	< 0.01	< 0.01	< 0.01	< 0.01	12
Swan Lake	< 0.01	< 0.01	< 0.01	< 0.01	13
Edziza	< 0.01	< 0.01	< 0.01	< 0.01	33
Level-Kawdy	< 0.01	< 0.01	< 0.01	< 0.01	6

Collaboration

This research was done in collaboration with multiple governments and scientists. During project conception, I worked with ideas from Conrad Thiessen, Dr. Chris Johnson, Lance Nagwan, Norm MacLean, Kelsey Russell, and Dorothy Cooley to outline the project within the constraints of data availability and feasibility. Further refinement of the research ideas occurred following engagement with the Tahltan Central Government, Teslin Tlingit Council, Kaska Dena Council, and the BC Caribou Recovery Program's Science Team. Important to me was linking the research to ongoing Indigenous-led caribou projects and recovery programs with the Tahltan Central Government, Teslin Tlingit Council, and Kaska Dena Council. I worked with the Tahltan Central Government and Teslin Tlingit Council to ensure that the research questions were relevant and that the study design was inclusive to the work these governments were leading.

Chu Cho Environmental and Wildlife Infometrics were informal project partners that provided wildlife hair samples and contributed their collective knowledge to this research. The Wildlife Conservation Society of Canada and BC Caribou Recovery Program were my two primary funders and provided mentorship and guidance to me as a student. Lastly, I partnered with the Skeena Sustainability Assessment Forum who provided grizzly bear hair samples.

Reflexivity

As a researcher, I approached my research by identifying available data, fitting methodologies to those data, and developing research questions that could be addressed with those data and methods. Once I had a general sense for what was possible within the constraints of my methodology, I sought opportunities to partner with people and organizations that helped refine the research. My life experience, world view, and soul-journey have profoundly shaped my research. I inherently introduced my own perceptions of what constituted relevant research and how that research could be approached. I sought research questions that were first and foremost of interest to me. I acknowledge that the information I brought forward through this thesis was influenced by the way I looked at caribou conservation. Indeed, through partnership and trust-based relationships, my goal of an inclusive research project that benefited the needs of others has worked out. I continue to seek opportunities to share my experiences and learnings from graduate school with as many people as possible. I committed to ensuring that others benefited from my research as much, if not more than me.

My research was guided by the Western or Eurocentric tradition. I designed my research methodology based on information that fit within a postpositivist paradigm (Mertens, 2015). This philosophy is based on the assumption that there are mechanistic relationships that are discoverable by sourcing and analysing information to determine one knowable truth. Quantitative empirical hypothesis testing is at the core of this paradigm and my research methodology. The underpinnings of this paradigm govern what constitutes knowledge, shapes the perspective of the researcher, and guides the choices and actions of the researcher (Held, 2019). Indeed, myself as a researcher, and by extension my methodologies, are not naive to these underpinnings. I recognize that there are equally relevant ways of knowing, yet knowledge power dynamics continue to inhibit true bridging of knowledge systems (Nadasdy, 1999, 2005). My research is no exception as there was no bridging of knowledge systems.

My research philosophy considered the distribution and ecology of NMC through the lens of Western science. A number of key principles guided the methodological design: data that conform to Western traditions, quantitative methods to test empirical hypotheses, statistical analysis to model relationships, and knowledge that is objective and independent of personal biases. Following from these principles, I developed a methodology that fit the scope of a thesis-based research project.

Due to the significant contributions of research collaborators to the information presented in this thesis, the pronoun "we" will be used instead of "I" when referring to Chapters 2, 3, and 4. Though the information presented in this thesis represents my thinking, and may not represent the thinking of my collaborators.

Chapter 2 | Altered predator diet in response to habitat disturbance signals disturbance mediated apparent competition

Introduction

Land use and climate change continue to alter ecosystems and as part of that process shape and reshape ecological communities (Barnosky et al., 2012; Sinclair & Byrom, 2006). The corresponding gain and loss of individual species has fundamentally changed competition and predator-prey dynamics (Rosenblatt & Schmitz, 2016; Shapira et al., 2008; Stoner et al., 2018). Although the mechanisms can be indirect and complex, the consideration of interspecific interactions is important for not only understanding community dynamics but also the resilience and vulnerability of individual species to a changing world.

The introduction or increases in the abundance of predator or prey can have important implications for community dynamics. For instance, the decline or extirpation of one prey species may be driven by a shared predator that is responding numerically to a more abundant, second prey species (Bryant & Page, 2005; DeCesare et al., 2010; Roemer et al., 2001). In this predator-prey dynamic, termed apparent competition, asymmetrical predation allows one prey species to persist while the other declines to a lesser abundance or is extirpated from the system, mirroring the effects of direct competition (Holt, 1977). DMAC occurs when human land use shapes the distribution or abundance of predator and primary prey, which can endanger alternate prey (DeCesare et al., 2010; Sinclair & Byrom, 2006).

Anthropogenic activities have contributed to the expansion of moose across the range of woodland caribou in western North America (Anderson et al., 2018; Darimont et al., 2005; Santomauro et al., 2012). Following from the DMAC hypothesis, human-caused increases in the distribution and abundance of moose will elicit a numerical and spatial response in wolves (Fuller et al., 2003; Hayes & Harestad, 2000; Holt, 1977; Mumma et al., 2018). The result is asymmetrical and unregulated predation of caribou. DMAC is increasingly recognized as the proximate cause for declines of woodland caribou across Canada (Festa-Bianchet et al., 2011).

Environmental change is thought to play a crucial role in mediating DMAC between caribou and moose (Neufeld et al., 2021). Yet there are considerable challenges in empirically assessing the emergence and measuring apparent competition. In theory, one would need to identify the mechanism, for example a change in the amount or quality of forage, that would lead to the relative increase in one prey species within this three-species dynamic. Assessment of the rate and ultimate outcome of apparent competition would require direct measurement of the abundance of the prey and predator. Classic apparent competition theory dictates that the alternate prey (i.e., caribou) becomes less abundant relative to the primary prey (i.e., moose) as the predator (i.e., wolf) increases in abundance and distribution (Holt, 1977; Holt et al., 1994). More recently, some have postulated that apparent competition can be expressed as the product of a numeric and distributional predator-prey dynamic. In such cases, habitat change facilitates the movement or distribution of the primary prey and predator, leading to increased encounters and predation of the secondary prey. Although the mechanism differs, the outcome of spatial and numeric DMAC are the same: a decline or extirpation of the less fit prey species.

The precise estimation of the distribution and abundance of moose, caribou, and wolves is difficult and expensive for many ecosystems. Thus, directly quantifying apparent competition is challenging. Dietary analysis is particularly suited and efficient at quantifying trophic interactions and allows researchers to explore some elements of community dynamics, including predator-prey dynamics (Ben-David & Flaherty, 2012; Hobson et al., 2000). Several methods are available for quantifying diet and resource partitioning (e.g., gut content, scat analysis), but are limited by sampling constraints or spatial and temporal resolution (Bowen & Iverson, 2013). Innovations in technology, such as the use of biotracers (e.g., stable isotopes and fatty acids), are increasingly being used as potentially non-invasive methods for quantifying the longer-term diet of predators, omnivores, and herbivores (Merkle et al., 2017; O'Donovan et al., 2018). These dietary biotracers are based on the theory that organisms 'are what they eat, isotopically' (DeNiro & Epstein, 1978). Whereby, consumers incorporate unique prey or forage biomarker profiles into their tissue after consumption (Ben-David & Flaherty, 2012).

Ecologists are increasingly using stable isotope analysis (SIA) to explore diet and the resulting trophic interactions. SIA has been used to measure spatial variation in resource use by predators (Adams et al., 2017), dietary niche partitioning (Merkle et al., 2017), and track seasonal diet shifts (Darimont & Reimchen, 2002). Although there are a number of stable isotopes, SIA of diet most commonly quantifies differences in the ratios of ^{13}C:^{12}C and ^{15}N:^{14}N within the growing tissue of the predator and the consumed tissue of the prey (Ben-David & Flaherty, 2012). The ratios are measured as deviations from a standard ($\delta^{13}C$, $\delta^{15}N$) in parts per thousand. There are a range of tissues that can be used to measure the consumer and source $\delta^{13}C$ and $\delta^{15}N$, including hair, but the isotopic ratios are specific to the period of metabolic activity.

Isotopic landscapes of dietary data can geographically characterize how the relative contributions of prey from different habitats structure predator-prey dynamics (Adams et al., 2017). In this chapter, we used SIA of two biotracers, $\delta^{13}C$ and $\delta^{15}N$, to reconstruct the diet of wolves and grizzly bears across two study landscapes with contrasting disturbance footprints in northcentral and northwestern BC. Our goal was to determine whether the relative contribution of caribou and moose in predator diets could represent the relative abundance of these sympatric prey for high- and low-disturbance study landscapes. We used the ratio of caribou to moose in the diet of the predator to assess DMAC within the two study landscapes (Neufeld et al., 2021). Whereby, the prevalence of an extensive disturbance footprint provides the mechanistic foundation for DMAC.

We predicted that predator diets would be enriched with more moose relative to caribou across caribou ranges with relatively greater habitat disturbance, an expectation of DMAC (southern distribution). We based this hypothesis principally on the observed increase in moose density across landscapes that have considerable human or natural disturbance, and the concurrent decline in the abundance of caribou linked to increased predation (DeCesare et al., 2010; Mumma et al., 2018; Santomauro et al., 2012; Serrouya et al., 2019). As a corollary to this relationship, we predicted that caribou and moose would be equally depredated by wolves and bears across low-disturbance ranges (northern distribution; Bergerud & Elliot, 1986; Bergerud & Elliott, 1998; Merkle et al., 2017). We based this prediction on the assumed abundance-disturbance relationships for NMC in northern BC (Cichowski et al., 2022), and evidence that in regions with relatively little anthropogenic activity and associated landscape disturbance caribou are an important diet item for wolves and bears (Merkle et al., 2017; Milakovic & Parker, 2011, 2013). Moreover, a lack of habitat disturbance eliminates the primary mechanism for DMAC, which we expected would reduce predation risk for caribou.

We did not have direct evidence that apparent competition was active across the study area. Moreover, we lacked empirical evidence that apparent competition was mechanistically responsible for the observed decline of caribou for some of the study subpopulations. Therefore, we made three critical assumptions: 1) anthropogenic habitat disturbance increased the potential for apparent competition via DMAC; 2) changes in the proportional composition of caribou and moose in the diet of wolves and bears was a reflection of the abundance of the two prey species; and 3) inferred declines in the abundance of caribou relative to moose was a result of predation and not some other limiting or regulating factor (e.g., disease, nutritional limitations).

Materials and methods

Wildlife hair sample collection

To estimate the diet of wolves and grizzly bears we collected hair samples to derive two common isotopic biotracers: $\delta^{13}C$ and $\delta^{15}N$. All consumer and source hair samples were collected through community science and Indigenous and non-Indigenous government programs. We developed a community science program to sample wildlife hair with Indigenous guardians, resident hunters, guide outfitters, trappers, and Indigenous and non-Indigenous government officials. We applied our community science program over two years (2022–2023). We provided sampling kits that included coin envelopes, hair sample labels, and a project infographic. Community science participants collected samples of guard hairs following harvest (hunted or trapped), and opportunistic sampling of bear hair from rub trees.

In addition to hair provided by community science participants, we gathered samples from provincial and territorial government programs that included compulsory inspection of hunted species, wildlife capture (e.g., GPS-collaring), and predator removal programs. That included samples provided by two projects focused on mark-recapture estimates of grizzly bear populations (Wetzin'kwa and Omineca). These hair samples were collected from barbed-wire corrals with non-reward scent lure. The secondary use of hair samples was approved by the University of Northern British Columbia's Animal Care and Use Committee (Protocol 2021-06).

Sample preparation and analysis

Wolves and grizzly bears molt annually beginning in late spring and terminating in late fall (Darimont & Reimchen, 2002; Jacoby et al., 1999). Accordingly, all wolf hair samples were collected during the fall and winter months. That maximized our opportunity to look at seasonal diet estimates. Grizzly bear hair samples were collected mostly during spring and fall. We partitioned each guard hair into three equal sections to estimate seasonal differences in diet. The tip, middle, and base sections reflected spring, summer, and fall diets respectively. We only partitioned hair samples when adequate hair was available; otherwise, complete guard hairs were used. This was the case for 34% of the grizzly bear samples. For prey hair samples, we processed whole guard hairs to register a single diet end-point per-individual. All hair samples were processed and analysed by Aquatech Enviroscience Laboratories Inc. (Saanich, British Columbia).

Hair samples were cleaned of surface oils with repeated rinses of a 2:1 chloroform/methanol solution and then dried in an oven at 60°C overnight. Approximately 0.2 to 0.8 mg of hair was weighed into a tin cup. Carbon and nitrogen isotope compositions were determined using a thermal combustion elemental analyzer (NA 1500 NC) coupled via a flow reducing interface (ConFlow IV) with continuous flow isotope ratio mass spectrometer (Thermo Finnigan MAT253). Each batch of samples included quality assurance and quality control (QA/QC) samples: four reference standards analyzed before and after each batch of samples, a sample duplicate, and a procedural blank. Both carbon and nitrogen isotope data were reported in conventional delta (δ) notation in units of per mil (‰) with reference to atmospheric nitrogen (air) and Vienna Pee Dee Belemnite (VPDB) carbonate standard, respectively.

Source selection

A critical assumption of Bayesian isotopic mixing models is that $\delta^{13}C$ and $\delta^{15}N$ values are unique among dietary prey (Ben-David & Flaherty, 2012; Phillips, 2012). Moreover, prey sources must be a plausible component of the diet of the consumer (Phillips et al., 2014). We used the *a priori* approach to assign known dietary items to source mixtures (Phillips et al., 2005, 2014). We referenced geographically and ecologically relevant diet studies, including those based on SIA (Merkle et al., 2017; Milakovic & Parker, 2011, 2013), scat analyses (Milakovic & Parker, 2011), and kill-site investigations (Anderson et al., 2023), to identify prey species for inclusion in the prey equations used to parameterize the Bayesian isotopic mixing models.

Wolves across much of their sub-boreal and boreal range are obligate consumers of ungulates (Hayes and Gunson, 1995; Peterson and Ciucci, 2003). We included moose and caribou as potential diet sources across the complete study area as both ungulates are important diet items for wolves (Bergerud & Elliott, 1998; Hayes et al., 2000; Merkle et al., 2017; Milakovic & Parker, 2011). In the low-disturbance study landscape, we included Stone's sheep (*Ovis dalli stonei*), an important prey species that occurred at moderate to high densities (Denny and Kriss, 2021; Lance Nagwan, personal communications, 2022). Stone's sheep are rare in the high-disturbance study landscape; thus, we excluded that species and included more abundant mountain goat (*Oreamnos americanus*). We excluded elk (*Cervus canadensis*) and mule deer (*Odocoilus hemionus*) based on their rarity across both study landscapes. Beaver (*Castor* *canadensis*) is a well documented diet item for wolves (Peterson and Ciucci, 2003) and was included for both study landscapes.

Grizzly bears are an omnivore with a wide-ranging feeding ecology that varies in relation to regional prey availability (Lamb et al., 2017; Mowat & Heard, 2006). Like wolves, we included both moose and caribou for the complete study area. In the low-disturbance study landscape, we included hoary marmot (*Marmota caligata*; Jung et al., 2023). In the high-disturbance study landscape, we included sockeye and kokanee salmon (*Oncorhyncus nerka*) given high concentrations in select major watersheds (Gottesfeld and Rabnett, 2008). For vegetation, we applied the Merkle et al (2017) isotope signature for combined vegetation to the entire study area.

We performed a K-nearest neighbour (KNN) randomization test to evaluate the isotope signature of individual and aggregated diet groups (Rosing et al., 1998). As part of the KNN procedure, samples for each diet item were split into training and test data. During this step, diet items with small sample sizes were excluded from either the training or test data. For these diet items, we randomly assigned samples to both training and test datasets.

Trophic fractionation

One of the most challenging components of stable isotope analysis of diet is identification of trophic enrichment factors (TEF; Bond & Diamond, 2011; Caut et al., 2009). Consumers have species-specific physiological processes that influence the isotopic ratios of the prey that are expressed in their tissue (i.e., fractionation; Ben-David & Flaherty, 2012; Caut et al., 2009). The application of the correct TEF accounts for differences in source macromolecular content and the consumer's assimilation process (Ben-David & Flaherty, 2012). Researchers have quantified

TEFs for several consumers (Derbridge et al., 2015; Felicetti et al., 2003; Hilderbrand et al., 1996). For wolves, we used the TEFs developed by Derbridge et al (2015) that closely matched our prey landscapes (mean ± SD; $\Delta^{13}C = 1.972‰ \pm 0.705‰$, $\Delta^{15}N = 3.04‰ \pm 0.313‰$).

There is not a universally accepted TEF for grizzly bear with particular uncertainty associated with the application of carbon isotopes (Felicetti et al., 2003; Mowat & Heard, 2006; Van Daele et al., 2013). We explored the effect of different $\delta^{13}C$ fractionation values and methods, as reported in the literature, and used a fixed carbon rate of 3.7‰ (SD ± 0.2‰; Fortin et al. 2007 and Van Daele et al. 2013). Following from past studies (Fortin et al., 2007; Mowat & Heard, 2006; Van Daele et al., 2013), we chose the Felicetti et al. (2003) regression equation to apply source specific nitrogen TEFs.

$$\Delta\delta 15N = (0.88 \times \delta 15N + 5.28) - \delta 15N.$$

Stable isotope mixing models

We used the MixSIAR Bayesian isotopic mixing model (R package MixSIAR, Stock and Semmens, 2016), to estimate relative proportions of prey within the seasonal and global diet of sampled wolves and grizzly bears respectively (Stock et al., 2018). A lack of *a priori* empirical information of the diet of wolves and grizzly bears in our study area eliminated the potential to use informative priors. Therefore, we specified uninformative prior Dirichlet distributions ($\alpha_k = 1$), with 1,000,000 iterations and a burn-in of 500,000, and evaluated model convergence using the Gelman-Rubin statistic (Brooks & Gelman, 1998). We elected to parameterize the mixing models with raw source data that included covariance between isotopes (Stock et al., 2018). We coupled the user-specified source isotope distributions with user-specified fractionation distributions to account for uncertainty in fractionation rates (Moore & Semmens, 2008). We specified season (spring, summer, fall) as a fixed effect. We assumed that wolves and grizzly bears sampled food items randomly through predation, scavenging, and foraging. Therefore, we parameterized the error structure as process *x* residual error (Stock & Semmens, 2016). We used the mean posterior values to represent the proportion of each diet item in an individual's diet.

Caribou and moose abundance ratios

A requirement of DMAC is that the primary prey (i.e., moose), should be more abundant or have greater available consumable biomass than the alternate prey (i.e., caribou; Holt et al., 1994; Holt & Polis, 1997). We would expect the more abundant prey to be more prevalent in the diet of the predator. Thus, we quantified the relative proportion (i.e., ratio) of caribou and moose in the diet of wolves and bears and used that measure as an index for DMAC.

As supporting evidence of DMAC, we summarised estimates of the abundance of caribou and moose. Population estimates of caribou were derived using a range of survey methods including mark-resight (Maricle et al, 2021; Thiessen et al, 2018), extrapolation based on estimated densities in different habitat types (Klaczek and Anderson, 2023), and total populations census (Wong and Greene, 2020). For the Horseranch subpopulation, we applied a published expert-based estimate of abundance (Cichowski et al., 2022). We calculated density as the reported estimate of abundance divided by the subpopulation boundary, as defined by the BC Government. Moose density was estimated using the stratified random block method (Anderson et al, 2022; Gasaway et al, 1986). In some instances, the survey area for moose did not correspond directly with the caribou subpopulation ranges but was the best approximation for the purpose of this study. Indeed, seven estimates of moose density directly overlapped with caribou subpopulation ranges. In total, the two ratios allowed us to index DMAC across the study area.

The estimates of abundance of caribou for most subpopulation in the low-disturbance study landscape were preliminary and did not include a measure of precision. Thus, we were unable to assess statistical differences in the ratio of the density of caribou and moose with the ratio of caribou and moose in the diet of sampled wolves and grizzly bears.

Ethics approval

All capture and handling of wildlife was approved by the University of Northern British Columbia's Animal Care and Use Committee (Protocol 2021-06).

Results

Source selection

The source $\delta^{13}C$ and $\delta^{15}N$ estimates were derived from hair samples of caribou, moose, Stone's sheep, mountain goat, hoary marmot, and beaver, and flesh samples of sockeye salmon (Table 2). Isotope data for plants and kokanee salmon were previously reported for projects that overlapped our study area (Merkle et al., 2017). We observed significant overlap in the isotopic signature of mountain goats and Stone's sheep (Figure 3). We chose not to combine these two sources. Following our *a priori* prey equation assignments, we included Stone's sheep in the low-disturbance and mountain goat in the high-disturbance study areas, respectively. Results from the KNN tests revealed that the prey equations used to parameterize the Bayesian isotopic mixing models had classification accuracies of > 75%, which indicates adequate uniqueness (Table 3).

Table 2 Mean (SE) isotope values of diet items used in Bayesian isotopic mixing models to estimate relative diets of wolf (*Canis lupus*) and grizzly bear (*Ursus arctos horribilis*). Samples were collected in two regions in northwest and northcentral British Columbia, Canada, between 2021–2023.

Region	**Source**	**n**	**δ^{13}C ± SE**	**δ^{15}N ± SE**
High-disturbance study landscape (south)	Caribou	80	-23.51 ± 0.09	4.87 ± 0.22
	Moose	73	-25.99 ± 0.09	2.34 ± 0.11
	Mountain goat	60	-24.54 ± 0.08	2.06 ± 0.12
	Sockeye Salmon	5	-21.15 ± 0.21	10.81 ± 0.34
	Kokanee	15	-31.62 ± 0.20	9.20 ± 0.06
	Beaver	24	-25.08 ± 0.21	4.64 ± 0.37
Low-disturbance study landscape (north)	Caribou	55	-23.72 ± 0.05	3.62 ± 0.14
	Moose	49	-25.81 ± 0.10	1.64 ± 0.12
	Stone's sheep	50	-24.20 ± 0.08	2.23 ± 0.11
	Marmot	3	-24.46 ± 0.07	2.18 ± 0.17
	Vegetation	66	-27.61 ± 0.20	0.14 ± 0.23

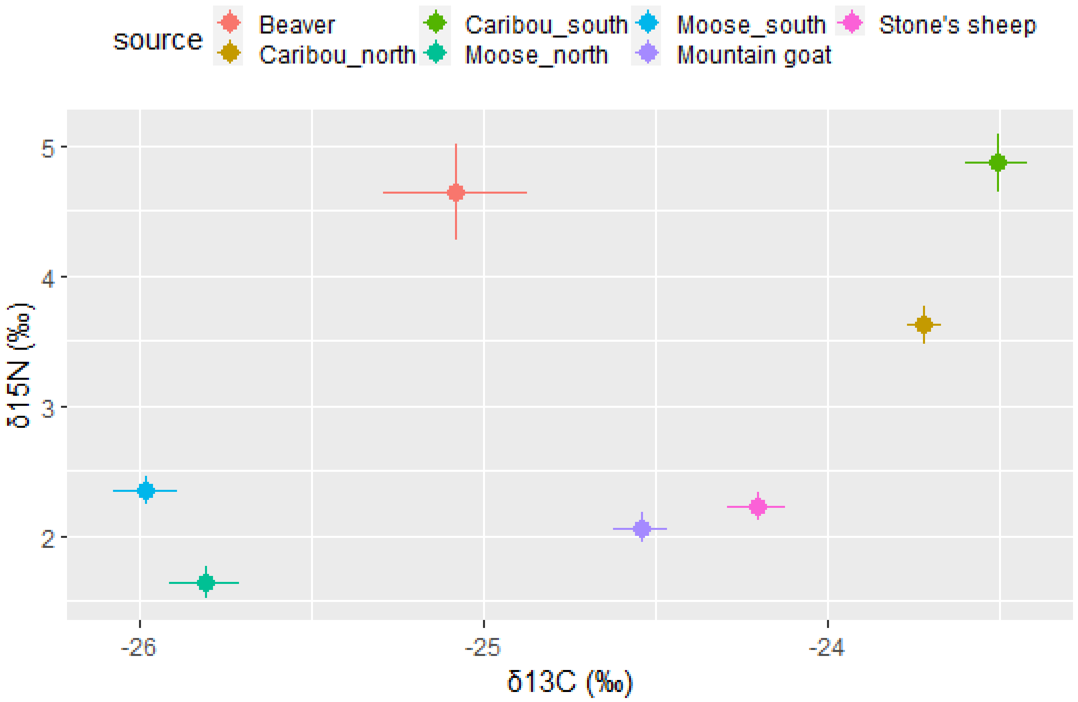

Figure 4 Mean (SE) source carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values from hair samples (guard hairs) used to parameterize Bayesian isotopic mixing models for estimating the diet of wolves (*Canis lupus*) in a low- (north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada, between 2021–2023.

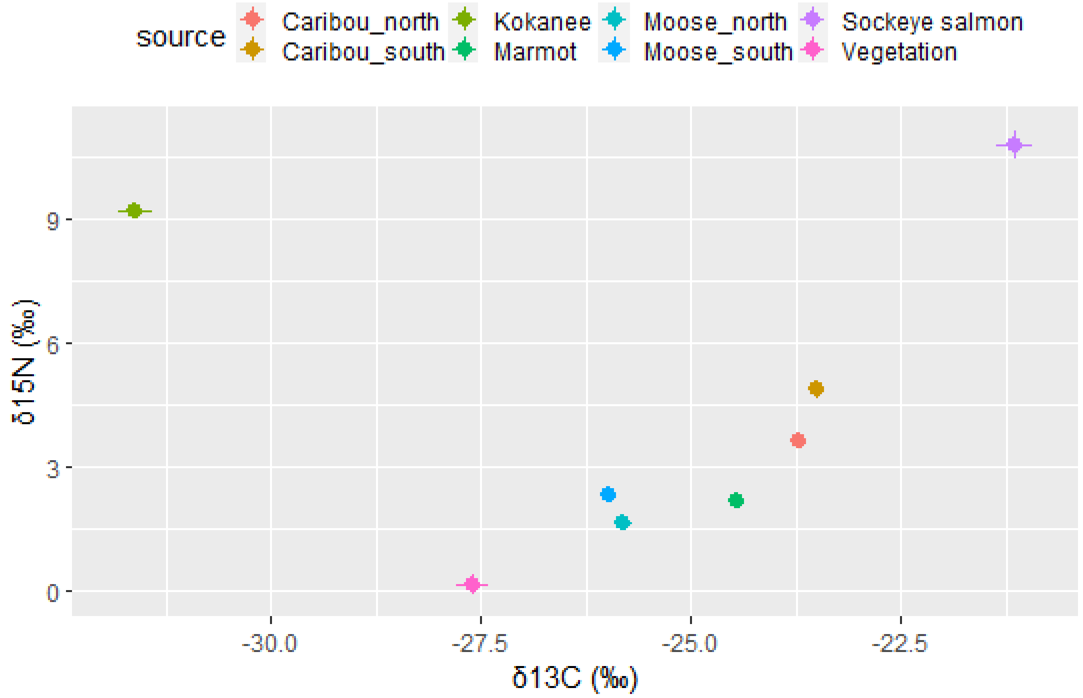

Figure 5 Mean (SE) source carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from hair samples (guard hairs) used to parameterize Bayesian isotopic mixing models for estimating the diet of grizzly bears (*Ursus arctos horribilis*) in a low- (north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada, between 2021–2023.

Table 3 Results of K-nearest neighbour test of isotopic uniqueness among prey within each source for Bayesian isotopic mixing models of diet of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*) in a low- (north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada, between 2021–2023.

Consumer	**Source mixture (study landscape)**	**Accuracy**	**P-value**
Wolf	caribou+moose+beaver+mountain goat (high-disturbance)	0.76	< 0.001
	caribou+moose+beaver+stone's sheep (low-disturbance)	0.81	< 0.001
Grizzly bear	caribou+moose+sockeye salmon+kokanee+vegetation (high-disturbance)	1.00	0.001
	caribou+moose+marmot+vegetation (low-disturbance)	0.88	< 0.001

Wolf diet estimates

We collected 208 samples of wolf hair from across the study area. Due to quality and quantity, some samples could not be processed and analyzed. We obtained $\delta^{13}C$ and $\delta^{15}N$ estimates from 68 and 57 wolves within the low- and high-disturbance study landscapes, respectively. In the high-disturbance study landscape (south), the proportional diet of wolves was dominated by beaver (fall 68% [0.50–0.91, 90% BCI], spring 66% [0.47–0.92], summer 67% [0.49–0.92]), followed by moose (fall 28% [0.04–0.46], spring 32% [0.03–0.49], summer 30% [0.03–0.48]). Caribou (fall 2% [0.00–0.07], spring 1% [0.00–0.07], summer 1% [0.00–0.06]) and mountain goat (fall 2% [0.00–0.08], spring 1% [0.00–0.10], summer 1% [0.00–0.09]) constituted a small proportion of the diet of wolves. In the low-disturbance study landscape (north), Stone’s sheep (fall 33% [0.14–0.55], spring 47% [0.11–0.69], summer 41% [0.15–0.62]) and moose (fall 33% [0.20–0.44], spring 30% [0.15–0.47], summer 31% [0.17–0.44]) contributed the most to the diet of wolves followed by caribou (fall 18% [0.02–0.36], spring 13% [0.01–0.38], summer 17% [0.01–0.37]) and beaver (fall 16% [0.06–0.25], spring 10% [0.02–0.20], summer 12% [0.03–0.22]). There was no notable seasonal variation in the diet of wolves across either study landscape (Table 4).

Table 4 Seasonal mean posterior density estimates (90% Bayesian credible interval; BCI) of the relative proportion of prey items in the diet of wolves (*Canis lupus*) sampled during 2021–2023 in a low- (north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada. Estimates were derived from Bayesian isotopic mixing models generated with hair samples from 57 and 68 wolves in the high-disturbance and low-disturbance study landscapes, respectively.

Region	**Source**	**Season**	**90% BCI**	**Mean**
High-disturbance study landscape (south)	Beaver	fall	0.50–0.91	0.68
		spring	0.47–0.92	0.66
		summer	0.49–0.92	0.67
	Caribou	fall	0.00–0.07	0.02
		spring	0.00–0.07	0.02
		summer	0.00–0.06	0.02
	Moose	fall	0.04–0.46	0.27
		spring	0.03–0.49	0.29
		summer	0.03–0.48	0.28
	Mountain goat	fall	0.00–0.08	0.03
		spring	0.00–0.10	0.03
		summer	0.00–0.09	0.03
Low-disturbance study landscape (north)	Beaver	fall	0.06–0.25	0.16
		spring	0.02–0.20	0.10
		summer	0.03–0.22	0.12
	Caribou	fall	0.02–0.36	0.18
		spring	0.01–0.38	0.15
		summer	0.01–0.37	0.18
	Moose	fall	0.20–0.44	0.32
		spring	0.15–0.47	0.30
		summer	0.17–0.44	0.31
	Stone's sheep	fall	0.14–0.55	0.34
		spring	0.11–0.69	0.44
		summer	0.15–0.62	0.39

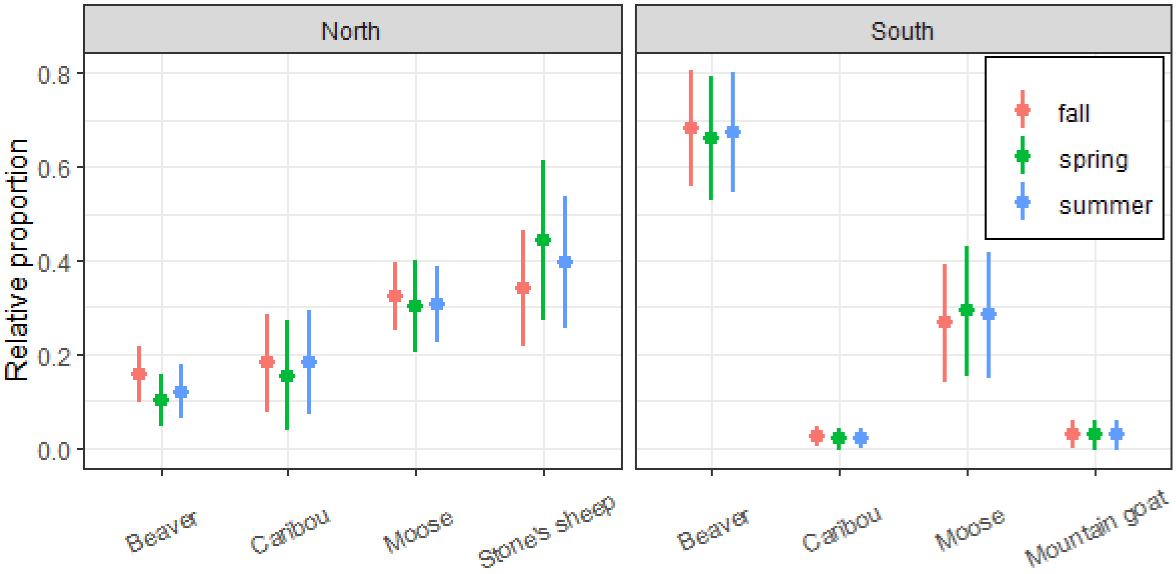

Figure 6 Mean (SD) posterior distributions of the seasonal diets for wolves (*Canis lupus*) in a low-(north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada, between 2021–2023. Distributions were calculated using hair samples and Bayesian isotopic mixing models.

Grizzly bear diet estimates

We obtained δ^{13}C and δ^{15}N estimates from 86 and 43 grizzly bears from within the low- and high-disturbance study landscapes, respectively. We did not complete seasonal diet analysis due to insufficient sample volume for many of the hair samples. Diet of sampled grizzly bears consisted mainly of vegetation within both study landscapes (north 79% [0.45–0.89, 90% BCI], south 94% [0.06–0.98]). Fish (kokanee 1% [0.00–0.52], sockeye salmon 1% [0.00–0.24]) were a small component of grizzly bear diets in the study area (i.e., high-disturbance study landscape) where they were available. Grizzly bears in the low-disturbance study landscape consumed a greater proportion of meat relative to the diet of grizzly bears in the high-disturbance, southern landscape. The proportional contribution of caribou (north 3% [0.00–0.12], south 1% [0.00–0.12]) and moose (north 7% [0.01–0.23], south 3% [0.00–0.22]) to grizzly bear diet was greater in the low-disturbance study landscape, but the differences were relatively small (Table 5).

Table 5 Seasonal mean posterior density estimates (90% Bayesian credible interval) of the relative proportion of prey items in the diet of grizzly bears (*Ursus arctos horribilis*) in a low- (north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada. Estimates were derived from Bayesian isotopic mixing models generated with hair samples from 43 and 86 grizzly bears in the high- and low-disturbance study landscapes, respectively.

Region	**Source**	**90% BCI**	**Mean**
High-disturbance study landscape (south)	Caribou	0.00-0.12	0.03
	Kokanee	0.00-0.52	0.14
	Moose	0.00-0.22	0.06
	Sockeye	0.00-0.24	0.06
	Vegetation	0.06-0.98	0.71
Low-disturbance study landscape (north)	Caribou	0.00-0.12	0.04
	Marmot	0.01-0.32	0.11
	Moose	0.01-0.23	0.09
	Vegetation	0.45-0.89	0.76

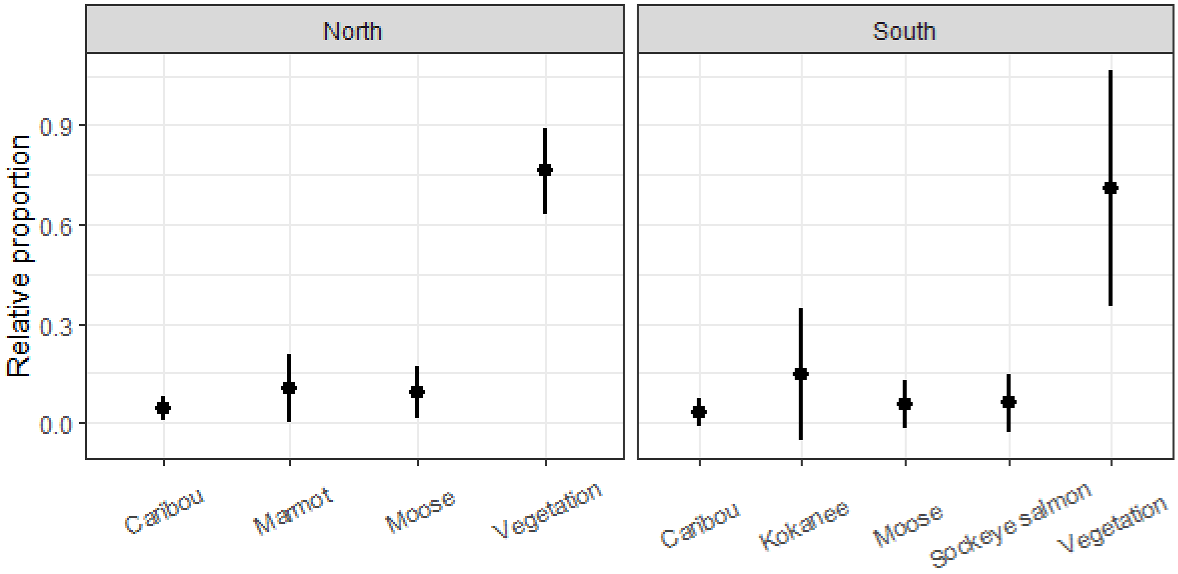

Figure 7 Mean (SD) posterior distributions of the proportional assimilation of annual (June-November) diets for two populations of grizzly bears (*Ursus arctos horribilis*) in a low-(north) and high-disturbance (south) study landscape in northwest and northcentral British Columbia, Canada, between 2021–2023. Distributions were calculated using hair samples and Bayesian isotopic mixing models.

Caribou to moose ratios

We compiled 11 mark-resight population estimates for caribou and 7 stratified random block surveys for moose that temporally overlapped with this study (2015–2023). Caribou subpopulations in the low-disturbance study landscape varied in density with a low of 0.03 caribou/km^2 and high of 0.34 caribou/km^2. Estimates of density in the high-disturbance study landscape varied between 0.01 and 0.04 caribou/km^2. Moose density was similar across both study landscapes (north 0.28–0.32 moose/km^2, south 0.22–0.35 moose/km^2). The SIA diet analysis suggested a lower relative proportion of caribou in the diet of wolves sampled from the high-disturbance landscape (caribou to moose diet proportion – high-disturbance = 0.07, caribou to moose diet proportion – low-disturbance = 0.55). This finding was consistent with the ratios of animal density quantified using population estimates (Table 6). Indeed, we did not have sufficient population estimate data to perform a statistical test for the relationship between the two quantified caribou to moose ratios. Moreover, the Bayesian credible intervals for the diet estimates of wolves demonstrated considerable variability in the diet proportions of caribou and moose.

Table 6 Density estimates of caribou (*Rangifer tarandus caribou*) and moose (*Alces americanus*) across a low- (north) and high-disturbance (south) landscape in northwest and northcentral British Columbia, Canada. Caribou and moose abundance ratios were derived from direct estimates of population density and an index of population density defined by the proportional diet of wolves (*Canis lupus*) estimated with stable isotope analysis (SIA). The SIA ratio was calculated as the proportions of caribou to moose in the diet of wolves (*Canis lupus*).

Region	**Subpopulation**	**Caribou density (caribou/km^2) and year of estimate**	**Moose density (moose/km^2) and year of estimate**	**Density ratio**	**SIA ratio**
High-disturbance study landscape (south)	Tweedsmuir	0.01 (2021)	0.22 (2019)	0.04	0.07
	Telkwa	< 0.01 (2020)	0.35 (2023)	0.01	0.07
	Wolverine	0.03 (2023)	0.29 (2022)	0.11	0.07
	Chase	0.04 (2021)	0.34 (2020)	0.13	0.07
Low-disturbance study landscape (north)	Little Rancheria	0.11 (2023)	NA	NA	0.55
	Swan Lake	0.13 (2021)	0.32 (2021)	0.40	0.55
	Level-Kawdy	0.14 (2023)	0.32 (2021)	0.43	0.55
	Tsenaglode	0.34 (2021)	NA	NA	0.55
	Horseranch	0.03 (NA)	NA	NA	0.55
	Spatsizi	0.10 (2023)	0.28 (2017)	0.35	0.55
	Edziza	0.01 (2018)	NA	NA	0.55

Discussion

We quantified the diet of two sympatric predators in similar multiprey ecosystems yet contrasting disturbance regimes. We used those data as an index of the occurrence of DMAC for NMC, an evolutionarily and ecologically distinct type of woodland caribou (i.e., Designatable

Unit; COSEWIC, 2014). Notably, previous studies of woodland caribou have used estimates of vital rates or abundance to identify the occurrence of apparent competition (Frenette et al., 2020; Serrouya, Wittmann, et al., 2015; Wittmer, Sinclair, et al., 2005). This is the first study to use diet of the predator, correlated with landscape disturbance, as an index of DMAC.

Wolf diet can serve as an indirect measure of the relative proportion of available prey in an ecosystem (Jędrzejewski et al., 2012). Although wolves across our study area likely consumed many prey species, including small mammals, fish, and birds (Peterson and Ciucci, 2003), we were most interested in determining if wolf diet could serve as an estimate of the availability of caribou and moose across the study area. Our results suggested that across landscapes with a high-disturbance footprint, a requirement of DMAC, wolves consumed primarily beaver and moose, and trace amounts of caribou and mountain goat. By contrast, wolves in relatively intact ecosystems consumed markedly more caribou, yet similar amounts of moose as in the high-disturbance study landscape. Moreover, wolves sampled from the low-disturbance study landscape had a diet with more equal contribution from the four prey types (Figure 6).

Apparent competition rests on a particular mechanism, namely a numerical or spatial response of a predator to a primary prey with corresponding unsustainable predation and decline of the alternate prey (Holt et al., 1994). Habitat disturbance, particularly from human sources (Demars et al., 2019), has the potential to increase moose populations eliciting a numerical or spatial response by wolves while increasing predation risk for caribou (Anderson et al., 2018; Dickie et al., 2017; Seip, 2011). Thus, we assumed that a lower proportion of caribou in the diet of wolves in combination with an increase in anthropogenic disturbance would serve as correlative evidence of DMAC (Demars et al., 2019b; Neufeld et al., 2021). As a corollary to that relationship, a predator diet with similar parts caribou and moose would suggest that numeric or spatial DMAC was not occurring in the system or that it was occurring with a magnitude that could not be detected using SIA. Moreover, a lack of habitat disturbance would sever the mechanistic link between disturbance and moose abundance, and the numerical or distributional response of predators (Dickie et al., 2017), both fundamental requirements for DMAC as observed in western Canada (Demars et al., 2019).

For both study landscapes, the caribou to moose ratio derived from SIA diet estimates was consistent with the abundance ratios that we quantified using population estimates (i.e., Table 6). Indeed, our results demonstrated considerable variability in the diet of wolves (i.e., Figure 6). Yet, the pattern of decreased caribou abundance and proportion of caribou in the diet of wolves with increasing habitat disturbance is evident. An extensive set of studies from across western North America support the assumed relationship between increasing moose and wolves, following disturbance, with a corresponding decrease in abundance of caribou (DeMars & Boutin, 2018; Serrouya et al., 2017, 2019, 2021; Wittmer et al., 2007).

For declining caribou subpopulations, predation is spatially associated with anthropogenic disturbance (DeCesare et al., 2014a; Derguy et al., 2025; Mumma et al., 2018). As a result, the two-fold impacts from anthropogenic disturbance whereby moose sustain wolf populations that efficiently predate on caribou drive the ratio of caribou relative to moose down (Latham et al., 2011; Neufeld et al., 2021). Indeed, our findings support other research that demonstrates a low ratio of caribou, relative to moose, when DMAC is suspected or observed in highly disturbed landscapes (Hervieux et al., 2014; Latham et al., 2011; Serrouya et al., 2019).

The relatively greater area of disturbance and absence of caribou from the diet of wolves sampled from the high-disturbance landscape suggested the occurrence of DMAC. Yet, the available monitoring data did not reveal large differences in the density of moose, a condition necessary to support the hypothesis of numerical DMAC. It is possible that the estimates of moose densities were incorrect, possibly due to an incorrect assessment of the area of habitat within each subpopulation area. Alternatively, caribou in the high-disturbance landscape may be suffering from spatial DMAC. Other studies from western Canada have suggested that the distribution of predators, or the vectors of their distribution, in particular roads and other linear corridors, is the most important factor influencing the mortality of caribou across disturbed landscapes (Apps et al., 2013; Mumma et al. 2018; McKay et al., 2021; Lochhead et al., 2022; Wilson 2024).

Other researchers used SIA and reported that caribou were an important component of the diet of wolves in landscapes relatively void of anthropogenic disturbance (Merkle et al., 2017; Milakovic & Parker, 2011). Similarly, Neufeld et al. (2021) quantified a caribou to moose abundance ratio not far from unity in a low productivity landscape that was assumed to be decoupled from DMAC. Thus, the relatively balanced diet of wolves in the low-disturbance study landscape suggested no measurable DMAC across the northern distribution of caribou that we studied.

We did not have data representing the density or distribution of wolves across the study area. Those data are necessary for a definitive test of apparent competition. Indeed, existing models of wolf-prey relationships can be used to estimate wolf densities associated with the abundance of moose (Messier, 1994) and more generally prey biomass (Kuzyk & Hatter, 2014). For both study landscapes, moose densities (> 0.2 moose/km^2) could in theory support a wolf population (> 5 wolves/1,000km^2) capable of driving caribou numbers down (Bergerud & Elliot, 1986; Messier, 1994; Neufeld et al., 2021; Serrouya et al., 2021; Appendix D). However, the functional response of wolves to linear features and the distribution of moose at the landscape scale are important factors when considering variation in caribou predation (Mumma et al., 2018; Lochhead et al., 2021; Dickie et al., 2022; Wilson, 2025). The southern subpopulations of caribou ranged across areas with a greater density of anthropogenic disturbance, including roads, and are likely exposed to higher predation risk as a result.

As an omnivore, grizzly bear diets can vary across space and time. Mowat and Heard (2006) reported a trend of increasing meat-based diet for populations that ranged across northern latitudes. Van Elslander (2024) described two major dietary niches in BC: salmon on the BC coast and plants inland. Our results are similar to past diet studies of grizzly bear in northwest and northcentral BC. For example, Merkle et al. (2017) and Milakovic and Parker (2013) used SIA and reported that grizzly bears predominantly consumed vegetation. In our study, regardless of landscape disturbance, grizzly bears predominantly consumed vegetation. Grizzly bears consumed more moose than other terrestrial prey and caribou were a relatively small component of the diet in both study landscapes. Interestingly, grizzly bears from the high-disturbance study landscape consumed little to no fish even though some bears were sampled within salmon bearing watersheds (Figure 7).

Our analyses provided no evidence of apparent competition between caribou, moose, and grizzly bears. Although, grizzly bears may have been consuming ungulates during the early spring or late fall, before and after the period of hair growth. Also, individual bears are known to be specialists on the calves of ungulates (Bastille-Rousseau et al., 2011; Lesmerises et al., 2015; McLaren et al., 2021; Støen et al., 2022). Thus, even if the stable isotope signature of meat were to occur in the hair growth of grizzly bears, those individuals may only be a small proportion of the population and missed as a result of sampling variation (Lesmerises et al., 2015). However, a small number of predatory bears could have a significant impact on the trajectory of small and declining caribou populations (Johnson et al., 2019). Given the prevalence of a plant-based diet, SIA appears to be insensitive to differential consumption of moose and caribou or grizzly bear do not play an important role in apparent competition within the systems that we sampled.

Methodological considerations and limitations

As is typical of SIA, the estimate of wolf and grizzly bear diet was temporally coarse and limited to the period of hair growth for the predator. Some researchers have suggested that bear hair only starts to grow mid-June (VanElslander et al., 2025), after the peak in parturition of caribou and moose (Mueller et al., 2022). Salmon represents another time-sensitive caloric landscape for grizzly bears and wolves (Bryan et al., 2013; Darimont & Reimchen, 2002; Hilderbrand et al., 1999). The run timing of salmon populations is specific to the life-histories of those fish and that may occur after or near the completion of hair growth for bears and wolves (Gottesfeld and Rabnett, 2008). Moreover, bears are hibernating during winter, but wolves may differentially hunt moose or caribou during that time. This method did not allow us to quantify winter diets of wolves.

The Bayesian mixing models used statistical distributions to characterize uncertainties in source and consumer isotopic values (Moore & Semmens, 2008; Phillips et al., 2014). A large sample of isotopic signatures for prey can reduce uncertainty in estimating the mean $\delta^{13}C$ and $\delta^{15}N$ ratios

(Pearson & Grove, 2013). We invested considerable effort in gathering a relatively large sample of hair from across the study area for both the predator and their diet items. That allowed us to account for potential spatial and temporal variation in $\delta^{13}C$ and $\delta^{15}N$ signatures (Ben-David & Flaherty, 2012). Although, isotopic signatures in black-tailed deer had little variation across a large geographic area of coastal British Columbia (Darimont et al., 2009). Also, the large and spatially extensive sample size likely controlled for intraspecific variability in $\delta^{13}C$ and $\delta^{15}N$ signatures. The large number of hair samples for most diet items reduced the influence of using uninformative priors (Moore & Semmens, 2008), which was important given the lack of information for our study area to derive informative priors.

All isotopic samples for prey were collected from adults, which can potentially underestimate consumption if there are differences in isotopic signatures between age classes. We included neonate hair samples for caribou from the Klinse-za maternity pen (Lamb et al., 2022) to test for trophic enrichment between offspring and maternal caribou that was observed in other studies (Jenkins et al., 2001). Consistent with Jenkins et al. (2001), we observed intraspecific differences in $\delta^{13}C$ and $\delta^{15}N$ between neonate and adult caribou (Appendix C). However, the bias in diet estimates associated with those differences was likely small given milk-dependent neonates are only available to predators during a short period of time (Jenkins et al., 2001; Milakovic & Parker, 2011). Jenkins et al. (2001) reported no difference in $\delta^{13}C$ and $\delta^{15}N$ between those age classes of moose. We did not test for age-related differences in isotopic signature for moose.

Modelling of diet with stable isotopes is most precise when trophic enrichment in isotopic ratios increase through the food web, from primary producer to herbivore to predator (Ben-David & Flaherty, 2012). Yet it is common to observe trophic enrichment within guilds (i.e., terrestrial mammals; Breault et al., 2021), and among sympatric species with a similar ecology (see Darimont et al., 2007). Consistent with our data, multiple authors reported unique isotopic signatures among ungulate species (Merkle et al., 2017; Milakovic & Parker, 2011). Our research also found an isotopically heterogeneous landscape for wolves, grizzly bears, and their prey. Isoscapes generated for this research can be used for future research focused on the diet of wolves, bears and other predators of caribou and moose (e.g., wolverine *Gulo gulo*, cougar *Puma concolor*) in this region (Appendix C).

Although the SIA method was efficient and relatively inexpensive, the estimates of diet proportion for our sample were relatively imprecise. Large measures of variance are not unusual for ungulates sampled from similar ecosystems (Milakovic and Parker, 2011; Merkle et al., 2017). That imprecision ultimately influences the strength of inference, especially when using diet as an index of a complex process such as DMAC. Although the data and method could resolve differences in diet for some items within a study landscape, we could not statistically differentiate differences when comparing the diet of wolves between landscapes. Alternative methods for assessing diet (e.g., O'Donovan et al., 2018) may lead to more precise estimates that could better reveal DMAC among subpopulations of caribou or landscapes.

Stewardship implications

More information is needed to better understand the temporal ebb-and-flow of apparent competition. For instance, in both study landscapes, population declines, and extirpation of caribou, corresponded with an era of increased human footprint and the emergence of moose (Bergerud & Elliot, 1986; Santomauro et al., 2012). Accordingly, there is precedent for apparent competition in both study systems during the early and mid 20th century. During the course of this study (2015–2023), the abundance of caribou in the high-disturbance study landscape appeared to be relatively stable, or the pace of population decline observed during the early 2000s had slowed (Lamb et al., 2024), while moose populations have declined and stabilized (Boucher et al., 2022). In the low-disturbance study landscape, moose and caribou populations trends are unknown but likely stable (Cichowski et al., 2022). It is possible that in recent years apparent competition is weakening as moose populations stabilize at low densities in both disturbed and undisturbed landscapes.

Our research advances a new, indirect method, for monitoring changes in the apparent competition dynamic between caribou and moose. Stable isotope analysis of the diet of wolves is a cost-effective, community-driven, and a scalable monitoring tool that can complement other methods for assessing the occurrence of DMAC. Many of the efforts focused on the conservation and recovery of caribou are a response to unsustainable predation as a result of DMAC. That includes efforts to reduce moose populations to elicit a negative numerical response in wolf populations (Lamb et al., 2024; Serrouya et al., 2017, 2019). More directly, wolf populations are being reduced through lethal control efforts (Lamb et al., 2024). Both moose and wolf reductions are controversial. Also, the efficacy of these conservation actions, in particular the reduction of moose populations, is dependent on an understanding of the occurrence of DMAC, a process that is inherently difficult to monitor.

The natural regulation of the caribou-moose-wolf system may occur in-lieu of recovery efforts such as moose or wolf reductions. For instance, there is evidence of recent (2014–2023) stability of caribou populations with (i.e., Tweedsmuir) and without (i.e., Chase, Telkwa, Wolverine) predator management (Lamb et al., 2024). Northern subpopulations across the low-disturbance study landscape are relatively abundant despite cooccurrence with moose densities ($\geq$0.28 moose/km^2) that, in theory, could support wolf population capable of reducing caribou populations (Bergerud & Elliot, 1986; Serrouya et al., 2021). Future research should focus on monitoring and quantifying the prevalence and impacts from apparent competition in systems with little to no habitat disturbance. Moreover, future research should focus on whether apparent competition is being naturally regulated by recent moose population declines across the range of NMC.

The recent stability of caribou in the high-disturbance study landscapes may be a reflection of recent declines of 50–70% in moose populations across some portions of central BC. Those declines could be the result of extensive salvage harvest of trees that were killed by mountain pine beetle (*Dendroctonus ponderosae*) and the resulting reduction in the quality of habitat or increased predation of moose (e.g., Mumma et al., 2021). Declines in moose abundance would dampen apparent competition with caribou and illustrate limits or nonlinearities in that relationship. Despite the uncertainty in our understanding of the population dynamics of moose and caribou in BC, our results suggest that conservation efforts are needed to recover and expand caribou habitat to approximate the conditions in the north that appear to facilitate caribou and moose coexistence. The principal condition being relatively little human-caused forest disturbance across low-elevation habitat.

Chapter 3 | Northern mountain caribou range contraction with increasing habitat loss and altered predator-prey dynamics

Introduction

Shifts in species distribution occur across spatial and temporal scales in response to a suite of natural and human-mediated processes. For instance, past climate regimes had major biogeographical (e.g., geographical distribution shifts as species track suitable habitats) and evolutionary (e.g., in situ adaptation to new climates and habitats) effects that influenced species distribution across western North America (Meiri et al., 2020; Polfus et al., 2017; Williams & Blois, 2018). Humans are the primary drivers of contemporary ecological change that has increased the pace of range shifts with resulting strong effects on community structuring and interactions (Boivin et al., 2016; Lendrum et al., 2018; Service et al., 2014; Stuart et al., 2000). In some cases, novel communities emerge from changes in the distribution of individual species that can have cascading trophic effects through interspecific interactions (Wisz et al., 2013). Thus, understanding the distributional response of wildlife to anthropogenic land use and species interactions is critical to predicting future range shifts.

Woodland caribou in North America has demonstrated a dramatic change in distribution as a result of climate, habitat loss, and altered predator-prey dynamics (Labadie et al., 2023; Morineau et al., 2023; Taylor et al., 2021). Pleistocene glaciation resulted in subpopulation expansion, contraction, and introgression that shaped the evolutionary path and current distribution of woodland caribou (Letts et al. 2012, Yannic et al. 2014, Polfus et al. 2017, Taylor et al. 2021). Caribou have an inherent capacity for plasticity in distribution that is the result of genetic traits or learned behaviour (Cavedon et al., 2022; Theoret et al., 2022). However, those historic ecological factors likely pale in comparison to the effects of contemporary anthropogenic land use that is outpacing the ability of caribou to respond (Morineau et al., 2023). As a result, we are witnessing range contraction and the extirpation of subpopulations (Festa-Bianchet et al., 2011).

As habitat disturbance increases, caribou move less (Dyer et al., 2002), reduce the size of their range (Beauchesne et al., 2014; Donovan et al., 2017; Smith et al., 2000; Wilson et al., 2019; Wittmer, McLellan, et al., 2005), and shift their seasonal range to lower-quality habitats (e.g., MacNearney et al., 2016; Poole et al., 2000). Yet the mechanisms that are responsible for these behavioural and distributional responses are complex and intertwined. For example, across much of western North America, resource development has changed the structure, species composition, and age of forests occupied by caribou (Nagy-Reis et al., 2021; Serrouya et al., 2021). The loss of mature forests has resulted in broad-scale reductions in functional habitat (COSEWIC, 2014; Courtois et al., 2007; Maltman et al., 2024). Moreover, increased rates of disturbances (natural and anthropogenic) have resulted in a more contiguous arrangement of early successional forest. These forest types increase the number and extent of generalist herbivores such as moose and deer (Bergerud & Elliot, 1986; Decesare et al., 2020; Latham et al., 2011; Santomauro et al., 2012). The expansion of moose and deer has increased the abundance and distribution of wolves, a shared predator with caribou (Fuller et al., 2003; Kuzyk & Hatter, 2014; Serrouya et al., 2021). As a result, caribou are facing increased and often unsustainable predation as a component of an asymmetrical predator-prey dynamic (Beauchesne et al., 2014; Courtois et al., 2007; Festa-Bianchet et al., 2011a; Latham et al., 2011; Serrouya et al., 2021). This process, known as DMAC, is often a product of human-caused forest disturbance.

Given that distributional dynamics are mediated by both environmental conditions and species interactions (Wisz et al., 2013), it is important to account for biotic interactions to enhance our understanding of range shifts (Trainor et al., 2014). Indeed, the ecology of woodland caribou in western Canada is well described (Seip & Cichowski, 1994; Theoret et al., 2022; Wittmer, McLellan, et al., 2005). That includes theoretical expectations for the distribution of caribou (e.g., “spacing out” from predators; Bergerud & Page, 1987) and documentation of population decline as well as rapid range contraction and extirpation (Festa-Bianchet et al., 2011). However, there have been few studies directly testing for a relationship between range contraction and DMAC at the scale of the subpopulation. Accounting for the spatial response of woodland caribou to DMAC can enhance our understanding of how caribou distribution is shaped by habitat disturbance.

We used a space-for-time experimental design to investigate differences in caribou distribution across contrasting habitat disturbance footprints for 11 subpopulations of NMC. We used GPS-collar locations to quantify the seasonal home ranges and elevational profiles of individual female caribou from those subpopulations. We quantified the effects of both top-down (i.e., DMAC) and bottom-up (i.e., habitat disturbance) factors on home range area and elevation use. Caribou to moose abundance ratios (Chapter 2), an index of DMAC, allowed us to account for the potential effect of altered predator-prey dynamics on caribou distribution.

Given the assumed relationship between the decline of caribou and DMAC, we expected range contraction to be most apparent for subpopulations with a greater extent of anthropogenic disturbance and low caribou to moose ratio (i.e., signal for DMAC). We hypothesised a reduction in home range area and a greater use of high-elevation range following a proportional increase in disturbance and subsequent DMAC (MacNearney et al., 2016; Poole et al., 2000; Smith et al., 2000; Williams et al., 2021; Wittmer, McLellan, et al., 2005). As a corollary to that relationship, caribou confronted with less disturbance and no DMAC (i.e., higher caribou to moose abundance ratio) would range across larger areas that included low-elevation habitats that is typical of the ecology of this ecotype of caribou (COSEWIC, 2014). Our research provided new insights into the distributional response of NMC to habitat disturbance and DMAC (Trainor et al., 2014). Moreover, our space-for-time study design allowed us to anticipate future range shifts in the face of accelerating habitat loss and potential for DMAC (Nagy-Reis et al., 2021; Tucker et al., 2018).

Materials and Methods

Experimental design

We used a space-for-time experimental design to quantify the relationship between the distribution of NMC caribou and landscape change. We selected 11 subpopulations of NMC according to data availability. These caribou subpopulations differed according to the area of wildfire and anthropogenic disturbance across low-elevation ecosystems. Generally, subpopulations at the southern extent of NMC had greater anthropogenic disturbance and lower caribou to moose abundance ratio. That trend of increasing disturbance, DMAC, and decline is consistent with other types of woodland caribou in Canada (Morineau et al., 2023; Schaefer, 2003).

We used available GPS-collar locations to estimate seasonal home range area and mean elevational profiles of 295 female caribou. Each caribou was assigned to a subpopulation (i.e., Telkwa, Spatsizi, etc.,) during the process of capture and GPS-collaring. Thus, subpopulation assignment dictated the range-wide covariates that were attributed to the individual caribou.

We used generalized linear mixed effects models to relate home range area and mean elevation profile to anthropogenic and wildfire disturbance footprints, an index of DMAC derived from the caribou to moose ratios quantified in Chapter 2, and six environmental factors that allowed us to control for ecological variability among subpopulations (Table 7). The analysis tested for a relationship between landscape-scale factors that might result in changes in the distribution of caribou across the broader range of the subpopulation, not a relationship between home range area and mean elevation profile at any one place in the range. The focus on range-wide attributes allowed for an analysis and test of displacement, not selection of seasonal ranges within the broader distribution of the subpopulation.

GPS data

Adult female caribou were captured between 2014 and 2023 using aerial netgunning and fitted with GPS collars. We collaborated with three governments who permitted and supervised the capturing and collaring of caribou. Those governments included the Tahltan Central Government, BC Government, and Yukon Territorial government. All protocols were approved by UNBC's Animal Care and Use Committee (ACUC 2021-06). Collars were programmed to provide a range of fix rates (i.e., 2–6 locations/day).

Prior to data analysis, we used the animal movement tools (AMT) R package to clean the GPS-collar data (Signer et al., 2019). That process included removing low-quality locations based on the dilution of precision (i.e., DOP < 6) and removing locations that displayed unreasonably fast movements or that occurred outside the expected range of the collared caribou (i.e., outliers). We divided the data into two seasons, roughly corresponding with snow (November 1 – May 15), and snow-free (May 16 – October 31) periods. To ensure sufficient location data, we only included individual caribou with a minimum of 90 locations per season.

Environmental data

Methods for quantifying the spatial area of habitat disturbance were described in Chapter 1. We generated a measure of anthropogenic habitat disturbance that included cutblocks, roads, and static disturbances. We included wildfire as a separate disturbance agent. All disturbances were 40 years or less to account for the temporal response of caribou to disturbance (Courtois et al., 2007), and the seral transition to a state that is less compatible with moose occurrence (Fisher & Wilkinson, 2005).

We statistically controlled for other environmental factors that were known to influence caribou distribution yet were not directly related to the primary hypotheses of the research. Those controls also allowed us to account for large-scale ecological and environmental differences among subpopulations. Caribou are known to modify their seasonal distribution in response to snow depth (Farnell et al., 1996; Lessard et al., 2025). For example, variation in snow depth can influence the energetic costs associated with movement and feeding, and subsequently habitat selection (Kinley et al., 2006; Lessard et al., 2025). For each regression model, we included a measure of the Normalized Difference Snow Index (NDSI) for the year during which GPS-locations were collected. The NDSI was generated using Google Earth Engine derived from NASA’s Moderate Resolution Imaging Spectroradiometer at a resolution of 500m (MODIS, MOD09GA_006_NDSI; Riggs et al. 1994).

We used the Enhanced Vegetation Index (EVI) to represent annual net primary productivity for each seasonal caribou range. The EVI allowed us to control for potential differences in vegetation productivity that can influence moose abundance (Dickie et al., 2022), and how moose respond to disturbances (Neufeld et al., 2021). Those responses by moose will directly influence the magnitude of DMAC. The EVI was generated with MODIS Terra Vegetation Indices 16-Day Global data (500m cell) compiled with Google Earth Engine. For each year, the median leaf-off was subtracted from the median leaf-on to calculate the change in EVI (ΔEVI).

To account for the potential for topography to influence the habitat, disturbance and, ultimately, the distribution of mountain caribou (Oosenburg & Theberge, 1980), we used a digital elevation model to calculate a topographic ruggedness index (TRI) using the Terra package in R (Hijmans, 2025). Additionally, we wanted to control for the relative availability of low-elevation habitats for each subpopulation range as this has implications for the elevation use by caribou. We quantified the percentage of each range that was below the approximate treeline (< 1200m) for sub-boreal forested landscapes.

Demographic data

Generally, small populations have smaller seasonal ranges (Balluffi-Fry et al., 2025; Gaston & Blackburn, 1996; Wilson et al., 2019). Indeed, small and declining populations of caribou have demonstrated range contraction (MacNearney et al., 2016; Morineau et al., 2023; Wilson et al., 2019). Thus, we included a contemporary estimate of density for each of the 11 subpopulations within each regression model. Aerial mark-resight surveys and resulting population estimates were conducted (2015–2023) by Indigenous and non-Indigenous governments for most of the study subpopulations. The estimate for the Horseranch subpopulation was based on the expert opinion of staff with the BC provincial government. We used the subpopulation range boundaries from the BC provincial government to generate a density estimate from the total population estimate.

Apparent competition index

We used estimates of the density of caribou and moose to quantify the ratio of caribou to moose for each subpopulation. The differential abundance of two prey species is a component of apparent competition (Holt, 1977; Neufeld et al., 2021). In subpopulations that did not have overlapping estimates of caribou and moose density (Little Rancheria, Tsenaglode, Horseranch, Edziza), we used the ratio of caribou to moose in the diet of wolves (Chapter 2) to represent the abundance ratio of the two species.

Statistical analysis

We used an autocorrelated kernel density estimator (AKDE) from the continuous-time movement modeling (CTMM) package in R to quantify seasonal home range area (Fleming and Calabrese, 2023). Unmodelled autocorrelation or bias, oversmoothing, and unrepresentative sampling in time can result in over-estimation of home range size. This is common in other home range estimators and the primary reason we chose the AKDE method (Fleming & Calabrese, 2017; Silva et al., 2022). We chose a 50% isopleth core home range (Fieberg & Börger, 2012; Wilson et al., 2010), with a 95% confidence interval (Fleming & Calabrese, 2017). The 50% isopleth was more likely to represent the core area of use for NMC, an ecotype of caribou that are atypical range residents with large seasonal movements (Cavedon et al., 2022; Theoret et al., 2022).

We developed home ranges for two seasons, winter (snow November 1 – May 15) and summer (snow free May 16 – October 31). During winter, NMC are more sedentary, typically using low-elevation forested areas or wind-swept ridges (COSEWIC, 2014). During the growing season (snow-free), NMC move more widely to accommodate a greater number of life-history requirements that include seeking out high-quality forage, parturition and support of a calf, and participating in the rut (COSEWIC, 2014). There are subtleties and nuances in range use by each subpopulation that can be mediated by the condition of the landscape. Yet, these two seasons represent periods of relative range residency for caribou, which is an important assumption for AKDEs (Fleming & Calabrese, 2017). We also developed mean elevation profiles during the snow and snow-free seasons for individual caribou. We used GPS locations and a digital elevation model to quantify the elevation for each point location. We averaged those elevations for each individual caribou/season/year combination. Each caribou had 1–12 unique caribou/season/year/AKDE and caribou/season/year/elevation profile combinations based on two seasons/year and 1–6 years of monitoring.

Table 7 Description of variables used with generalized linear mixed effect models to explain seasonal (snow and snow free) home range area and elevation use for northern mountain caribou (*Rangifer tarandus caribou*) monitored between 2015–2023 in northcentral and northwestern British Columbia, Canada.

Variable	**Type**	**Description**
Home range area	Response	Autocorrelated kernel density estimate for seasonal home range area (km^2) for each unique caribou/season/year combination
Mean elevation profile	Response	Mean elevation derived from GPS locations and a digital elevation model for each unique caribou/season/year combination
Anthropogenic (An)	Explanatory	% area of the subpopulation range area consisting of forestry cutblocks and roads (< 40 years old), and static disturbances (settlement, agriculture, mining, and linear infrastructure) at < 1200m in elevation
Fire (Fi)	Explanatory	% area of the subpopulation range area consisting of wildfire (< 40 years old) at < 1200m in elevation
C:M Ratio (Cm)	Explanatory	Ratio of caribou to moose derived from the SIA estimate of the diet of wolves and population estimates of caribou and moose quantified at the subpopulation level
Net primary productivity (EVI)	Control	Terra vegetative indices derived from MODIS (MOD13A1) data; averaged over a 16-day period at a 500m resolution quantified at the subpopulation level
Snow cover index (NDSI)	Control	Snow depth derived from MODIS (MOD09GA_006_NDSI) data; averaged daily at a 500m resolution quantified at the subpopulation level
Season	Control	Categorical variable for snow and snow-free seasons
Low-elevation range (LER)	Control	% of subpopulation range area < 1200m
Terrain Ruggedness Index (TRI)	Control	Index from 0 to 1 representing topographic heterogeneity quantified at the subpopulation level
Caribou abundance (Pop)	Control	Total abundance estimate divided by subpopulation range area at the subpopulation level
Subpopulation and Individual caribou (1|subpop/ind)	Nested random effect	Subpopulation and individual caribou from which home range area and elevation profile was calculated and averaged to the respective subpopulation

We developed seven *a priori* model hypotheses to explore the relationship between the distribution of monitored caribou and habitat disturbance and DMAC. We built models that included combinations of the two "bottom-up" explanatory factors: anthropogenic and wildfire disturbance footprints (Table 7). We developed a model hypothesis for "top-down" effects that included the DMAC index (i.e., caribou to moose abundance ratio). Additionally, we developed model hypothesises that represented the combined effects of habitat disturbance and DMAC, such as anthropogenic disturbance and DMAC, wildfire and DMAC, and finally our global model of anthropogenic and wildfire disturbances, and DMAC (Table 9). For comparisons of model fit, we included a random intercept model and a null model that only included the control covariates.

We derived the model hypotheses to represent our understanding of the ecology of the study area and the literature focused on the predator-prey dynamics of caribou. For example, anthropogenic disturbance is well established as a principal factor that affects caribou distribution (MacNearney et al., 2016; Wilson et al., 2019). Although the impacts of wildfire are still debated, there is evidence that caribou avoid burned habitat (Konkolics et al., 2021; Palm et al., 2022; Russell, 2018; Stevenson et al., 2024). Caribou are known to "space-out" to avoid predators and other prey (Bergerud & Elliot, 1986; Wilson et al., 2019). Moreover, caribou are functionally extirpated from parts of their range (i.e., low elevations; Santomauro et al., 2012), the proximate cause being unsustainable predation (i.e., top-down effects; Courtois et al., 2007; Wittmer, Sinclair, et al., 2005). Thus, we tested the DMAC index (Chapter 2) as an explanation of observed changes in caribou distribution (Trainor et al., 2014). Whereby, a low caribou to moose ratio in conjunction with high habitat disturbance footprint signals DMAC. For each model, we consistently included the variables that served as statistical controls for environmental and demographic variation among study subpopulations.

We used the variance inflation factor (VIF) to test for multicollinearity (VIF < 10) among independent variables (Vittinghoff et al. 2012). We used a z-transformation to standardize the explanatory and control covariates (Base R). We log transformed the measure of home range area to reduce the influence of large, infrequent values, typical of home range data, and increase normality of residuals.

We used generalized linear mixed models (GLMM; family=Gaussian, link=identity) to test for a statistical relationship between home range area or average seasonal elevation of monitored caribou and the hypothesised explanatory variables. We included a nested random intercept term (1|subpopulation/individual) to statistically account for repeated sampling within clusters (i.e., subpopulation) of sample units (i.e., individual collared caribou). We used Akaike's information criterion corrected for small sample size (AIC_c) and the difference in in AIC_c scores (ΔAIC_c) to rank model hypotheses and the null and random intercept models (Anderson et al., 2000). According to this criterion, the model with the lowest AIC_c value is the most parsimonious. We reported models with a $\Delta AIC_c < 2$ (Anderson et al., 2000; Anderson & Burnham, 2002). We assessed overall model fit by comparing the most parsimonious models to the null and intercept only models. Also, we reported the coefficient of determination (R^2) for the top-ranked models. Finally, model coefficients were considered influential when the 95% confidence interval did not overlap zero.

Results

Caribou locations

A total of 699,742 GPS locations were collected from 2015–2023. We estimated 1317 unique caribou/season/year seasonal home ranges and mean elevation profiles for 295 individual female caribou from 11 subpopulations of NMC (Table 8). The home range sample included 738 snow and 579 snow-free home ranges.

Table 8 Mean home range area quantified using an auto-correlated kernel density estimator and mean elevation profile quantified using the average elevation from locations collected for GPS-collared female caribou (*Rangifer tarandus caribou*). Sample size represents the number of unique caribou/year/season for each of the 11 northern mountain caribou subpopulations monitored between 2015–2023 in northcentral and northwestern British Columbia, Canada. Subpopulations were classified as low disturbance (LD) or high disturbance (HD) according to the extent of anthropogenic disturbance.

	Home Range Size (km^2)			**Elevation Profile (m)**		
	mean	SD	n	mean	SD	n
Level-Kawdy (LD)	7340	6354	105	1317	180	105
Little Rancheria (LD)	3532	2918	175	1273	237	175
Swan Lake (LD)	2274	3455	77	1304	200	77
Horseranch (LD)	1635	1785	16	1433	212	16
Tseneglode (LD)	1577	2375	50	1561	123	50
Spatsizi (LD)	1158	1282	88	1598	176	88
Tweedsmuir (HD)	1469	1972	345	1352	222	345
Chase (HD)	665	1176	292	1657	150	292
Wolverine (HD)	578	1206	90	1606	180	90
Edziza (LD)	323	391	13	1520	132	13
Telkwa (HD)	230	232	66	1722	62	66

Home range area and model selection

Caribou subpopulations in the high-disturbance study landscape had smaller mean home range areas compared to caribou in the low-disturbance study landscape (Table 8). Small home ranges were particularly evident in subpopulations with the greatest anthropogenic disturbance footprint (e.g.., Telkwa, Wolverine 28% and 19% anthropogenic disturbance, respectively). Conversely, caribou in the low-disturbance study landscape had larger mean home range sizes (Table 8). Caribou from the Edziza subpopulations were the exception.

Two regression models had nearly equal support in explaining the area of seasonal home ranges. The first model included the anthropogenic and wildfire disturbance covariates and supported the "bottom-up" hypothesis that greater footprint of habitat disturbance resulted in smaller home ranges ($AIC_c w = 0.59$, $R^2 = 0.31$). The second-ranked model was the global model that included an additional covariate representing the ratio of caribou to moose, and our hypothesis that both habitat disturbance and DMAC influence home range area ($AIC_c w = 0.36$, $R^2 = 0.28$). The two top models were ranked considerably higher than the random intercept and null models, and both explained a reasonable amount of the variation (R^2) in home range area (Table 9). For the global model, anthropogenic disturbance, wildfire disturbance, and caribou to moose abundance ratio were negatively correlated with home range area. The standardized coefficients from the top ranked model revealed that anthropogenic disturbance had the strongest effect size ($\beta = -1.22$, 95% CI = -2.13, -0.32) relative to observed variation in home range area (Table 9). Wildfire had the least variation of the coefficients. The 95% confidence intervals for the caribou to moose abundance ratio overlapped 0 for all models. The relationship between range size and caribou abundance was negative in the global model, but positive in lesser ranked, more simple models suggesting considerable covariation with anthropogenic disturbance (Figure 8).

Table 9 A *priori* hypotheses with explanatory and control covariates (ΔEVI + NDSI + SSN + LER + TRI + POP), and nested random effect (1|subpop/ind) used to explain home range area of female northern mountain caribou (*Rangifer tarandus caribou*) between 2015–2023 in northcentral and northwestern British Columbia, Canada. For each model the effect size of explanatory covariates and 95% confidence interval (CI), Akaike score (ΔAIC_c) and weight (AIC_c *w*), and coefficient of determination (R^2) are shown.

Hypothesis	**ΔAIC_c**	**AIC_c *w***	**R^2**	**An (CI)**	**Fi (CI)**	**Cm (CI)**
An + Fi + Controls + (1|subpop/ind)	<0.01	0.59	0.31	-1.22 (-2.13, -0.32)	-0.85 (-1.41, -0.55)	
An + Fi + Cm + Controls + (1|subpop/ind)	0.96	0.36	0.28	-1.92 (-3.51, -0.33)	-0.91 (-1.23, -0.60)	-0.82 (-2.41, 0.76)
Cm + Fi + Controls + (1|subpop/ind)	5.59	0.04	0.29		-0.70 (-0.97, -0.44)	0.71 (-0.24, 1.67)
Fi + Controls + (1|subpop/ind)	7.28	0.02	0.21		-0.68 (-0.94, -0.42)	
Null: Controls + (1|subpop/ind)	22.37	<0.01	0.25			
An + Controls + (1|subpop/ind)	22.69	<0.01	0.24	-0.17 (-0.73, 0.39)		
Cm + Controls + (1|subpop/ind)	22.93	<0.01	0.25			0.24 (-0.35, 0.82)
An + Cm + Controls + (1|subpop/ind)	24.67	<0.01	0.24	0.21 (-0.92, 1.33)		0.41 (-0.77, 1.58)
Random intercept: (1|subpop/ind)	35.68	<0.01	<0.01			

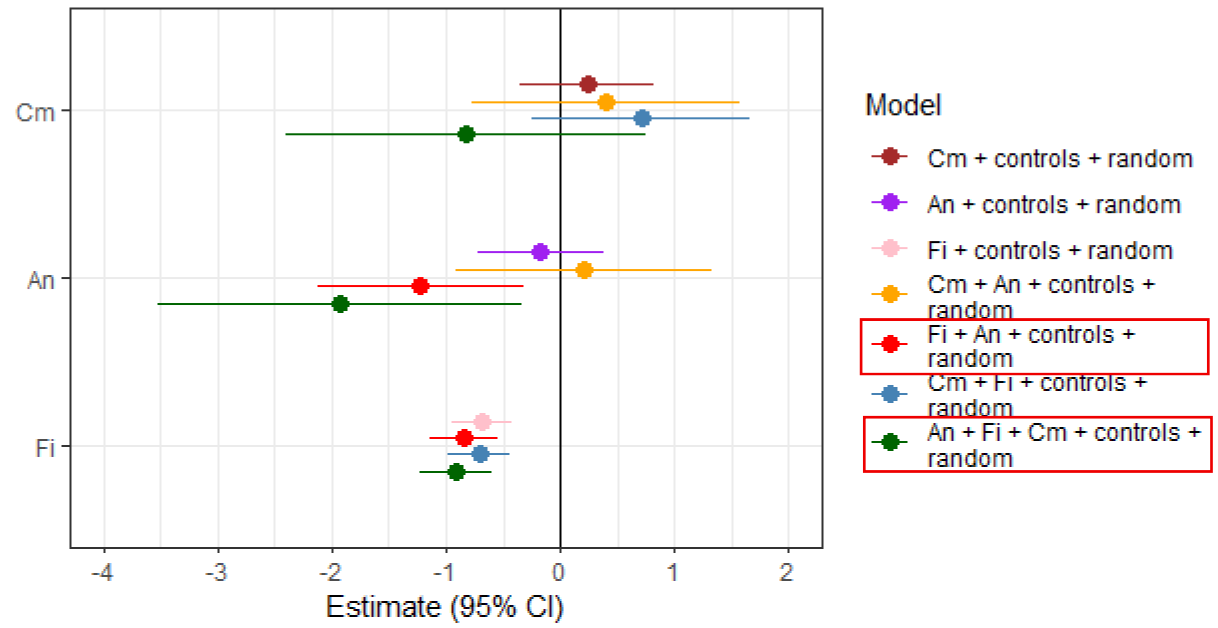

Figure 8 Effect size for explanatory covariates (CM: caribou to moose abundance ratio, An: anthropogenic disturbance footprint, Fi: wildfire disturbance footprint) and 95% confidence intervals from linear regression models explaining variation in home range area for female northern mountain caribou (*Rangifer tarandus caribou*) between 2015–2023 in northcentral and northwestern British Columbia, Canada. Values with confidence intervals that did not overlap zero were considered to have a relatively strong influence on area of home range. Red box identifies top ranked model.

Elevation profile and model selection

Caribou in the high-disturbance study landscape used habitats that typically were higher in elevation (Table 8). The top-ranked regression model was consistent with the summary data, revealing an empirical relationship between the elevation of habitat used by collared caribou and the amount of habitat disturbance and DMAC ($AIC_cw = 0.63$). The most parsimonious model ranked considerably higher than the random intercept and null models, and explained a reasonable amount of the variation ($R^2 = 0.50$) in home range area (Table 10).

As with the most parsimonious home range model, anthropogenic habitat disturbance had the greatest effect size (β = 291.58, CI = 143.44, 439.72) followed by the area of wildfire (β = 48.32, CI = 14.78, 81.86). The caribou to moose ratio was positively correlated with elevation use (β = 141.40, CI = 1.48, 281.31; Figure 9). However, as with the home range regression models, the relationship was negative in lesser ranked, more simple models suggesting considerable covariation with disturbance. The top-ranked model for elevation explained more variation in the data when compared to the top-ranked model for home range area ($R^2 = 0.50$; $R^2= 0.31$, respectively).

Table 10 A *priori* hypotheses with explanatory and control covariates (ΔEVI + NDSI + SSN + LER + TRI + POP), and nested random effect (1|subpop/ind) used to explain mean elevation use of female northern mountain caribou (*Rangifer tarandus caribou*) between 2015–2023 in northcentral and northwestern British Columbia, Canada. For each model the effect size of explanatory covariates and 95% confidence interval (CI), Akaike score (ΔAIC_c) and weight (AIC_c *w*), and coefficient of determination (R^2) are shown.

Hypothesis	**ΔAIC_c**	**AIC_c *w***	**R^2**	**An (CI)**	**Fi (CI)**	**Cm (CI)**
An + Fi + Cm + Controls + (1|subpop/ind)	<0.01	0.63	0.50	291.58 (143.44, 439.72)	48.32 (14.78, 81.86)	141.40 (1.48, 281.31)
An + Cm + Controls + (1|subpop/ind)	2.30	0.20	0.49	186.88 (79.89, 293.87)		82.76 (-26.79, 192.31)
An + Fi + Controls + (1|subpop/ind)	3.54	0.11	0.48	169.54 (84.13, 254.95)	38.59 (6.49, 70.68)	
An + Controls + (1|subpop/ind)	4.46	0.07	0.47	118.77 (55.89, 181.64)		
Cm + Controls + (1|subpop/ind)	15.18	<0.01	0.38			-78.17 (-170.61, 14.28)
Cm + Fi + Controls + (1|subpop/ind)	16.70	<0.01	0.37		19.31 (-10.27, 48.89)	-91.79 (-196.23, 12.66)
Null: Controls + (1|subpop/ind)	17.80	<0.01	0.36			
Fi + Controls + (1|subpop/ind)	19.59	<0.01	0.29		16.45 (-12.85, 45.75)	
Random intercept: (1|subpop/ind)	365.97	<0.01	<0.01			

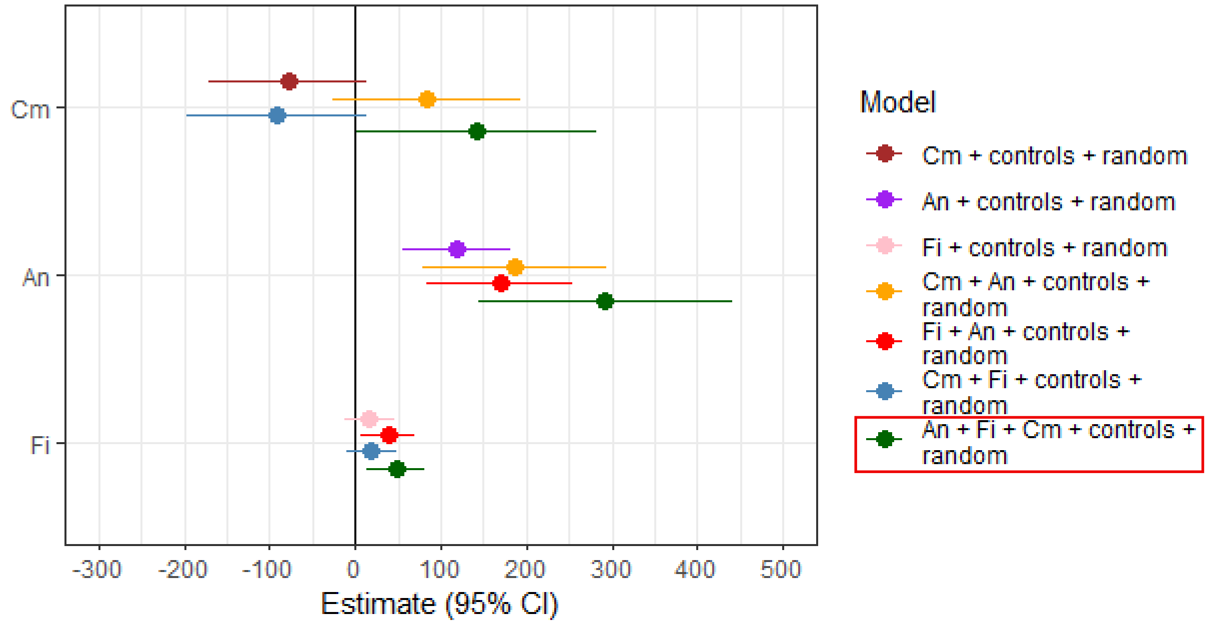

Figure 9 Effect size for explanatory covariates (CM: caribou to moose abundance ratio, An: anthropogenic disturbance footprint, Fi: wildfire disturbance footprint) and 95% confidence intervals from linear regression models explaining variation in mean elevation for female northern mountain caribou (*Rangifer tarandus caribou*) between 2015–2023 in northcentral and northwestern British Columbia, Canada. Values with confidence intervals that did not overlap zero were considered to have a relatively strong influence on area of home range. Red box identifies top ranked model.

Discussion

The strong correlation between increasing anthropogenic disturbance and range contraction of caribou is well documented (Wilson et al., 2019). We found that area of home range decreased and use of higher elevation habitats increased for caribou subpopulations with greater area of anthropogenic disturbance. In contrast, some have reported larger seasonal home ranges for caribou in response to anthropogenic disturbance (Courtois et al., 2007). For such cases, anthropogenic disturbance may initially cause caribou to increase the area of their range to avoid human activity or predators (Beauchesne et al., 2014; Courtois et al., 2007; Donovan et al., 2017). In general, however, long-term reduction in home range area in response to increasing anthropogenic disturbance is symptomatic of declining caribou populations (MacNearney et al., 2016; Santomauro et al., 2012; Wilson et al., 2019). That relationship suggests declining caribou populations that are a function of a habitat loss and DMAC (DeCesare et al., 2010; Festa-Bianchet et al., 2011), display diminished home range area. Our research substantiates that relationship.

Our research adds to the mounting evidence of landscape-scale retreat of mountain caribou to high elevations in response to anthropogenic disturbance (MacNearney et al., 2016; Morineau et al., 2023; Poole et al., 2000; Schaefer, 2003; Wilson et al., 2019). For example, MacNearney et al. (2016) reported that caribou were “heading for the hills” and abandoning low-elevation habitats in response to increasing anthropogenic disturbance. NMC typically range across low-elevations during winter, although they may be found across high-elevation windswept ridges. Low-elevation habitats may be used during spring and summer (COSEWIC, 2014). However, some subpopulations of mountain caribou in BC and Alberta now exclusively use high-elevation habitats (MacNearney et al., 2016; Poole et al., 2000). That distributional pattern appears to be correlated with extensive anthropogenic disturbance and increases in moose, deer, and their shared predators across low-elevation habitats (Hebblewhite et al., 2010; Johnson et al., 2015; MacNearney et al., 2016; Poole et al., 2000).

A shift in the range used by caribou may be a behavioural response to habitat loss, increasing predation risk, or disturbance related to human activities (Courtois et al., 2007; Dyer et al., 2002; Gill et al., 2024; MacNearney et al., 2016; Seip et al., 2007). Mechanistically, caribou may shift their distribution to smaller areas of suboptimal habitats (i.e., alpine), possibly to increase survival (MacNearney et al., 2016). Rettie and Messier (2000) suggested that the most broad-scale distributional responses should align with the most limiting factor for fitness. Numerous studies have shown that caribou and other species limit or attempt to limit predation risk by avoiding risk-prone habitats at a range of spatial scales (Apps et al., 2013; DeCesare et al., 2014b; Derguy et al., 2025; Mumma et al., 2017; Wittmer et al., 2007). The observed shift to less productive, high-elevation habitats (e.g., MacNearney et al., 2016) is a strategy that suggests predation associated with DMAC is a strong limiting factor for mountain caribou. Range contraction and even extirpation suggests that such a strategy is only partially successful or, for some subpopulations, completely unsuccessful. Yet this strategy likely explains the shift to high-elevation habitats that are less productive and have less disturbance and thus less conducive to DMAC (e.g., Neufeld et al., 2021).

A species' distribution is not solely determined by abiotic environmental variables (Wisz et al., 2013). In the case of mountain caribou, consideration of the effects of DMAC can enhance our understanding of how caribou alter their distribution in response to changing environments (Thaker et al., 2011; Trainor et al., 2014). Others have looked at DMAC, but in the context of caribou survival (Labadie et al., 2023; Wittmer et al., 2007), resource selection (DeCesare et al., 2014b), and conservation interventions (DeCesare et al., 2010; Serrouya et al., 2019). We are the first to integrate a measure of DMAC, an assumed species interaction that influences caribou distribution (MacNearney et al., 2016; Morineau et al., 2023; Wilson et al., 2019), into the study of caribou biogeography.

In areas where DMAC is expected to be a limiting factor for caribou, researchers have reported caribou to alternate prey abundance ratios of <0.5 (Latham et al., 2011; Neufeld et al., 2021;

Serrouya et al., 2017). We found caribou to moose ratios of ≤ 0.13 and ≥ 0.35 in the high- and low-disturbance study landscapes respectively. That contrast suggests that numeric or spatial DMAC is likely occurring in the high-disturbance study landscape with a corresponding influence on caribou distribution. The top ranked regression models explaining home range size and elevation included that index of DMAC. Considering that the caribou to moose ratio coefficient was relatively imprecise (i.e., overlapping confidence interval with zero) it is possible that this coefficient was an uninformative parameter in our models (Leroux, 2019). Moreover, it is possible the covariation among anthropogenic disturbance and the DMAC index contributed to model uncertainty and change in coefficient sign. Covariation between anthropogenic disturbance and DMAC represents the interconnectedness of this ecological process and the challenge in disentangling causal relationships between habitat disturbance, altered predator-prey dynamics, and caribou range contraction. Nonetheless, the occurrence of DMAC in the high-disturbance landscape is consistent with theoretical expectations and empirical observations of woodland caribou (Wittmer et al., 2007), and likely contributed to the range contraction we quantified.

Wildfire had a relatively small, but measurable effect on home range area and mean elevation of monitored caribou. Given that wildfire represents a single disturbance agent it was not surprising to see a smaller coefficient when compared to anthropogenic disturbance, which is comprised of multiple disturbance agents (i.e., roads, cutblocks, static). In other study systems, wildfire had relatively less or little effect on the spatial distribution and vital rates of caribou (Dalerum et al., 2007; Johnson et al., 2020). Moreover, wildfire appears to have minimal influence on DMAC (Demars et al., 2019a; Neufeld et al., 2021). The range contraction that we observed was partly driven by wildfire but anthropogenic disturbance and subsequent DMAC likely had a stronger influence.

Past research that focused on the spatial response of boreal caribou to disturbance revealed a temporal lag of approximately two decades between habitat loss and range shift (Fortin et al., 2017; Vors et al., 2007). A similar lag time may exist between habitat disturbance, DMAC, and population declines (Serrouya, Wittmann, et al., 2015). For example, we observed a large wildfire footprint across both study landscapes where some of the larger wildfires occurred during the time of this study. Thus, it is possible that caribou have not adjusted their distributional behaviour to habitat change related to wildfire or that moose abundance and DMAC have not increased following fire. However, there is growing evidence of functional differences between wildfire and human disturbance when considering caribou range use (Dalerum et al., 2007), recruitment and survival (Johnson et al., 2020; Konkolics et al., 2021), and DMAC (Demars et al., 2019; Stevenson et al., 2024). For example, caribou continue to use burned habitats post-fire (Dalerum et al., 2007; Konkolics et al., 2021). That is generally not the case for anthropogenic disturbance (MacNearney et al., 2016; Wilson et al., 2019).

We used the contrast in habitat disturbance as a surrogate for time to demonstrate how caribou in the low-disturbance study landscape may respond to future habitat loss. We recognise that the study of temporal phenomena is best done using time-series data sampled from a spatial scale and at a frequency that is relevant to the ecological process (Damgaard, 2019). When spatiotemporal data are unavailable, space-for-time substitutes are useful especially when studying large-scale ecological processes (Lovell et al., 2023; Srivathsa et al., 2018). Although we did not document the temporal patterns of distribution for individual subpopulations of NMC, the aggregate response of caribou within the high-disturbance study landscape suggests that increases in human-caused disturbance will result in range contraction and greater use of high-elevation habitats by caribou found across the northern distribution of NMC. This is an important consideration for prioritising conservation planning and actions given continued and projected increase in habitat loss across portions of northwestern BC (Festa-Bianchet et al., 2011; Nagy-Reis et al., 2021).

Methodological considerations and limitations

There is no standard approach to delineate annual and seasonal ranges of caribou subpopulations. Range delineation is typically based on data availability and those data can range in accuracy and precision. Also, there are a number of methods for calculating seasonal, annual, or multi-year range boundaries (Fleming & Calabrese, 2017; Noonan et al., 2019). Thus, range delineation is as much an art, as it is a science. We used the herd range boundaries that were made public by the BC government's Caribou Recovery Program. These boundaries dictated the extent of the disturbance and environmental covariates, as applied to the area and elevation used by individual caribou. However, habitat disturbances beyond the provincial range boundaries likely contributed to ecological processes that influenced the distribution of caribou. We applied coarse-scale measures of snow cover (500m resolution), net primary productivity (500m resolution), and topographic ruggedness. Those data were averaged across the herd range area and did not represent within range variation. Nevertheless, the study design allowed us to make relative comparisons among caribou with no obvious spatial bias between the extent of disturbance and the area and elevation use of caribou in the high- and low-disturbance landscapes.

Our measure of anthropogenic disturbance was an amalgamation of disturbance types including a combination of polygonal and linear features. We did not test for a relationship between the distribution of caribou and individual disturbance types, such as forestry cutblocks or roads (Donovan et al., 2017). This approach limited our ability to identify the sources of disturbance with the greatest influence on caribou. Also, we could not disentangle the effects of spatial and numerical DMAC (Mumma et al., 2018). However, our decision to identify two classes of disturbance was not unprecedented (Environment Canada 2012; Johnson et al. 2020). Also, this approach simplified the analysis and interpretation of results and avoided challenges such as ranking the relative influence of overlapping features (Arias-Patino et al., 2024).

Our measure of anthropogenic disturbance and DMAC index covaried, which is not surprising considering that habitat disturbance is an intrinsic component of theis ecological phenomenon. However, disentangling habitat from predation is challenging. Future work could test the effectiveness of causal inference (e.g., Arif & MacNeil, 2023) for partitioning the effects of habitat change (i.e., displacement, reduction in forage) and predator-prey dynamics, both of which are defining elements of DMAC (Arif et al., 2022).

We identified two seasons that influenced the distribution of caribou. The dates of those seasons aligned with those reported by authors who quantified migration and range residency. However, caribou respond to finer temporal scales of ecological variation (Grant et al., 2019; MacNearney et al., 2016; Williams et al., 2021). For example, Lessard et al. (2025) identified 6 biological periods that differed in timing among subpopulations of boreal caribou in BC and Québec. Thus, we failed to represent some seasonal differences in distribution and the relationship with disturbance and the other ecological factors that we included in the regression models (e.g., primary productivity, snow cover).

Stewardship implications

There is strong empirical evidence of a negative relationship between the recruitment or survival of caribou and the extent of anthropogenic disturbance (DeCesare et al., 2010; Rudolph et al., 2017). We, alongside other researchers, found a similarly strong and negative relationship between disturbance and caribou distribution (MacNearney et al., 2016; Morineau et al., 2023; Wittmer et al., 2005). When studying the disturbance-distribution relationship, Wilson et al (2019) concluded that smaller annual home ranges among subpopulations may signal anthropogenic habitat loss for forest-dwelling caribou. Our findings support this statement and suggest that shifts in species distribution can provide an early warning that underlying ecological change is occurring within an ecosystem (Service et al., 2014).

Concurrent range contraction and subpopulation declines have been documented over the past century (Santomauro et al., 2012), and it appears the trend is continuing for caribou (Johnson et al., 2015; MacNearney et al., 2016; Morineau et al., 2023; Wilson et al., 2019; Wittmer et al., 2005). Indeed, this same trend is observed in other species (Gaston & Blackburn, 1996). Generally, abundant species are more widely distributed than less abundant species (Hanski, 1982). Monitoring the distribution dynamics of individual animals is efficient, cost effective, and can compliment other uses of GPS-collar data (e.g., population estimation, calculation of vital rates). Moreover, the calculation of seasonal range area and elevation use has fewer methodological assumptions when compared to more complex resource selection analyses (Boyce et al., 2002). Also, monitoring the spatial distribution of caribou provides mechanistic insights into limiting factors that are not easily observed from demographic trends alone (MacNearney et al., 2016).

The primary difference between the two study landscapes was the intactness of low-elevation habitats. Caribou within low-disturbance areas exemplified distributional patterns that were typical of the known spatial ecology of NMC. Thus, our data suggest that it is paramount to focus habitat protections and restoration in low-elevation habitats especially for subpopulations that are enduring increasing anthropogenic disturbance (Nagy-Reis et al., 2021). Currently, population-based actions (e.g., predator management, maternity pens) are the focus of caribou conservation and recovery in BC (Lamb et al., 2024). However, if there is increasingly less habitat, then these activities will need to increase in intensity and for an indefinite period of time. Equal emphasis must be placed on meaningful action to enhance and restore the integrity of low-elevation caribou habitats at a landscape-scale.

Chapter 4 | Conclusion

We used an innovative space-for-time experimental design to quantify the relationship between anthropogenic disturbance and the predator-prey dynamics and distribution of 11 subpopulations of NMC. We demonstrated that habitat disturbance and DMAC were correlated with smaller seasonal ranges and greater use of high-elevation habitat. Those measures can serve as indicators of range contraction and potentially changes in abundance and increases in the risk of extirpation. Our research offered a unique perspective into how increasing human-caused and natural disturbance could influence the future distribution of NMC (Morineau et al., 2023; Wilson et al., 2019).

For many species, small and isolated populations are at the greatest risk of extirpation (Channell & Lomolino, 2000). Indeed, small and declining caribou populations have experienced range contraction across Canada (MacNearney et al., 2016; Morineau et al., 2023; Wilson et al., 2019). Range contraction is part of the extirpation process that is linked to landscape-scale anthropogenic disturbance (Wilson et al., 2019). Eventually, extirpation coincides with complete abandonment of range, such has been observed in close proximity to our study area (Santomauro et al., 2012). The smallest home range areas we quantified were from the two subpopulations with the fewest caribou (Telkwa and Edziza). The distribution dynamics of the caribou in the high-disturbance study landscapes are troubling and suggest a greater risk of possible extirpation. Monitoring for future changes in range use, including smaller seasonal ranges and greater use of high-elevation habitat, can help track the population trajectory of caribou. In particular, multi-year monitoring, similar to this study design, is important to account for inter-annual variation in distribution dynamics.

In the low-disturbance study landscape, we observed distribution dynamics that were typical of the known spatial ecology of this ecotype of caribou (COSEWIC, 2014). These subpopulations of NMC have minimal exposure to human activities and can freely range across low- and high-elevation habitats. There is a unique conservation opportunity to implement proactive stewardship, not reactionary management, to safeguard these caribou. That includes protecting the integrity of this landscape to maintain these distribution dynamics that, as we showed, can quickly trend to range contraction with increasing habitat disturbance and DMAC. We expect that projected increases in anthropogenic disturbance in the northern range of NMC will result in range contraction similar to that observed in the high-disturbance study landscape (Nagy-Reis et al., 2021).

Much of NMC range is remote or inaccessible, challenging the feasibility of typical monitoring programs designed to assess population change. As a result, abundance trends are unknown for approximately 50% of NMC subpopulations (Cichowski et al., 2022). Furthermore, the overall trend for the NMC Designatable Unit is unknown largely due to a lack of survey or vital rate data (COSEWIC, 2014). Even less is known of the occurrence or magnitude of apparent competition simply because there are few or no estimates of the density of caribou, moose, and their predators.

We developed a novel method to index DMAC, the most referenced cause of caribou declines (Festa-Bianchet et al., 2011). We demonstrated that SIA could be used to quantify wolf diet. In combination with a measure of habitat disturbance, the proportion of caribou to moose in the diet of wolves was a reasonable index of DMAC. To quantify a similar ratio using population estimates would be less collaborative, more costly, and less repeatable given the challenges of using aircraft to count caribou, moose, and wolves across large and remote landscapes. Moreover, quantifying diet provides mechanistic insights into the ecology of wolves and their prey.

Our results, and those of others (Dickie et al., 2022; Serrouya et al., 2021), suggest that vegetation productivity, whether a function of ecosystem condition or disturbance, is a strong causal agent of apparent competition. Neufeld et al. (2021), for example, reported a near unity in caribou to moose abundance and argued that there was no evidence of apparent competition in a low-productivity ecosystem in northern Saskatchewan. We demonstrated that relatively little anthropogenic disturbances across northwest BC also resulted in a near unity in the ratio of caribou to moose. In our system, the management of the extent of anthropogenic habitat disturbance may be the single most important factor for mitigating apparent competition.

Achieving a state of coexistence for sympatric populations of caribou and moose is an ideal outcome for wildlife conservation and stewardship in BC. Both moose and wolf populations are being managed to targeted densities that in theory stabilize DMAC and increases survival of caribou (Lamb et al., 2024; Serrouya et al., 2017; Serrouya et al., 2015). These conservation actions have shown some success at arresting the decline or increasing the abundance of caribou over the short term (Lamb et al., 2024), but they have not been proven effective in achieving resilient and self-sustaining caribou populations. For instance, research that continued monitoring after cessation of predator management discovered a short-term (i.e., <3 year) effect on ungulate demography due to wolf populations quickly rebounding (Bergerud & Elliott, 1998; Boertje et al., 2010; Farnell, 2009; Seip, 1991; Valkenburg et al., 2004). Moreover, post predator management high, and stable, prey populations have not been met (Mech and Peterson, 2003).

Our research provides evidence that landscapes with few anthropogenic disturbances demonstrate no DMAC and potential coexistence among caribou and moose. The ability for caribou to range freely and minimize exposure to anthropogenic features that exacerbate DMAC (e.g.,Dickie et al., 2017; Mumma et al., 2018), may be the only realistic scenario for caribou-moose coexistence, and self-sustaining caribou populations.

Future research should assess if occupancy of high-elevation habitats (i.e., spatial DMAC refugia) is a viable strategy for caribou to achieve self-sustaining populations in the face of extensive anthropogenic disturbance. That question would require an assessment of the potential carrying capacity of “mountain islands in a sea of wolves and moose” (Poole et al., 2000). Across much of western Canada, mountain caribou may have abandoned low-elevation habitats as an adaptation to reduce predation and increase survival (MacNearney et al., 2016). However, some have suggested that the continuous use of high-elevation habitats is maladaptive over the long-term and eventually results in further population declines (Williams et al., 2021).

Our research documented increasing use of high elevations with increasing disturbance footprints. This distributional shift towards high-elevation habitats coincides with recent populations stability (Lamb et al., 2024), including subpopulations that have not experienced wolf or moose management actions. Thus, these caribou may be experiencing stable population dynamics while they remain spatially separated from DMAC (i.e., low-elevations). Perhaps we are at a point in time where caribou subpopulations have reached the carrying capacity of high-elevation predator refugia. This question requires investigation and could potentially provide new insights into realistic population goals for caribou conservation in areas where continued resource extraction is expected.

One of the greatest contrasts we observed between the two study landscapes was the extensive anthropogenic footprint in the south. Relatively little disturbance across low-elevation habitat is likely the reason that we did not observe range contraction or a strong signal of DMAC across the northern study area. Our research, and that of others, suggests that caribou range must be managed to limit DMAC (Palm et al., 2020). Our results suggest that conservation efforts are needed to recover and expand caribou habitat to approximate the conditions in the north that seemingly provide a blueprint for caribou self-sustainability. Yet, from my home office I write this thesis with a view of the Telkwa range. Matter of fact, my little round home is situated in historic Telkwa caribou range. Just how much low-elevation habitat can we give to caribou? This, in my opinion, is the most important conservation question we need to ask ourselves.

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Appendix A | Low-elevation habitat disturbance for each caribou study subpopulation and caribou locations (GPS points)

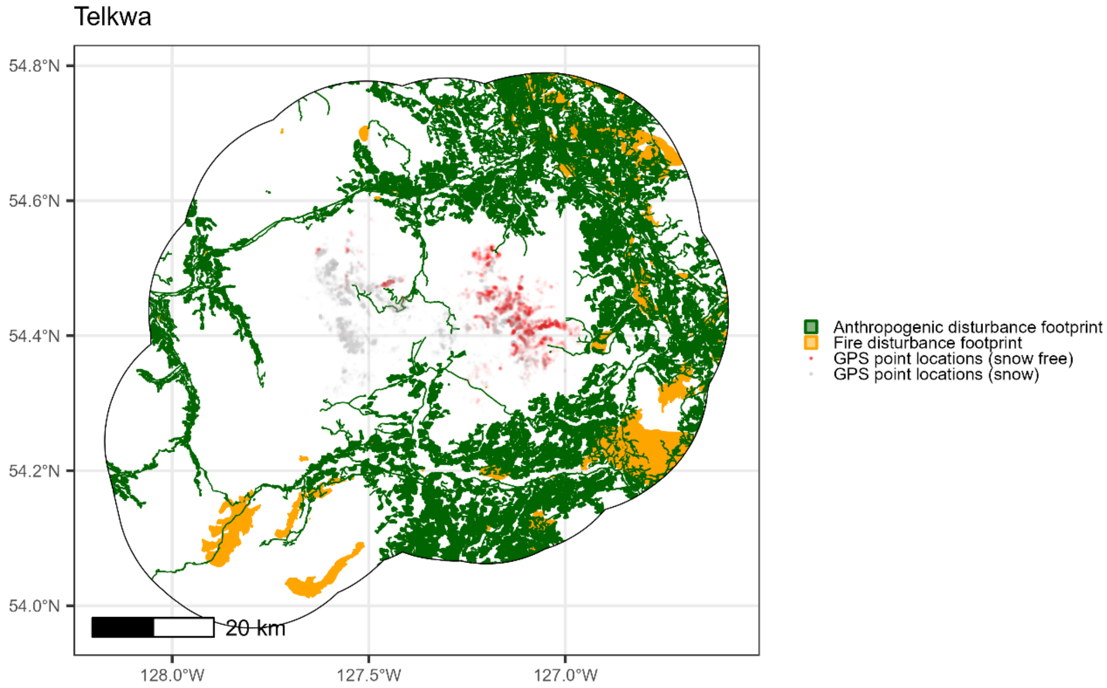

Figure 10 Anthropogenic and wildfire disturbance footprint in the Telkwa subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

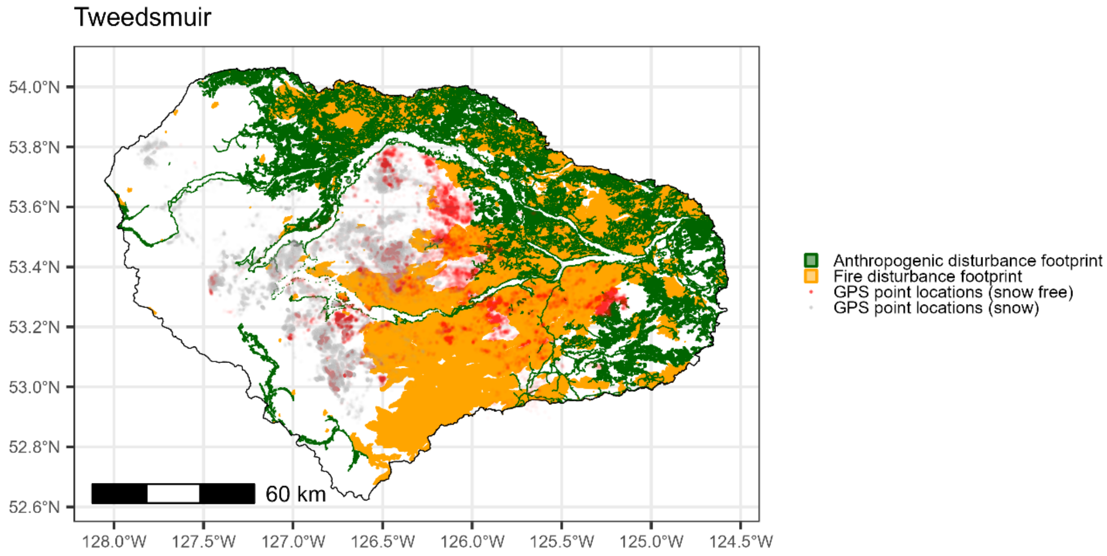

Figure 11 Anthropogenic and wildfire disturbance footprint in the Tweedsmuir subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

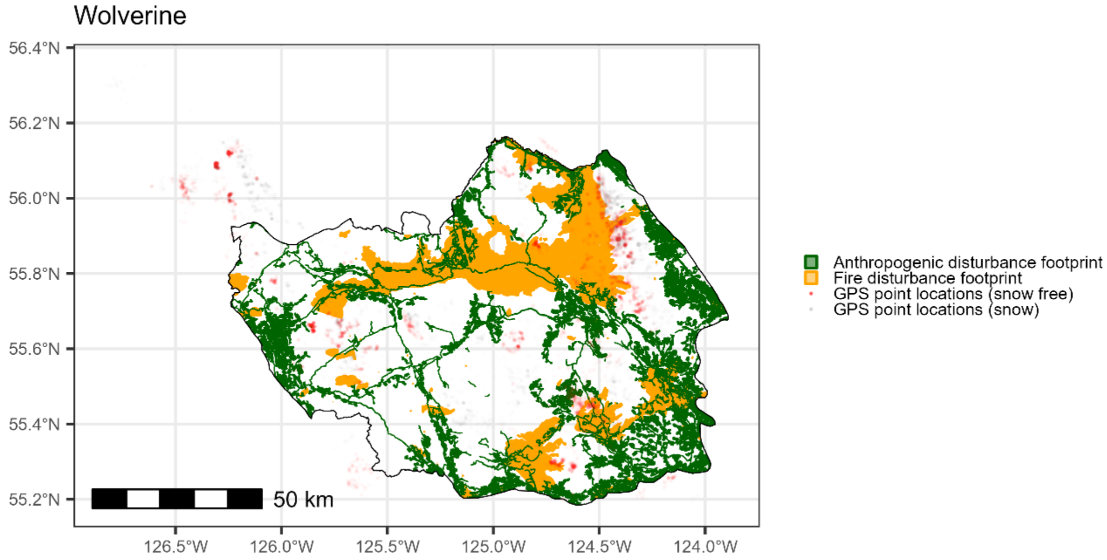

Figure 12 Anthropogenic and wildfire disturbance footprint in the Wolverine subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

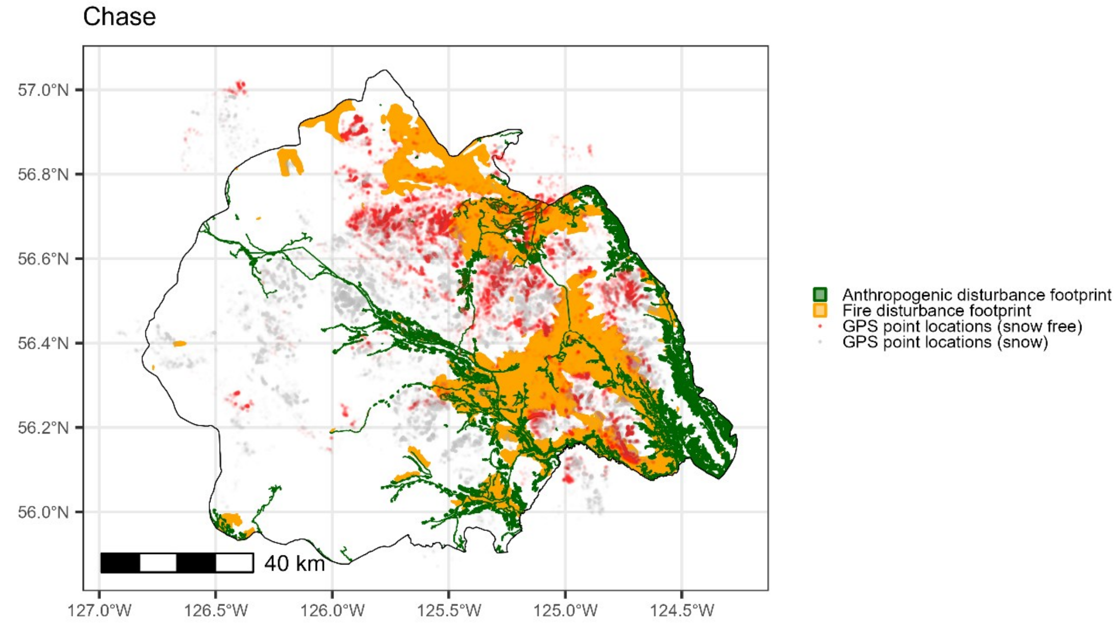

Figure 13 Anthropogenic and wildfire disturbance footprint in the Chase subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

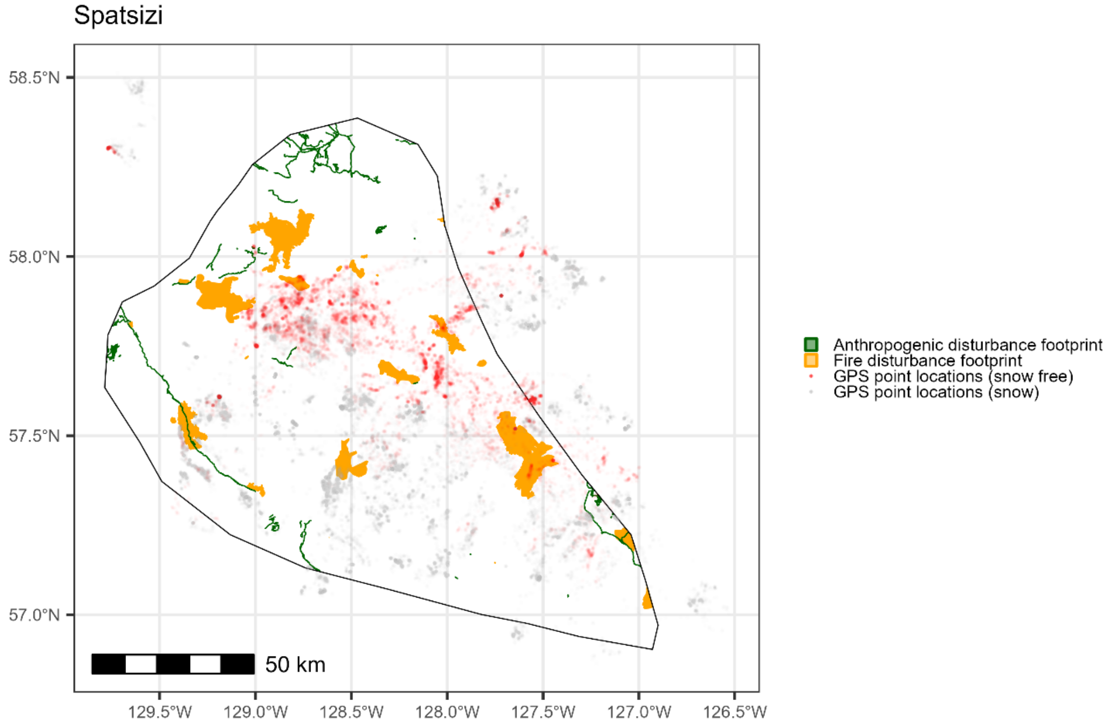

Figure 14 Anthropogenic and wildfire disturbance footprint in the Spatsizi subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

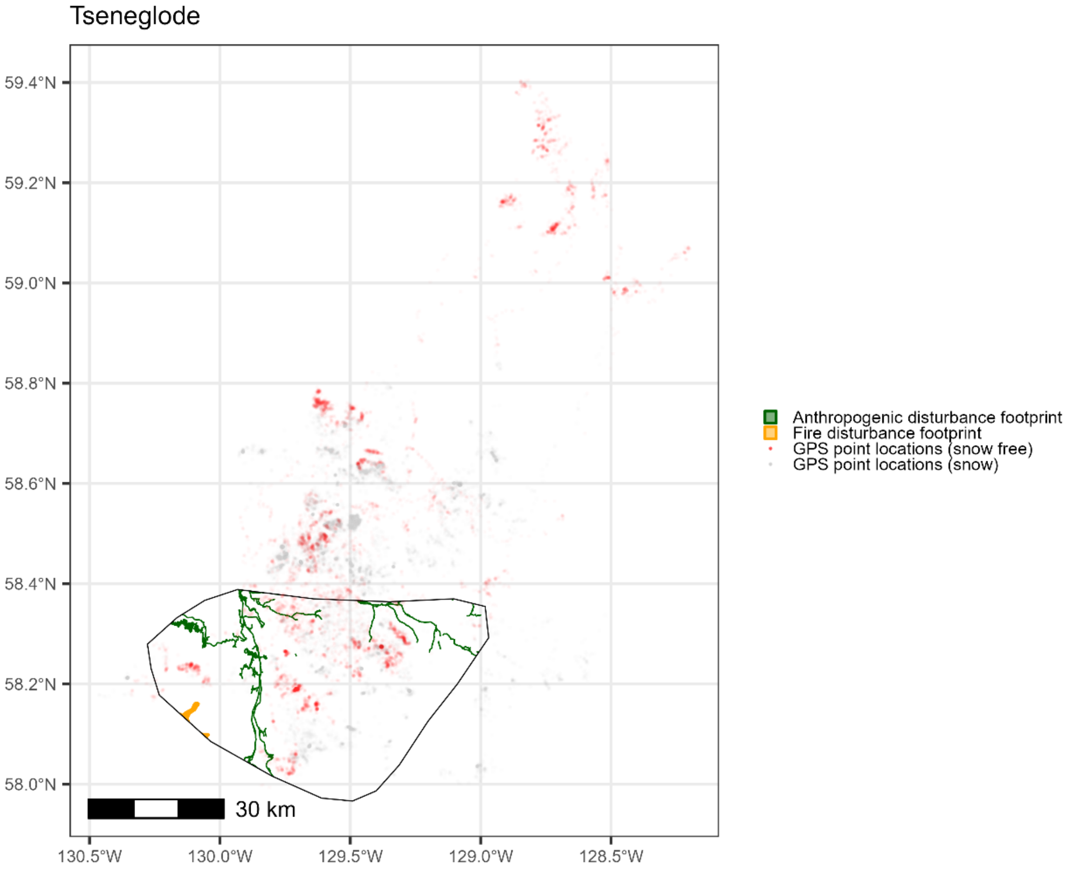

Figure 15 Anthropogenic and wildfire disturbance footprint in the Tseneglode subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

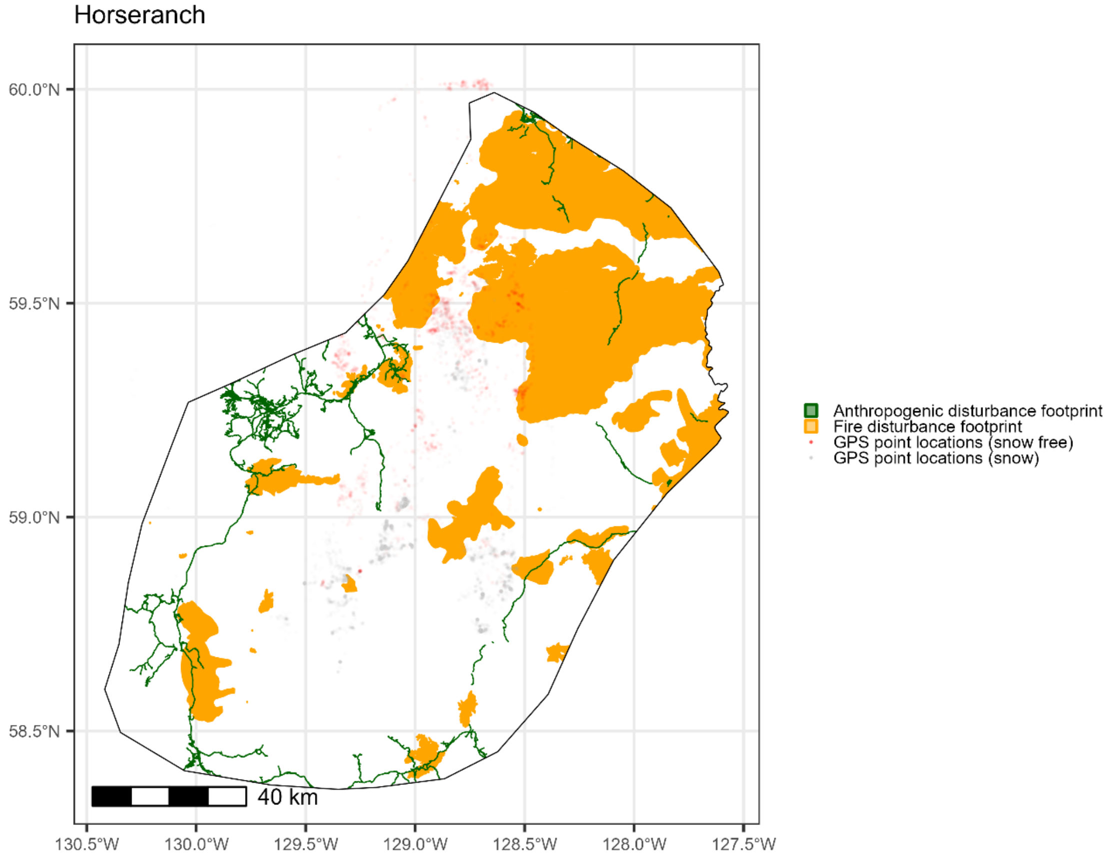

Figure 16 Anthropogenic and wildfire disturbance footprint in the Horseranch subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

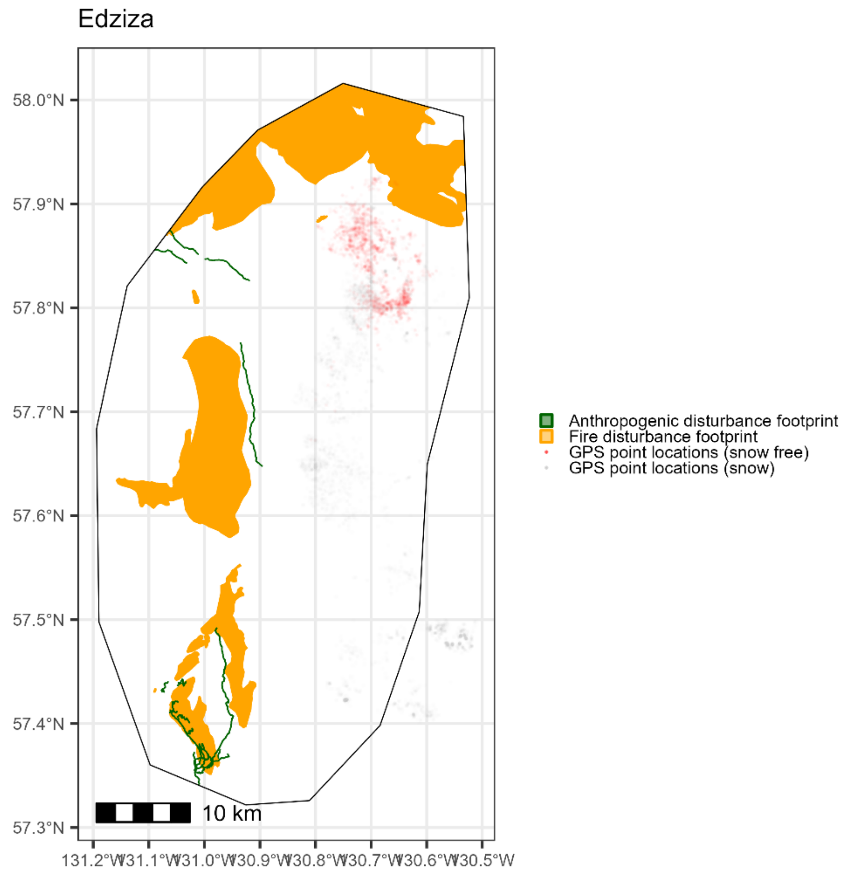

Figure 17 Anthropogenic and wildfire disturbance footprint in the Edziza subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

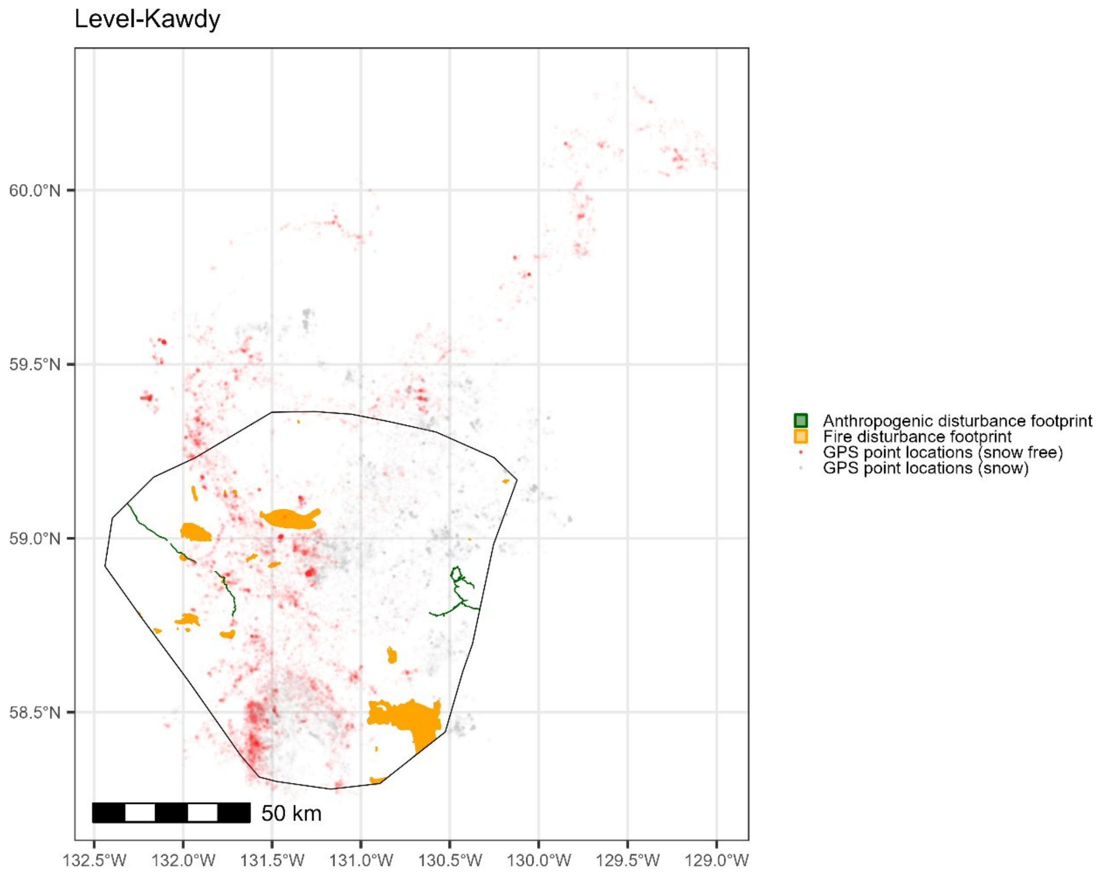

Figure 18 Anthropogenic and wildfire disturbance footprint in the Level-Kawdy subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

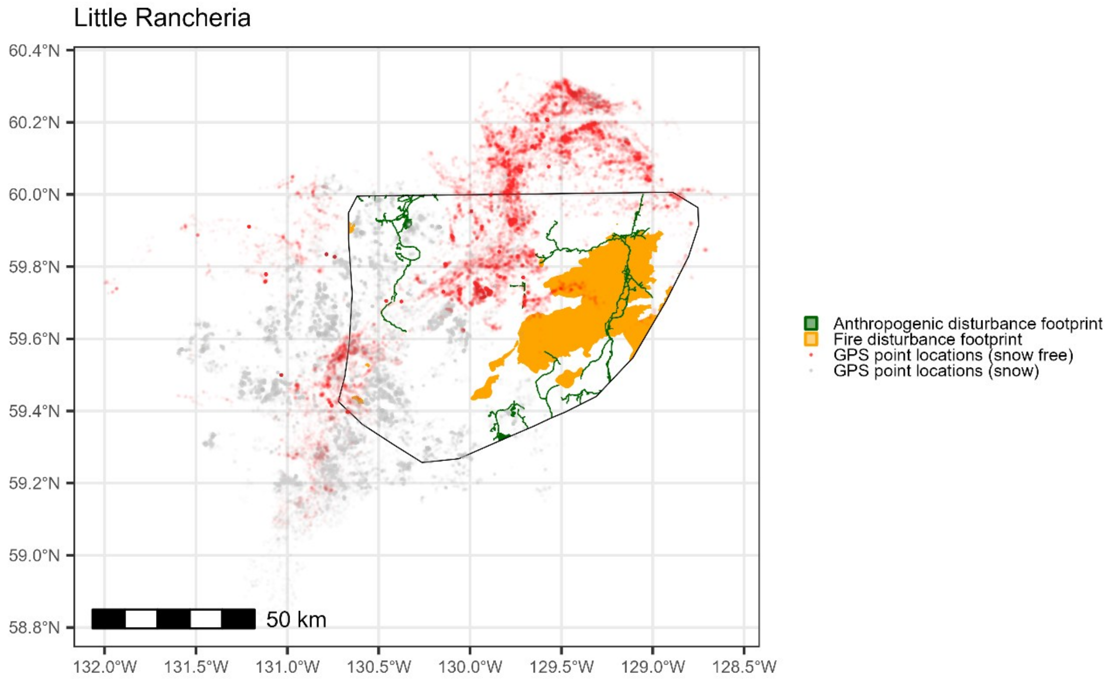

Figure 19 Anthropogenic and wildfire disturbance footprint in the Little Rancheria subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

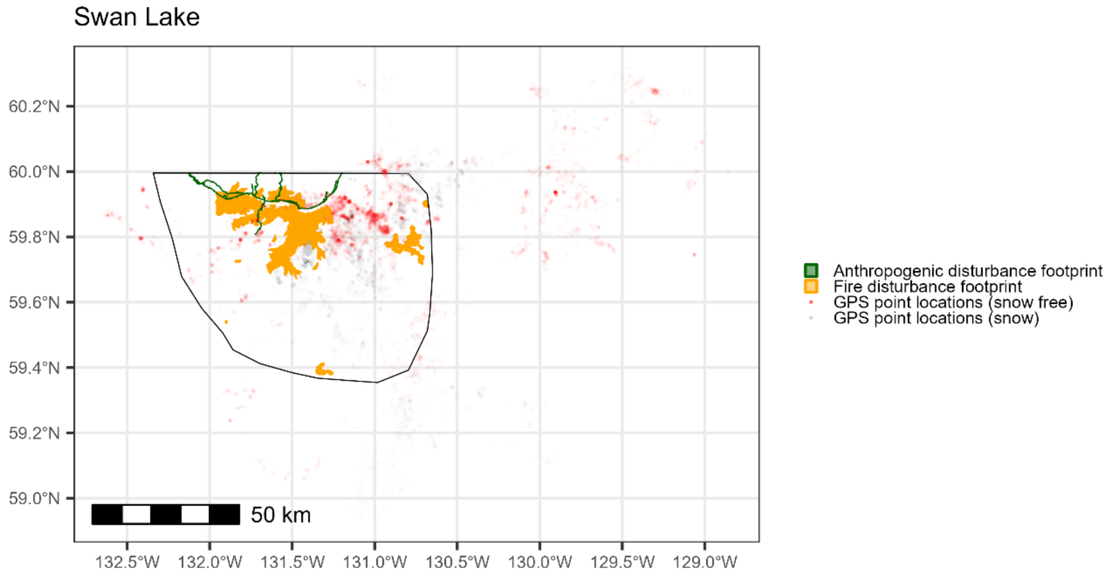

Figure 20 Anthropogenic and wildfire disturbance footprint in the Swan Lake subpopulation range for 2023. Each subsequent year (2015–2023) these same disturbance footprints were calculated to include disturbance as a principal factor for the linear regression analysis of home range area and elevation profile. GPS-collar locations are included for each year (2015–2023).

Appendix B | Data source and vector layers used to quantify disturbance footprints

Table 11 Data source and vector layers for data used to develop the dominant disturbance analysis used to create disturbance anthropogenic and wildfire disturbance footprints for each of the 11 subpopulations of northern mountain caribou (*Rangifer tarandus caribou*).

DISTURBANCE CATEGORY	DISUTRBANCE	DATA SOURCE	LAYER
STATIC	Agriculture	BCCE - 2021 Disturbance Data	CEF_DISTURB_GROUP = 'Agriculture_and_Clearing'
	Airstrip	BC Gov Database	WHSE_BASEMAPPING.TRIM_EBM_AIRFIELDS
	Dam	BC Gov Database	WHSE_WATER_MANAGEMENT.WRIS_DAMS_PUBLIC_SVW
	Mine	BCCE - 2021 Disturbance Data	CEF_DISTURB_GROUP = 'Mining_and_Extraction'
	Pipeline	BC Gov Database	WHSE_MINERAL_TENURE.OG_PIPELINE_AREA_PERMIT_SP
	Rail	BC Gov Database	WHSE_BASEMAPPING.GBA_RAILWAY_TRACKS_SP
	Reservoir	BC Gov Database	WHSE_WATER_MANAGEMENT.WLS_RESERVOIR_PMT_LICENSEE_S
	Road (25m buffer to create polygon)	BCCE - Roads - 2021	N/A
	Seismic	BCCE - 2021 Disturbance Data	CEF_DISTURB_GROUP = 'OGC_Geophysical'
	Transmission Line	BC Gov Database	WHSE_BASEMAPPING.GBA_TRANSMISSION_LINES_SP
	Urban	BCCE - 2021 Disturbance Data	CEF_DISTURB_GROUP = 'Urban'
	Well	BC Gov Database	WHSE_MINERAL_TENURE.OG_WELL_FACILITY_PERMIT_SP
CUTBLOCK	Cutblocks (no buffer) past 40 years	BC Gov Database	WHSE_FOREST_VEGETATION.VEG_CONSOLIDATED_CUT_BLOCKS_SP
WILDFIRE	Wildfires past 40 years	BC Gov Database	WHSE_LAND_AND_NATURAL_RESOURCE.PROT_HISTORICAL_FIRE_POLYS_SP

Appendix C | Complete isoscape for all prey (mammals, fish, and vegetation) that were sampled to allow for the *a priori* selection process of determining prey equations for Bayesian stable isotope mixed modeling of the diets of wolves and grizzly bears

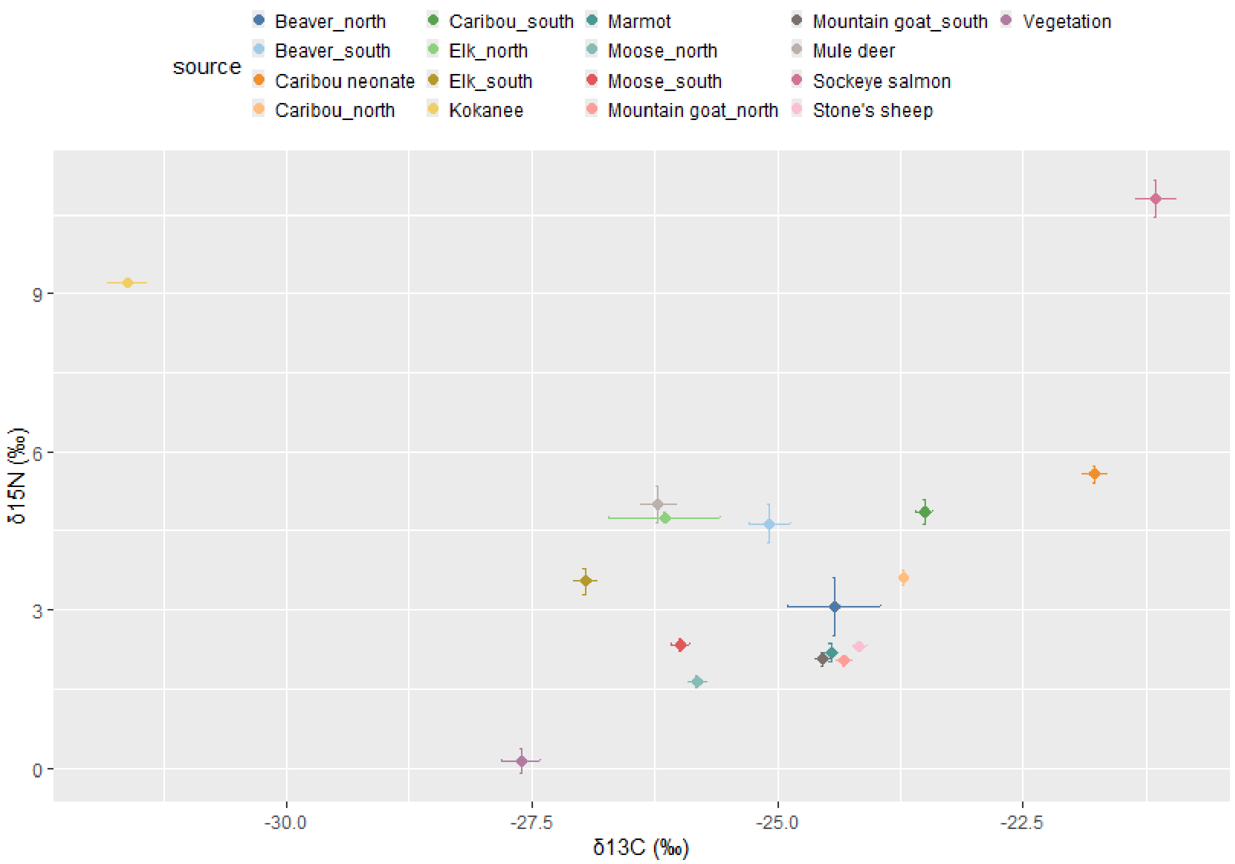

Figure 21 Mean (SD bars) source carbon (δ13C) and nitrogen (δ15N) isotope values from hair samples (guard hairs) for all sampled prey sources in a low- (north) and high-disturbance (south) landscape in northwest and northcentral British Columbia, Canada, between 2021–2023.

Appendix D | Estimates of moose density (standard error) and associated trend across subpopulations of northern mountain caribou

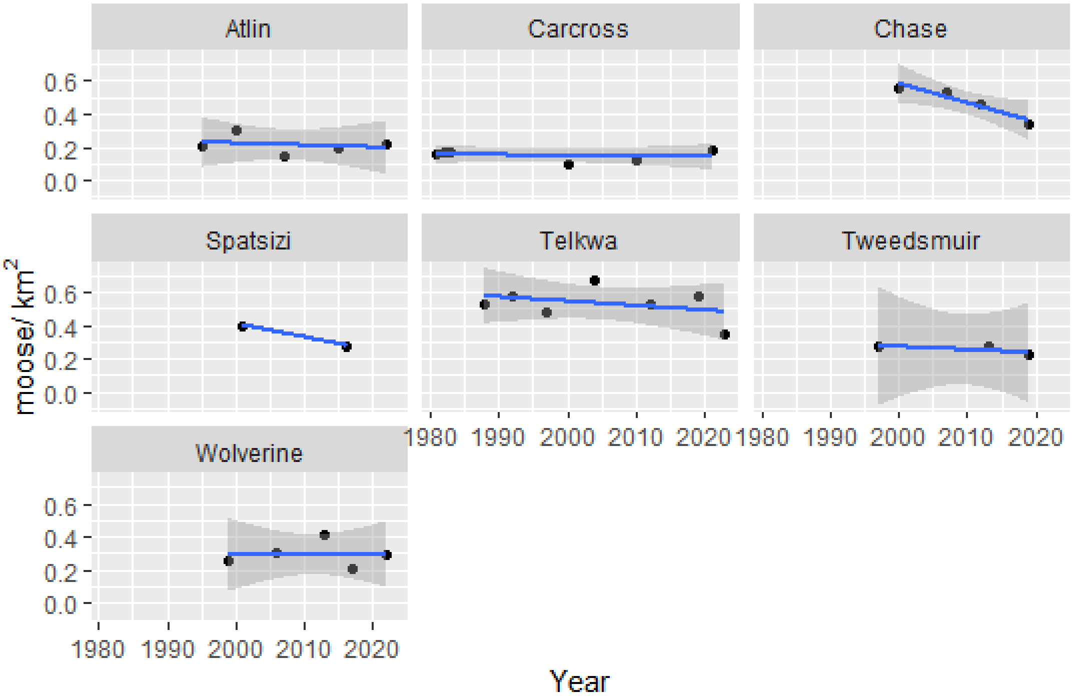

Figure 22 Estimates of moose (*Alces americanus*) density and associated trend and standard error (grey area) for subpopulations of northern mountain caribou (*Rangifer tarandus caribou*) monitored between 1980–2023 in northcentral and northwest, British Columbia and southern, Yukon, Canada. Monitoring programs were managed by provincial and territorial governments.