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LINKING HABITAT, POPULATIONS AND POLICY FOR CARIBOU IN THE FACE OF INCREASING DISTURBANCE

By

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Linking Habitat, Populations and Policy for Caribou in The Face of Increasing Disturbance

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ABSTRACT

In North America's boreal forest, wildfire has long been the dominant form of natural disturbance. However, the human footprint in the region is steadily growing. Large-scale forest harvest and energy development have fragmented late-successional forests, leading to habitat loss for species such as caribou (*Rangifer tarandus*) that rely on these ecological communities. Caribou have experienced widespread population declines and local extirpation throughout the western boreal forest in recent decades. I first analyzed caribou resource selection responses to fires in >685 female caribou across 15 populations that span a wide gradient of fire frequency but are exposed to relatively little human disturbance. Caribou generally avoided burned areas, but season, burn severity and time since fire affected the magnitude of avoidance. Consistent avoidance of burns in winter and avoidance of high severity burns across the range of burn availability suggested that future increases in fire frequency and severity will lead to habitat loss for caribou. Disturbance-caused habitat loss (whether direct or indirect) does not necessarily translate to negative demographic effects. My second set of analyses linked disturbances to caribou behavior and demography throughout western Canada by relating resource selection responses to vital rates. I found a strong negative relationship between human disturbance footprint and calf recruitment. I also found evidence of adaptive resource selection, where increased road avoidance in summer predicted higher recruitment. Increased road avoidance by caribou in winter decreased mortality hazard in adult females, but disturbance and behavior were less predictive of adult female survival than of recruitment. Many of the most imperiled caribou populations live in mountainous areas in British Columbia, where extensive forestry and energy development have facilitated increased predation on caribou. Southern mountain caribou are listed as Threatened under Canada's federal Species at Risk Act (SARA), yet critical habitat identified under the law provides incomplete protection for southern mountain caribou. My spatial analysis showed that nearly 1,000 square kilometers of critical habitat were logged in the five years following its legal identification under SARA. Halting or reversing caribou population declines requires innovative, multi-pronged policy efforts combining short-term efforts to reduce predation with long-term habitat restoration.

ACKNOWLEDGEMENTS

I am thankful for our Alaska Native and First Nations partners, upon whose traditional lands caribou depend. Many of these communities supported the radiocollaring efforts that made this dissertation possible. Caribou are an essential element of Indigenous cultures in the boreal forest, providing a source of spirituality and sustenance that is intrinsic to their holistic values.

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Finally, I acknowledge how lucky I am to spend my days pondering questions about ecology and conservation. The intellectual challenges I faced during my PhD were trivial in comparison to daily struggles endured by hundreds of millions of people who are less privileged and fortunate than me.

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CHAPTER 1: OVERVIEW AND INTRODUCTION

Disturbances are major sources of global change and are drivers of species, community, and ecosystem responses (Johnstone et al. 2010). Ecosystems have been exposed to, and in fact are structured by disturbances of varying frequency, duration, and magnitude throughout evolutionary time, yet the current rate at which disturbance regimes are changing is unprecedented (Ricciardi 2007).

Human disturbance is the most important contributor to biodiversity loss around the world (Pereira et al. 2010, Wilson et al. 2016, IPBES 2018). Human land use change leads directly to habitat loss and fragmentation through resource extraction and energy development, conversion of forest to agricultural lands, urban and transportation network development, fire suppression or initiation, and outdoor recreation development (Johnson et al. 2016). The effects of these changes are consistent with island biogeography theory, where fragmented habitat patches are smaller and spatially isolated, often with reduced richness, species persistence, energy flow across trophic levels, nutrient retention, and dispersal (MacArthur and Wilson 2001, Haddad et al. 2015). Human-induced climate change has also modified global fire regimes, with the potential to profoundly affect ecological processes across spatial scales (Dale et al. 2001, Keith et al. 2008, de Groot et al. 2013). In North America's boreal forest, these changes include increased fire frequency, intensity, duration, and/or total area burned (Weber and Flannigan 1997, de Groot et al. 2013).

The combination of increasing human disturbance and potentially larger, more frequent, and more severe fires may affect the distribution and availability of late-successional boreal forest communities on which many animal species depend, including caribou (*Rangifer tarandus*). Caribou are an iconic and umbrella species of the boreal region that are uniquely adapted to live in large tracts of old growth forests (Festa-Bianchet et al. 2011, Bichet et al. 2016), and are increasingly threatened or endangered by climate and land use change (Hebblewhite 2017).

An effective way to understand potential responses of species such as caribou to changing fire regimes is through the lens of resource selection. Animal resource selection is an ecological process driven by natural selection whereby animals evolve to select resources and conditions that favor their reproductive fitness (Boyce and McDonald 1999, Manly et al. 2002). Ecologists use resource selection analyses to estimate a species' habitat in ecological space, known as their ecological niche. These analyses estimate relative probabilities of selection for or avoidance of environmental attributes by comparing those attributes at locations used by animals (e.g., GPS locations) to those that were available to animals but may or may not have been used. (Manly et al. 2002). However, when environmental conditions change dramatically, or provide novel threats—such as with changes to land use or climate—animals may not adjust to these new conditions and selection of resources may not be adaptive, leading to population declines (Robertson and Hutto 2006, Fletcher et al. 2012). Animals may also often vary their selection for key resources as resource availability changes (Mysterud and Ims 1998). This phenomenon, known as a functional response, can clarify how species respond to global change and help identify thresholds in behavioral and demographic responses to disturbances. Functional responses in resource selection can help improve predictions about animal responses to future increases in disturbance frequency and intensity (Paton and Matthiopoulos 2016).

Predicting responses to global change for wide-ranging animals such as caribou is a continental-scale problem that requires linking population dynamics to habitat characteristics and resource selection across populations (Gill et al. 2001, Aldridge and Boyce 2007). Yet collecting sufficient data on survival and recruitment over large spatial scales, integrating demographic data across populations, and directly relating them to spatial data is exceedingly difficult (Aldridge and Boyce 2007, Lukacs et al. 2009). The boreal forest is rich in natural resources for human economic development, and anthropogenic disturbance in the area is increasing through continued extraction of oil and gas, minerals, and forest products (Johnson et al. 2005). Forests, mountains, and boreal peatland complexes have been transformed into industrialized landscapes with a large network of energy-related infrastructure including roads, transmission lines, pipelines, seismic exploration lines, and well sites (Pickell et al. 2015, Hebblewhite 2017). Apparent competition, directly facilitated by this human development, is the leading hypothesis for widespread woodland caribou declines in recent decades (DeCesare et al. 2010, Festa-Bianchet et al. 2011). Under apparent competition, post-fire early seral vegetation attracts primary ungulate prey species, which bolsters predator populations and increases predation on caribou as alternate prey (Holt 1977, DeCesare et al. 2010). Continued research characterizing mechanisms that link caribou habitats, behavior and population decline are crucial for long-term management of the species, but it will be of little use without effective habitat protection and restoration.

The general theme of my dissertation is linking habitat disturbance and caribou resource selection to their demography and habitat protection. Here, I present a brief overview of each of the following three chapters. First, in Chapter 2, I analyze caribou resource selection in fifteen caribou populations that all experience different levels of burn availability (measured as percent of available habitat burned in the past 40 years). These populations each experienced relatively low levels of human disturbance, limiting the potential for any confounding effects of human disturbance and fire on caribou. My analyses consisted of three separate parts, each addressing different factors associated with fire disturbance. Past studies showing that caribou avoid burns have primarily focused on winter resource selection. More recent work has indicated that fires may not affect caribou through top-down affects such as disturbance-mediated apparent competition in all areas of their range.

My research questions for Chapter 2 were composed of three parts, each of which focuses on different aspects of fire that might affect caribou behavior: burn presence, burn severity, and within burn conditions such as post-fire lichen abundance and distance to burn perimeter. I conducted the burn presence analysis at two spatiotemporal scales because animal selection behavior is scale dependent. I found that avoidance of burns was consistent across populations in winter, including at the highest existing levels of burn availability. This result strongly suggests that future increases in fire frequency (and therefore, burn footprint) will lead to habitat loss through behavioral avoidance. However, caribou displayed a functional response in summer at the coarser spatiotemporal scale, as relative selection for burns decreased at the highest levels of burn availability. This functional response may be explained in part by a spatial constraint; it is difficult to avoid burn if burns dominate available habitat. Further, previous research shows that recent burns can provide important sources of protein-rich foods during summer when lactating adult female caribou have their highest energy demands. Caribou showed the strongest avoidance of severely burned areas, but their relative selection for unburned residual patches within fire perimeters was similar to unburned evergreen forest outside of fire perimeters. This result provides support for the idea that bottom-up factors such as lichen availability are important drivers of caribou responses to burns. My finding that increased burn severity was negatively correlated with lichen abundance and that avoidance of severely burned areas attenuated over time is also evidence of bottom-up effects of fire on caribou.

In Chapter 3, I related human and fire disturbance to caribou behavior, testing how disturbance and caribou behavioral responses to disturbance affect survival and calf recruitment. The first step of this chapter included defining zones of influence of disturbances. Zones of influence represent the ecological footprint of these features and help quantify indirect habitat loss due to behavioral avoidance (Polfus et al. 2011, Boulanger et al. 2012). I then used these estimated zones of influence as buffers to create disturbance footprints, which served as explanatory variables in subsequent analyses of resource selection and demography. As the human footprint expands and fire frequency increases in the boreal forest, I tested whether the two disturbance types have interactive effects on caribou behavior and population dynamics. I found no evidence that selection for one disturbance type varied as a function of the other, indicating that human and fire disturbance have an additive effect on caribou resource selection. However, caribou decreased their avoidance of roads as overall human disturbance increased, and similarly, decreased their avoidance of burns as burn footprint increased. As in Chapter 2, this finding may indicate a behavioral constraint where caribou are no longer able to avoid roads and burns at extremely high disturbance densities.

Later in Chapter 3, I related population-level selection coefficients from resource selection analyses to test whether the degree to which caribou avoided disturbances could predict demographic vital rates. Many resource selection studies assume that selection is adaptive and that behavioral responses directly affect fitness. However, an animal's behavioral plasticity or its ability to balance tradeoffs between factors such as foraging and predation may decouple habitat changes from fitness consequences (Garshelis 2000, Robertson and Hutto 2006). I found that human footprint was the best predictor of caribou recruitment, which is more sensitive than adult female survival to environmental stochasticity in ungulates. In addition to finding a strongly negative correlation between human footprint and recruitment, I found evidence of adaptive resource selection in the summer. Caribou populations that more strongly avoided roads during the summer had higher recruitment. This result may reflect a strategy by caribou to spatially separate themselves from wolves (which often use roads as travel corridors for hunting) during the first few weeks of life when calf mortality is highest. The relationship between disturbance, behavior and survival in adults was weaker than with recruitment, but increased avoidance of roads during winter did lower the mortality risk of adult females. Neither burn footprints nor caribou behavioral responses to burns were statistically significant predictors of demography, corroborating several recent studies suggesting that fire may not have negative effects on caribou population dynamics in large portions of the boreal forest.

In Chapter 4, I first review the provisions for protecting critical habitat on non-federal lands within Canada's federal Species at Risk Act (SARA). Identifying habitat that is essential to the recovery of species at risk, known as critical habitat, is a major focus of species at risk legislation, yet there has been little research on the degree to which these areas are protected. I used southern mountain caribou (*Rangifer tarandus caribou*) as a case study to show that identification of critical habitat does not guarantee its protection on non-federal lands. I found that nearly 1,000 km^2 of critical habitat identified on provincial lands were logged in the five years after it was legally identified under SARA. British Columbia is among several Canadian provinces without dedicated species at risk legislation, and their existing legislation and policies have provided incomplete protection of caribou critical habitat. Even though the federal government has the authority to mandate critical habitat protection on non-federal lands, it has yet to do so. I explain why the federal government is reluctant to exercise environmental authority over matters on provincial lands. I conclude this chapter by outlining potential alternative mechanisms for protecting critical habitat, which involve all levels of government, Indigenous people, and industry.

No single species can adequately represent the conservation issues currently facing an ecosystem as expansive as North America's boreal forest, but the caribou comes close (Bichet et al. 2016, Drever et al. 2019). Its spatial distribution covers most of the boreal region, and it relies on old growth forests that help store a considerable portion of the world's terrestrial carbon. Caribou are culturally important for Indigenous communities throughout Alaska and Canada for food and ceremonial purposes. The boreal and southern mountain ecotypes of woodland caribou have been listed as Threatened under SARA for nearly two decades, yet during this period, approximately seven subpopulations of southern mountain caribou have been extirpated.

The challenge of halting caribou population declines and successfully recovering the species highlight many political, economic, and societal issues that face major biodiversity conservation efforts. The economies of Alberta and British Columbia currently rely on revenue from extractive industries such as forestry, oil and natural gas, and caribou inhabit many of the same areas that help drive enormous profits for those sectors. The situation is dire enough that scientists, conservationists, government agencies and Indigenous groups are using invasive treatments such as predator reduction and maternity penning to prevent additional extirpation of local caribou populations. These emergency measures are temporary. They are likely necessary to prevent imminent extirpation of local populations, yet inadequate to maintain population viability in the long term. My dissertation increases our understanding of behavioral mechanisms that link disturbance to caribou demography. It also clarifies how and why federal and provincial governments have failed to protect critical habitat and offers guidance on ways to achieve habitat protection through an innovative suite of existing legislative and policy tools, many of which involve collaboration with Indigenous governments.

A note on authorship

I use the first-person plural voice, “we”, throughout the rest of this dissertation to reflect the highly collaborative nature of my research. I relied on co-authors for data on caribou locations, survival and recruitment, as well as for their invaluable insight on caribou ecology and management. I recognize their contributions at the beginning of each chapter. Chapter 2 is under review at *Ecological Applications,* Chapter 3 is being prepared for *Ecological Monographs*, and Chapter 4 is published in *Conservation Science and Practice.*

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CHAPTER 2: Increasing fire frequency and severity will increase habitat loss for a boreal forest indicator species[1]

INTRODUCTION

The frequency, duration, timing and magnitude of ecological disturbances, collectively known as a disturbance regime, are changing rapidly in response to human-induced climate change across the globe (Turner 2010, Sergio et al. 2018). Changes to natural disturbance regimes vary widely across space and time, are difficult to predict, and potentially lead to novel environmental conditions (Flannigan et al. 2009). Rapidly shifting disturbance regimes can alter ecosystem states in unpredictable and non-linear ways (Seidl et al. 2017). How species respond to future changes in environmental conditions is a central question for ecologists, managers, and conservationists (Sutherland et al. 2013).

There are few places experiencing changes to disturbance regimes more rapidly than in North America's boreal forests, where temperatures are rising at a rate twice the global average (Callaghan et al. 2004). Wildfire has shaped boreal ecosystems for millennia and remains their dominant source of disturbance (Stocks et al. 2001, Flannigan et al. 2009). Boreal forest fires create a diversity of tree stand ages, physical structure, successional trajectories and species compositions (Dale et al. 2001, Burton et al. 2008). Climate warming is expected to increase the frequency, severity, duration, and spatial extent of fires in some areas of boreal forests, especially western North America, yet

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[1] This chapter is under review at *Ecological Applications* as:
Palm, E. C., M. J. Suitor, K. Joly, J. D. Herriges, A. P. Kelly, D. Hervieux, K. L.M. Russell, T. W. Bentzen, N. C. Larter, and M. Hebblewhite. Increasing fire frequency and severity will increase habitat loss for a boreal forest indicator species. *Under review*.

models predict spatial variability in these changes due to variation in precipitation, vegetation, soil composition, and fuel load (Weber and Flannigan 1997, Kasischke et al. 2010, de Groot et al. 2013). Larger, more frequent, and more severe fires in boreal forests will affect the distribution and availability of late-successional communities and alter habitat for boreal biodiversity that rely on these areas (Joly et al. 2012).

Characterizing habitat selection patterns helps ecologists understand how animals respond to changing disturbance regimes, and their habitat needs. Resource selection analysis (RSA) clarify how animals respond to a variety of disturbances, including human development (e.g., Hebblewhite and Merrill 2008, Martin et al. 2010), fires (DeMars et al. 2019), and insect outbreaks (Rota et al. 2014). RSAs estimate the relative strength of animal selection for (or avoidance of) environmental resources and the relative probability (or intensity) of animal occurrence in a given spatiotemporal extent by comparing resources at locations used by animals to resources at “available” locations that could have been used (Manly et al. 2002, Johnson et al. 2006). Therefore, RSAs estimate the multivariate Hutchinsonian niche (Hutchinson 1957), defined as habitat, for a given species (Hirzel and Le Lay 2008, Holt 2009), and behavioral avoidance of any resources (e.g., fire disturbance) leads to an indirect loss of habitat (e.g., Hirzel and Le Lay 2008).

For wide-ranging species, defining available habitat using a movement-based approach, such as a step selection function (SSF), may provide better predictive performance than traditional static RSAs (i.e., resource selection functions; Thurfjell et al. 2014, Avgar et al. 2016). Integrating animal movement into RSAs is also key to account for the changing availability of resources in space and time, exemplified by dynamic fire disturbance in the boreal forest (Avgar et al. 2016).

To predict animal habitat selection in response to future changes in disturbance regimes, we must first understand how selection varies across the full range of conditions that animals encounter. Variation in behavior across such a gradient of resource availability is known as a functional response in resource selection (Mysterud and Ims 1998, Matthiopoulos et al. 2011, Aarts et al. 2013). Increased fire frequency in parts of western North America's boreal forests would decrease availability of spruce (*Picea* spp.) dominated late-successional habitats, which may transition to deciduous forests, shrubs, or even to a grassland state in some portions of the region (Rupp et al. 2000, Barber et al. 2018). Functional responses improve predictions of resource selection under these novel conditions (Matthiopoulos et al. 2011) and can help identify thresholds in behavioral responses to disturbances that serve as targets for management and recovery (Beyer et al. 2013).

As a long-lived and wide-ranging species whose ecology is inextricably linked to fire, the forest-dwelling caribou (*Rangifer tarandus*) is an iconic indicator of changing disturbance regimes and their effects on boreal biodiversity (Festa-Bianchet et al. 2011, Bichet et al. 2016). Most populations of forest-dwelling caribou in western North America are declining and listed as threatened under Canada's federal Species at Risk Act (SARA), while others are classified under SARA as species of special concern (Ray et al. 2015). The primary hypothesis for explaining caribou population declines in Canada's southern boreal forest is that habitat loss and fragmentation from human disturbance have facilitated increased predation on caribou (Sorensen et al. 2008a, Festa-

Bianchet et al. 2011). For most populations inhabiting northern boreal forests such as those in Alaska (AK), Yukon (YT) and Northwest Territories (NT), human disturbance is considerably lower, and fire remains the major source of habitat alteration (Neufeld et al. 2020). In these areas, the degree to which changing fire regimes will affect caribou resource selection and drive population dynamics is unclear, and is a pressing challenge for conserving caribou and the boreal biodiversity they represent (Bichet et al. 2016).

Forest-dwelling caribou have coexisted with fire for thousands of years. Fire heavily influences the abundance and distribution of boreal forest lichen (Payette et al. 2000), potentially resulting in direct bottom-up effects on caribou through food limitation in winter in areas with very large burn footprints. Terrestrial lichens provide the bulk (usually > 50%) of the diet for many northern caribou in winter, when the availability of high-protein forage is limited (Person et al. 1980, Thomas et al. 1996, Joly and Cameron 2018). Lichen is easily destroyed by fire due to its low moisture content, and takes multiple decades to recover to sufficient biomass for caribou foraging (Morneau and Payette 1989, Coxson and Marsh 2001, Joly et al. 2003). Thus, caribou generally avoid burns in winter (e.g., Schaefer and Pruitt 1991, Rettie and Messier 2000, Joly et al. 2003) due to the negative effects of fire on lichen. However, caribou may benefit from some post-fire habitat conditions, especially during summer. Early seral vegetation in burns may provide crucial protein for caribou during summer, the period of peak nutritional demand for adult females (Brown and Mallory 2007), and caribou resource selection studies during summer have shown more variable responses to burns (DeMars et al. 2020). The relationship between lichen cover and burn severity is less clear, but increasing severity could exacerbate the negative effects of fire on caribou resource selection in winter if it has strong effects on lichen abundance and regeneration (Russell and Johnson 2019).

Here, we used hierarchical mixed-effects RSAs to test for mechanisms by which changing fire disturbance regimes could affect resource selection, and potentially exacerbate existing population declines of forest-dwelling caribou. We tested the overall hypothesis that caribou avoid burned areas, but predicted that factors such as season, spatiotemporal scale, burn severity and availability of burns influenced the strength of avoidance. Within this working hypothesis, we addressed two main questions: (1) How do caribou alter their resource selection of burns across seasons, spatiotemporal scales, and the wide range of spatiotemporal fire frequency in western North America's boreal forests? (2) How does burn severity across and within burns drive caribou resource selection?

For Question 1, our analyses included GPS location data from 15 caribou populations and ~600,000 km^2 of western Canada and eastern AK (Figure 1). We predicted caribou would avoid burns more strongly in winter in part due to the negative effects of fire on lichen. Habitat selection theory predicts that a species' primary limiting factors (e.g., predation risk) drive selection at coarser scales, while selection at finer scales may be influenced by multiple factors such as local food availability (Rettie and Messier 2000, Spitz et al. 2019). We also tested for a functional response to burns, where caribou alter their relative selection for burns across the range of burn availability in our study area. We also tested whether caribou ecotype or burn availability explained more variation in relative selection for burns. We refer to Question 1 analyses as the *burn perimeter RSA* in corresponding subsections.

To answer Question 2, we conducted two separate analyses. The first analysis focused on how different levels of burn severity influenced caribou resource selection relative to unburned areas across the same 15 populations as Question 1. We refer to this analysis as the *burn severity RSA*. Caribou management decisions that consider influence of disturbances on caribou populations primarily rely on polygonal fire perimeter data, overlooking variation in burn severity within burn perimeters, including the presence of completely unburned forest patches that may act as refuges and important food sources (Johnstone and Chapin 2006b, Skatter et al. 2017). We tested the hypothesis that caribou avoidance of burned areas was influenced by burn severity due to its possible negative effects on lichen cover and regeneration. Alternatively, fire may destroy lichen regardless of its severity, in which case we would predict severity would be less important for caribou resource selection. We predicted stronger effects of burn severity on caribou during winter because winter caribou diets include more lichens and fewer forbs and graminoids (Brown and Mallory 2007) that flourish in recently burned areas. Conversely, because caribou select protein-rich forbs and deciduous shrubs in the summer, we predicted weaker avoidance of burns in the summer (Denryter et al. 2017).

The second analysis under Question 2 aimed to test how burn severity and other conditions within burns influence caribou resource selection at a finer spatiotemporal scale through their effects on lichen abundance and distribution. This fine-scale analysis included a subset of four populations in AK and YT for which we had previously developed, satellite-derived data on percent cover of terrestrial lichens and burn severity (Macander et al. 2020; Figure 1). If lichen abundance decreases with increasing burn severity (Pinno and Errington 2016), we predicted increased avoidance by caribou of severely burned areas during the winter, when lichen dominates their diet. Similarly, we predicted that avoidance of these areas during winter would continue longer after a fire than in summer due to the long post-fire recovery time of lichens (Jandt et al. 2008). We also predicted that caribou would avoid areas deeper within burn perimeters (Joly et al. 2003). Finally, we predicted that the strength of avoidance of severely burned areas and areas deeper within burns would decrease as lichen and vegetation recovered over time. We refer to this analysis as the *within-burn RSA*.

METHODS

We conducted three separate sets of RSAs for forest-dwelling caribou responses to fire disturbance in northwestern North America (Figure 2). Below, we first describe our *burn perimeter RSA* focused on caribou responses to burns, along with functional responses to burns. We then provide details on our *burn severity* and *within-burn RSA*s.

Study area

We analyzed resource selection in caribou from 15 populations across eastern AK, YT, NT and northern Alberta (AB). Each population was exposed to relatively low human disturbance (~2–20% of range disturbed by humans, including 500-m buffer, Johnson et al. 2020). Our populations included migratory (*R.t. granti*, n = 2), mountain woodland (*R.t. caribou*; n = 4), and boreal woodland (*R.t. caribou*; n = 9) caribou ecotypes (Ray et al. 2015). Estimated mean fire return intervals varied widely by dominant tree species, but were <100 years for northern AB boreal ranges (Larsen 1997, Johnstone and Chapin 2006a), ~40–200 years in southern NT (Larsen 1997, Bothwell et al. 2004), and 100–200 years in YT and eastern AK (Kasischke et al. 2010). Interior sections of eastern AK and

YT consisted of rolling hills, rugged peaks, subalpine and alpine areas, and large forested river valleys. In the boreal ranges of northern AB and NT, topography is gently rolling, except in localized upland areas and a few deeply incised river valleys. Common tree species throughout the study area include spruces (*Picea mariana, P. glauca*), poplars (*Populus tremuloides, P. balsamifera*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), and birch (*Betula papyrifera*).

Capture and data summary

Caribou were generally captured from a helicopter by net gun and were subsequently fitted with GPS collars following approved federal, provincial, state, and territorial animal care protocols and permits (Appendix 2A: Table 2A-1). Prior to filtering and analyses, our dataset included 1,804,829 GPS locations from 721 GPS-collared female caribou from 15 populations whose collars collected data from between 2006 and 2019 (Appendix 2A: Table 2A-2).

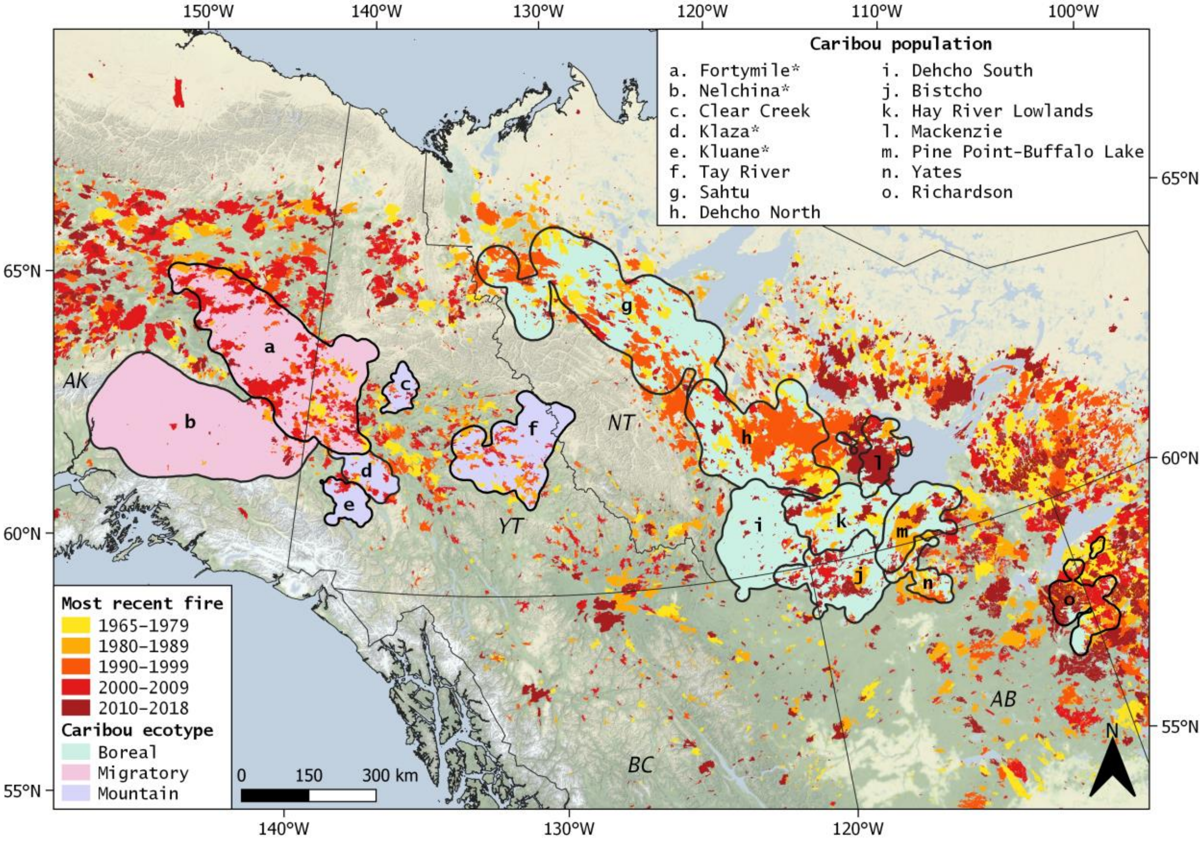
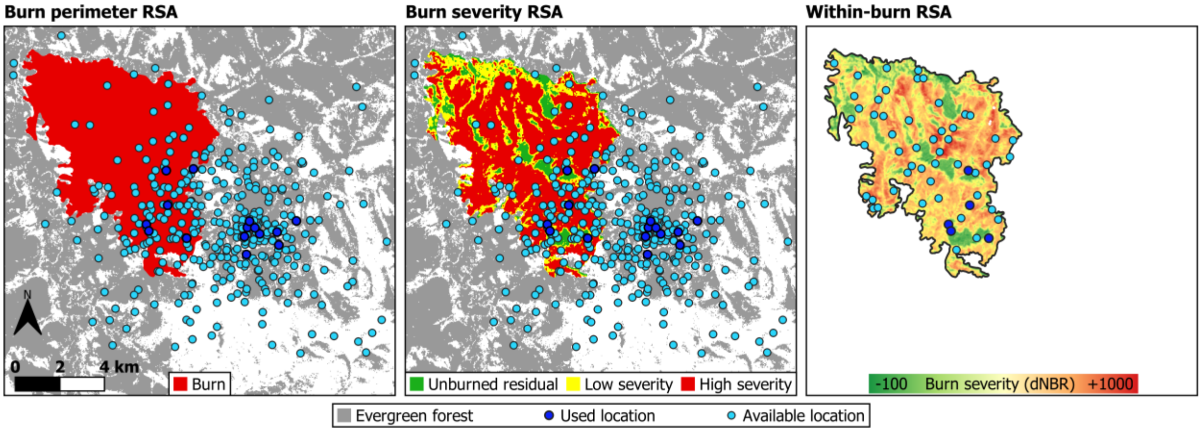


Figure 2-1. Map of fire history and location of 15 population ranges from three ecotypes of forest-dwelling caribou (*Rangifer tarandus*) that were included in analyses. Asterisks denote four populations included in the within-burn RSA.

Burn perimeter RSA

We filtered GPS location data to create separate datasets for relocation intervals of two weeks and 24 hours. Hereafter, we refer to these time periods as ‘spatiotemporal scales’, because the relocation interval determined both the spatial and temporal extent of the domain available to an animal (e.g., Mahoney et al. 2018). These spatiotemporal scales roughly represent opposite ends of Johnson’s (1980) third-order selection (within an individual’s seasonal range). We further divided these two datasets into two seasons, defining summer as May 25–October 5 and winter as October 6–May 5 based on general patterns in movement rates across populations (Appendix 2A: Figure 2A-1; see Appendix

2A: Table 2A-2 for details on analysis subsets). The spatial extent of available habitat varied widely across ecotypes and populations, reflecting different movement behaviors. For example, the mean distances between consecutive locations (step length) at the two-week and 24-hour spatiotemporal scales during the summer were 71.6 km and 7.6 km, respectively, for the migratory Fortymile population, versus 5.4 km and 1.9 km for the relatively sedentary boreal Dehcho South population (Appendix 2A: Figure 2A-2). We explicitly accounted for variation in movement behavior across individuals and populations by sampling availability from step length and turning angle distributions fit for each individual at these two spatiotemporal scales.



Caribou populations: 15
Availability sample: SSF
Spatiotemporal scales: Two weeks, 24 hours
Land cover classes: 7 + burn
Burn severity: none
Other covariates: tree cover, TPI, TRI

Caribou populations: 15
Availability sample: SSF
Spatiotemporal scales: Two weeks, 24 hours
Land cover classes: 7 + 3 severity + old burn
Burn severity: 4 levels
Other covariates: tree cover, TPI, TRI

Caribou populations: 4
Availability sample: conditional RSF
Spatiotemporal scale: 8–17 hours
Land cover: 6 pre-fire classes, within burns only
Burn severity: continuous
Other covariates: lichen cover, years since fire, distance to fire perimeter, TPI, TRI

Figure 2-2. Example of spatial distribution of used and available caribou locations, and different burn characteristics for three separate resource selection analyses of female caribou (*Rangifer tarandus*) in eastern Alaska and western Canada. Panels show a 1998 fire in the Kluane caribou range, YT, and GPS locations from one caribou during February 2014. Evergreen forest is the reference land cover category for the left two panels, and pre-fire evergreen forest is the reference land cover category for the right panel. All other land cover categories are not shown. For simplicity, the fourth burn severity category (‘regrowth’) is not shown in the middle panel.

We used point-based SSFs in a generalized linear mixed modeling (GLMM) framework (Muff et al. 2019) to analyze caribou resource selection across the 15 caribou populations. This approach divides an animal’s movement path into discrete steps based on a user-defined time interval, restricting resource availability in the model by the animal’s current location in space and time. Using the R package amt, version 0.1.2 (Signer et al. 2019), we generated 10 available locations per used location by making random draws from gamma distributions fitted to used step lengths and von Mises distributions fitted to turning angles between consecutive used locations (Signer et al. 2019). Each set of one used location and 10 available locations represented a stratum.

Our GLMMs accounted for correlated observations within individual caribou and within populations and for differences in sample sizes across individuals and populations (Gillies et al. 2006). Random coefficients allowed the effect of a covariate on resource selection to vary by individual caribou, population, or both (Muff et al. 2019). We estimated selection coefficients for each covariate using a Poisson regression with stratum-specific intercepts, which is a likelihood equivalent of a conditional logistic regression often used in SSFs (McCullagh and Nelder 1989, Muff et al. 2019). Within conditional Poisson GLMMs, we treated stratum-specific intercepts as random effects with a fixed large variance using the R package glmmTMB, version 1.0.2.1 (Brooks et al. 2017), following Muff et al. (2019).

Because we were interested in estimating resource selection responses across and within populations while accounting for varying responses and sample sizes across individuals, our models included random coefficients at the population and individual level for every covariate. Each candidate model included all possible covariates (described below) that we hypothesized would affect caribou resource selection. We used Akaike's Information Criterion (AIC) to assess support for including linear versus non-linear (i.e., second order) covariate terms in the models. Given p caribou populations, n animals, and a matched set of j used and available locations, we used the following Poisson function (Muff et al. 2019) to estimate the relative selection intensity y at each time point t:

$$\mathrm{E}\left(y_{pntj}\right) = \mu_{pntj} = \exp\left(\alpha_{pnt} + \boldsymbol{\beta}^{\mathrm{T}}\mathbf{x}_{pntj} + \mathbf{u}_{pn}^{\mathrm{T}}\mathbf{z}_{pntj}\right),$$

$$\text{with } y_{pnt} \sim \mathrm{Po}(\mu_{pntj}) \text{ and } \alpha_{pnt} \sim \mathrm{N}(0, \sigma_{\alpha}^{2}), \ (1)$$

where α_{pnt} is a stratum-specific random intercept (with variance σ_{α}^{2} fixed at 10^6) for individual animal n within population p at time t, $\boldsymbol{\beta}^{\mathrm{T}}$ is the transpose of the covariate vector $\boldsymbol{\beta}$ selection coefficients estimated for a vector of covariates $\mathbf{x}_{pntj}$, $\mathbf{u}_{pn}^{\mathrm{T}}$ is a vector of population- and individual-level random coefficients, and $\mathbf{z}_{pntj}$ is a sub-vector of covariates from $\mathbf{x}_{pntj}$. All used-available RSAs estimate relative probabilities (or relative intensities in a Poisson regression) of selection that are proportional, but not equivalent, to true probabilities of selection (Manly et al. 2002).

We tested for functional responses in selection for burns by including an interaction between the burn landcover category and the average seasonal burn availability for each animal (Matthiopoulos et al. 2011). We estimated average seasonal burn availability by calculating the proportion of available locations at each movement step (i.e., stratum) that fell within a burn, and averaging over all steps along an animal's seasonal movement path. To test the effect of ecotype on relative selection for burns, we included a model with an interaction between ecotype and the burn landcover category. We used AIC to select the top model for each combination of season and scale from a candidate set that included models with linear or second-order polynomial functional responses, those with the burn_01:ecotype interaction, and those without interaction terms.

Environmental covariates

We used burn perimeter polygons from the Alaska Large Fire Database (Kasischke et al. 2002) from 1965–2018 and from the Canada National Fire Database (Stocks et al. 2003) from 1965–2018. We excluded burn perimeters from fires that occurred prior to 1965 because not all regions reported burn perimeter data from this period. State, provincial and federal agencies typically rely on simple burn perimeters in caribou management plans (e.g., Environment Canada 2012). Our models included land cover, tree cover, and indices of terrain ruggedness and terrain position to account for these additional habitat attributes. We used percent tree cover data estimated for year 2000 (Hansen et al. 2013). We derived terrain indices from ~30-m resolution elevation data from NASA's Shuttle Radar Topography Mission (≤ 60°N; Farr et al. 2007), the National Elevation Dataset (> 60°N, > 120°W; Gesch et al. 2002), and the Canadian Digital Elevation Model (> 60°N, ≤ 120°W; Natural Resources Canada 2015).

We used land cover data from a 30-m resolution, Landsat-based product with separate land cover classes estimated for each year from 1984–2014 (Wang et al. 2019). The 10 land cover classes were: evergreen forest, deciduous forest, shrubs, grass, sparse vegetation, barren, fen, bog, shallows/littoral, water. We collapsed barren, bog, and shallows/littoral into an "other" category, added in a "burn" category for all locations within burns (regardless of time since fire), and assigned evergreen forest as the reference land cover category. For caribou locations in unburned areas, we annotated land cover values from the year the animal was present unless it was after 2014, in which case we used the 2014 land cover value.

Burn severity RSA

We tested the degree to which caribou responded to different levels of burn severity relative to unburned areas outside burn perimeters by replacing the burn land cover category in our functional response models with five categories of burn severity. The levels for burn severity were regrowth areas within burns, residual unburned areas within burns, burns from <1985 (with no available burn severity data), low severity burns and high severity burns. We define cutoffs for burn severity categories below in *burn severity RSA covariates* following categories in Key and Benson (2006). Model coefficients for all five burn severity categories represented selection relative to unburned evergreen forest. After splitting burns into these five categories, we only had sufficient sample sizes for model convergence at the 24-hour spatiotemporal scale.

Burn severity RSA environmental covariates

Aside from the addition of burn severity categories, models with categorical burn severity retained the same suite of covariates as the burn perimeter RSA above. For fires that occurred between 1985 and 2015, we used differenced normalized burn ratio (dNBR) burn severity data that was derived from Landsat image pairs collected the year preceding and the year following the fire year (Loboda et al. 2018). We classified burn severity into four severity categories by collapsing Key and Benson’s (2006) seven categories. We defined dNBR values within burn perimeters between –500 and –100 as “regrowth” (1.8% of available locations within burn perimeters from 1985–2015 across both seasons at the 24-hour scale). These areas were likely dominated by herbaceous and deciduous shrub vegetation that was exposed to low severity burn and recovered quickly to exceed pre-fire productivity (Key and Benson 2006). We defined dNBR values between –100 and +100 as “residual unburned patches” (12.5%), which represented areas within burn perimeters with little to no change in productivity between pre- and post-fire productivity. “Low severity” (39.4%) encompassed dNBR values between +100 and +439, while “high severity” (46.2%) included dNBR between +440 and +1300. We classified locations within burns from 1965–1984, for which we had no burn severity data, as “old burns”. We excluded locations within burns that occurred after 2015 because we lacked burn severity data for these burns.

Within-burn RSA

We analyzed fine-scale resource selection within burned areas for four populations in eastern AK and western YT (Appendix 2A: Table 2A-2, Figure 1) within the spatial domain of a previously developed model of terrestrial lichen cover (Macander et al. 2020). Prior to analysis, we filtered GPS locations to an interval of one location every 5–8 hours. This relocation interval maximized sample size of locations within burns while avoiding dropping populations (e.g., Clear Creek, Tay River) with longer intervals between locations from the analysis. We used burn perimeters to constrain availability in a static (not movement-based) RSA, randomly sampling ten available locations within the same burn perimeter containing the corresponding used location. We defined a stratum as all used and available locations within a single burn for an individual-year-season. We modeled resource selection within burns using conditional Poisson GLMMs, which allowed for multinomial strata with a varying number of used points per stratum (y_{pntj} from Eq. 1). Because >90% of locations in this analysis were from the Fortymile population, we estimated random coefficients at the individual level but not at the population level. We used interaction terms to account for our hypotheses that time since most recent fire would effect caribou responses to burn severity (severity:time_since_fire) and distance to burn perimeter (dist_fire_perimeter:time_since_fire).

Within-burn RSA environmental covariates

We restricted this analysis to locations that occurred within burns from 1985–2015 for which we had burn severity data. We used percent cover of terrestrial lichens estimated for year 2015 (Macander et al. 2020), which fell within the temporal range of most of our caribou location data. We estimated distance to burn perimeter by calculating the distance from each location within a burn to the burn perimeter, so larger distances indicated locations that were deeper within a burn. Time since fire represented the amount of time (in years) elapsed between the fire and the caribou GPS location timestamp. We used Wang et al.'s (2019) land cover layer to estimate pre-burn land cover (for the year preceding the fire) within burn perimeters. We lumped "water" into the "other" land cover category because it was extremely rare in the spatial domain of this analysis.

Model validation

For the *burn perimeter* and *burn severity RSA*s, we evaluated all models using an out-of-sample cross-validation where we iteratively withheld one population as a test data set (Roberts et al. 2017) and fitted models to the remaining 14 populations. We estimated predicted values for the test datasets using fixed-effects terms (omitting random coefficients) from fitted models. Within each stratum, we ranked predictions from used locations against those from available locations (from 1 to 11, i.e., 1 used and 10 available locations). We tallied used locations across all strata and calculated the Spearman rank correlation (r_s) for each withheld population to test whether higher ranking bins include more used locations (Fortin et al. 2009). We used a similar out-of-sample cross-validation procedure for *within-burn RSA* models, but divided the dataset into 10 random folds (instead of withholding by population), each with an equal number of individuals.

RESULTS

After thinning and filtering our data, models in the *burn perimeter and burn severity RSAs* included between 9,551 and 266,768 GPS locations from between 539 and 685 caribou, depending on season and spatiotemporal scale, from 15 populations (Appendix 2A: Table 2A-3A). Our *within-burn RSA* models included 13,295 GPS locations from 148 caribou in winter and 7,918 GPS locations from 107 caribou in summer from four populations (Appendix 2A: Table 2A-3B). The median time between successive locations across all individuals included in the *within-burn RSA* after excluding locations with burn severity dNBR values below –500 and above +1100 (Key and Benson 2006) was 10.4 hours in summer and 12.5 hours in winter. Across all three analyses, we excluded random coefficients at the individual level for all land cover categories except burn because they often prevented model convergence. All final models within an analysis included the same set of random coefficients.

General patterns in caribou use of burns across populations and ecotypes

Caribou use of burns throughout the year varied widely across caribou ecotypes and populations. Boreal caribou populations generally spent a higher proportion of time in burned areas during the summer and early fall than during the rest of the year (Appendix 2A: Figure 2A-3). For example, 75% of caribou GPS locations from the Yates population in AB/NT between mid-April and mid-November were in burns versus 26–62% between December and March. However, the Mackenzie population in NT almost exclusively used burns all year, as very little of their range remained unburned. Peak caribou use of burns in mountain populations typically occurred in April and May (7%–34% of annual burn use), with low use of burns during September and October (2%–7% of annual burn use). There were dissimilar temporal patterns of burn use between the two migratory populations (Fortymile and Nelchina) in AK/YT. Nelchina caribou only used burns during the winter (fire was virtually absent from its summer range), while Fortymile used burns throughout the year except during the weeks prior to and immediately following calving (Appendix 2A: Figure 2A-3).

Burn perimeter RSA

Summary of non-burn-related covariates

In all four combinations of seasons (summer, winter) and spatiotemporal scales (24 hours, two weeks), caribou avoided areas with higher tree cover (βsummer, 24 hours = –0.21 ± 0.12 [SE]; βsummer, two weeks = –0.34 ± 0.11; βwinter, 24 hours = –0.36 ± 0.04; βwinter, two weeks = –0.59 ± 0.05). Negative quadratic terms for tree cover during winter indicated that the strength of avoidance increased as tree cover increased (see Appendix 2A: Table 2A-4A for remaining coefficient estimates). Relative to unburned evergreen forest, caribou avoided “other” land cover (category including barren, bog, and shallows/littoral land cover types) across all seasons and scales, and avoided shrubs and grass land cover types except during summer at the two-week scale (Appendix 2A: Table

2A-4A). Significant positive coefficients for terrain position index in all four models (β range: 0.05 to 0.09, Appendix 2A: Table 2A-4A) indicated that caribou selected ridgetops and avoided incised valleys. Caribou avoided more rugged terrain at all seasons and spatiotemporal scales (β range: –1.85 to –0.29, Appendix 2A: Table 2A-4A).

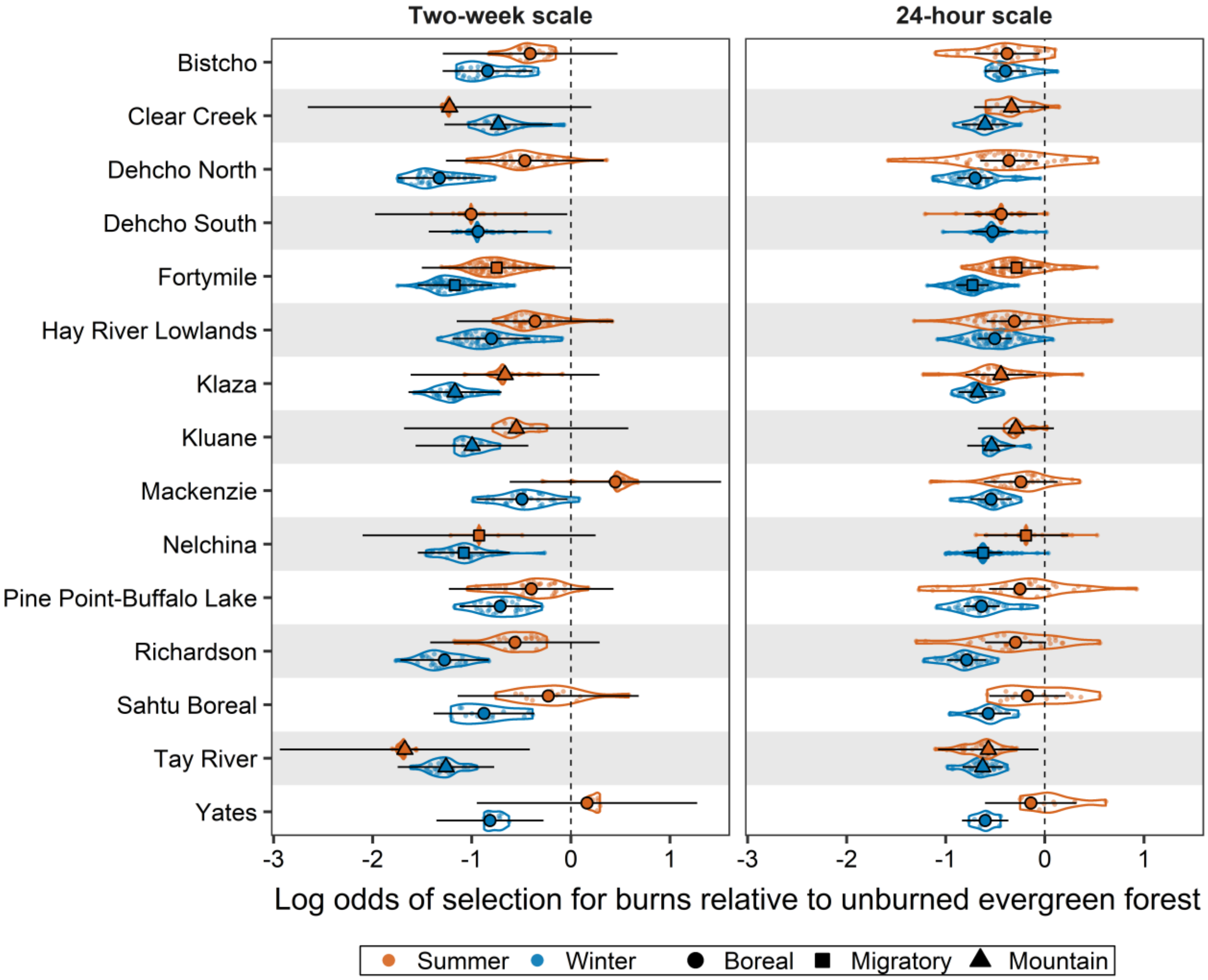


Figure 2-3. Individual- and population-level selection coefficients (conditional modes) for burns, shown by season and spatiotemporal scale, for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska. Values are log odds of selection relative to unburned evergreen forest, the reference land cover category. Violins with small points show the distribution of individual-level coefficients, while bold circles and lines indicate population-level coefficients for burns with their 95% confidence intervals (calculated using the sum of conditional and fixed-effect variances).

Summary of burn-related coefficients

Fixed-effects coefficients for burns indicated that caribou generally avoided burns (β range: –1.85 to –0.29; Appendix 2A: Table 2A-4A). Caribou consistently avoided burns during winter at both spatiotemporal scales across nearly all populations, but avoidance was generally stronger at the larger two-week spatiotemporal scale (Figure 3, Appendix 2A: Table 2A-5). During summer, caribou in most populations showed weaker avoidance of burns at the two-week scale. Caribou use of burns was nearly proportional to burn availability at the 24-hour scale during summer.

Functional response in burn perimeter RSA

Burn availability explained more variation in relative selection for burns than ecotype (Figure 4, Appendix 2A: Table 2A-6). The top models during winter at both spatiotemporal scales included a second-order polynomial functional response to burns (Figure 4, Appendix 2A: Table 2A-6), wherein selection for burns slowly increased as burn footprint increased but leveled off at higher levels of burn availability (i.e., 60–70% of seasonal range burned; winter two weeks: $\beta_{\text{burn\_01:burn availability}} = 0.39 \pm 0.06$, $\beta_{\text{burn\_01:burn availability}^2} = –0.18 \pm 0.05$; winter 24 hours: $\beta_{\text{burn\_01:burn availability}}$ 0.12 ± 0.03, $\beta_{\text{burn\_01:burn availability}^2} = –0.07 \pm 0.02$. During summer, the top model at both scales included a linear functional response to burn availability, indicating caribou decreased their avoidance of burns as burn availability increased (summer two weeks: $\beta_{\text{burn\_01:burn availability}} = 0.70 \pm 0.09$, summer 24 hours: $\beta_{\text{burn\_01:burn availability}} = 0.41 \pm 0.05$).

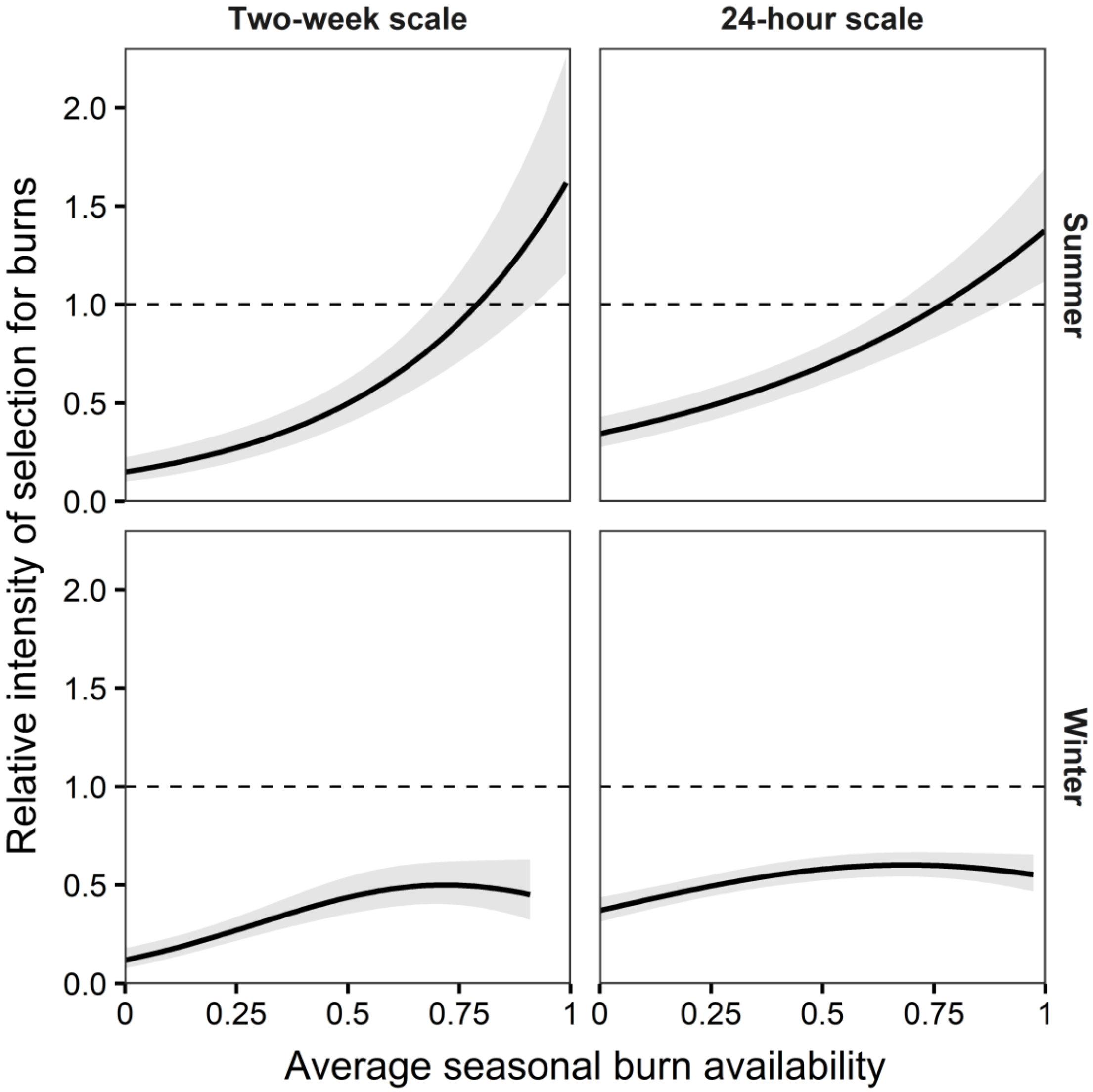


Figure 2-4. Functional responses to burns for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska shown by season and spatiotemporal scale. Gray shaded region indicates 95% confidence interval.

Burn severity RSA

Our second analysis modeled caribou resource selection in response to different levels of burn severity relative to unburned evergreen forest across the same 15 populations as above. These models replaced simple burn perimeters from the first analysis with five levels of burn severity but retained the same suite of non-burn-related covariates (Appendix 2A: Table 2A-4). Coefficients for non-burn-related covariates only changed slightly from the those (average change of <3.0%) in the *burn perimeter RSA* (Appendix 2A: Table 2A-4A), confirming that there was no evidence of confounding with burn severity.

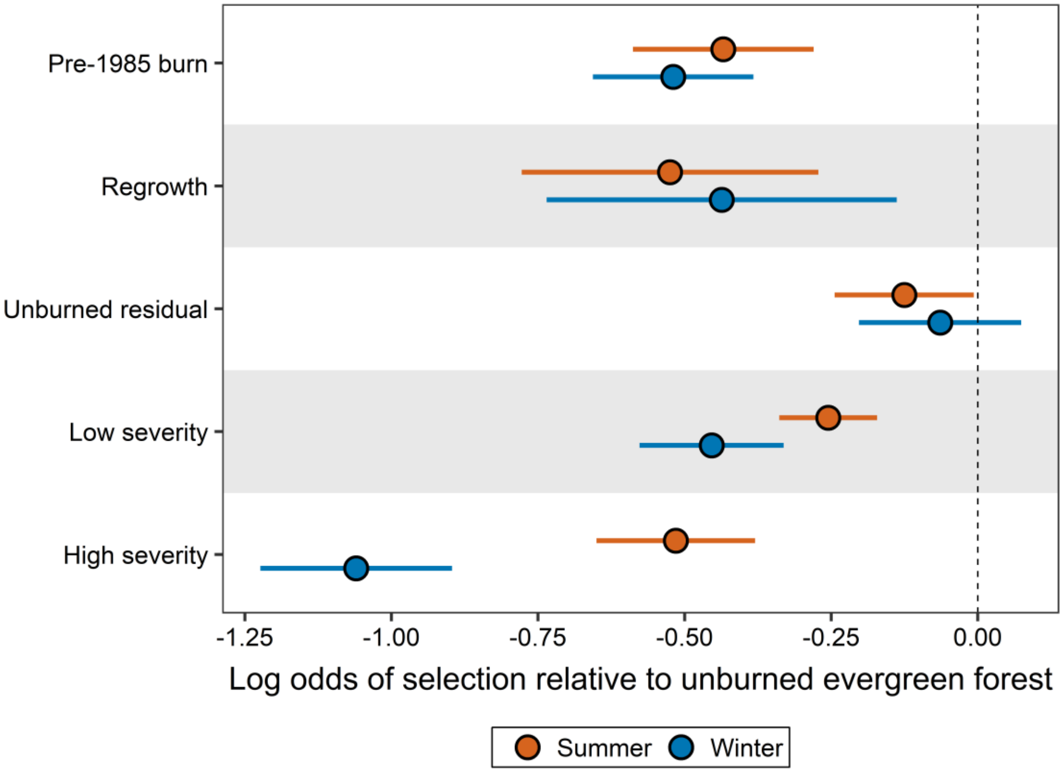


Figure 2-5. Fixed-effect selection coefficients and their 95% confidence intervals for different levels of burn severity at the 24-hour scale, shown by season, for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska. Values indicate log odds of selection relative to unburned evergreen forest, the reference land cover category.

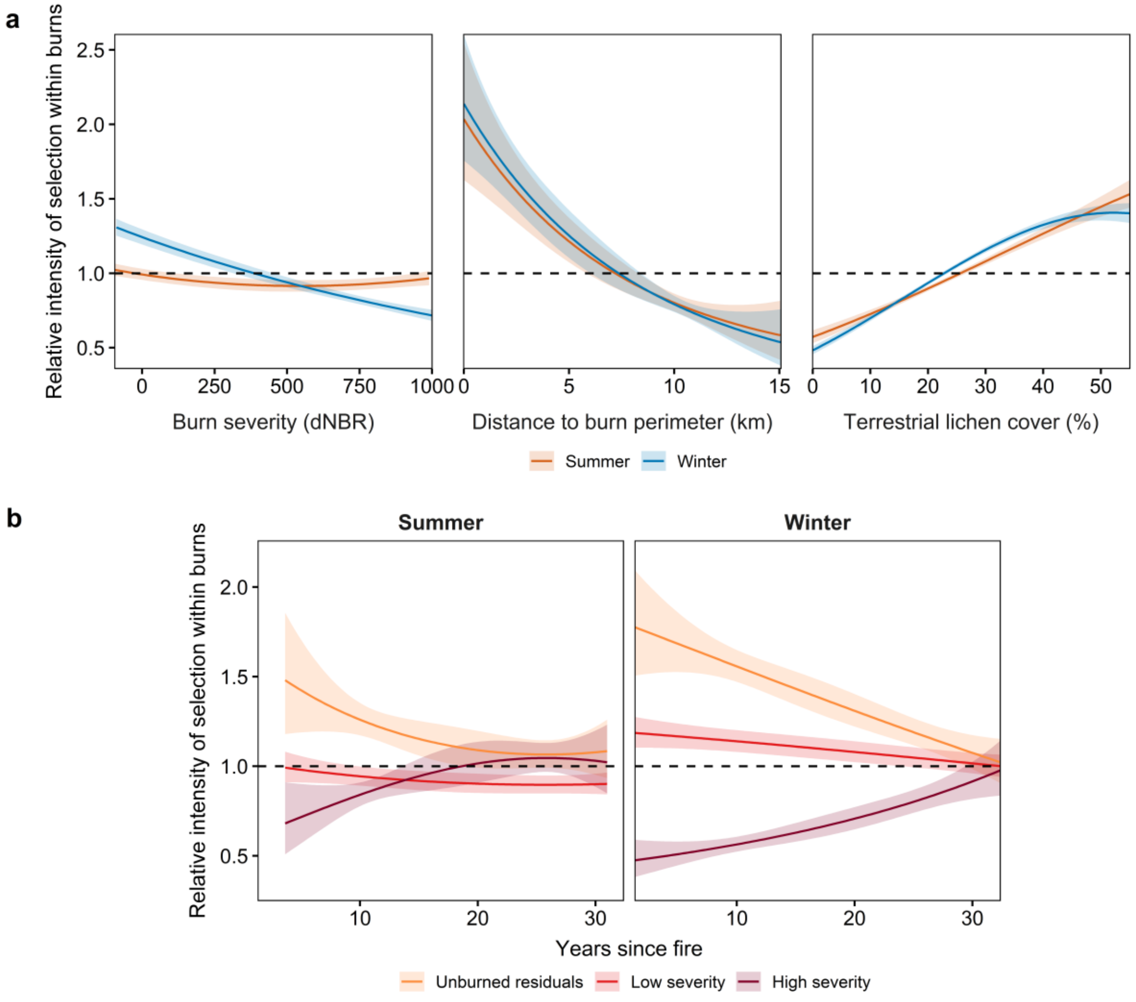


Figure 2-6. Predicted effects of burn severity, distance to burn perimeter, terrestrial lichen cover (a), and time since fire (b) on the relative intensity of selection within burn perimeters for female caribou (*Rangifer tarandus*) across four populations in eastern Alaska and western Yukon. In panel B, dNBR values for unburned residuals, low severity, and high severity categories were 0, 270 and 900, respectively. Predictions and 95% confidence intervals (shaded regions) are based on fixed effects only. All other model covariates were held at their mean values (pooled across all observations). Dashed lines indicate proportional habitat use.

We found stronger avoidance of low- and high-severity burns during winter than during summer ($\beta_{\text{winter, low severity}} = -0.45 \pm 0.06$, $\beta_{\text{summer, low severity}} = -0.26 \pm 0.04$, $\beta_{\text{winter, high severity}} = -1.06 \pm 0.08$, $\beta_{\text{summer, high severity}} = -0.51 \pm 0.07$; Figure 5, Appendix 2A: Table 2A-4B). Relative to the reference category of unburned evergreen forest, fixed-effect coefficients showed avoidance of all levels of burn severity during winter except unburned residuals. During winter, caribou avoided high-severity burned areas more than low-severity burned areas, old burns and regrowth areas, and avoided low-severity burned areas more than unburned residuals. During summer, fixed-effect coefficients indicated avoidance of all burn severity levels relative to the unburned evergreen forest, but the strength of avoidance was weaker than during the winter.

Population-level coefficients showed that all caribou populations avoided high-severity burned areas and most populations avoided low-severity burned areas relative to unburned evergreen forests during winter (Appendix 2A: Table 2A-7). During summer, caribou showed weak avoidance of high and low severity areas relative to unburned evergreen forest, and there were fewer differences between burn severity levels.

Within-burn RSA

Our third analysis modeled fine-scale caribou resource selection within burns in response to a suite of burn characteristics across four populations (two migratory and two mountain ecotypes) in AK and YT. Within burns, caribou consistently selected areas with a higher percent cover of terrestrial lichen ($\beta_{\text{winter}} = 0.31 \pm 0.01$, $\beta_{\text{summer}} = 0.29 \pm 0.02$) and areas closer to perimeters ($\beta_{\text{winter}} = –0.46 \pm 0.06$, $\beta_{\text{summer}} = –0.52 \pm 0.07$) during both summer and winter (Figure 6, Appendix 2A: Table 2A-4C). During winter, caribou avoided areas within burns that were more severely burned (Figure 6), but avoidance attenuated with increasing time since fire (Figure 6). Burn severity was a weaker driver of resource selection within burns during the summer (Figure 6), but selection for more severely burned areas did increase with increasing time since fire. During winter, our model predicted that relative intensity of selection for high severity areas did not reach the relative intensity of selection for unburned residuals until nearly 30 years after a fire, approximately ten years later than during summer (Figure 6). Finally, caribou selected areas closer to burn perimeters, avoiding areas deeper within burns during both seasons (Figure 6). We did not find evidence that this pattern weakened with increasing time since fire. We found a negative relationship between 2015 lichen cover and burn severity regardless of time since fire, except for dNBR values classified as post-fire regrowth, i.e., below –100 (Appendix 2A: Figure 2A-4).

Model validation

Models from our *burn perimeter and burn severity RSA*s showed better predictive performance for winter than summer, while the within-burn RSA models showed similar performance across seasons (Appendix 2A: Table 2A-8 and Figure 2A-5). The mean (± SD) r_s across each of the 15 withheld populations was 0.96 ± 0.05 in winter and 0.84 ± 0.12 in summer at the two-week scale and 0.94 ± 0.12 in winter and 0.89 ± 0.15 in summer at the 24-hour scale in the *burn perimeter RSA*. The mean r_s in the *burn severity RSA* was 0.96 ± 0.10 in winter and 0.88 ± 0.17 in summer. In the *within-burn RSA*, the mean r_s across the 10 withheld folds was 0.81 ± 0.06 in winter and 0.81 ± 0.13.

DISCUSSION

Our results provide strong support for the prevailing paradigm that caribou avoid burned areas very consistently across spatiotemporal scales during winter. Caribou generally avoided burns during the summer, but their responses were much more variable. Our analyses of burn severity and fine-scale burn characteristics help clarify the mechanisms driving these seasonal patterns in resource selection and confirmed that increasing fire severity will decrease lichen cover. Consistently strong avoidance of burns during winter at both spatiotemporal scales across a wide gradient of burn availability suggests that increasing fire frequency will accelerate habitat loss for caribou across huge swaths of North America’s boreal forests.

The large spatial extent of our analysis and wide variability across our 15 caribou populations in their exposure to burns greatly increased our scope of inference for resource selection behavior compared to existing RSA studies focused on one or few populations inhabiting a limited geographic area. Caribou more strongly avoided burns at larger spatiotemporal scales in many populations, supporting the idea of hierarchical habitat selection (Rettie and Messier 2000, Robinson et al. 2010). Strong avoidance of burns during winter, but weaker avoidance during summer, corroborates previous studies on migratory caribou in AK (Joly et al. 2003, 2007, 2010) and boreal woodland caribou in Quebec (Courtois et al. 2007) that attributed burn avoidance to decreases in lichen cover, their main winter forage. Stronger caribou avoidance of burns during winter compared to other seasons is also consistent with studies of mountain woodland caribou in AB (Robinson et al. 2010) and boreal woodland caribou in NT (DeMars et al. 2020). Consistent avoidance of burns across a gradient of burn availability and across spatiotemporal scales, implies that caribou will continue to avoid burns and experience habitat loss as fire frequency increases.

Our results cast a more complex picture of the relationship between caribou resource selection and fire in the summer. During summer, caribou avoided burns at the larger (two-week) scale but showed weaker to no avoidance of burns at the smaller (24-hour) scale and exhibited positive functional responses to burns both scales (see below). Our results suggest that weaker avoidance of burns in summer by adult female caribou may reflect a shift from a lichen-dominated winter diet to a more diverse, protein-rich diet to help meet increased nutritional demands after calving (Parker et al. 2009). Deciduous shrubs such as willow (*Salix* spp.) and birch (*Betula* spp.) are among the most important forage species for forest-dwelling caribou in summer (Boertje 1984, Denryter et al. 2017), and are particularly abundant early in post-fire successional forests (Schaefer and Pruitt 1991). Further, variation in burn severity within burn perimeters may provide a diverse suite of forbs, deciduous shrubs, and fungi that are important in summer caribou diet (Thompson et al. 2015) yet are unavailable in winter. We speculate that the need for protein-rich forage during summer (White et al. 2014) may override any potential increase in predation risk associated with burns (Robinson et al. 2010).

Our analyses of caribou resource selection responses to burn severity suggest that the effects of fire on species reliant on late successional boreal forest communities are more nuanced than what is revealed by quantifying responses merely to burns (presence only) or to time since fire. An important factor in fire ecology is burn severity, the proportion of organic matter consumed by a fire (Keeley 2009), which can drive biodiversity across species and scales. Burn severity has been shown to affect a diverse array of biodiversity responses and ecological processes governing post-fire vegetation recovery in forest ecosystems (Romme et al. 2011). For example, burn severity levels have been shown to affect seed germination and net seedling establishment of dominant boreal tree species (Johnstone and Chapin 2006a), relative abundance of birds species in western Montana (Smucker et al. 2005), species richness and abundance of ground beetles in northeast Alberta's boreal forest (Koivula and Spence 2006). Here, we identified a clear negative relationship between burn severity and lichen cover. This result corroborates previous work in Alberta, wherein lichen cover was negatively correlated with burn severity in jack pine forests (Pinno and Errington 2016). Caribou avoidance of areas with high burn severity and low lichen cover during winter, coupled with the observed negative relationship between burn severity and lichen cover in AK and YT (Appendix 2A: Figure 2A-4), supports the supposition that lichen destruction by severe fires contributes to the lack of functional response to burns during that season.

Legacy effects of pre-burn forest characteristics can affect post-fire vegetation trajectories, future fire conditions, and biodiversity (Johnstone et al. 2010, Romme et al. 2011). We found that pre-burn land cover may be an important predictor of fine-scale caribou resource selection within burns in summer, presumably through its effects on post-burn successional trajectory. Strong selection of pre-burn grasslands and shrubs relative to pre-burn evergreen forests within burns during summer might reflect more abundant graminoids (e.g., *Eriophorum* spp.), forbs, and deciduous shrubs in these areas after a fire (Schaefer and Pruitt 1991, Jandt et al. 2008). More detailed data on pre- and post-fire land cover could provide additional information on caribou selection responses to successional trajectory. In addition, increased deadfall in burned evergreen forests might impede caribou movement and contribute to stronger avoidance of those areas relative to pre-burn grasslands.

Predicted increases in fire frequency in the central and western portions of the boreal forest will lead to younger forest stands, reducing the average time that forest tracts exist in a mature state and potentially decreasing caribou food availability, especially in winter (Rupp et al. 2006). Depending on factors such as soil type, soil moisture, and fire timing, more frequent and/or more severe fires may result in post-fire successional trajectories dominated by deciduous species or even graminoids (Stralberg et al. 2018, Roland et al. 2019). Several studies based on projections from climate models predict broad-scale shifts in successional trajectories that will produce novel conditions in North America's boreal forests (e.g., Rupp et al. 2000, Stralberg et al. 2018). With more frequent fires, boreal land cover will continue to shift towards younger, deciduous-dominated vegetation communities, especially in the southern fringes of the region (Barber et al. 2018), that are favored by other ungulates such as moose (*Alces alces*) and deer (*Odocoileus* spp.). Our results show that caribou tend to avoid these land cover types relative to evergreen forests, especially in winter (Appendix 2A: Table 2A-4). Collectively, this suggests that important consequences of increasing fire frequency and severity and its effects on boreal biodiversity will be through the direct loss of late successional vegetation communities, the resources therein (e.g., lichen in winter for caribou), and through land cover change and compounding effects on future fire. There is considerable uncertainty around rates of predicted changes to forest composition and structure resulting from climate warming and changing fire regimes (Roland et al. 2019).

It is important to understand how animals reliant on late-successional forests might alter their selection of burned areas as fire frequency increases in the future, and how these changes may affect habitat use. For example, California spotted owls (*Strix occidentalis occidentalis*), a subspecies of spotted owl adapted to relatively small patches of severe fires, more strongly avoided severely burned areas when a higher proportion of their home ranges were severely burned (Jones et al. 2020). If caribou maintain strong avoidance of burns as the footprint of burns within their ranges increases, they will experience increasing habitat loss. Alternatively, caribou might relax their avoidance, indicating less habitat loss as fire availability increases. However, if burned habitat is of lower quality, increasing use of burns could ultimately have negative demographic impacts for caribou.

Many studies have used climate projections to predict future declines in caribou habitat quality and distribution based on present avoidance of burns by caribou (e.g., Rupp et al. 2006, Gustine et al. 2014, Barber et al. 2018). However, our functional response results in summer showed decreasing avoidance burn availability increased, to the point where selection of burns was equal to or greater than selection of evergreen forests. The difference in functional response to burns between seasons may stem from seasonal differences in diet composition and nutritional demands. Caribou may also be constrained in their ability to avoid burns at extremely high levels of burn availability (Beyer et al. 2010). During winter, caribou rely on old growth habitats with sufficient lichen abundance and may be unable to shift to burned areas where lichen has been destroyed. As burn frequency and overall burn footprint increases, some burns may be adequate substitutes for unburned areas during summer because they can provide a diverse suite of protein-rich forage. Our functional response models suggest that at least in winter, future fires are likely to continue to result in increasing indirect habitat loss.

Several additional factors may also contribute to variation in relative selection for burns beyond burn availability and seasonal diet differences. During the winter, increased sun and wind exposure within burns may impede caribou movement and foraging due to snow density and surface crust thickness (Schaefer and Pruitt 1991). In addition, historical exposure to burns in Quebec helped predict caribou responses to forest harvest in Quebec, and may influence relative selection for burns in our study area (Lafontaine et al. 2019). We found that any potential effects of ecotype on caribou responses to burns were outweighed by seasonal burn availability.

Given their large ranges and reliance on late-successional vegetation, forest-dwelling caribou are important umbrellas of broadscale biodiversity (Bichet et al. 2016) and indicators of boreal carbon stocks, which account for roughly one-third of the world's terrestrial carbon (Pan et al. 2011). Although most carbon beneath older, wetter forests is typically protected from combustion, shallower organic matter layers in warmer, drier, and younger forests allow fires to release more carbon, which could shift North American boreal region from a net sink to a net source of carbon (Walker et al. 2019). The area affected by greater fire frequency in boreal forests (de Groot et al. 2013) will likely dwarf the area harvested by the forestry industry, even though continued forestry and energy development throughout the region are main causes of population declines for many boreal species (Venier et al. 2014). As fire frequency increases, species that require late-successional communities may retreat to climate refugia such as mountains and peatlands (Stralberg et al. 2020). Protecting late successional habitats that experience fires of increasing frequency and considerable spatiotemporal unpredictability is a major conservation challenge and underscores the need to minimize negative effects of new human disturbance in remaining mature forests. In addition, our study also has implications for other types of boreal forest disturbances, such as insect outbreaks, that may interact with fire to affect late-successional communities (Bradshaw et al. 2009, Labadie et al. 2021). Future work directly linking animal demography to habitat selection in response to both fire and human disturbance would provide a clearer picture of the degree to which fire may affect boreal biodiversity.

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APPENDIX 2A

Table 2A-1. Animal care permit details for captures of female caribou (*Rangifer tarandus*) in eastern Alaska and northwestern Canada.

Region	Populations	Animal care permit #s
AB	Richardson, Yates	University of Montana IAUCUC # 05606MHECS_010207
AK	Fortymile, Nelchina	2012-034, 2013-031, 2015-03, 2016-10
NT	Bistcho, Dehcho North, Dehcho South, Hay River Lowlands, Mackenzie, Pine Point-Buffalo Lake, Sahtu	Government of Northwest Territories Wildlife Act authority and internal permits and capture reviews.
YT	Clear Creek, Klaza, Kluane, Tay River	Government of Yukon Territory wildlife act authority and internal permits and capture reviews.

Table 2A-2. Summary of available GPS location data from female caribou (*Rangifer tarandus*) in eastern Alaska and northwestern Canada prior to filtering for all resource selection analyses.

Ecotype	Region	Population	Years marked	# of animals	Mean # of years marked per animal	Mean # of locs per animal	Median relocation interval (hours)	Range of median relocation interval (hours)
Boreal	AB/NT	Bistcho	2006–2011	30	2.4	2046	8.0	8–16
Boreal	NT	Dehcho North	2007–2019	64	1.9	1781	8.0	2–25
Boreal	NT	Dehcho South	2007–2019	66	2.0	1699	8.0	4–24
Boreal	NT	Hay River Lowlands	2008–2019	86	2.1	1946	8.0	2–24
Boreal	NT	Mackenzie	2015–2019	37	2.2	5371	2.0	2–8
Boreal	NT	Pine Butte-Buffalo Lake	2015–2019	44	2.0	2241	8.0	2–8
Boreal	AB	Richardson	2008–2016	36	1.4	4632	2.0	2–23
Boreal	NT	Sahtu	2003–2011	16	2.6	1441	12.0	8–24
Boreal	AB	Yates	2014–2016	13	1.1	4674	2.0	2–23
Migratory	AK/YT	Fortymile	2013–2019	118	2.2	4357	2.5	1–26
Migratory	AK/YT	Nelchina	2012–2015	78	1.3	1707	4.0	4–12
Mountain	YT	Clear Creek	2017–2019	39	1.5	305	23.0	13–69
Mountain	YT	Klaza	2012–2019	43	1.6	1742	8.0	5–13
Mountain	YT	Kluane	2014–2018	12	2.6	3875	5.0	5–13
Mountain	YT	Tay River	2016–2018	39	1.9	550	23.0	23–46

Table 2A-3. Summary of GPS location data from adult female caribou (*Rangifer tarandus*) in eastern Alaska and northwestern Canada used in resource selection analyses. We excluded the Nelchina population from the *within-burn RSA* summer model due to a lack of GPS locations within burns.

A. *Burn perimeter* and *burn severity RSAs*

				Summer				Winter			
Ecotype	Region	Population	Years marked	24-hour scale		Two-week scale		24-hour scale		Two-week scale	
				# of animals	Mean # of locs per animal	# of animals	Mean # of locs per animal	# of animals	Mean # of locs per animal	# of animals	Mean # of locs per animal
Boreal	AB/NT	Bistcho	2006–2011	29	264.4	28	20.8	30	498.8	28	38.7
Boreal	NT	Dehcho North	2007–2019	49	221.3	44	18.0	58	385.9	46	33.5
Boreal	NT	Dehcho South	2007–2019	56	181.0	50	15.8	65	376.2	52	32.8
Boreal	NT	Hay River Lowlands	2008–2019	71	195.2	61	16.9	85	381.8	67	34.3
Boreal	NT	Mackenzie	2015–2019	30	315.4	30	19.3	37	523.6	32	38.8
Boreal	NT	Pine Point-Buffalo L.	2015–2019	34	262.5	33	18.5	44	460.7	35	39.0
Boreal	AB	Richardson	2008–2016	30	255.8	26	16.0	36	386.6	27	27.5
Boreal	NT	Sahtu	2006–2011	14	278.3	13	23.5	15	392.3	14	30.5
Boreal	AB	Yates	2014–2016	8	258.4	8	14.6	8	496.8	8	28.2
Migratory	AK/YT	Fortymile	2013–2019	110	342.4	102	22.0	112	513.2	102	36.5
Migratory	AK/YT	Nelchina	2012–2015	64	173.6	55	13.7	77	232.6	38	27.4
Mountain	YT	Clear Creek	2017–2019	20	114.3	16	11.5	22	160.4	19	18.1
Mountain	YT	Klaza	2012–2019	33	173.9	32	13.1	43	345.7	41	26.2
Mountain	YT	Kluane	2014–2018	10	418.9	11	22.9	12	601.6	27	36.1
Mountain	YT	Tay River	2016–2018	32	180.7	8	16.0	36	265.6	29	24.8

Table 2A-3. (continued)

B. Within-burn RSA

				Summer				Winter			
Ecotype	Region	Population	Years marked	# of animals	Mean # of locations per animal	Mean # of burns visited per animal	Median location interval within burns (hours)	# of animals	Mean # of locations per animal	Mean # of burns visited per animal	Median location interval within burns (hours)
Migratory	AK/YT	Fortymile	2013–2019	91	76.8	13.3	9.9	94	106.0	18.8	12.0
Migratory	AK/YT	Nelchina	2012–2015	-	-	-	-	30	47.1	5.5	12.6
Mountain	YT	Klaza	2012–2019	12	52.6	1.5	12.7	7	50.3	3.3	8.0
Mountain	YT	Kluane	2014–2017	4	74.8	1.5	15.1	17	153	1.6	16.5

Table 2A-4. Fixed effect coefficients and 95% confidence intervals for covariates in resource selection analyses for female caribou (*Rangifer tarandus*) in eastern Alaska and northwest Canada.

A. *Burn perimeter RSA* (*n* = 15 populations). Land cover coefficients indicate selection relative to the reference category of evergreen forest.

	Summer						Winter					
Covariate	24-hour scale			Two-week scale			24-hour scale			Two-week scale		
	β	LCI	UCI	*β*	LCI	UCI	*β*	LCI	UCI	*β*	LCI	UCI
burn	–0.32	–0.43	–0.21	–0.61	–0.96	–0.25	–0.61	–0.68	–0.54	–0.99	–1.15	–0.82
fen	–0.48	–0.66	–0.31	–0.54	–0.82	–0.26	–0.45	–0.66	–0.24	–0.63	–0.97	–0.28
grass	–0.07	–0.35	0.21	0.25	–0.06	0.56	–0.20	–0.49	0.09	–0.16	–0.46	0.14
other	–0.41	–0.51	–0.30	–0.23	–0.44	–0.02	–0.53	–0.68	–0.38	–0.74	–1.03	–0.45
shrubs	–0.49	–0.69	–0.28	–0.50	–0.86	–0.14	–0.55	–0.79	–0.32	–0.94	–1.34	–0.54
sparse	0.08	0.05	0.12	0.32	0.21	0.44	0.02	–0.01	0.04	–0.16	–0.25	–0.07
water	–4.26	–4.95	–3.56	–9.76	–13.14	–6.37	–2.59	–2.93	–2.25	–3.37	–4.04	–2.71
tree cover	–0.21	–0.45	0.03	–0.34	–0.56	–0.11	–0.35	–0.44	–0.27	–0.59	–0.70	–0.49
tree cover^2	–0.09	–0.22	0.05	–0.14	–0.32	0.04	–0.25	–0.30	–0.19	–0.38	–0.45	–0.31
TRI	–0.29	–0.54	–0.05	–0.41	–0.82	–0.01	–1.85	–3.31	–0.40	–0.63	–0.97	–0.28
TRI^2	0.04	–0.08	0.17	0.04	–0.22	0.31	–0.80	–1.44	–0.15	0.04	–0.12	0.19
TPI	0.05	0.05	0.06	0.07	0.04	0.09	0.08	0.08	0.08	0.09	0.07	0.11
log sl	0.07	0.06	0.08	0.16	0.12	0.19	0.06	0.06	0.07	0.13	0.11	0.15

B. *Burn severity RSA* at the 24-hour spatiotemporal scale (*n* = 15 populations). Land cover coefficients indicate selection relative to the reference category of unburned evergreen forest.

Covariate	Summer			Winter		
	β	LCI	UCI	*β*	LCI	UCI
old burn	–0.43	–0.59	–0.28	–0.52	–0.66	–0.38
regrowth	–0.52	–0.78	–0.27	–0.44	–0.74	–0.14
unburned residual	–0.13	–0.24	–0.01	–0.06	–0.20	0.07
low severity	–0.26	–0.34	–0.17	–0.45	–0.58	–0.33
high severity	–0.51	–0.65	–0.38	–1.06	–1.22	–0.90
fen	–0.49	–0.67	–0.32	–0.45	–0.66	–0.24
grass	–0.07	–0.36	0.22	–0.22	–0.51	0.06

other	–0.39	–0.51	–0.28	–0.52	–0.68	–0.35
shrubs	–0.48	–0.69	–0.28	–0.55	–0.79	–0.32
sparse	0.10	0.06	0.13	0.02	0.00	0.05
water	–4.26	–4.96	–3.56	–2.55	–2.89	–2.21
tree cover	–0.20	–0.44	0.05	–0.34	–0.44	–0.24
tree cover^2	–0.09	–0.22	0.05	–0.25	–0.31	–0.20
TRI	–0.34	–0.68	–0.01	–1.79	–3.31	–0.27
TRI^2	0.02	–0.13	0.18	–0.77	–1.47	–0.06
TPI	0.05	0.04	0.06	0.08	0.08	0.09
log sl	0.05	0.04	0.05	0.05	0.04	0.05

C. *Within-burn RSA* (*n* = 4 populations). Land cover categories represent pre-fire land cover, and their coefficients indicate selection relative to the reference pre-fire land cover category of evergreen forest.

Covariate	Summer (~10-hour scale)			Winter (~12-hour scale)		
	β	LCI	UCI	β	LCI	UCI
severity	–0.08	–0.12	–0.04	–0.30	–0.35	–0.26
severity^2	0.08	0.04	0.12	0.00	–0.03	0.04
lichen	0.29	0.25	0.32	0.31	0.29	0.34
lichen^2	–0.03	–0.05	–0.01	–0.09	–0.10	–0.08
distance to perimeter	–0.52	–0.66	–0.38	–0.46	–0.58	–0.33
distance to perimeter^2	0.04	–0.05	0.13	0.01	–0.08	0.11
severity:tsf	0.09	0.04	0.13	0.16	0.11	0.20
severity:tsf^2	–0.04	–0.11	0.03	0.01	–0.04	0.06
distance to perimeter:tsf	–0.11	–0.28	0.05	0.12	–0.02	0.25
distance to perimeter:tsf^2	–0.24	–0.43	–0.04	–0.02	–0.15	0.11
fen	0.54	0.43	0.65	0.04	–0.07	0.14
grass	1.18	1.08	1.29	0.36	0.23	0.49
other	0.10	–0.13	0.32	–0.36	–0.57	–0.14
shrubs	0.46	0.36	0.57	–0.09	–0.18	0.00
sparse	0.53	0.38	0.68	0.33	0.22	0.45
TRI	–0.10	–0.28	–0.04	–0.09	–0.02	–0.03
TRI^2	–0.29	–0.43	–0.24	–0.20	–0.15	–0.15
TPI	0.08	–0.17	0.10	0.04	–0.14	0.06
TPI^2	–0.04	–0.33	–0.01	0.01	–0.24	0.03

Table 2A-5. Population-level random selection coefficients and their 95% confidence intervals (calculated using the sum of conditional and fixed effects variances) for burns (in the *burn perimeter RSA*) at two spatiotemporal scales and seasons, for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska. Values indicate log odds of selection relative to the reference land cover category of unburned evergreen forest.

		Summer						Winter					
Ecotype	Population	Two-week scale			24-hour scale			Two-week scale			24-hour scale		
		β	LCI	UCI	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI
Boreal	Bistcho	–0.41	–1.29	0.47	–0.38	–0.71	–0.05	–0.84	–1.29	–0.39	–0.40	–0.61	–0.19
Boreal	Dehcho North	–0.46	–1.26	0.33	–0.36	–0.65	–0.07	–1.33	–1.74	–0.91	–0.70	–0.88	–0.52
Boreal	Dehcho South	–1.01	–1.98	–0.04	–0.44	–0.81	–0.07	–0.94	–1.43	–0.44	–0.52	–0.73	–0.32
Boreal	Hay River Lowlands	–0.36	–1.15	0.43	–0.31	–0.59	–0.02	–0.80	–1.19	–0.41	–0.51	–0.68	–0.33
Boreal	Mackenzie	0.45	–0.62	1.52	–0.24	–0.61	0.13	–0.49	–0.95	–0.03	–0.54	–0.75	–0.34
Boreal	Pine Point-Buffalo Lake	0.00	–1.23	0.43	–0.25	–0.56	0.06	–0.71	–1.12	–0.30	–0.64	–0.82	–0.46
Boreal	Richardson	–0.56	–1.42	0.29	–0.30	–0.60	0.01	–1.27	–1.72	–0.83	–0.79	–0.98	–0.59
Boreal	Sahtu	–0.23	–1.14	0.68	–0.18	–0.56	0.21	–0.88	–1.39	–0.37	–0.57	–0.80	–0.34
Boreal	Yates	0.16	–0.95	1.27	–0.14	–0.60	0.32	–0.82	–1.36	–0.28	–0.60	–0.84	–0.37
Migratory	Fortymile	–0.75	–1.50	0.01	–0.29	–0.54	–0.03	–1.17	–1.55	–0.79	–0.73	–0.89	–0.57
Migratory	Nelchina	–0.93	–2.10	0.25	–0.19	–0.62	0.24	–1.08	–1.54	–0.62	–0.62	–0.82	–0.43
Mountain	Clear Creek	–1.22	–2.65	0.21	–0.34	–0.71	0.04	–0.73	–1.27	–0.19	–0.6	–0.84	–0.37
Mountain	Klaza	–0.66	–1.62	0.29	–0.44	–0.80	–0.09	–1.17	–1.64	–0.70	–0.67	–0.87	–0.47
Mountain	Kluane	–0.55	–1.68	0.58	–0.29	–0.68	0.09	–1.00	–1.57	–0.43	–0.54	–0.78	–0.29
Mountain	Tay River	–1.68	–2.94	–0.41	–0.57	–1.08	–0.06	–1.26	–1.75	–0.77	–0.63	–0.83	–0.42

Table 2A-6. Delta AIC values for candidate models testing for functional responses to burns and those testing for the effect of ecotype on relative selection for burns for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska in the *burn perimeter RSA*. Bolded values indicate top models for each combination of spatiotemporal scale and season. df indicates degrees of freedom.

Model	df	Two-week scale		24-hour scale	
		Summer	Winter	Summer	Winter
First order functional response	33	**0.0**	8.8	**0.0**	9.2
Second order functional response	34	1.4	**0.0**	2.0	**0.0**
Burn:ecotype interaction	34	64.3	49.4	80.8	30.8
No functional response or interaction	32	69.1	48.0	85.1	28.3

Table 2A-7. Population-level random selection coefficients and their 95% confidence intervals (calculated using the sum of conditional and fixed effects variances) for burn severity levels (in the *burn severity RSA*) at the 24-hour spatiotemporal scale during summer and winter for female caribou (*Rangifer tarandus*) across 15 populations in western Canada and eastern Alaska. Values indicate log odds of selection relative to the reference land cover category of unburned evergreen forest.

A. Summer

Ecotype	Population	Old burn			Regrowth			Residual			Low severity			High severity		
		β	LCI	UCI	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI	β	LCI	UCI
Boreal	Bistcho	–0.42	–0.89	0.05	–0.56	–1.11	–0.01	–0.13	–0.45	0.19	–0.33	–0.59	–0.07	–0.54	–0.91	–0.18
Boreal	Dehcho North	–0.45	–0.83	–0.07	–0.52	–0.98	–0.06	–0.24	–0.55	0.07	–0.16	–0.41	0.08	–0.54	–0.88	–0.21
Boreal	Dehcho South	–0.57	–1.06	–0.09	–0.51	–1.00	–0.02	–0.08	–0.43	0.26	–0.28	–0.50	–0.05	–0.48	–0.87	–0.08
Boreal	Hay River Lowlands	–0.38	–0.74	–0.02	–0.52	–0.99	–0.04	–0.07	–0.38	0.24	–0.27	–0.48	–0.05	–0.45	–0.82	–0.08
Boreal	Mackenzie	–0.47	–0.97	0.02	–0.51	–0.99	–0.04	–0.05	–0.37	0.27	–0.19	–0.45	0.07	–0.69	–1.08	–0.31
Boreal	Pine Point-Buffalo L.	–0.29	–0.68	0.10	–0.55	–1.03	–0.06	–0.26	–0.59	0.08	–0.26	–0.47	–0.05	–0.61	–0.99	–0.24
Boreal	Richardson	–0.25	–0.64	0.14	–0.54	–1.00	–0.07	–0.12	–0.43	0.18	–0.27	–0.47	–0.06	–0.74	–1.12	–0.36
Boreal	Sahtu	–0.36	–0.82	0.09	–0.52	–0.99	–0.05	–0.16	–0.50	0.18	–0.22	–0.47	0.03	–0.33	–0.78	0.12
Boreal	Yates	–0.21	–0.74	0.31	–0.52	–1.00	–0.05	–0.14	–0.50	0.23	–0.27	–0.51	–0.03	–0.39	–0.90	0.12
Migratory	Fortymile	–0.67	–1.04	–0.31	–0.40	–1.36	0.55	0.07	–0.22	0.36	–0.27	–0.46	–0.07	–0.30	–0.60	0.01
Migratory	Nelchina	–0.46	–0.99	0.06	–0.53	–1.00	–0.05	–0.11	–0.48	0.25	–0.27	–0.51	–0.03	–0.43	–0.91	0.05
Mountain	Clear Creek	–0.37	–0.90	0.16	–0.53	–1.00	–0.05	–0.10	–0.47	0.26	–0.24	–0.48	0.00	–0.48	–0.95	–0.02
Mountain	Klaza	–0.47	–0.94	0.00	–0.53	–1.01	–0.05	–0.16	–0.50	0.18	–0.25	–0.48	–0.03	–0.41	–0.81	–0.01
Mountain	Kluane	–0.47	–0.99	0.05	–0.52	–1.00	–0.05	–0.11	–0.47	0.26	–0.23	–0.48	0.01	–0.49	–0.94	–0.04
Mountain	Tay River	–0.52	–1.03	–0.01	–0.52	–0.99	–0.05	–0.12	–0.49	0.24	–0.29	–0.54	–0.03	0.00	–1.22	–0.18

Table 2A-7. (continued)
B. Winter

Ecotype	Population	Old burn			Regrowth			Unburned residual			Low severity			High severity		
		B	LCI	UCI	*β*	LCI	UCI	*β*	LCI	UCI	*β*	LCI	UCI	*β*	LCI	UCI
Boreal	Bistcho	–0.29	–0.68	0.10	–0.24	–1.01	0.53	0.23	–0.11	0.57	–0.19	–0.49	0.10	–0.49	–0.91	–0.07
Boreal	Dehcho North	–0.73	–1.07	–0.40	–0.26	–0.95	0.43	–0.25	–0.57	0.08	–0.43	–0.71	–0.15	–1.14	–1.52	–0.75
Boreal	Dehcho South	–0.46	–0.86	–0.06	0.13	–0.81	1.08	0.03	–0.34	0.40	–0.26	–0.58	0.05	–0.55	–0.99	–0.11
Boreal	Hay River Lowlands	–0.53	–0.84	–0.23	–1.24	–2.08	–0.41	–0.13	–0.46	0.19	–0.42	–0.72	–0.13	–0.91	–1.32	–0.50
Boreal	Mackenzie	–1.02	–1.54	–0.50	–0.58	–1.33	0.17	0.07	–0.26	0.41	–0.19	–0.49	0.12	–1.26	–1.67	–0.86
Boreal	Pine Point-Buffalo L.	–0.48	–0.8	–0.16	–0.76	–1.45	–0.06	–0.46	–0.80	–0.11	–0.57	–0.87	–0.28	–1.05	–1.47	–0.64
Boreal	Richardson	–0.52	–0.85	–0.19	–0.29	–1.01	0.43	–0.30	–0.64	0.04	–0.86	–1.16	–0.56	–1.47	–1.89	–1.06
Boreal	Sahtu	–0.49	–0.90	–0.08	–0.07	–0.89	0.76	0.13	–0.27	0.54	–0.59	–0.96	–0.22	–1.21	–1.72	–0.7
Boreal	Yates	–0.59	1.00	–0.18	–0.44	–1.58	0.70	0.11	–0.43	0.66	–0.47	–0.91	–0.03	–1.03	–1.64	–0.42
Migratory	Fortymile	–0.57	–0.88	–0.26	–0.75	–1.48	–0.02	–0.18	–0.49	0.12	–0.66	–0.93	–0.39	–1.11	–1.48	–0.75
Migratory	Nelchina	–0.41	–0.77	–0.05	–0.37	–1.21	0.47	–0.33	–0.71	0.05	–0.55	–0.87	–0.22	–0.87	–1.29	–0.44
Mountain	Clear Creek	–0.21	–0.73	0.32	–0.27	–1.21	0.66	0.07	–0.39	0.53	–0.56	–0.99	–0.13	–1.33	–1.87	–0.79
Mountain	Klaza	–0.66	–1.04	–0.28	–0.17	–1.09	0.74	0.08	–0.29	0.46	–0.48	–0.80	–0.15	–1.01	–1.44	–0.58
Mountain	Kluane	–0.20	–0.76	0.36	–0.44	–1.58	0.70	0.03	–0.47	0.54	–0.17	–0.58	0.23	–1.02	–1.53	–0.50
Mountain	Tay River	–0.48	–0.86	–0.10	–0.25	–1.31	0.82	0.06	–0.38	0.49	–0.27	–0.62	0.08	–1.06	–1.50	–0.61

Table 2A-8. Spearman rank correlations for resource selection models for female caribou (*Rangifer tarandus*) in western Canada and eastern Alaska. For the *burn perimeter* and *burn severity RSAs*, models were fit using 14 of 15 populations, and model coefficients were used to predict RSF scores for the withheld population. For the *within-burn RSA*, models were fit to 90% of individual caribou, and model coefficients were used to predict RSF scores for the remaining 10% of animals.

		Burn perimeter RSA				*Burn severity RSA*	
Ecotype	Population	Summer		Winter		Summer	Winter
		Two weeks	24 hours	Two weeks	24 hours	24 hours	24 hours
Boreal	Bistcho	0.92	1.00	1.00	0.98	1.00	0.99
Boreal	Dehcho North	0.85	0.88	0.99	1.00	0.98	1.00
Boreal	Dehcho South	0.91	0.99	1.00	1.00	0.97	1.00
Boreal	Hay River Lowlands	0.90	0.86	0.99	0.98	0.87	1.00
Boreal	Mackenzie	0.78	0.50	0.94	0.66	0.95	0.81
Boreal	Pine Point-Buffalo Lake	0.90	0.64	0.99	0.98	0.95	0.98
Boreal	Richardson	0.83	0.99	1.00	0.97	0.98	0.98
Boreal	Sahtu Boreal	0.73	0.76	0.89	1.00	0.94	1.00
Boreal	Yates	0.67	0.81	0.98	0.99	0.44	0.99
Migratory	Fortymile	0.95	1.00	0.99	1.00	0.99	1.00
Migratory	Nelchina	0.99	1.00	0.96	1.00	1.00	1.00
Mountain	Clear Creek	0.57	0.97	0.91	0.64	0.73	0.62
Mountain	Klaza	0.81	0.93	0.92	0.99	0.54	0.99
Mountain	Kluane	0.87	0.99	0.85	0.96	0.90	0.99
Mountain	Tay River	0.97	1.00	0.99	1.00	0.96	1.00

	Within-burn RSA	
Random fold	Summer	Winter
	10–15 hours	12–17 hours
1	0.54	0.78
2	0.73	0.74
3	0.96	0.88
4	0.86	0.76
5	0.93	0.84
6	0.84	0.84
7	0.89	0.92
8	0.80	0.75
9	0.86	0.77
10	0.70	0.77

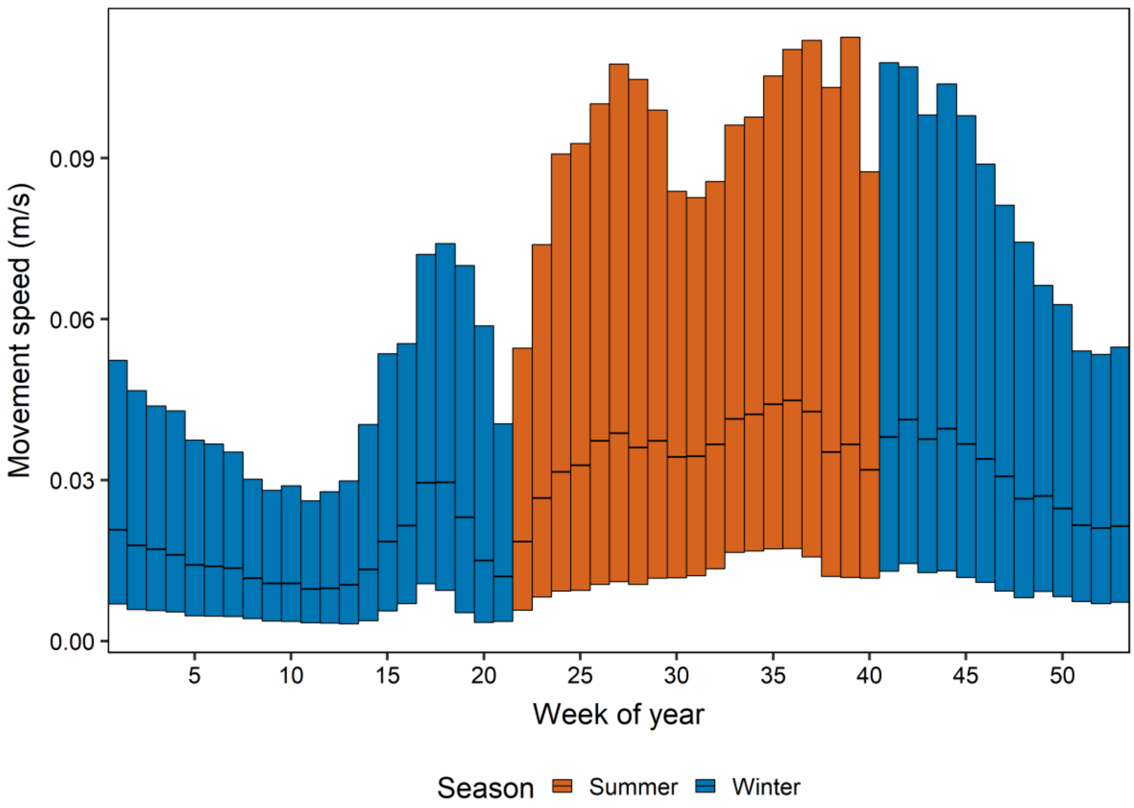

Figure 2-A-1. Movement speeds by week of year across all 15 populations of caribou included in the *burn perimeter* and *burn severity RSAs*. Black horizontal bars indicate median values and colored bars represent values between 0.25 and 0.75 quantiles.

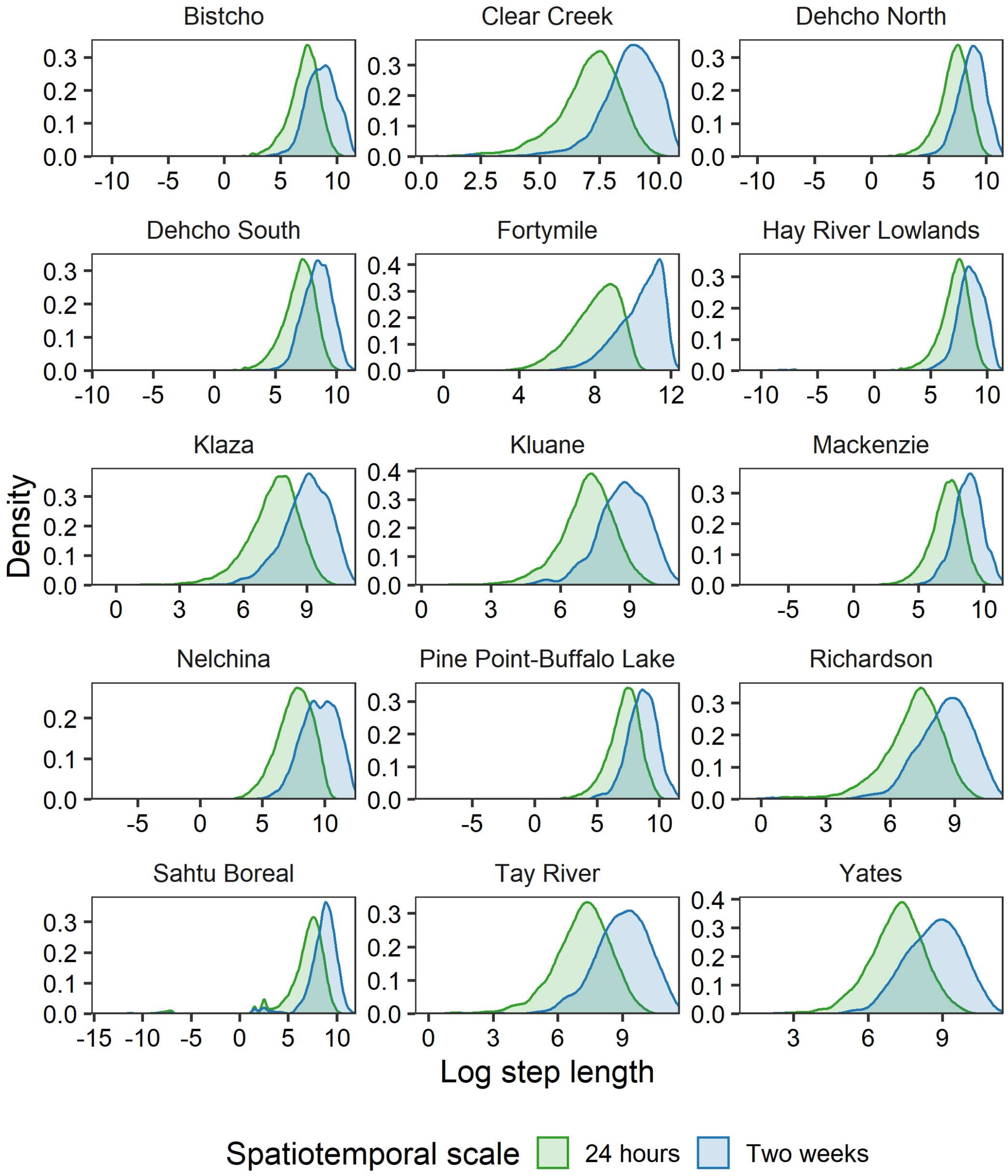

Figure 2-A-2. Distribution of log-transformed step lengths at the 24-hour and two-week spatiotemporal scales for adult female caribou (*Rangifer tarandus*) from 15 populations throughout eastern Alaska and northwest Canada.

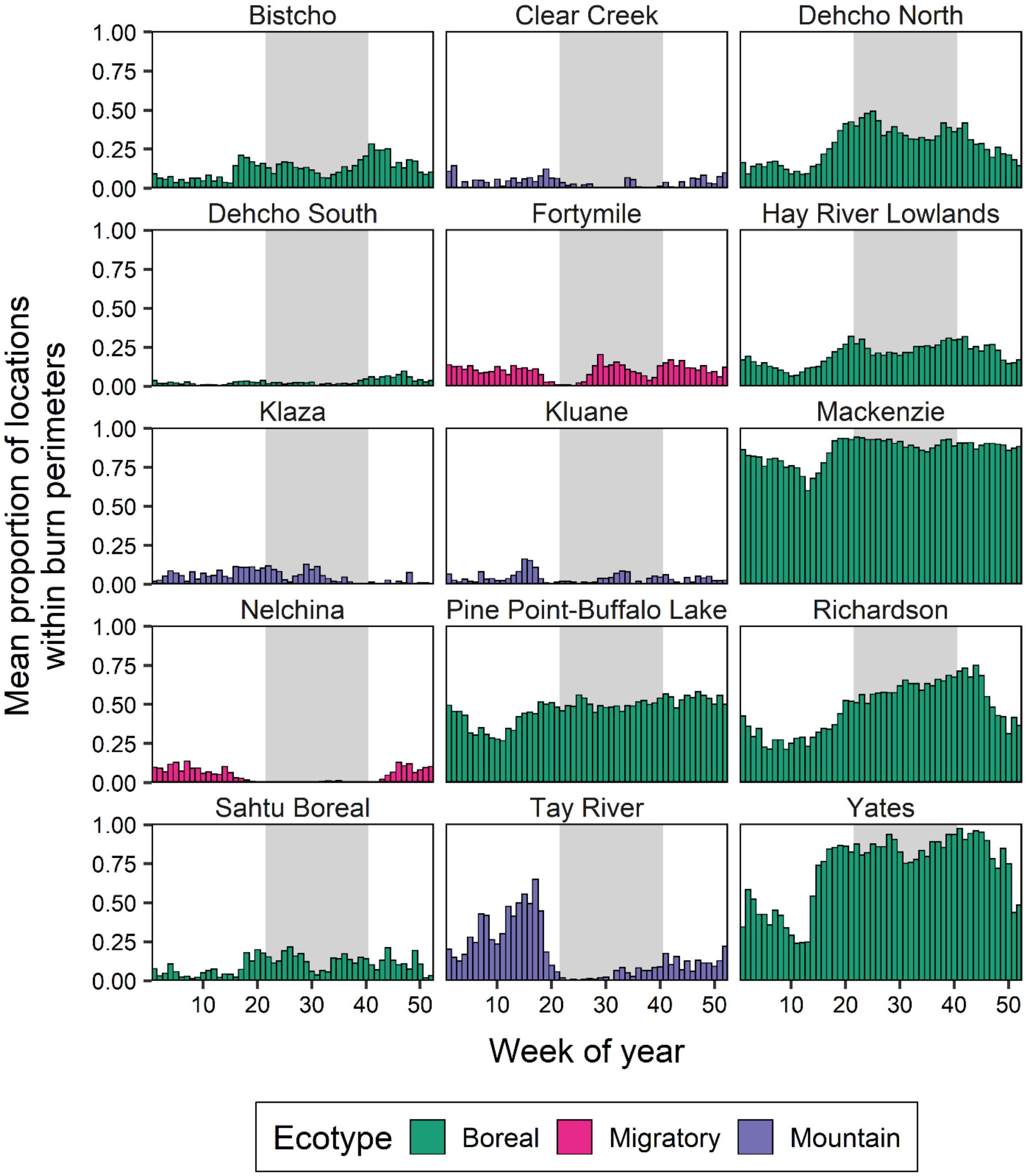

Figure 2-A-3. Proportion of GPS locations within burn perimeters by week of year for female caribou (*Rangifer tarandus*), averaged across all individuals within a population, from 15 populations in eastern Alaska and northwest Canada. Gray shaded areas depict summer season used for models.

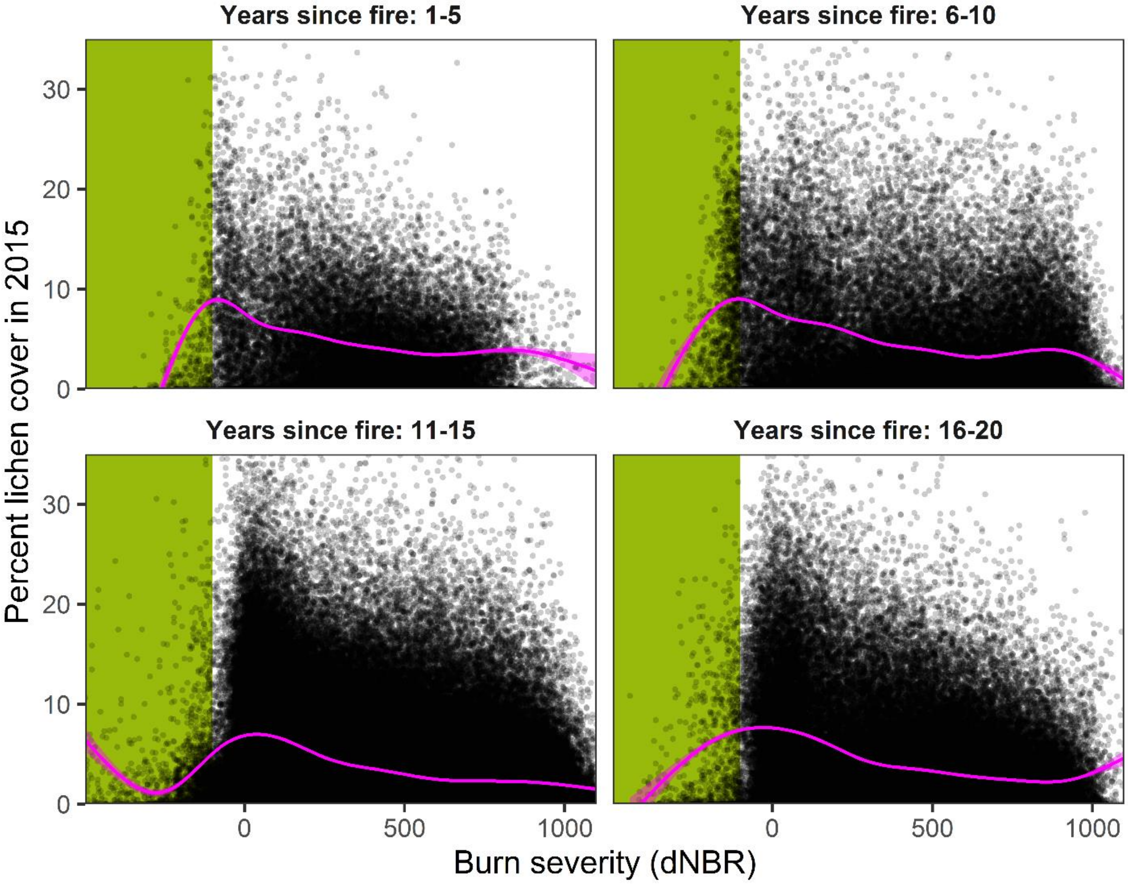

Figure 2-A-4. Relationship between percent cover of terrestrial lichens estimated for year 2015 and burn severity within burns used by female caribou (*Rangifer tarandus*) in the Fortymile, Klaza, Kluane, and Nelchina populations in eastern Alaska and western Yukon. Data are separated into separate panels by number of years before 2015 that the fire occurred. Green shaded areas correspond to dNBR values between –500 and –100, which Key and Benson (2006) classified as "regrowth". Magenta lines depict cubic spline curves fit to the data.

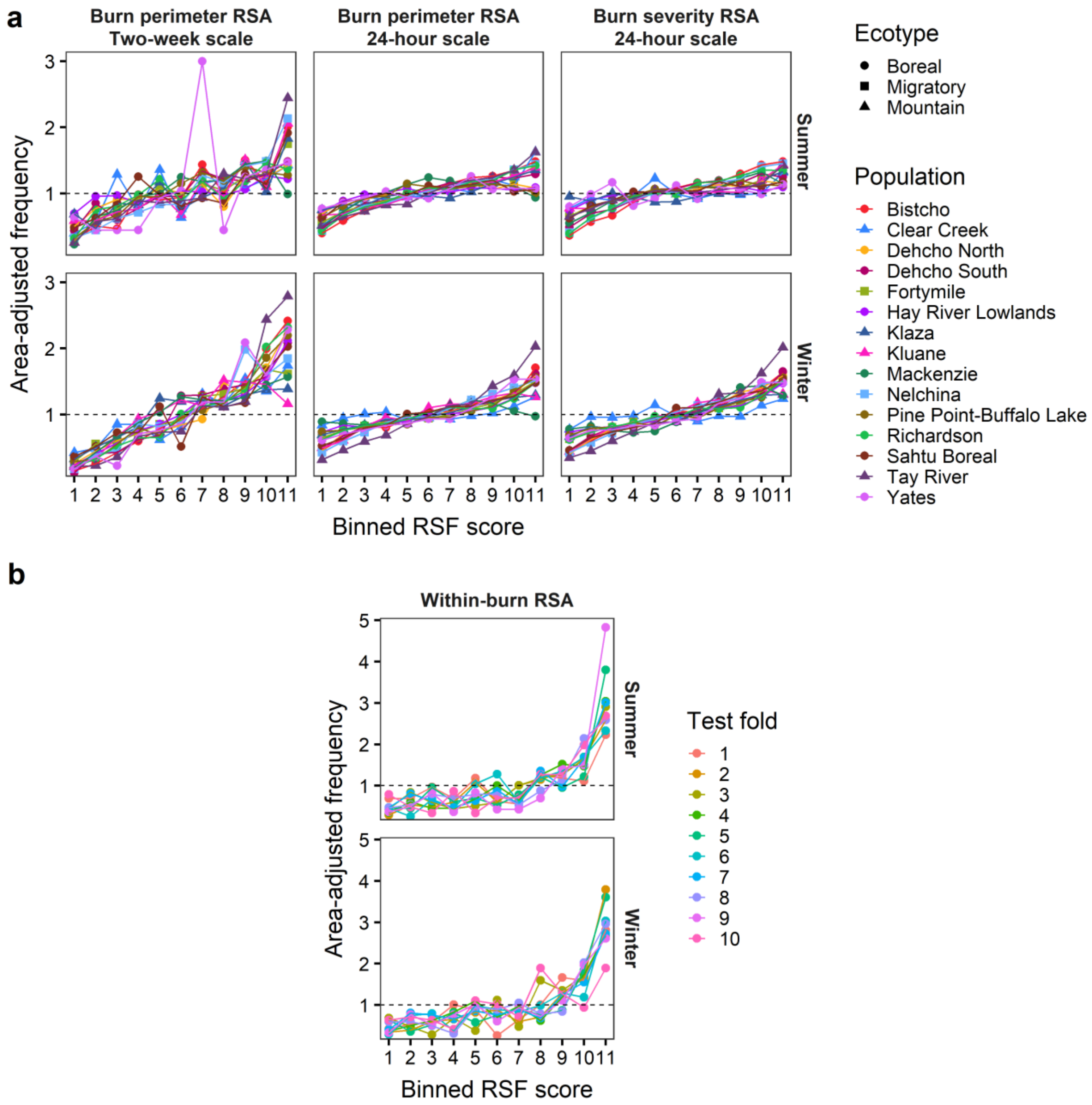

Figure 2-A-5. Out-of-sample cross validation results from the *burn perimeter* and *burn severity RSA*s (a) and the *within-burn RSA* (b) for caribou in eastern Alaska and western Yukon. Area-adjusted frequencies for each test fold (or population) represent the cumulative frequency of predicted RSF scores for used locations that fall into each of 11 equal-interval bins (10 available location + 1 used location per stratum). Values above 1 indicate that cross-validated used locations occur at rates higher than expected by chance. For the *burn perimeter* and *burn severity RSAs*, models were fit using 14 of 15 populations, and model coefficients were used to predict RSF scores for the withheld population. For the *within-burn RSA*, models were fit to 90% of individual caribou, and model coefficients were used to predict RSF scores for the remaining 10% of animals.

CHAPTER 3: Linking caribou behavior and demography across a gradient of disturbances in western North America's boreal forest

INTRODUCTION

Human land-use change is among the largest drivers of species endangerment and declines in biodiversity (Sala et al. 2000, Newbold et al. 2015). Human-induced habitat loss, fragmentation and modification has led to changing animal behavior (Tuomainen and Candolin 2011), declines in functional and phylogenetic diversity (Brodie et al. 2021), decreased animal vagility (Tucker et al. 2018), expansion of invasive species (Brook et al. 2008), and declines in demographic rates (Kerley et al. 2002). In response to land-use change, mammals have shifted their geographic ranges (Pineda-Munoz et al. 2021), and many larger-bodied terrestrial mammals have experienced range contraction (Pacifici et al. 2020). The predominant effects of human land use on wildlife and biodiversity will be exacerbated by climate change (Brodie et al. 2012). However, it can be difficult to disentangle the relative importance of human activity and climate change on ecological processes (Berteaux et al. 2006, Oliver and Morecroft 2014).

Quantifying behavioral responses to disturbances such as human activity can help clarify the ecological processes by which these disturbances affect animal populations (Bro-Jørgensen et al. 2019). The recent proliferation of animal tracking systems with increasing spatiotemporal resolution allows for detailed assessments of habitat selection in response to disturbances and how these behaviors vary across a range of conditions. Further, animal selection for resources varies as the availability of resources changes, a phenomenon known as a functional response in resource selection (Mysterud and Ims 1998). Incorporating functional responses into habitat selection models can improve predictions of animal behavior under novel conditions such as human footprints and fire frequencies that are above current levels (Matthiopoulos et al. 2011). Inference to population consequences from habitat selection analyses often relies on the assumptions that behavioral responses directly affect fitness, and that habitat selection is free or adaptive (Fretwell and Lucas 1969, McLoughlin et al. 2010). However, correlations between habitat selection and environmental characteristics are not necessarily predictive of animal susceptibility to changes in ecosystem processes (Garshelis 2000, Gill et al. 2001). For example, animals may exhibit behavioral plasticity to mitigate short-term risk from disturbances, potentially decoupling habitat changes from fitness consequences. Further, animals may fail to balance tradeoffs between factors such as foraging and predation risk, and therefore may select habitats maladaptively (Robertson and Hutto 2006, DeCesare et al. 2014).

Few wildlife studies assess the consequences of behavioral responses to population dynamics, in part because collecting sufficient data to detect demographic responses is time consuming and expensive (Pulliam and Danielson 1991, Matthiopoulos et al. 2015). However, linking habitat, behavior and demography may be necessary to gain a complete understanding of animal responses to disturbances and to guide management decisions (King et al. 2015). For example, analyzing habitat use and survival concurrently can help target management to prioritize source habitats (Aldridge and Boyce 2007) and to potentially eliminate ecological traps (Simon and Fortin 2019). As human development continues to encroach into previously undisturbed landscapes (Allan et al. 2017), its effects may be confounded by interactions with natural disturbances that are increasing in frequency, duration or severity as a result of climate change (Franklin 2010).

One area experiencing recent increases in human land-use change coupled with pronounced climate change is western North America’s boreal forest. Forestry and energy development have contributed to major losses in net primary productivity in the region (Butt et al. 2013, Allred et al. 2015) and are growing threats to an ecosystem that retains a high level of biodiversity intactness (Newbold et al. 2016, Allan et al. 2017). Its vast area and ability to regulate global climate by storing ~30% of the world’s terrestrial carbon (Pan et al. 2011) means that conserving the boreal forest also represents a huge opportunity and a potential buffer against climate change. However, large swaths of boreal forests, mountains, and peatland complexes have been transformed into industrialized landscapes with an extensive network of forestry and energy-related infrastructure including roads, transmission lines, pipelines, seismic exploration lines, and well sites (Venier et al. 2014, Pickell et al. 2015).

In addition to experiencing increasing land use change, western North America’s boreal forest is undergoing climate change-induced shifts in its fire regime. Many parts of the region are experiencing earlier spring phenology, shifts in climate, more frequent and more severe forest fires, and longer fire seasons (Price et al. 2013). Fires have long been the dominant type of disturbance in the region (Stocks et al. 2001, de Groot et al. 2013). Yet intensifying fire regimes due to rapidly warming temperatures, coupled with increasing human disturbance, may lead to unprecedented levels of landscape change that preclude animal adaptation to novel conditions (Turner 2010). These changes may have dire consequences for boreal species that depend on late-successional communities, such as forest-dwelling caribou (*Rangifer tarandus*).

Caribou serve as a key ecological umbrella species for boreal biodiversity (Bichet et al. 2016, Drever et al. 2019). Along with changing climatic conditions, extensive development of forest harvesting and energy sector activities are quickly transforming caribou habitat, threating their population persistence across Canada (Hebblewhite 2017). In North America's western boreal forest, declines in boreal and southern mountain populations of woodland caribou led to their 2002 listing as "Threatened" under Canada's Species at Risk Act. After a decade of recovery planning and critical habitat assessments, the federal government published recovery strategies for boreal and southern mountain caribou in 2012 and 2014, respectively (Environment Canada 2012, 2014). The leading hypothesis in the recovery strategy for widespread woodland caribou declines is apparent competition, which is directly facilitated by human development (DeCesare et al. 2010, Festa-Bianchet et al. 2011). Logged forests contain more early seral vegetation and support higher densities of moose (*Alces alces*) and deer (*Odocoileus* spp.), which maintain higher densities of wolves (*Canis lupus*) that subsequently prey upon caribou. Linear features such as roads and seismic exploration lines for oil and gas extraction increase caribou predation risk by providing travel corridors for predators to move through mature forest and increase their chances of encountering caribou (Latham et al. 2011, Whittington et al. 2011). In addition to forest harvest, fires may create habitat favorable to primary wolf prey (Maier et al. 2005) or decrease spatial separation between caribou and their predators (Robinson et al. 2010), potentially accelerating caribou declines. Together, human land use and climate change could exacerbate risks to caribou population persistence and boreal biodiversity.

Challenging our ability to disentangle climate and landuse change effects on caribou is their correlation with the latitudinal gradient in human disturbance in North America's western boreal forest. Most population ranges in the southern portion of the region have larger human development footprints, while more northerly populations are relatively undeveloped. Not surprisingly, most studies from western North America addressing effects of human land-use change on caribou are from AB and BC (e.g., Polfus et al. 2011, Mumma et al. 2019). Wildlife managers and First Nations in these two provinces have resorted to wolf control and maternity penning to save caribou populations from extirpation (e.g., Serrouya et al. 2019, Lamb et al. 2021). However, commensurate habitat recovery actions outlined in the federal recovery strategies for boreal and southern mountain caribou have not slowed the rate of habitat loss (Nagy-Reis et al., *In press*). Human development continues to expand throughout the western boreal forest, including in some Yukon caribou ranges, where there are several large mining projects currently seeking territorial government approval.

Several studies have already found a strong link between disturbance and caribou demography. Sorensen (2008) found that fire and human disturbance had an additive effect on boreal caribou population growth rates in AB. The Canadian federal government found that across 24 populations, the proportion of population range disturbed, including both anthropogenic (with non-overlapping 500 m buffers around all features) and fire disturbance (≤ 40 years old), explained ~70% of the variation in mean caribou recruitment (Environment Canada 2011). Most recently, Johnson et al. (2020)

found that the negative effect of human disturbance on caribou survival and recruitment across 46 caribou populations throughout the boreal forest was far greater than that of fire. These previous studies have focused on the boreal ecotype of woodland caribou. The extent to which disturbance affects caribou behavior and demography in other ecotypes and western boreal regions is unclear and remains a major conservation concern (Environment Canada 2012). Continued increases in human development in northern areas coupled with predicted increases in fire frequency and severity may interact to amplify negative effects on caribou populations trajectories observed across many parts of the region (Gustine et al. 2014).

Here, we tested hypotheses about the degree to which human and fire disturbance throughout northwestern North America affected caribou resource selection and demography. We took advantage of a large Global Positioning System (GPS) location dataset to assess resource selection across 30 caribou populations that each experienced different levels and combinations of human disturbance and fire. In our resource selection analyses, we estimated the relative influences of fire and several types of human disturbance on caribou by quantifying both the strength of behavioral responses and how relative selection for resources changes across a gradient of disturbance availability. Our first behavioral hypothesis was that human disturbance and fire have an additive effect on caribou resource selection (Sorensen et al. 2008, Environment Canada 2012). Under this hypothesis, we predicted that the caribou would avoid both human and fire disturbance, but the degree of avoidance of one disturbance type would not change in areas with a higher density of the other disturbance type. Alternatively, human disturbance and fire could have a synergistic effect on resource selection, where an increasing human or fire footprint would influence the strength of caribou responses to the other disturbance type. This is an example of a functional response in resource selection (Mysterud and Ims 1998, Holbrook et al. 2019). Understanding whether caribou showed a functional response to disturbance would allow for more accurate predictions of caribou behavior and more informed management decisions. For example, if caribou avoidance of roads changed as burn footprint increased, future predictions that failed to account for this interaction would under or overestimate effects of climate change or human disturbance on caribou behavior (Paton and Matthiopoulos 2016).

Second, we evaluated how disturbances and caribou behavioral responses to these disturbances influenced demographic processes at the population level (e.g., Johnson et al. 2020). We estimated calf recruitment (n=20 populations) and adult female survival (n = 24) for a subset of populations in the resource selection analyses. We tested for links between disturbance, resource selection and demography (*sensu* Boyce and Mcdonald 1999) by regressing these vital rates against range-level disturbance footprints that were informed by our resource selection analyses.

We tested whether the amount of disturbance itself or the behavioral responses to those disturbances best explained variation in caribou demography. First, we tested a suite of hypotheses related to how disturbances footprints might influence caribou recruitment and adult female survival based on previous studies (Sorensen et al. 2008, Fortin et al. 2017, Johnson et al. 2020). We considered models representing the hypotheses that either human disturbance or fire on their own would negatively affect caribou demography. We then tested whether these disturbance footprints might have additive or interactive effects on caribou demography. Next, we estimated the degree to which behavioral responses to disturbance affected recruitment and adult female survival by using population-level selection coefficients from our resource selection models. Increased relative avoidance of disturbance leading to higher vital rates would provide evidence of adaptive selection, while decreased avoidance of disturbance that predicted lower vital rates might indicate an ecological trap (DeCesare et al. 2014).

METHODS

Study area

We analyzed resource selection in caribou from 31 populations across eastern Alaska (AK), Yukon (YT), Northwest Territories (NT), British Columbia (BC) and Alberta (AB, Figure 3-1). Caribou populations spanned a wide gradient of human and burn footprints (Figure 3-1C). Our populations included three caribou ecotypes; migratory (*R.t. granti*, n = 2), mountain woodland (*R.t. caribou*; n = 10), and boreal woodland (*R.t. caribou*; n = 18) caribou (Ray et al. 2015). Land cover and topography throughout the study area included rolling hills, rugged peaks, subalpine and alpine areas, forested river valleys, upland forests, peatlands, marshes, and lakes. Dominant tree species in the study area included black spruce (*Picea mariana*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*) and Engelmann spruce (*Picea engelmanni*). The prevalence and distribution of human disturbance types also varied across the study area (Figure 3-1C). Density of human disturbance, which included roads, clear cuts, oil and gas exploration seismic lines, pipelines, mines, and wells for oil and gas, was high across most southern caribou ranges in BC and AB. Seismic lines accounted for most linear disturbance in NT but were absent from caribou ranges in AK and YT. Throughout AK, YT and NT, roads were relatively sparse and clear cuts were mostly absent.

Capture and data summary

Caribou were captured from a helicopter by net gun and were subsequently fitted with GPS collars following approved federal, provincial, state, and territorial animal care protocols and permits (Table 3A-1). Prior to filtering, thinning, and analyses, our dataset included 4,906,202 GPS locations from 1,701 GPS-collared female caribou from 31 populations whose collars collected data from between 2000 and 2020 (Table 3A-2).

Resource selection analysis

We filtered GPS location data to a relocation interval of two weeks. We further divided these two datasets into two seasons. The summer season (May 25–October 5) generally included the period between calving and rut across all populations, while winter (October 6–May 24) encompassed the remainder of the year (see Table 3-1 for details on analysis subsets).

We used point-based step selection functions (SSF; Thurfjell et al. 2014, Avgar et al. 2016) in a generalized linear mixed-modeling (GLMM) framework (Muff et al. 2019; as described in Chapter 2) to analyze caribou resource selection across the 30 caribou populations. We generated 10 available locations per used location, which together composed a stratum. Following guidance from Muff et al. (2019), our models included random coefficients at the population level for every covariate. We used Akaike Information Criterion (AIC) to assess support for including linear versus non-linear (i.e., second order polynomial) covariate terms in the resource selection models.

Our resource selection analyses consisted of three steps. In Step 1, we determined the zones of influence for burns and five types of human disturbance in two broad categories; 1) clear cuts and other polygonal disturbance (e.g., mines, oil pads, cultivated areas), and 2) linear disturbances like roads, seismic lines, and other linear features (e.g., oil and gas pipelines, powerlines). Defining zones of influence can help determine cumulative effects of disturbances on wildlife, prioritize areas for mitigating negative effects, and inform population models (e.g., Polfus et al. 2011). We transformed "distance-to" measures using an exponential decay function:

$$-\exp(-\alpha \mathrm{d}), \text{ (Equation 1)}$$

where α is the decay rate and d is the distance to disturbance feature. This transformation accounted for caribou responses to disturbance attenuating at a certain distance from disturbance features (e.g., Nielsen et al. 2009). We fit a series of univariate models for each disturbance type with a range of decay rates (α) and used AIC to determine the α value above which responses to the distance below which disturbance attenuated (Carpenter et al. 2010). Transformed distance values ranged from 1 at the feature to 0 at far distances. We considered the distance corresponding to a transformed value of 0.05 to be the cutoff below which caribou no longer respond to the disturbance.

In Step 2, we fit a series of SSF models to determine the relative influence of each disturbance type on caribou resource selection across our study area. All candidate models in this step consisted of the same base suite of landcover categories and topographic indices (see Chapter 2 for details on these covariates). We first added a single disturbance covariate, such as roads or burns, formulated using the best fitting exponential decay transformation for each disturbance type-season combination from

Step 1. For example, our winter roads model included the base suite of covariates plus the distance to roads covariate, which was transformed so that avoidance of roads attenuated at 2000 m (Figure 3-2). We then fit a model with all five human disturbance types but withholding burns, before fitting a model with all human disturbance and burns. Prior to fitting all SSF models, we tested covariates for pairwise correlations and considered collinear variables ($|r| > 0.7$) independently within model sets (Dormann et al. 2013). We excluded all GPS location data from population-years with ongoing wolf-control measures (see Table 3A-3 for details) to avoid confounding effects of predator reduction on caribou behavior.

Functional responses in resource selection

We tested whether relative section for (or avoidance of) a disturbance depended on changes in that resource's availability. To do this, we ran models with an interaction between a covariate and its mean value within an animal's seasonal range (e.g., burns:burn_footprint), an approach known the generalized functional response (Matthiopoulos et al. 2011). We extended this approach to test our hypothesis that human and fire disturbance synergistically (i.e, interact) affect caribou resource selection. Specifically, we tested whether caribou selection for human disturbance varied by burn footprint, and whether their selection for burns varied by human footprint, by including interactions between one disturbance type and the other's availability (e.g., roads:burn_footprint).

We estimated individual-level seasonal footprints for burns and total human disturbance by buffering each disturbance type by its zone of influence distance from Step 1 and calculating the proportion of available points within an animal-season that occurred within the cumulative buffered area. We tested for functional responses to roads (and not other human disturbance types) across a gradient of total human and fire disturbance footprints because roads were present in all population ranges and other types of human disturbances were not. Functional response models included an interaction between a disturbance covariate (e.g., burns or distance to roads) and a disturbance footprint (either burn or human) within an animal's seasonal range. We evaluated statistical support for different functional responses by calculating delta AIC values across candidate models and by measuring the significance of the coefficients representing these responses.

Environmental covariates

We used human disturbance data downloaded from state, provincial, and territorial government datasets (Table 3A-4 for details). We used burn perimeter polygons from the Alaska Large Fire Database (Kasischke et al. 2002) and the Canada National Fire Database (Stocks et al. 2003) from 1960–2018, excluding burn perimeters from fires that occurred prior to 1960. We only considered caribou GPS locations to be within a burn if the burn occurred < 40 years before the location timestamp, because the Canada National Fire Database lacked fire perimeter data > 40 years prior to the earliest GPS locations in NT. Our models included land cover, tree cover, and indices of terrain ruggedness and terrain position to account for these additional habitat attributes (see Chapter 1 for details on each of these covariates).

Resource selection model validation

We evaluated our top seasonal SSF models using out-of-sample cross-validation where we iteratively withheld one population as a test data set (Roberts et al. 2017) and fit models to the remaining 30 populations. We used the same procedure as in Chapter 1 to test, within each stratum, whether our model predicted higher probabilities of use for GPS locations than randomly generated available locations.

Demographic analyses

We monitored caribou adult female survival in 25 populations and calf recruitment in 22 populations. We filtered these demographic data to only include population-years coinciding with those in our resource selection analyses (Table 3-1). We tested the statistical support for our hypothesis that disturbance footprints drive caribou demographic rates. We predicted that higher human and fire footprints would be correlated with lower adult female survival and calf recruitment (Fortin et al. 2017, Johnson et al. 2020). Compared to adult female survival, recruitment in ungulates generally shows higher temporal variability and greater sensitivity to limiting factors such as predation and environmental stochasticity (Gaillard et al. 1998). Therefore, we predicted that both disturbance footprint and behavior would have stronger effects on recruitment than on survival. For burns and total human disturbance, we averaged the individual-level seasonal footprints estimated during our resource selection analyses to create population-level annual footprints, weighting each season by the proportion of the year it represented. In addition to human and burn footprints, we created a non-overlapping cumulative footprint for both disturbances, which represented the hypothesis that total footprint was a more important predictor of caribou demography than disturbance type (Environment Canada 2011).

We used population-level selection coefficients for disturbance from our additive (all human disturbance types + burns) resource selection models (without functional responses) to test our behavioral hypotheses that caribou strength of disturbance avoidance affected their demographic indices. We predicted that summer behavior (e.g., increased road avoidance) might be more correlated with recruitment than with survival because most calf mortality occurs during the first few weeks of life (Gustine et al. 2006, Pinard et al. 2012). We predicted that behavioral responses to human disturbance would be more strongly correlated with demography than responses to burns because early seral vegetation in recent burns may be an important food source during snow-free periods (Thompson et al. 2015).

We analyzed survival data in a continuous time framework using left-staggered entry and a recurrent survival time origin of May 1 (Fieberg and Delgiudice 2009). Following DeCesare et al. (2012a) and Eacker et al. (2019), we used monthly monitoring intervals and right-censored individuals one month after they were last observed alive. We estimated the relative effects of disturbance footprints and behavior on a constant baseline hazard rate over time using mixed-effects Cox proportional hazards models, fit in the R package ‘coxme’ (Therneau 2020). We included random intercepts for population and year to account for repeated observations and correlation within these groupings. We tested whether our models satisfied the proportional hazards assumption using Schoenfeld residuals (Therneau and Grambsch 2000). We also calculated annual survival rates by population using the Kaplan-Meier estimator (Pollock et al. 1989).

We pooled all aerial survey observations from a population-year to estimate recruitment, which we defined as the ratio of calves to adult females. We only included aerial surveys conducted between February and April. Both female and male caribou can have antlers during the survey period, making it difficult to estimate the calf:adult female ratio denominator (DeCesare et al. 2012a). Therefore, we converted the ratio denominator from total adults (what were surveyed) to female adults by partitioning 65% of surveyed adult caribou that were not classified by sex as females based on Edmonds (1988). We tested the effects of disturbances and behavioral responses on recruitment using a mixed-effects beta regression (*sensu* Johnson et al. 2020) with a logit link in the R package 'glmmTMB' (Brooks et al. 2017), including random intercepts for population and year.

RESULTS

Resource selection

After filtering data to include one location every two weeks, our GPS location dataset for resource selection spanned 1999–2020 and included 29,801 locations from 1,296 caribou across 31 populations.

Caribou avoidance of disturbances varied by disturbance type and season. Caribou avoidance of human activity extended to farther distances in winter than during summer (Figure 3-2; Table 3A-5). Across both seasons, the estimated zones of influence for human disturbance ranged from 300–600 m for seismic lines to 3–4 km for other polygonal disturbance (e.g., mines, oil and gas wells). Seasonal zones of influence for cutblocks, roads and other linear features range from 1,500–3,000 m. We found that avoidance of burns rapidly diminished beyond the burn perimeter during both seasons such that there was effectively no zone of influence around burns (Figure 3-2). Therefore, we only considered the impacts of burns on caribou with a binary variable that indicated whether a GPS location was within a burn. Models with only one disturbance type (using transformed distance values for human disturbance and a binary variable for burns) indicated that during summer, roads had the largest effect on caribou resource selection (Figure 3; ΔAIC = 318 compared to top seasonal functional response models, described below, that included all disturbance types), followed by clear cuts (ΔAIC = 424) and then burns (ΔAIC = 629). During winter, burns were a more important driver of caribou resource selection (ΔAIC = 926) than any single type of human disturbance, followed by cutblocks (ΔAIC = 1140) and roads (ΔAIC = 1143). Seismic lines, other linear and polygonal disturbances were less important predictors of caribou resource selection during both seasons (Figure 3-3, ΔAIC range = 1338–1386). On average, population-level human footprints estimated using disturbance type-specific buffers from our ZOI analysis were 11% larger than those using a 500-m buffer applied to all human disturbance (as in the boreal caribou recovery strategy). Other linear and other polygonal disturbances were highly correlated ($|r| > 0.7$) in both seasons). Because other linear features explained more variation in caribou resource selection than other polygonal features (Figure 3-3), we dropped other polygonal disturbance from models that included all human disturbance types (see Table 3A-6 for selection coefficients for models with all human disturbance and burns).

Functional responses in resource selection

We found evidence for functional responses in resource selection for both roads and burns. However, selection for roads and burns did not vary significantly as a function of the other disturbance type's availability, indicating additive, not interactive (see Figure 3-3), effects of these two disturbances on caribou. The interactive functional response models that included the terms roads:burn_footprint and burn:human_footprint were between 59.5 and 93.1 AIC units worse than the top seasonal functional response models (burn:burn_footprint + roads:human_footprint; Figure 3-3).

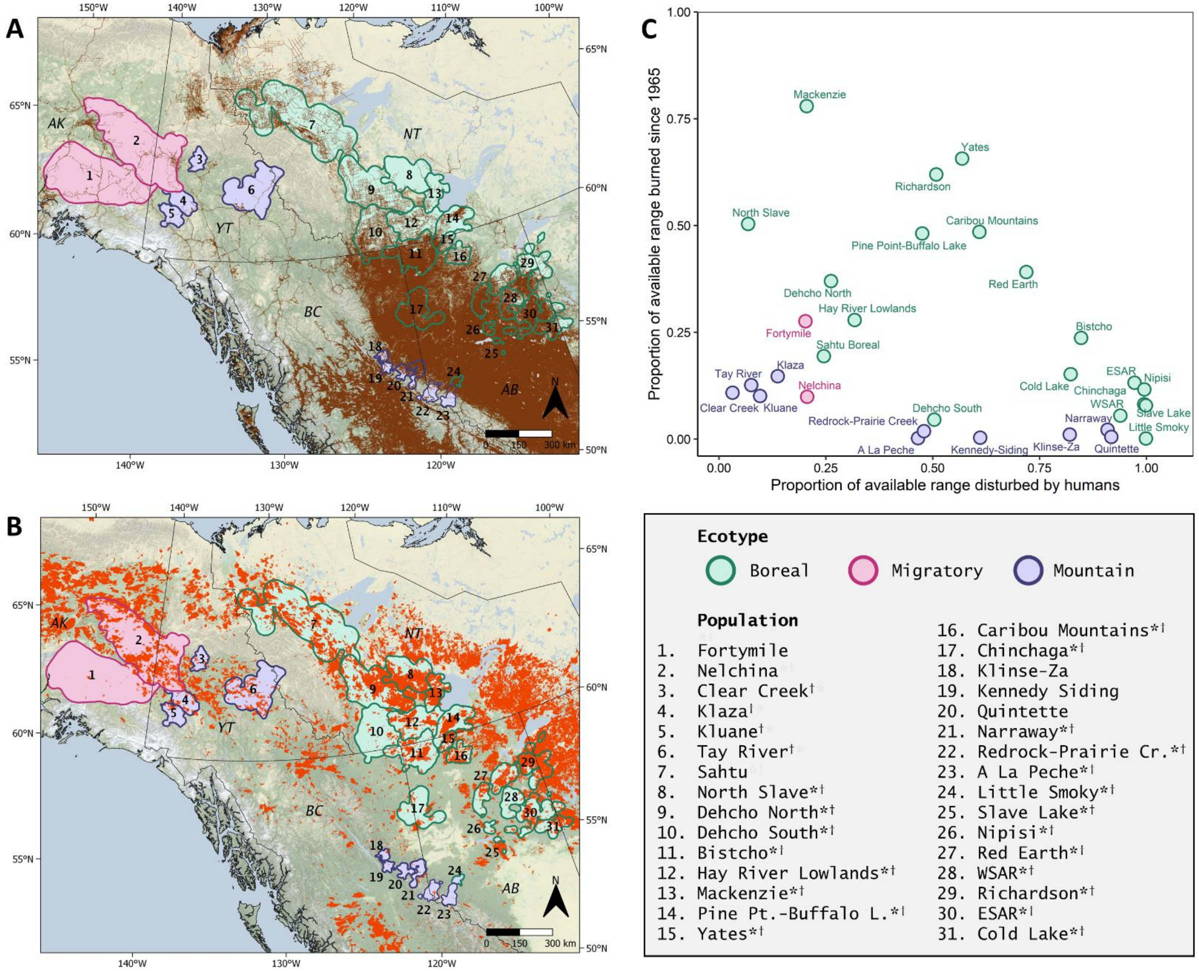

Figure 3-1. Thirty-one caribou (*Rangifer tarandus*) population ranges showing current estimated footprints of human disturbance (A) and burns since 1965 (B). Panel (C) shows the relationship between human and fire footprints for each population. ESAR and WSAR denote East Side and West Side of Athabasca River, respectively. * and † indicate populations with available data on recruitment and survival, respectively.

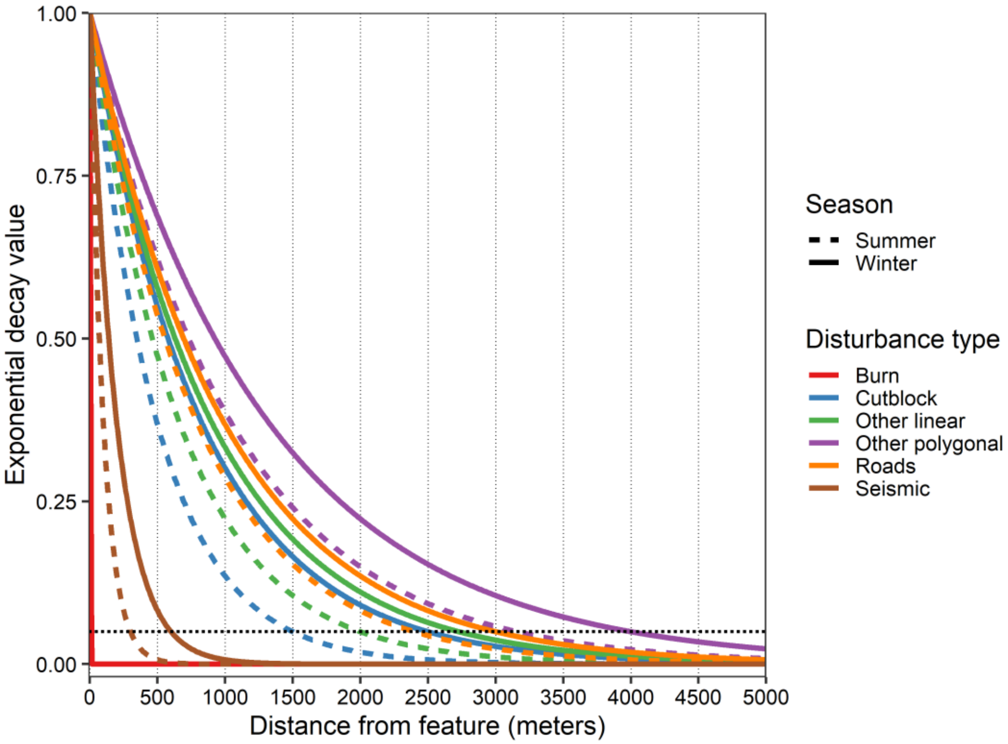

Figure 3-2. Exponential decay curves depicting the zone of influence distances for different human disturbance types on 31 populations of adult female caribou (*Rangifer tarandus*) in eastern Alaska and western Canada. The dashed black line at an exponential decay value of 0.05 indicates the approximate distance at which caribou avoidance of disturbance features attenuates. The zone of influence distance for burns was 0 m in both seasons. Some lines are jittered slightly to avoid overlap.

The top resource selection models (Figure 3-3, dAIC = 0) in both seasons included functional responses for burns (burns:burn_footprint) and roads (roads:human_footprint; Figure 3-4). For both roads and burns and in both seasons, caribou decreased their avoidance of disturbance as the disturbance footprint increased ($\beta_{\text{burns:burn\_footprint}}$: summer = 0.46 ± 0.06 [SE], $\beta_{\text{burns:burn\_footprint}}$: winter = 0.30 ± 0.04, $\beta_{\text{roads:human\_footprint}}$: summer = 0.18 ± 0.03, $\beta_{\text{roads:human\_footprint}}$: winter = 0.11 ± 0.03; Figure 3-4). Caribou responses to burns did not significantly vary by human disturbance footprint ($\beta_{\text{burns:human\_footprint}}$: summer = 0.09 ± 0.06, winter = 0.02 ± 0.05), nor did their responses to roads vary by burn footprint ($\beta_{\text{roads:burn\_footprint}}$: summer = –0.03 ± 0.03, winter = –0.02 ± 0.02).

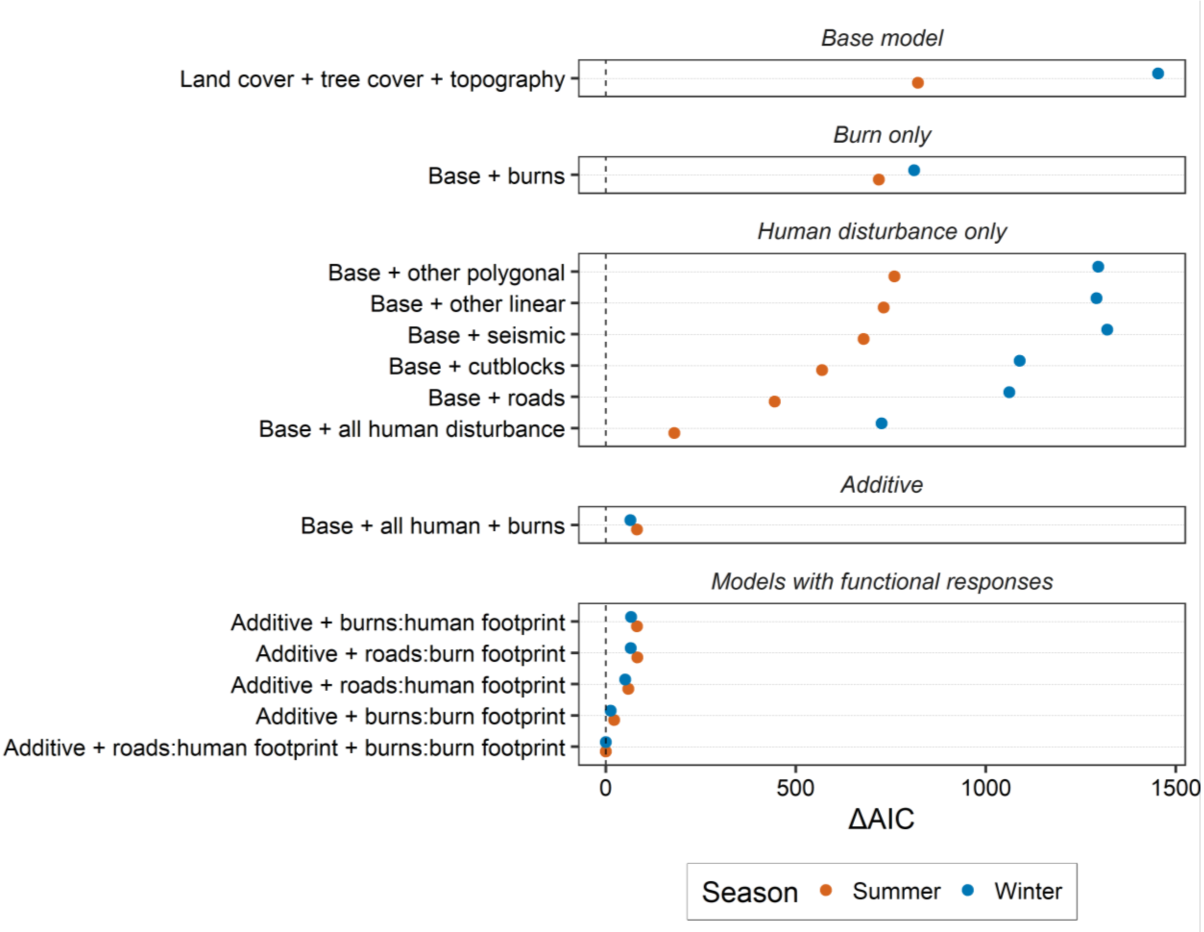

Figure 3-3. Delta AIC (DAIC) values indicating variable importance for candidate resource selection models of disturbance effects on adult female caribou (*Rangifer tarandus*) across 30 populations in eastern Alaska and Canada. Top models for each season had DAIC values of 0. DAIC values are not comparable across seasons.

Model validation

Our top ranked seasonal resource selection models showed better predictive performance for winter than summer. The mean (± SD) Spearman rank correlation across the 31 withheld populations was 0.95 ± 0.07 in winter and 0.81 ± 0.25 in summer (Figure 3A- 1).

Demography

Our analysis of caribou survival included data from 1,951 female caribou from 25 populations. Caribou were monitored for an average (± SD) of 3.0 ± 2.3 years for a total of

6,119 caribou-years. The geometric mean annual survival rate for adult female caribou was 0.88 across 25 populations. Our recruitment analysis included survey data from 21 populations. We calculated calf:adult female ratios for an average of 8.6 + 3.9 years (range: 3–16 years) per population, for a total of 181 survey-years. The pooled geometric mean recruitment ratio was 19.5 calves per 100 adult females.

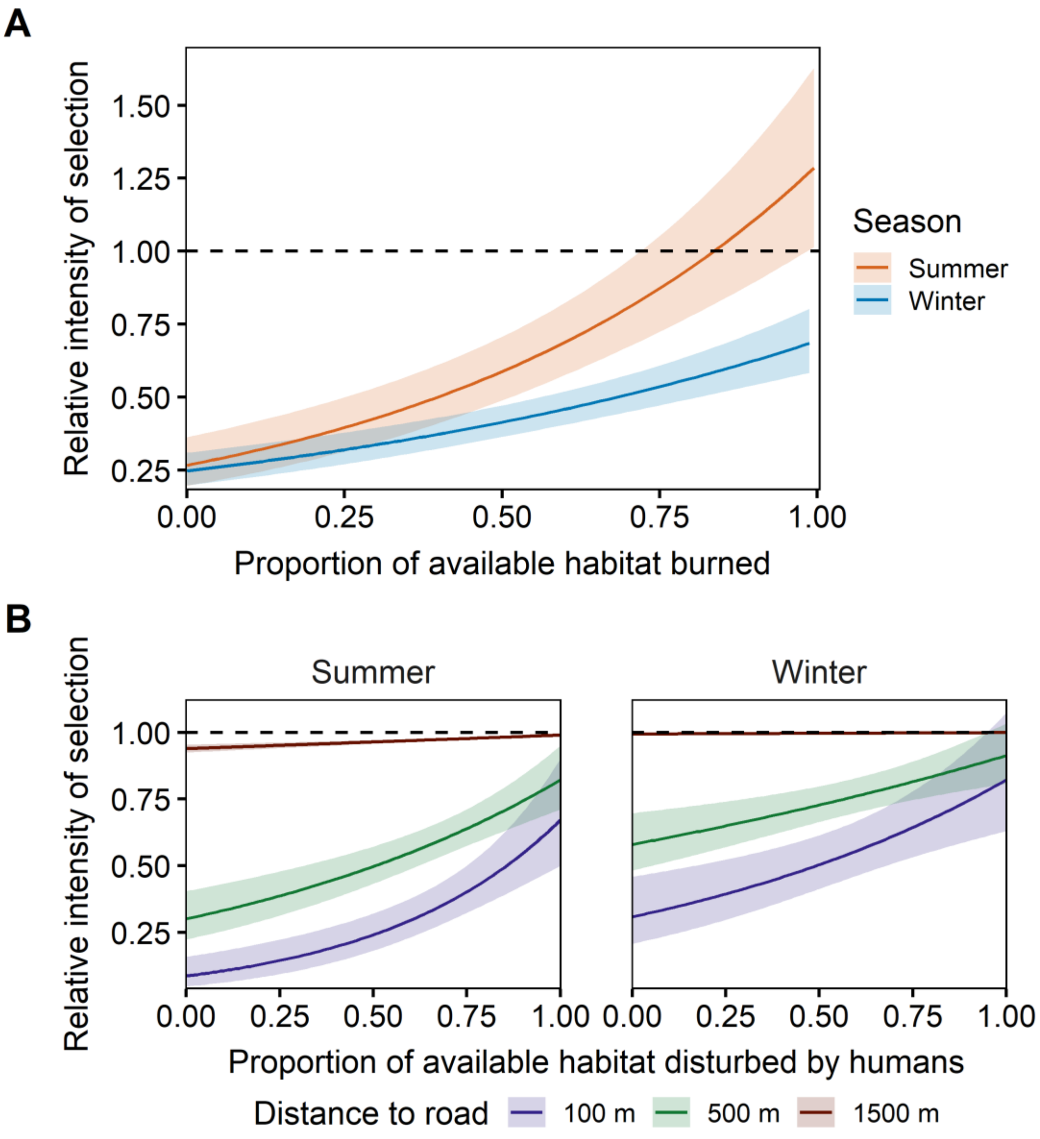

Figure 3-4. Functional response to burn (A) and distance to road (B) across a range of human disturbance footprints for 31 populations of caribou (*Rangifer tarandus*) in western Canada and eastern Alaska.

Table 3-1. Summary of GPS location data used in resource selection models for 31 populations of female caribou (*Rangifer tarandus*) from 31 populations across western North America.

Ecotype	Region	Population	Years marked	Summer		Winter	
				# of animals	Mean # of locs per animal	# of animals	Mean # of locs per animal
Boreal	AB/NT/BC	Bistcho	2006–2019	50	9.3	46	17.4
Boreal	AB	Caribou Mountains	2016–2019	16	9.6	11	13.1
Boreal	AB/BC	Chinchaga	2007–2019	46	9.3	46	16.5
Boreal	AB/SK	Cold Lake	2013–2017	16	8.7	22	13.0
Boreal	NT	Dehcho North	2007–2019	48	9.6	53	18.7
Boreal	NT/AB	Dehcho South	2007–2019	57	9.8	59	18.5
Boreal	AB/SK	ESAR	2009–2017	55	8.9	63	13.5
Boreal	NT	Hay River Lowlands	2008–2019	67	10.0	77	17.9
Boreal	BC	Little Smoky	2000–2005	24	9.0	23	10.8
Boreal	AB	Mackenzie	2015–2020	36	10.3	45	17.0
Boreal	NT	Nipisi	2006–2019	9	8.7	9	15.4
Boreal	AB	North Slave	2017–2020	31	9.0	30	15.7
Boreal	NT	Pine Point-Buffalo L.	2015–2019	53	9.4	57	16.0
Boreal	AB/NT	Red Earth	2011–2019	82	9.4	87	15.7
Boreal	AB	Richardson	2009–2019	45	9.2	42	14.6
Boreal	AB/BC	Sahtu Boreal	2006–2010	13	9.2	14	24.6
Boreal	AB/SK	Slave Lake	2006–2019	10	9.0	9	14.4
Boreal	NT	WSAR	2012–2019	27	9.7	25	18.0
Boreal	AB	Yates	2014–2019	14	9.2	13	17.7
Migratory	AB	Fortymile	2014–2018	102	9.0	102	14.6
Migratory	AB/NT	Nelchina	2013–2015	55	9.1	38	15.6
Mountain	AK/YT	A La Peche	2001–2010	22	9.0	26	13.5
Mountain	AK/YT	Clear Creek	2017–2018	16	9.8	19	14.7
Mountain	AB/BC	Kennedy-Siding	2004–2014	30	8.8	30	16.1
Mountain	YT	Klaza	2012–2017	32	8.9	41	18.7
Mountain	YT	Klinse-Za	2006–2013	13	8.9	15	14.1
Mountain	BC	Kluane	2014–2017	11	9.1	12	16.1
Mountain	YT	Narraway	2007–2012	6	10.0	7	14.4
Mountain	BC/AB	Quintette	2004–2014	37	8.8	41	14.5
Mountain	BC	Redrock-Prairie Creek	2000–2014	47	8.0	91	13.3
Mountain	YT/NT	Tay River	2016–2018	30	9.5	30	17.7

Population-level resource selection in response to disturbance was a more important predictor of individual-level caribou mortality hazard than the disturbance footprints themselves (ΔAIC = 4.3 between top resource selection and top disturbance model; see

Table 3-2). The top survival model showed that declining avoidance of roads at the population-level during winter predicted decreased caribou mortality hazard (β = 0.09 ± 0.04, *P* = 0.04), a result consistent with adaptive resource selection (Figure 3-6, Table 3-2). The second ranked survival model (dAIC = 1.8) included relative selection for roads and burns during winter. The effect of road avoidance on mortality risk remained relatively stable (β = 0.07 ± 0.05, *P* = 0.12) in this model compared to in the univariate model, but relative selection for burns was uninformative (β = –0.03 ± 0.04, *P* = 0.52). Increased selection for burns did not have a statistically significant effect on mortality hazard in either season in any model (Table 3-2). Schoenfield residuals indicated that all survival models satisfied the proportional hazards assumption.

Population-level recruitment was best explained by human footprint and behavioral avoidance of roads. Human footprint had a strong negative effect on the calf:adult female ratio (β = –0.37 ± 0.08 [SE], *P* < 0.01). The fixed effects in the human footprint model explained 36% of the variation in recruitment (marginal R^2), while the fixed and random effects together explained 66% of recruitment variation (conditional R^2). Models with footprints calculated using our behavior-based, disturbance type-specific zones of influence consistently performed better than the corresponding models where human footprint was calculated using 500-m buffers around all human disturbance (average improvement = 2.4 AIC units; see Table 3A-8 for comparison of models using footprints from different zones of influence). Relative selection for roads in summer was the second most important predictor of recruitment, which was only 0.8 AIC units higher than the top model (human footprint) (Table 3-2; Figure 3-5). Caribou populations that avoided roads more strongly during the summer had higher recruitment (Figure 3-5, panel B; β = –0.36 ± 0.06, *P* <

0.01). The effect of selection of roads during summer remained stable ($\beta_{rsf\_roads\_summer} = -0.36 \pm 0.09$, $P < 0.01$) when included in an additive model (rsf_roads_summer + rsf_roads_winter; dAIC = 2.8, Table 3-2) with selection for roads during winter, which was uninformative ($\beta_{rsf\_roads\_winter} = -0.02 \pm 0.10$, $P = 0.858$). Human footprint and relative selection for roads in summer were strongly correlated (r = 0.60), consistent with the positive summer functional response we found in resource selection to roads ($\beta_{burns:burn\_footprint} = 0.46 \pm 0.06$).

Table 3-2. Model selection evaluation of candidate models estimating effects of disturbance footprints and behavioral responses on calf:adult female ratios (n=21 populations) and adult female survival (n = 25 populations) for caribou (*Rangifer tarandus*) across western Canada. Calf:adult female ratios were modeled with a mixed-effects beta regression, while survival was modeled with a mixed-effects Cox proportional hazards regression. Bold highlight top ranking models. ΔAIC indicates delta AIC units, where the top model has a value of 0, df denotes degrees of freedom, and w indicates model weight. Shaded rows highlight models using population-level selection coefficients from resource selection analyses.

Model	Recruitment			Survival		
	ΔAIC	df	w	ΔAIC	df	w
Human footprint	**0**	**5**	**0.38**	6.2	21.0	0.01
Road selection summer	**0.8**	**5**	**0.25**	6.0	20.6	0.01
Human footprint + burn footprint	2.0	6	0.14	5.6	20.6	0.01
Human footprint X burn footprint	2.4	7	0.12	5.3	20.4	0.02
Roads and burn selection summer	2.6	6	0.10	6.8	21.2	0.01
Cumulative disturbance footprint	8.6	5	0.01	6.3	20.5	0.01
Road selection winter	12.3	5	0	**0.0**	**16.1**	**0.24**
Burn footprint	12.7	5	0	3.9	19.5	0.04
Road and burn selection winter	13.4	6	0	**1.6**	**17.1**	**0.11**
Burn selection winter	14.0	5	0	3.7	19.1	0.04
Burn selection summer	15.1	5	0	5.8	20.5	0.01

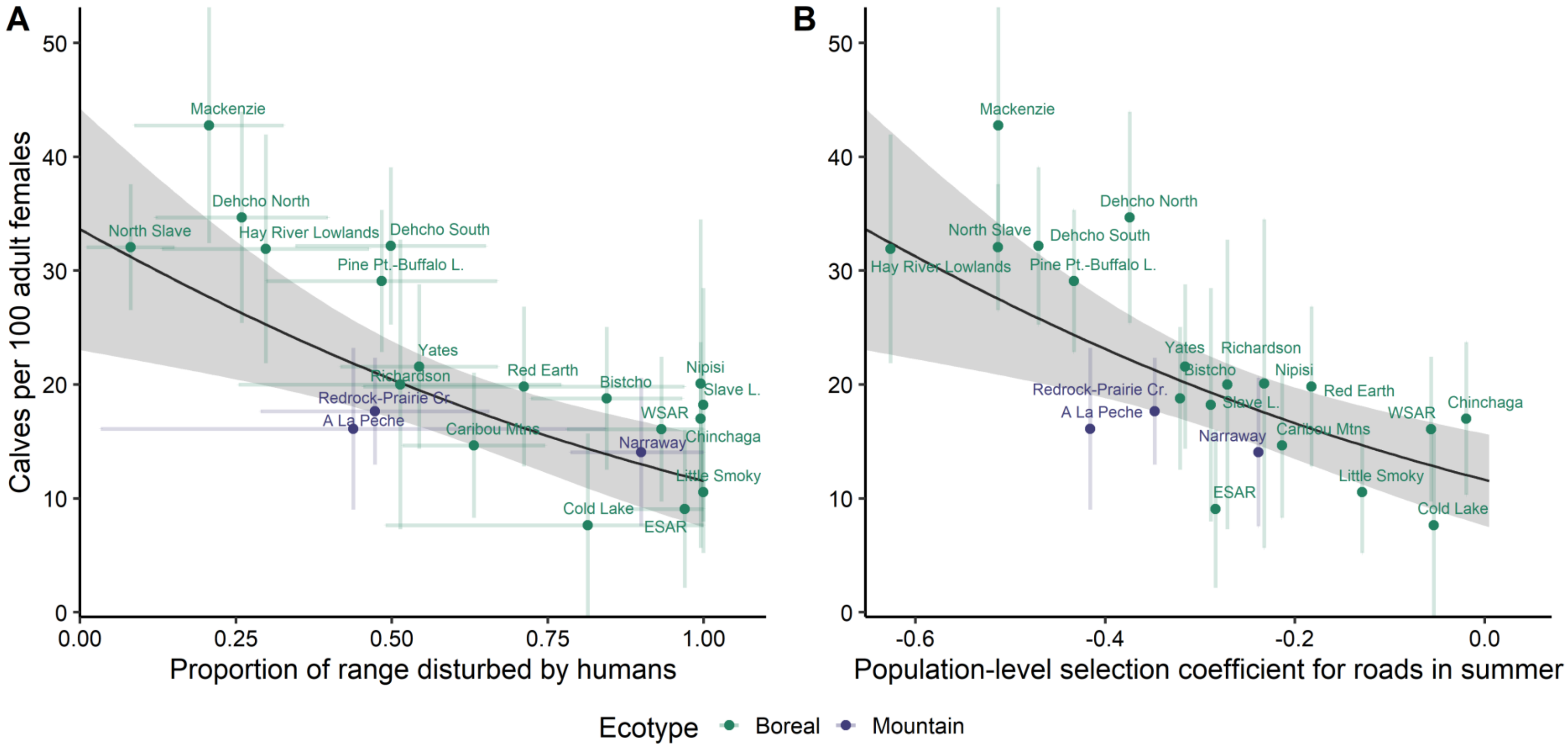

Figure 3-5. Predicted ratio (black lines) of calves per 100 adult females for 21 populations of caribou (*Rangifer tarandus*) in northwest Canada in as a function of human footprint (A) and relative selection for roads during summer (B). Gray shaded region indicates 95% confidence intervals around predictions. Vertical error bars indicate ± 1 standard deviation from the mean number of calves per 100 adult females across all survey years for each population. Horizontal error bars in Panel A indicate ± 1 standard deviation from the mean proportion of range disturbed by humans across all animals included in the resource selection analyses for each population.

Table 3-3. Coefficients and standard errors for models estimating effects of disturbance footprints and behavioral responses on calf:adult female ratios (n=21 populations) and adult female survival (n = 25 populations) for caribou (*Rangifer tarandus*) across northwest Canada. Calf:adult female ratios were modeled with a mixed-effects beta regression. Survival models were modeled as the effects of covariates on mortality risk using a mixed-effects Cox proportional hazards regression. Therefore, positive coefficients for mortality risk decrease the probability of survival. Bold highlight top ranking models for each dependent variable. ΔAIC indicates delta AIC units, where 0 is the top model, df denotes degrees of freedom, and w indicates model weight. Shaded rows highlight survival models for ease in interpretation.

Model	Dependent variable	Human footprint	Burn footprint	Cumulative footprint	Burn footprint: human footprint	Road selection winter	Road selection summer	Burn selection winter	Burn selection summer
Human footprint	Mortality risk	0.04 [0.05]							
Human footprint	Recruitment	**–0.37 [0.08]**							
Burn footprint	Mortality risk		–0.07 [0.05]						
Burn footprint	Recruitment		0.20 [0.10]						
Human footprint + burn footprint	Mortality risk	0.02 [0.05]	–0.07 [0.05]						
Human footprint + burn footprint	Recruitment	–0.38 [0.09]	–0.04 [0.08]						
Human footprint X burn footprint	Mortality risk	0.04 [0.05]	–0.03 [0.06]		0.09 [0.06]				
Human footprint X burn footprint	Recruitment	–0.38 [0.09]	–0.08 [0.10]		–0.11 [0.08]				
Cumulative footprint	Mortality risk			–0.02 [0.04]					
Cumulative footprint	Recruitment			–0.31 [0.10]					
Road selection summer	Mortality risk						0.03 [0.05]		
Road selection summer	Recruitment						**–0.37 [0.08]**		
Road selection winter	Mortality risk					**0.09 [0.04]**			
Road selection winter	Recruitment					–0.24 [0.11]			
Burn selection summer	Mortality risk								0.02 [0.04]
Burn selection summer	Recruitment								0.13 [0.11]
Burn selection winter	Mortality risk							–0.06 [0.04]	
Burn selection winter	Recruitment							0.20 [0.12]	
Road and burn selection summer	Mortality risk						0.04 [0.05]		0.03 [0.05]
Road and burn selection summer	Recruitment						–0.36 [0.08]		0.04 [0.08]
Road and burn selection winter	Mortality risk					0.07 [0.05]		–0.03 [0.04]	
Road and burn selection winter	Recruitment					–0.19 [0.11]		0.11 [0.12]	

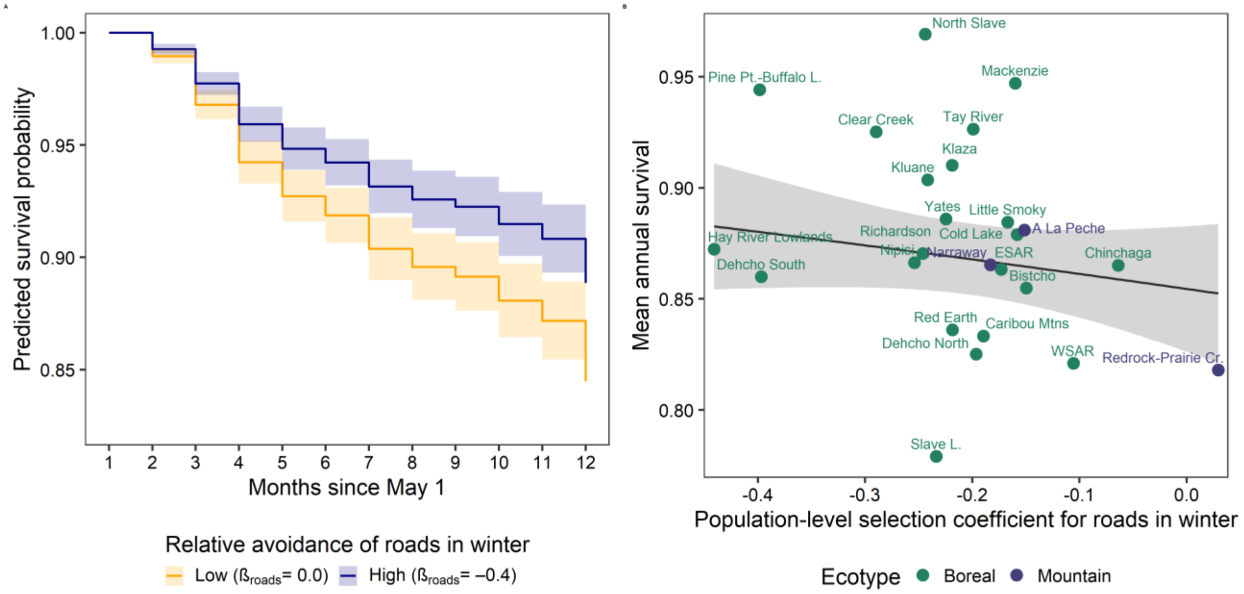

Figure 3-6. Predicted annual survival rates at two levels of relative avoidance of roads (A) and predicted mean annual survival rate (black line) as a function of relative intensity of selection for roads (B) during the winter for adult female caribou (*Rangifer tarandus*) from 25 populations. Points in B show geometric mean annual survival rates. Prediction in B derived from a mixed-effects beta regression using the mean annual survival rates.

DISCUSSION

We analyzed resource selection, recruitment, and adult female survival of caribou across western North America's boreal forest to test hypotheses about how human and fire disturbance affect their behavior and demography. Resource selection analyses showed total human disturbance to be a stronger predictor of caribou behavior than solely burns during both seasons. This supports the hypothesis that the two disturbance types have an additive but not synergistic effect on caribou resource selection. Therefore, future increases of one disturbance type will not necessarily affect the relative influence of the other disturbance type on caribou resource selection. Our study reaffirms the strong negative relationship between human disturbance and recruitment found in past caribou studies, including in the scientific assessment that informed the federal boreal caribou recovery strategy (Environment Canada 2011, Johnson et al. 2020). However, we make a novel contribution with our link between behavior and demography. We found increased behavioral avoidance of roads was the best predictor of adult female survival and a significant predictor of recruitment. Our results support the hypothesis that caribou avoidance of roads was adaptive, in that stronger avoidance behavior predicted lower risk of mortality for adult females. We found no evidence for a negative effect of fires on caribou demography, in contrast to previous national and regional analyses (Sorensen et al. 2008, Environment Canada 2011, Johnson et al. 2020).

We used disturbance-specific zones of influence as a primary metric to assess the effects of disturbance on caribou resource selection and demographic vital rates. Zones of influence have important management and conservation implications for wildlife as the human footprint expands into previously undisturbed areas (Fischer and Lindenmayer 2007, Haddad et al. 2015). The ecological footprint of disturbance features measured by zones of influence can help quantify indirect habitat loss due to behavioral avoidance (Polfus et al. 2011). For example, zones of influence for grizzly bears (*Ursus arctos*) varied by age and sex, and generally extend between 100 m and 1 km from roads, while migrating whooping cranes (*Grus americana*) avoided areas within 5 km of towers used to generate wind energy (Pearse et al. 2021). Land use planning, environmental assessments, and species recovery plans often rely on zone of influence estimates to minimize negative effects of human disturbance on wildlife (Parsons et al. 2020). Although zones of influence are usually informed by analyses of animal behavior, they can also be guided by relationships between disturbance and demography. Notably, Environment Canada (Environment Canada 2011) identified boreal caribou critical habitat using a 500-m buffer around human disturbance based on a sensitivity analyses of the recruitment-human disturbance relationship. This 500-m human disturbance footprint estimated habitat lost due to negative demographic effects, which can differ between linear and polygonal disturbance types. Past studies suggest linear disturbances negatively affect caribou primarily by decreasing caribou ability to maintain spatial separation from wolves, who use these features to travel more efficiently (DeMars and Boutin 2018). On the other hand, early seral vegetation following polygonal disturbance might attract numbers of primary wolf prey such as moose, supporting larger wolf populations and potentially increasing predation on caribou (Mumma et al. 2018).

Disentangling the effects of different types of human disturbance on wildlife can be difficult because they are often interdependent. For example, clearcutting requires logging roads and may also rely on existing seismic lines and oil and gas roads. We found that other linear disturbance and polygonal disturbance were highly correlated, while other pairwise correlations were low enough (<0.6) to including both covariates in the same resource selection model. Because our study included 31 caribou populations that included a wide range of combinations of burn and human footprints, we minimized the potential for confounding relationships between burns and human disturbances. However, correlations amongst human disturbance types (e.g., other linear + other polygonal human disturbances) prevented easy isolation of these effects. Although we initially partitioned roads into two classes (i.e., primary and secondary), separating roads into two categories did not improve overall model fit for our mixed-effects SSFs. Some of northern caribou populations had such low road densities that many collared animals rarely, if ever, traveled within a few kilometers of a road. Estimating relative selection for a resource at extremely low availabilities can lead to imprecise beta coefficients

(Holbrook et al. 2019). We minimized this effect by using mixed-effects models, which pulled less precise random coefficients towards the grand mean and effectively reduced their contribution to the overall (fixed-effects) covariates (Snijders and Bosker 2012). We found that caribou showed weaker avoidance of seismic lines and other linear features compared to roads and cutblocks, corroborating results from past studies of caribou resource selection (e.g., DeCesare et al. 2012b).

Past studies show the size of behavioral zones of influence for caribou and other wildlife can depend on many factors, including disturbance type, season and population (Johnson et al. 2015). Polfus et al. (2011) found northern mountain woodland caribou avoidance of mines extended out to 0.25 km in winter and 2 km in summer versus 2 km for primary roads in both seasons. Caribou road avoidance extended out to between 250 m and 1.25 km in three other studies of boreal caribou (Dyer et al. 2001, Leblond et al. 2011, Dussault et al. 2012), while zones of influence for seismic lines were generally lower (e.g., 100–250 m; Dyer et al. 2001). Johnson et al.'s (2015) estimated zones of influence for four southern mountain populations in BC ranged from 500 meters to ~4 km across human disturbance types. Our results showing caribou avoidance of human disturbance types extending out 300 m – 4 km was consistent with these studies.

There are a variety of approaches to estimate zones of influence for wildlife (Boulanger et al. 2012), including piecewise regressions, visual identification of thresholds in selection coefficients, and exponential decay transformations of distance (Nielsen et al. 2009). The exponential decay transformation allowed us to characterize caribou avoidance of disturbance with a continuous distance variable rather converting it to a binary or multilevel categorical variable. This same approach has been used to describe avoidance of linear disturbances and identify zones of influence in multiple caribou studies (e.g., Finnegan et al. 2018, Fullman et al. 2021), but also in large carnivores (Nielsen et al. 2009, Whittington et al. 2011), upland game birds (Carpenter et al. 2010), and mesopredators (Lai et al. 2017). In our study, defining zones of influence for human disturbances allowed us to estimate the amount of habitat indirectly lost to behavior avoidance and improved our ability to link resource selection to demographic outcomes.

Estimating the effects of dynamic covariates, such as disturbance footprints, on wildlife, also requires careful consideration of time. Our data on caribou behavior and demography spanned two decades. During this period, time stamps from BC and AB human disturbance data show an increasing human footprint across many disturbance types (Figures 3A-2 and 3A-3). Although disturbance footprints can change considerably over 20 years, their annual rate of change at the scale of a caribou range was relatively low. For example, the mean annual rate of habitat loss (measured as forest cover loss) from 2000–2018 across 70 caribou ranges in BC and AB was 0.39%, most of which was from fire (Nagy-Reis, *In Revision*). Further, the Canadian federal government's 2017 progress report on boreal caribou recovery showed that cumulative disturbance increased by 1.75% across all caribou ranges from 2012–2017 (Environment and Climate Change Canada 2017). Our population-level estimates of resource selection behavior and human and fire footprints represented average values from the period for which we had data from that population. Given that we had 4–15 years of data for each population, we do not expect there were substantial biases in our estimates of caribou behavior, demography, or disturbance footprints.

The strong relationship we observed between recruitment and disturbance is consistent with ungulate life-history theory. Despite being less elastic than adult female survival, ungulate recruitment may be more responsive to changing environmental conditions such as disturbance (Gaillard et al. 2000, Johnson et al. 2010). Our overall annual adult female survival rate of 0.88 for caribou was consistent with those from past studies that included many of the same populations (Eacker et al. 2019, Johnson et al. 2020). For example, the national average annual survival rate for adult females from the 2011 scientific assessment for boreal caribou was 0.85 (Environment Canada 2011). Similarly, annual adult female survival was 0.75 to 0.92 across 36 caribou populations throughout boreal Canada for which > 1 year of survival data existed (Johnson et al. 2020). Our average empirical estimate of recruitment (19.5 calves per 100 adult females) across 21 populations falls within squarely within the range of recruitment values in Johnson et al.'s (2020) national landscape condition analyses that included data from 58 boreal caribou populations. Both Johnson et al. (2020) and Fortin et al. (2017) found that disturbance was a much stronger predictor of recruitment than of adult female survival.

There was a seasonal difference in the demographic benefits associated with population-level road avoidance. Strong avoidance of roads by adult female caribou with calves during summer may help minimize calf mortality by maintaining spatial separation from predators (James and Stuart-Smith 2000, Pinard et al. 2012). In contrast, increased avoidance of roads during winter lowered the mortality risk for adult female caribou. Both findings suggest adaptive resource selection. McLoughlin (2005) also found a positive link between selection and demography in northeast AB, where caribou that avoided uplands experienced higher survival. On the other hand, mountain caribou in several AB populations failed to avoid areas of high predation risk, resulting in lower survival (DeCesare et al. 2014). This result may be explained in part by differential survival among migration strategies, which have shifted in response to increased human development in these mountain populations (Williams et al. 2021). Our results suggest caribou can avoid disturbance, and any associated mechanisms (such as apparent competition), to enhance demography in many of our populations.

The correlation between recruitment and degree of road avoidance in summer can be explained by a functional response in resource selection to roads. This positive functional response to roads in areas with more human disturbance (Figure 3-4) corroborates results from boreal caribou in Quebec (Mumma et al. 2019), and meant that relative selection of roads and human disturbance were positively correlated and have similar effects on recruitment. Because wolves have been shown to increase their selection of roads in areas of high road density (Muhly et al. 2019), the opposing caribou functional response to roads remains consistent with adaptive resource selection. In certain populations (e.g., Chinchaga, Little Smoky, Nipisi, and Slave Lake), nearly all available habitat for caribou was located within the cumulative zone of influence of human disturbance (as defined by our behavior-based buffers). Caribou in these populations were likely constrained in their ability to avoid human disturbance, even if human disturbance had negative effects on recruitment. Resource selection studies typically test for variation in responses to a resource as its availability changes. However, functional responses can also occur across resources, where relative selection for one resource varies by the availability of another (Matthiopoulos et al. 2011). This phenomenon may be especially common in categorical resources such as land cover (e.g., if burn availability increases, coniferous forest must decrease). For example, caribou selection of mature coniferous forest increased with increasing forest harvest in Quebec (Moreau et al. 2012), while their selection of high-quality forage habitat increased in areas with better cover from predators (Mason and Fortin 2017). Our results did not show evidence that selection for burn and human disturbance varied by the availability of the other disturbance. This suggests that fire and human disturbance do not have an interactive effect on resource selection, at least at their current levels. However, there are few population ranges with current disturbance footprints >40% for both human and fire.

Our results corroborate past work showing human disturbance and fire have an additive negative effect on caribou resource selection, but that human disturbance is the stronger of the two disturbance types. We did not find that the addition of burns explained more variation in recruitment or survival. These results are in contrast to past analyses of boreal caribou demography in relation to landscape-level disturbance (Sorensen et al. 2008, Environment Canada 2011, Johnson et al. 2020), all of which found fires had an additive negative effect on caribou demography by reducing calf and adult survival. If caribou avoidance of burns was adaptive, we expected increased burn avoidance to correlate with increased demographic rates, yet our analyses showed weak positive effects of burns on recruitment during both seasons and on survival during winter. Previous studies have suggested that fire may affect caribou through apparent competition (Robinson et al. 2010), the same top-down mechanism hypothesized to drive caribou population declines in areas with high levels of human disturbance (Serrouya et al. 2020). Under this hypothesis, predation on caribou increases after fires because primary prey such as moose may prefer post-fire habitats, thereby attracting more wolves, which feed on caribou as alternative prey. However, burned areas may provide an diverse suite of protein-rich foods during the summer (Thompson et al. 2015), when adult female energy demands are high (Parker et al. 2009). This may drive the stronger positive functional response to burns in summer compared to winter.

Several recent studies have suggested that disturbance-mediated apparent competition may not drive caribou population dynamics in large portions of the boreal forest, including some northern areas with relatively stable caribou populations. The lack of zone of influence around burns in our study is consistent with bottom-up forage effects, rather than increased predation risk. DeMars et al. (2019) found that moose avoided recently burned areas within several boreal caribou ranges, while McLoughlin (2019) observed that areas with frequent and spatially-extensive fires could support high densities of caribou. The pronounced latitudinal gradient in primary productivity across much of the boreal forest may contribute to limited post-fire deciduous growth and low moose densities in northern areas, thereby diminishing the effect of apparent competition (Gagné et al. 2016, Fortin et al. 2017, Neufeld et al. 2020). Consistent with this hypothesis, many of the populations in our study with the highest calf:adult female ratios were from areas in NT with the largest burn footprints. This finding suggests that management and recovery measures for caribou should consider factors such as primary productivity, and not just apparent competition, as potential drivers of caribou population dynamics in areas with relatively small human footprints.

When considered together, caribou adult female survival and recruitment can help predict population growth rate and population viability. Given our empirical estimates of annual vital rates and population viability predictions from past studies (Environment

Canada 2011), many populations in our study (e.g., those with adult female survival <0.85 and/or recruitment < 25 calves:100 females) may not be self-sustainable without short term predator control (Hervieux et al. 2014, Serrouya et al. 2019). Indeed, our demographic analyses include six populations with ongoing wolf removal aimed at increasing adult female survival, while some adjacent populations have maternity penning programs designed to increase recruitment. However, wolf reduction is highly controversial and does not address habitat loss driven by human development. Achieving self-sustainable caribou populations depends on a combination of short-term measures and enhanced government commitment to long-term habitat restoration and protection (Serrouya et al. 2019).

The negative effect of human disturbance on caribou recruitment throughout the boreal forest is strong (Environment Canada 2011, Fortin et al. 2017, Johnson et al. 2020) and is bolstered by our finding that increased road avoidance is a significant predictor of increased recruitment. This result identifies a potential behavioral mechanism that links habitat disturbance to population dynamics. Our analyses provide support for the existing buffer distances used to calculate range-level disturbance. The 500-m human disturbance buffer from the boreal caribou recovery strategy explained nearly as much variation in demography as our behavior-based buffers, and the recovery strategy's lack of buffer around burns is consistent with our results (Environment Canada 2012, Johnson et al 2020). Therefore, we recommend that future research focus on identifying and implementing the best approaches for restoring caribou habitat (see Palm et al. 2020; Chapter 4). The human footprint in northern mountain populations in YT and NT remains low and presents a major conservation opportunity. Without efforts to minimize effects of large-scale industrial development in these areas, human disturbance footprints will eventually exceed thresholds that threaten long-term population viability, mirroring the current situation in BC and AB. Protecting and recovering caribou populations in the western boreal forest will maintain boreal biodiversity, help Canada sequester carbon, meet its commitments to the Paris climate agreement, and fulfill its goal of protecting 30% of its terrestrial land by 2030.

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APPENDIX 3A

Table 3A-1. Animal care permit details for captures of female caribou (*Rangifer tarandus*) in western Canada and eastern Alaska.

Region	Populations	Animal care permit #s
AB	Bistcho, Caribou Mountains, Chinchaga, Cold Lake, ESAR, Little Smoky, Narraway, Nipisi, Red Earth, Redrock-Prairie Creek, Richardson, WSAR, Yates	University of Montana IAUCUC #05606MHECS_010207
BC	Kennedy-Siding, Klinse-Za, Quintette	BC Wildlife Act authority and internal permits and capture reviews.
AK	Fortymile, Nelchina	2012-034, 2013-031, 2015-03, 2016-10
NT	Bistcho, Dehcho North, Dehcho South, Hay River Lowlands, Mackenzie, North Slave, Pine Point-Buffalo Lake, Sahtu	Government of Northwest Territories Wildlife Act authority and internal permits and capture reviews.
YT	Clear Creek, Klaza, Kluane, Tay River	Government of Yukon Territory wildlife act authority and internal permits and capture reviews.

Table 3A-2. Summary of GPS location data before filtering for 31 populations of adult female caribou (*Rangifer tarandus*) across western Canada and eastern Alaska.

Ecotype	Region	Herd	Years marked	# of animals	Mean # of years marked per animal	Mean # of locs per animal	Median relocation interval (hours)	Range of median relocation interval (hours)
Boreal	AB/NT/BC	Bistcho	2006–2019	59	2.2	2580	8	2–46
Boreal	AB	Caribou Mountains	2016–2019	28	1.1	528	23	2–69
Boreal	AB/BC	Chinchaga	2007–2019	56	1.8	4546	2	2–23
Boreal	AB/SK	Cold Lake	2012–2019	56	1.5	2170	23	0–69
Boreal	NT	Dehcho North	2007–2020	72	2.1	1948	8	2–25
Boreal	NT/AB	Dehcho South	2007–2020	83	1.9	1762	8	2–24
Boreal	AB/SK	ESAR	2008–2019	112	1.6	3752	3	2–46
Boreal	NT	Hay River Lowlands	2008–2020	90	2.3	2206	8	2–24
Boreal	BC	Kennedy-Siding	2003–2016	41	1.5	1200	5	4–23
Boreal	AB	Little Smoky	1999–2020	84	1.5	2344	4	2–46
Boreal	NT	Mackenzie	2015–2020	53	2.2	5098	2	2–8
Boreal	AB	Nipisi	2006–2020	10	1.9	9820	2	1–23
Boreal	NT	North Slave	2017–2020	31	3	8261	4	1–4
Boreal	AB/NT	Pine Point-Buffalo Lake	2015–2020	72	2.1	1996	8	2–46
Boreal	AB	Red Earth	2011–2019	110	1.6	3343	2	2–46
Boreal	AB/BC	Redrock-Prairie Creek	1998–2018	136	1.3	3733	2	1–23
Boreal	AB/SK	Richardson	2009–2019	59	1.6	3065	4	2–46
Boreal	NT	Sahtu Boreal	2003–2011	16	2.6	1441	12	8–24
Boreal	AB	Slave Lake	2006–2019	13	1.2	5352	23	1–23
Boreal	AB	WSAR	2012–2019	36	2.0	3926	23	2–23
Boreal	AB/NT	Yates	2014–2019	16	2.1	4587	2	2–23
Migratory	AK/YT	Fortymile	2013–2019	118	2.2	4357	2	1–26
Migratory	AK/YT	Nelchina	2012–2015	78	1.3	1707	4	4–12
Mountain	AB/BC	A La Peche	2001–2019	47	1.5	2919	4	2–46
Mountain	YT	Clear Creek	2017–2019	39	1.4	305	23	13–69
Mountain	YT	Klaza	2012–2019	43	1.6	1742	8	5–13
Mountain	BC	Klinse-Za	2002–2015	18	1.5	1363	9	4–20
Mountain	YT	Kluane	2014–2018	12	2.6	3875	5	5–13
Mountain	BC/AB	Narraway	2006–2016	11	1.6	1472	9	7–23
Mountain	BC	Quintette	2003–2016	62	1.5	1362	7	4–23
Mountain	YT/NT	Tay River	2016–2018	39	1.9	550	23	23–46

Table 3A-3. Approximate dates of wolf reduction efforts across eight populations of caribou (*Rangifer tarandus*) in Alberta and British Columbia, Canada. Locations from these population-years were not included in resource selection analyses.

Region	Population	Dates of wolf reduction
AB	Cold Lake	January 2018 – Present
AB	ESAR	January 2018 – Present
AB	Little Smoky	January 2007 – Present
AB/BC	A La Peche	January 2015 – Present
BC	Kennedy-Siding	January 2015 – Present
BC	Klinse-Za	March 2014 – Present
BC	Quintette	January 2015 – Present
BC/AB	Narraway	January 2015 – Present

Table 3A-4. Summary of state and provincial human disturbance layers.

Region	Disturbance type(s)	Disturbance subtype	Organization	Layer name	Source	Most current data
AB	All human disturbance		Alberta Biodiversity Monitoring Institute	Wall-to-Wall Human Footprint Inventory	https://www.abmi.ca/home/data-analytics/da-top/da-product-overview/Human-Footprint-Products/HF-inventory.html	2018
AK	Roads		Alaska Department of Transportation & Public Facilities	Alaska Road Centerlines	https://opendata.arcgis.com/datasets/824e3282f9d14a9d8994d7b2a32a34a4_11.zip	2020
AK	Roads	Forestry roads	Alaska Department of Natural Resources	Forestry Roads	https://opendata.arcgis.com/datasets/8a7fec3fac5843cebdc6aa77904f1e80_2.zip	2020
AK	Seismic lines, forest harvest		-	-		-
AK	Other polygonal	Mining	Northwest Boreal Landscape Conservation Cooperative	Anthropogenic Footprint - Alaska and Canada Data	https://www.sciencebase.gov/catalog/item/5a554a3fe4b01e7be242be82	2018
AK	Other linear	Railways	Alaska Railroad Corporation	Alaska Railroad Track Centerline	https://opendata.arcgis.com/datasets/2eddb0d116e54e4aa7af4c52c69ab49e_0.zip	2020
AK		Transmission lines	State of Alaska	Electric Transmission Lines	https://opendata.arcgis.com/datasets/b122b04ec1e64ed08ada789f840c4379_15.zip	2020
BC	Roads		BC FLNRORD and BC Ministry of Environment and Climate Change Strategy	Cumulative Effects Framework Integrated roads layer	Request from BC FLNRORD	2020
BC	Seismic lines		BC Oil and Gas Commission	Surface Land Use Geophysical	Request from BC Oil and Gas Commission	2020
BC	Forest harvest		BC FLNRORD	Harvested Areas of BC (Consolidated Cutblocks)	https://catalogue.data.gov.bc.ca/dataset/b1b647a6-f271-42e0-9cd0-89ec24bce9f7	2020
BC	Other polygonal	Mining	Northwest Boreal Landscape Conservation Cooperative	Anthropogenic Footprint - Alaska and Canada Data	https://www.sciencebase.gov/catalog/item/5a554a3fe4b01e7be242be82	2018
BC		Oil and Gas wells	BC Oil and Gas Commission	Surface Land Use Geophysical	Request from BC Oil and Gas Commission	2020
BC		Agriculture	BC FLNRORD	Baseline Thematic Mapping Present Land Use	https://catalogue.data.gov.bc.ca/dataset/134fdc69-7b0c-4c50-b77c-e8f2553a1d40	2019
BC	Other linear	Oil and gas pipelines	BC Oil and Gas Commission	Surface Land Use Geophysical	Request from BC Oil and Gas Commission	2020

BC		Railways	BC FLNRORD	Railway Track Line	https://catalogue.data.gov.bc.ca/dataset/4ff93cda-9f58-4055-a372-98c22d04a9f8	2020
BC		Transmission lines	BC FLNRORD	BC Transmission Lines	https://catalogue.data.gov.bc.ca/dataset/384d551b-dee1-4df8-8148-b3fcf865096a	2020
NT	Roads, seismic lines, other linear		Forest Management Division, Dpt. of Environment and Natural Resources, Government of NT;	Linear disturbance history	Request from Government of NT	2018
NT	Roads, seismic lines, forest harvest, other polygonal, other linear		Environment and Climate Change Canada	Anthropogenic disturbance footprint within boreal caribou ranges (based on 15-m resolution imagery)	https://open.canada.ca/data/en/dataset/a71ab99c-6756-4e56-9d2e-2a63246a5e94	2015
NT	Forest harvest		-	-		-
SK	Roads, seismic lines, forest harvest, other polygonal, other linear		Environment and Climate Change Canada	Anthropogenic disturbance footprint within boreal caribou ranges (based on 15-m resolution imagery)	https://open.canada.ca/data/en/dataset/a71ab99c-6756-4e56-9d2e-2a63246a5e94	2015
SK	Roads		Government of SK	SK Upgraded Road Network (SURN)	https://geohub.saskatchewan.ca/datasets/4b3d6206ab7e424b8fe77b5132d33eba	2020
SK	Other polygonal	Agriculture	Government of SK	Saskatchewan Digital Landcover	https://geohub.saskatchewan.ca/datasets/a287612147ab4f0a9863148f76170f00	2020
YT	Roads, other polygonal, other linear		YT Government	Surface Disturbance	Request from YT Government	2018
YT	Roads		YT Government	Roads 50k	https://map-data.service.yukon.ca/geoyukon/Transportation/ROADS_50K_CANVEC	2018
YT	Seismic lines, forest harvest	-	-	-		
YT	Other linear	Utility lines	YT Government	YT Utilities Line 50k	https://map-data.service.yukon.ca/geoyukon/Utilities_and_Communication/UTILITIES_LINE_50K	2018

Table 3A-5. Estimated zones of influence by disturbance type and season for adult female caribou (*Rangifer tarandus*) from 31 populations in western Canada and eastern Alaska.

Disturbance type	Zone of influence (m)	
	Summer	Winter
Burns	0	0
Seismic lines	3,00	600
Forest harvest (clearcuts)	1,500	3,000
Roads	2,400	3,000
Other linear disturbance	2,000	3,000
Other polygonal disturbance	3,000	4,000

Table 3A-6. Fixed effect coefficients and 95% confidence intervals for covariates in resource selection models with all human disturbance and burns (without functional responses) for female caribou (*Rangifer tarandus*) from 31 populations across eastern Alaska and western Canada. Land cover coefficients indicate selection relative to the reference category of evergreen forest. ^{b} denotes binary or categorical variables.

Category	Covariate	Summer			Winter		
		β	LCI	UCI	β	LCI	UCI
Disturbance	burns^b	–0.387	–0.610	–0.164	–0.746	–0.873	–0.619
Disturbance	forest harvest	–0.327	–0.480	–0.174	–0.209	–0.287	–0.130
Disturbance	seismic	–0.170	–0.201	–0.139	–0.107	–0.130	–0.083
Disturbance	roads	–0.313	–0.403	–0.223	–0.205	–0.265	–0.144
Disturbance	linear	–0.093	–0.132	–0.054	–0.090	–0.117	–0.062
Land cover	barren^b	–0.695	–1.099	–0.292	–1.248	–1.553	–0.943
Land cover	deciduous^b	–0.952	–1.270	–0.634	–1.478	–1.826	–1.131
Land cover	fen^b	–0.607	–0.716	–0.498	–0.670	–0.868	–0.472
Land cover	grass^b	0.058	–0.171	0.287	–0.563	–0.864	–0.263
Land cover	other^b	–0.171	–0.312	–0.030	–0.043	–0.136	0.048
Land cover	shrubs^b	–0.443	–0.589	–0.297	–0.703	–0.882	–0.524
Land cover	sparse^b	–0.026	–0.175	0.123	–0.206	–0.366	–0.046
Land cover	water^b	–5.014	–7.627	–2.401	–3.087	–3.468	–2.706
Vegetation	tree cover	–0.244	–0.371	–0.116	–0.608	–0.710	–0.506
Vegetation	tree cover^2	–0.123	–0.221	–0.025	–0.361	–0.430	–0.291
Topography	terrain ruggedness	–0.316	–0.639	0.006	–0.600	–0.759	–0.442
Topography	terrain ruggedness^2	0.166	–0.200	0.533	–0.002	–0.077	0.072
Topography	terrain position	0.047	0.023	0.072	0.099	0.082	0.117
Movement	log(step length)	0.151	0.122	0.179	0.104	0.087	0.122

Table 3A-7. Comparison of parsimony for caribou (*Rangifer tarandus*) population-level recruitment models fit using different buffer distances for human disturbance footprints. Values indicate the improvement (measured in AIC units) of models using separate distance buffers for each human disturbance type compared to models where human footprint was created with uniform 500-m buffers for all human disturbance (as in boreal caribou recovery strategy).

Model	Improvement in AIC units
Human footprint	2.4
Human footprint + burn footprint	2.4
Human footprint X burn footprint	3
Cumulative human-burn footprint	1.6

Table 3A-8. Spearman rank correlations from resource selection models for female caribou (*Rangifer tarandus*) in western Canada and eastern Alaska. Models were fit using 30 of 31 populations, and model coefficients were used to predict RSF scores for the withheld population. Values above 0 indicate cross-validated used locations occur at rates higher than expected by chance, with 1 as the highest possible value.

Ecotype	Region	Population	Spearman rank correlation	
			Summer	Winter
Boreal	AB/NT/BC	Bistcho	0.96	0.99
Boreal	AB/NT/BC	Caribou Mountains	0.23	0.95
Boreal	AB/BC	Chinchaga	0.99	0.97
Boreal	AB/SK	Cold Lake	0.71	0.94
Boreal	NT	Dehcho North	0.87	1.00
Boreal	NT/AB	Dehcho South	0.93	0.99
Boreal	AB/SK	ESAR	0.94	0.99
Boreal	NT	Hay River Lowlands	0.88	0.98
Boreal	BC	Kennedy-Siding	0.95	1.00
Boreal	AB	Little Smoky	0.95	0.98
Boreal	NT	Mackenzie	0.95	0.90
Boreal	AB	Nipisi	0.77	0.97
Boreal	NT	North Slave	0.90	0.99
Boreal	AB/NT	Pine Point-Buffalo Lake	0.88	0.97
Boreal	AB	Red Earth	0.98	0.99
Boreal	AB/BC	Redrock-Prairie Creek	0.96	0.98
Boreal	AB/SK	Richardson	0.97	0.99
Boreal	NT	Sahtu Boreal	0.36	0.97
Boreal	AB	Slave Lake	0.86	0.91
Boreal	AB	WSAR	0.88	0.98
Boreal	AB/NT	Yates	0.66	0.90
Migratory	AB/NT	Fortymile	0.98	0.97
Migratory	AB/NT	Nelchina	0.99	0.97
Mountain	AB/BC	A La Peche	0.94	0.96
Mountain	YT	Clear Creek	-0.05	0.82
Mountain	YT	Klaza	0.46	0.91
Mountain	BC	Klinse-Za	0.70	0.97
Mountain	YT	Kluane	0.94	0.66
Mountain	BC/AB	Narraway	0.70	0.90
Mountain	BC	Quintette	0.94	0.91
Mountain	YT/NT	Tay River	0.75	0.98

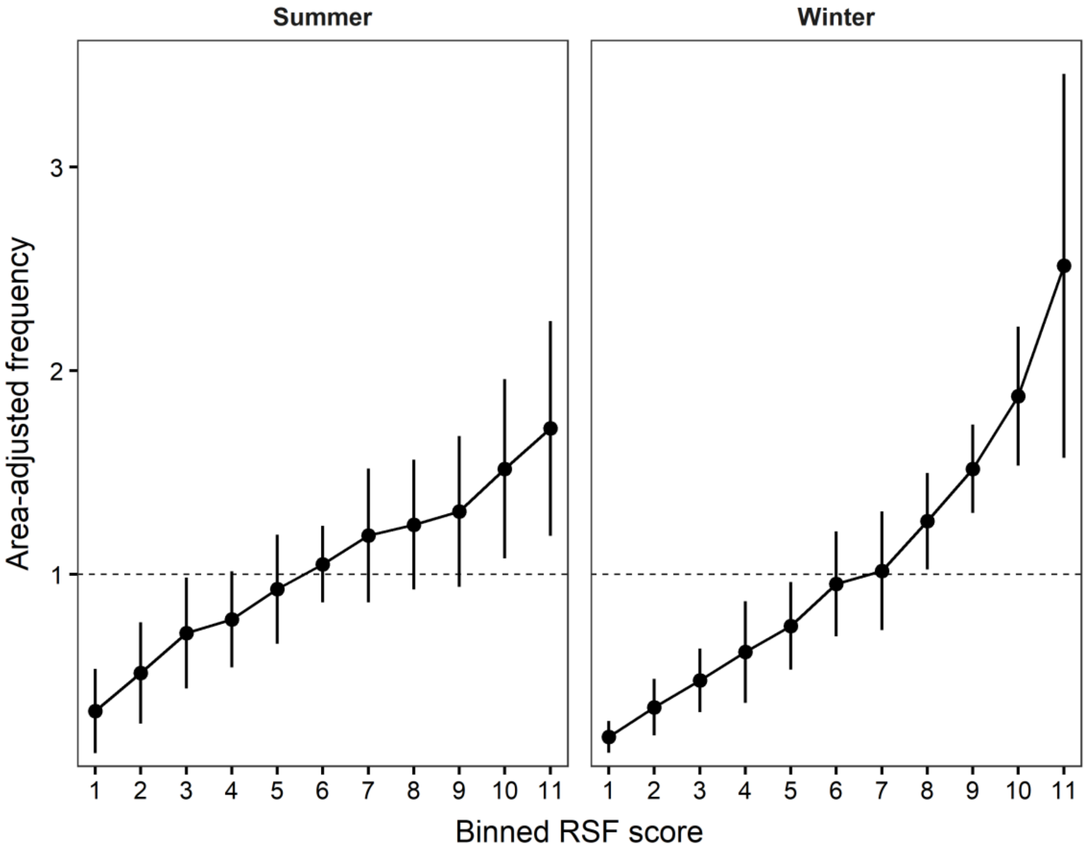

Figure 3A-1. Out-of-sample cross validation results from resource selection models for 31 populations of caribou (*Rangifer tarandus*) in western Canada and eastern Alaska. Y-axis values are mean (SD) area-adjusted frequencies across all test folds (populations), which represent the cumulative frequency of predicted RSF scores for used locations that fall into each of 11 equal-interval bins (10 available location + 1 used location per stratum). Values above 1 indicate that cross-validated used locations occur at rates higher than expected by chance. Models were fit using 30 of 31 populations, and model coefficients were used to predict RSF scores for the withheld population.

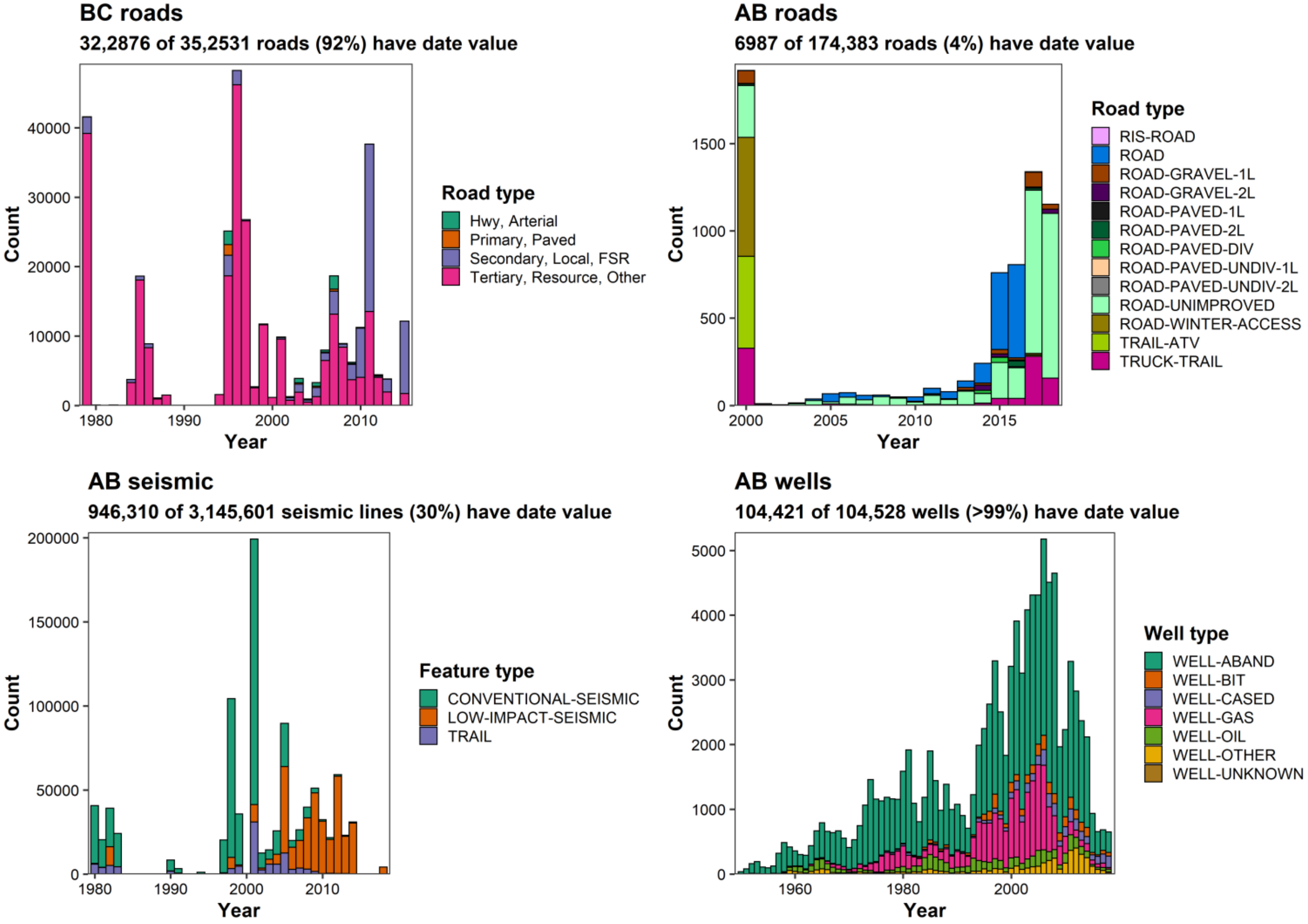

Figure 3A-2. Frequency distributions of construction years for roads, seismic lines and oil and gas wells over time within caribou (*Rangifer tarandus*) ranges in British Columbia and Alberta. Although most years indicate when the feature was constructed, many timestamps likely indicate when they were entered into the disturbance database (e.g., AB roads in year 2000).

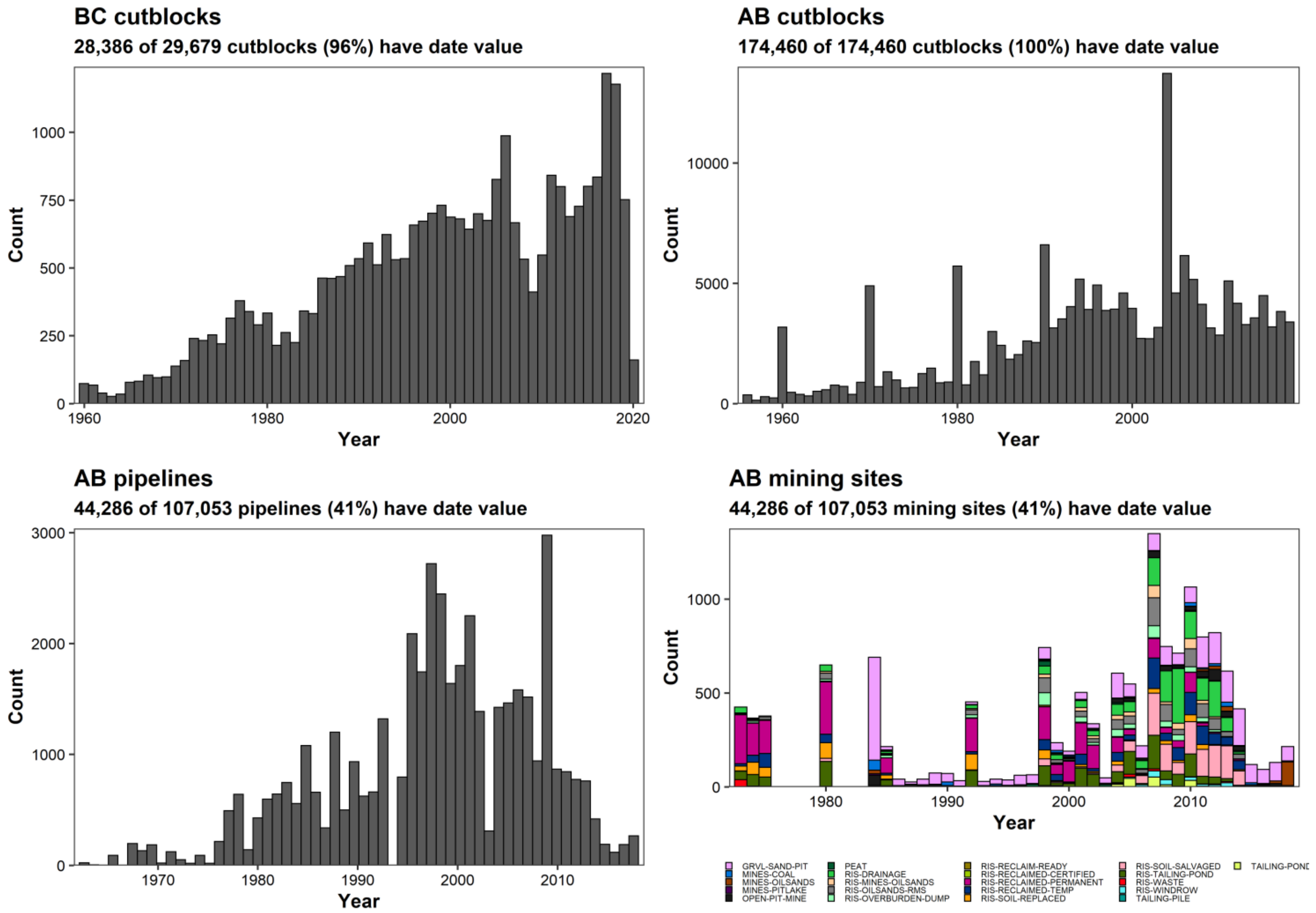

Figure 3A-3. Frequency distributions of construction years for cutblocks (forest harvest), oil and gas pipelines, and mining areas within caribou (*Rangifer tarandus*) ranges in British Columbia and Alberta. Although most years indicate when the feature was constructed, many timestamps likely indicate when they were entered into the disturbance database.

CHAPTER 4: The long road to protecting critical habitat for species at risk: the case of southern mountain woodland caribou[2]

INTRODUCTION

Habitat loss and degradation are the biggest threats to species at risk worldwide (Baillie et al. 2004, IPBES 2018). Identifying and protecting *critical habitat*, defined generally as the habitat required for the recovery of a listed species or population (Hall et al. 1997), are major focuses of species at risk (SAR) legislation around the world. Critical habitat identification is required for all species listed under the United States' Endangered Species Act (ESA) and for species listed as threatened, endangered or extirpated under Canada's Species at Risk Act (SARA), although it is optional in other jurisdictions, such as Australia under the Environment Protection and Biodiversity Conservation Act (EPBCA; Martin et al. 2016). SAR legislation typically protects critical habitat by prohibiting activities that adversely modify, damage, or destroy those areas. However, protection of SAR and their critical habitat is often at odds with social, economic, and political interests (Mooers et al. 2010), and may require multiple complementary approaches to succeed.

Despite the legal imperative to identify critical habitat for SAR, only 44% of species listed under the ESA, <12% of species listed as threatened, endangered or extirpated under SARA and <1% of species listed under the EPBCA had fully identified critical habitat as of 2015 (Martin et al. 2016, Bird and Hodges 2017). Many issues

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plague critical habitat identification, including bias across taxon, habitat type and lead agency (Schwartz 2008, Taylor and Pinkus 2013, Favaro et al. 2014), a lack of legal timelines (Mooers et al. 2010), delays in recovery planning (Ferreira et al. 2019), insufficient scientific information, expertise, and funding (Camaclang et al. 2015, Martin et al. 2016, Bird and Hodges 2017), and judicial and political intervention (Hagen and Hodges 2006).

For species whose ranges overlap with economically valuable natural resources, identification and subsequent protection of critical habitats are often contentious (Fortin et al. 2020). Westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in Alberta (Committee on the Status of Endangered Wildlife in Canada 2016), southern resident killer whales (*Orcinus orca*) in British Columbia (BC; Government of Canada, 2018c) and northern spotted owls (*Strix occidentalis caurina*) in Oregon and Washington (Proctor and Pincetl 1996) are examples of species whose critical habitat identification or protection was complicated in part because their ranges overlap economically valuable natural resources. Even if critical habitat is identified for a species, the degree to which these areas are protected is unclear.

In BC, the threatened Woodland Caribou, Southern Mountain Population (*Rangifer tarandus caribou*; as officially listed under Canada’s federal SARA; hereafter, “southern mountain caribou”), inhabits contiguous tracts of old growth, temperate rainforest that also help support a multi-billion dollar forestry industry. In the 2014 Recovery Strategy for southern mountain caribou, Environment Canada identified and mapped critical habitat for the species on non-federal lands, almost all of which is on BC provincial lands (Environment Canada, 2014b). Similar to Australia’s EPBCA but unlike the ESA, Canada's federal SARA does not automatically provide protection for critical habitat on non-federal lands (Bird & Hodges, 2017; Shumway, Lunney, Seabrook, & McAlpine, 2015). While the federal government has discretionary power to broaden the application of SARA onto provincial lands identified as critical habitat for southern mountain caribou, we review below why it has yet to do so. BC currently has no SAR legislation to provide legal protection for southern mountain caribou critical habitat on provincial land, so the province must rely on other laws to protect these areas. To our knowledge, there has been little research focusing on the degree to which critical habitat on non-federal lands has been protected after its identification for any SARA-listed species in Canada. Our analyses estimate that 909 km^2 of southern mountain caribou critical habitat on BC provincial land were logged in the five years after its identification through June 2019. Thus, for southern mountain caribou critical habitat on non-federal lands, identification has not yet equaled protection.

Here we provide a broad overview of Canadian federal and BC provincial legislation that offers varying degrees of protection of critical habitat. We describe provincial and federal legal authority over SAR and outline provisions under Canada's federal SARA that can be implemented to protect identified critical habitat. We then use southern mountain caribou in BC as a case study to highlight the institutional and practical challenges of protecting critical habitat in Canada via SAR legislation. We provide a brief background on southern mountain caribou population declines, describe what constitutes destruction of southern mountain caribou critical habitat as defined in the federal Recovery Strategy, outline specific existing tools for caribou critical habitat protection under SARA and BC provincial legislation, and discuss alternative mechanisms to protect their critical habitat. We determine the degree to which southern mountain caribou critical habitat has been protected by overlaying critical habitat data with publicly available data on timber harvest to estimate the area harvested in critical habitat in the five years following its identification in the Recovery Strategy in June 2014. Finally, we discuss how using existing legislative and policy tools, in combination with recognizing and affirming Indigenous rights, can help protect caribou critical habitat and recover imperiled species.

CANADA SAR LEGISLATION OVERVIEW

Provincial control over natural resources and wildlife

Lawmaking power over SAR is shared jurisdiction in Canada. The Constitution Act, 1867 did not explicitly allocate power on environmental protection amongst the federal and provincial governments. Instead, Canadian courts have allocated federal authority to make environmental laws based on listed federal powers to legislate over federal lands, inland fisheries, criminal law, matters of national concern, as well as enter into international treaties (Scott 2017). In relation to SAR, the federal government has clear authority to make laws protecting wildlife on federal lands, aquatic species, and migratory birds. However, the power to make laws governing SAR and their terrestrial habitats lies primarily with the provincial governments because the Constitution Act, 1867 gave provinces lawmaking power over provincial property (Olive 2014).

Canada is unique among jurisdictions with SAR legislation in that nearly 90% of its land base is public land, known as Crown land, over half of which is provincially owned (Government of BC 2011). In BC, 94% of the land is provincial Crown land, 5%

is privately owned and the remaining 1% is federally owned (Government of BC 2011). Because wildlife and habitat on provincial Crown land are considered provincial property and are therefore the legislative jurisdiction of the provinces rather than the federal government, the application of protection measures in SARA with respect to identified critical habitat in BC is constrained. Meaningful conservation of SAR in Canada will usually require provincial law and policy, or at the very least, provincial cooperation with federal SARA recovery plans.

Critical habitat identification and protection via SARA on non-federal lands

SARA requires the federal government to identify all critical habitat for threatened and endangered species in a recovery strategy, which also identifies threats to species survival and objectives for population recovery. Recovery strategies must include examples of specific activities that are likely to destroy critical habitat, such as, for example, mining exploration and logging. Sections 47 and 49 of SARA require Environment and Climate Change Canada (ECCC, formerly Environment Canada) to prepare action plans for listed species that, among other things, set out how the recovery and critical habitat protection objectives from recovery strategies will be achieved. SARA does not legislate a timeframe for the development of action plans but requires that recovery strategies indicate when action plans will be completed. Missing action plans are a systemic issue under SARA: as of January 2020, there were 304 completed recovery strategies and only 74 completed action plans on the SARA public registry (Government of Canada 2020a).

SARA Section 61 and Section 80 orders

There are two key provisions in SARA that provide for legal protection of terrestrial critical habitat located on non-federal lands. First, section 61 provides that for a specified portion of critical habitat, the federal government may issue an order on the recommendation of the responsible Minister that applies the critical habitat protections of SARA on provincial lands. The Minister must make this recommendation under section 61 if they form the opinion that an endangered or threatened species is not effectively protected through existing federal or provincial legislation (including any SARA section 11 conservation agreements – see ‘SARA section 11 conservation agreements’ below). Second, section 80 provides that the federal government may, on the recommendation of the responsible Minister, issue an emergency protection order that identifies *any* habitat that is necessary for the protection of a listed species and to prohibit activities that may adversely affect the species or its habitat. The Minister must make this recommendation under section 80 if they form the opinion that the species is experiencing an imminent threat to its survival or recovery.

One difficulty with protecting critical habitat on non-federal lands under SARA is that the federal government has considerable discretion with respect to forming opinions and issuing orders under sections 61 and 80 so that social and economic effects are considered in the decision. Further, the Canadian federal government has historically been reluctant to exercise environmental authority over matters on provincial lands (Fluker and Stacey 2012). Not surprisingly then, the federal government has yet to exercise its power under section 61 of SARA and has only issued two section 80 emergency protection orders since SARA was enacted in 2003; one for the western chorus frog (*Pseudacris triseriata*) in Quebec and one for greater sage-grouse (*Centrocercus urophasianus*) in southern Alberta and Saskatchewan. For the western chorus frog, the order prohibited critical habitat destruction from a housing subdivision development project near Montreal in a small spatial extent (2 km^2; Government of Canada 2016). For sage grouse, the order prohibited certain activities (e.g., operation and development of oil wells) across 1,672 km^2, costing an estimated CAD $10 million over five years in foregone gross revenues from oil production (Government of Canada 2013).

SARA section 11 conservation agreements

A third provision in SARA that provides for legal protection of terrestrial critical habitat on non-federal lands is section 11. This provision represents a collaborative approach in that it does not require the federal government to legislate over provincial jurisdiction. Section 11 allows the federal government to enter a "conservation agreement" with any government, organization, or private landowner to benefit a listed species, including by protecting its critical habitat. Such an agreement promotes coordination between two or more parties and, if implemented, may obviate the need for a federal order over non-federal lands issued under sections 61 or 80 of SARA. As of April 2020, all six finalized section 11 conservation agreements for terrestrial species relate to woodland caribou (Government of Canada 2020a). Despite the potential of section 11 conservation agreements to protect critical habitat and aid species recovery, it is unclear whether these agreements will provide strict legal protection of critical habitat.

Section 11 conservation agreements are similar in some ways to Habitat Conservation Plans (HCPs) under the US ESA, which protect listed species and their habitats on non-federal lands. HCPs balance species protection on private lands with property rights of landowners by allowing incidental "take" (e.g., killing, destroying habitat) of a listed species under an approved plan that includes habitat protection and minimizes take (Langpap and Kerkvliet 2012). As of August 2019, 697 approved HCPs provide habitat protection on private lands for 271 species listed under the ESA (US Fish and Wildlife Service 2019). The US Fish and Wildlife Service frequently signs HCPs with private companies involved in natural resources development and extraction.

Critical habitat protection via BC provincial legislation

Although it is the most biodiverse Canadian province and has the most species at risk, BC is one of four provinces and two territories without SAR legislation, and therefore must use other legislative tools to protect critical habitat identified on provincial land. The BC legislature has considered at least six SAR bills since 2010, yet none have advanced (Westwood et al. 2019). Instead, the province relies on a suite of existing provincial laws and policies, which so far has provided incomplete protection of critical habitat. We provide a detailed discussion of BC legislation and policy related to critical habitat protection in the following southern mountain caribou case study.

SOUTHERN MOUNTAIN CARIBOU CASE STUDY

Southern mountain caribou status

Woodland caribou are a subspecies of caribou that live in the boreal forests and mountains across Canada. They require large, contiguous tracts of mature forest and are considered a key ecological indicator and an umbrella species for boreal biodiversity (Bichet et al. 2016, Drever et al. 2019). Most woodland caribou populations across Canada are declining, ultimately due to decades of habitat loss and fragmentation from industrial development, which alter predator-prey dynamics and lead to increased caribou mortality (Wittmer et al. 2007, Festa-Bianchet et al. 2011). Activities such as logging and oil and gas extraction create productive early successional habitats that boost numbers of species such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginius*), both primary prey for wolves (*Canis lupus*; Seip 1992, Serrouya et al. 2011, Latham et al. 2011). Higher prey biomass supports higher wolf densities, increasing the probability of wolves encountering and killing caribou, and driving their populations towards extinction (DeCesare et al. 2010).

Southern mountain caribou, an ecotype of woodland caribou, range from north-central BC to southeast BC (they were extirpated from the US in 2019), including mountainous portions of western Alberta (Figure 4-1). They inhabit a range of biogeoclimatic zones that include low-elevation forests, subalpine parklands, and rugged alpine tundra (Hummel and Ray 2008). The process for listing and recovering southern mountain caribou under SARA began two decades ago. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC), a non-governmental body that assesses species at risk and recommends listing status under SARA, originally designated southern mountain caribou as threatened in 2000. Southern mountain caribou were listed as threatened under SARA in 2003. Although COSEWIC split the ecotype into three new designatable units in 2011 and upgraded their status to endangered in 2014, southern mountain caribou under SARA retain the population structure and threatened status from their 2003 listing. The Recovery Strategy, which included incomplete mapping of southern mountain caribou critical habitat, was posted to the SAR public registry in June 2014, seven years after its statutory due date under sections 42 and 43 of SARA. As required by SARA, the Recovery Strategy provided an action plan completion date, which was December 2017. No action plan exists as of May 2020.

The Recovery Strategy categorized southern mountain caribou by eco-evolutionary characteristics into the Northern, Central, and Southern Groups. Under SARA, they are further organized into local population units (LPUs), based on historical populations that have since declined and fragmented into recognized subpopulations (Ray et al. 2015). Since their listing under SARA in 2003, four subpopulations of southern mountain caribou have been extirpated and three more LPUs are likely functionally extirpated. ECCC estimated the total population of southern mountain caribou to be 3,746 animals in 2018, with 18 of 23 (78%) LPUs exhibiting declines and 22 of 34 (65%) subpopulations numbering < 100 animals (Government of Canada 2018b).

Southern mountain caribou recovery measures

Recovery of southern mountain caribou depends on both long-term critical habitat protection and restoration of disturbed habitats, along with short-term measures such as predator reduction (Serrouya et al. 2019). Southern mountain caribou have low reproductive potential and occupy relatively large areas at low densities to minimize their risk of predation and maximize survival and reproduction (Environment Canada 2008). Accordingly, they require large areas of critical habitat to recover. Critical habitat identified in the Recovery Strategy constitutes 34.8% and 40.5% of the total area within southern mountain caribou LPU and subpopulation boundaries, respectively, in BC. Failure to protect identified critical habitat from degradation can undermine recovery efforts because it takes decades to restore degraded habitats to late successional stages preferred by southern mountain caribou (Wittmer et al. 2007, Apps et al. 2013). The BC provincial government has attempted to address the proximate cause of population declines (increased predation on caribou) through predator reductions and maternity penning to boost calf survival (Serrouya et al. 2019). However, these emergency approaches do not address the ultimate cause of caribou declines and should only be used as tools to complement long-term efforts that protect and restore habitat.

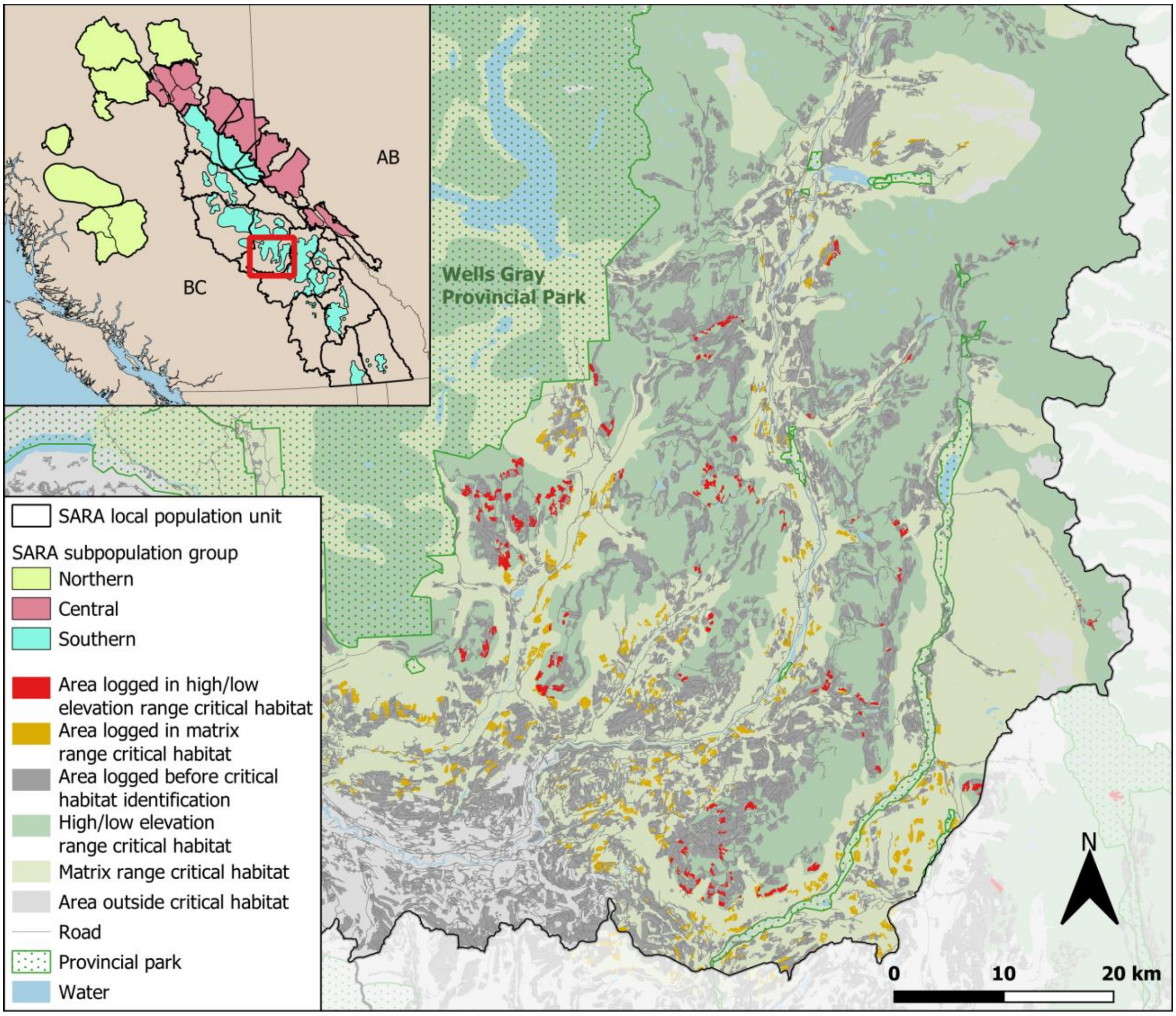

Figure 4-1. Map of logged areas and critical habitat types within the southern Wells Gray-Thompson local population unit of southern mountain caribou (*Rangifer tarandus caribou*), including portions of the Wells Gray and Groundhog subpopulations. Areas highlighted in red and orange were logged after critical habitat was identified in June 2014.

Southern mountain caribou critical habitat protection via SARA on non-federal lands

Specific activities that are likely to destroy critical habitat for southern mountain caribou, as defined in the federal Recovery Strategy, depend on the category of critical habitat identified, of which there are seven. The Recovery Strategy established thresholds for each of these critical habitat categories indicating the minimum amount of undisturbed habitat necessary to achieve recovery within the LPUs (Environment Canada 2014; see Table 4A-1 for details on different types of critical habitat). For most critical habitat categories, including high and low elevation summer and winter ranges, the Recovery Strategy identified any activities that result in the "direct loss", "degradation", or "cumulative loss" of critical habitat as activities that are likely to destroy it (e.g., logging, road construction). Areas in these categories were mapped as "high/low elevation range" critical habitat based on an elevation threshold that was putatively related to caribou life-history. The Recovery Strategy defined seasonal migration areas, areas with low caribou densities, and dispersal zones, as "matrix range" critical habitat. If not "sufficiently mitigated," logging and road construction are acknowledged to likely destroy certain types of matrix range critical habitat by increasing the likelihood of higher predator densities (by creating favorable conditions for more deer and/or moose) or by reducing the effectiveness of predator management. In other words, to avoid critical habitat destruction, logging and road construction must not increase predator densities and must maintain the effectiveness of predator management. However, it is unlikely that any mitigation measures for timber harvesting achieve both goals, nor does the Recovery Strategy offer guidance on this point.

We overlaid spatial polygons for high/low elevation range and matrix range southern mountain caribou critical habitat (Environment Canada, 2014a) with BC government data on logging clear cuts (British Columbia Data Catalogue 2019a) to estimate the area logged within critical habitat after its identification. We calculated that 314 km^2 of high/low elevation range critical habitat and 595 km^2 of matrix range critical habitat in BC were logged in the five years following critical habitat identification in June 2014 (see Figure 4-1 for example of critical habitat destruction and Supporting Information for details on spatial analyses). These areas reflect increases of 49% and 57%, respectively, in the area logged within high/low elevation and matrix ranges compared to the five years before critical habitat identification (Figure 4-2). The increase in critical habitat area logged from 2009–2018 mirrored observed increases in manufactured forest product sales and forest exports throughout the BC forestry industry during the same period following the 2008–2009 economic recession (Ministry of Forests, Lands Operations, 2019; Fortin, Mcloughlin, & Hebblewhite, 2020). These numbers show that critical habitat identification has not prevented timber harvest within critical habitat. Moreover, these results do not include indirect critical habitat loss, through avoidance and increased predation, in areas immediately adjacent to logged areas. The Recovery Strategy, borrowing from the boreal caribou recovery strategy, defines any habitat within a 500-m buffer of human development as disturbed (Environment Canada, 2011). Such areas no longer constitute critical habitat for critical habitat categories that are managed for minimal disturbance (see Table 4A-1). Applying the 500-m buffer to logged areas within these critical habitat types increases the total area of newly-disturbed critical habitat in the five years following its identification by 1,422

km^2 (to 1,736 km^2) in high/low elevation range and by 2,956 km^2 (to 3,551 km^2) in matrix range.

SARA section 61 and Section 80 orders for southern mountain caribou

Neither of the two emergency orders issued under section 80 to date (for the western chorus frog and sage grouse) carried the potential for negative social and economic consequences that may result from a similar order for southern mountain caribou, which inhabit large tracts of old-growth forests that help support a BC forestry industry that contributed CAD $7 billion to provincial GDP in 2018 (Statistics Canada 2019). In comparison, a proposed moratorium on timber harvest for 2,245 km^2 in portions of six southern mountain caribou LPUs could decrease provincial GDP by an estimated CAD $94 million annually (Stantec Consulting Ltd. 2019). While section 64 of SARA contemplates the possibility that parties may be compensated for losses in cases of “extraordinary impact” resulting from critical habitat protection, we are not aware of any such compensation being paid to date. The prospect of job losses and fewer recreation opportunities has sparked local opposition to southern mountain caribou habitat protection achieved through moratoria on timber harvest and recreation. A 2013 study found that local interest groups in Revelstoke, BC each cited different causes for local caribou population declines and assigned blame to other groups, highlighting the polarization and political challenges surrounding the issue of caribou conservation (Bixler 2013).

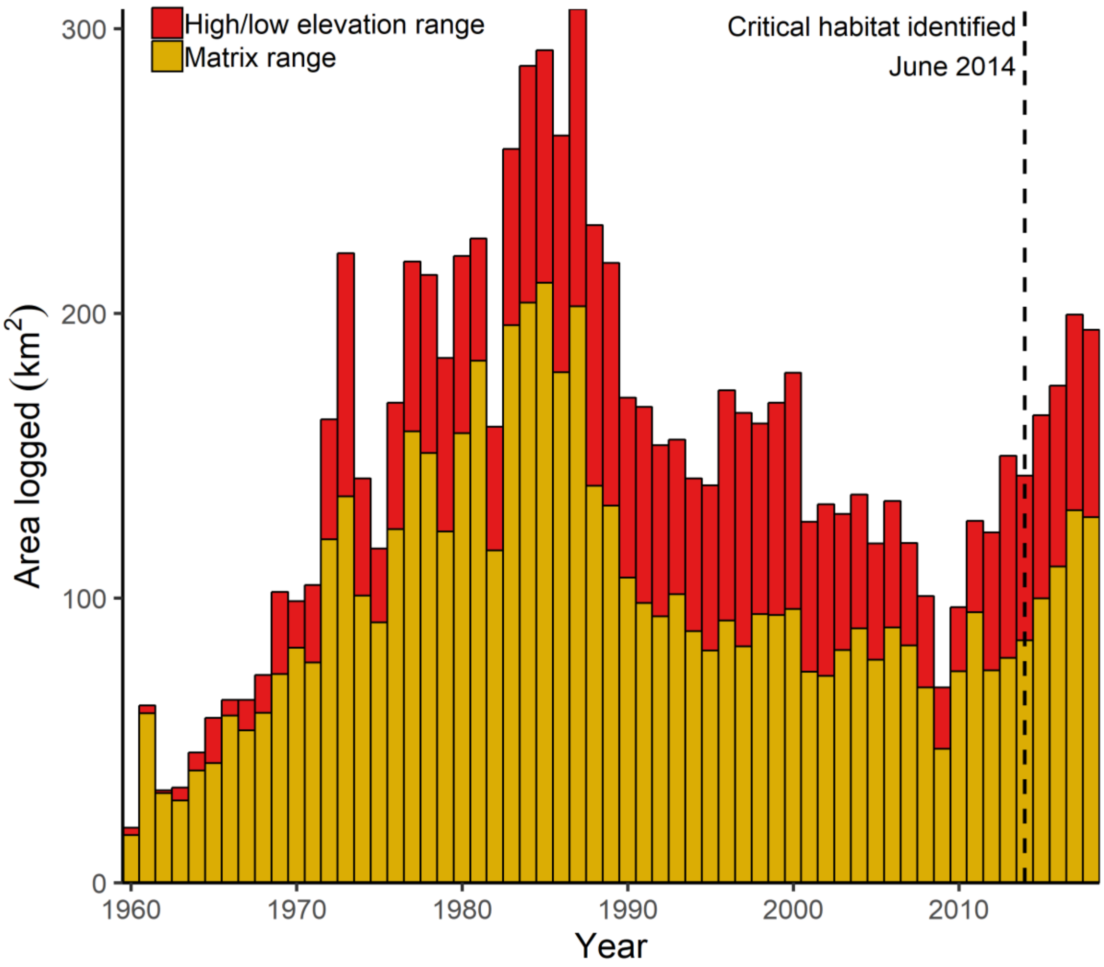

Figure 4-2. Area logged by year within current southern mountain caribou (*Rangifer tarandus caribou*) critical habitat boundaries in British Columbia.

The likelihood of a SARA section 80 emergency order to protect southern mountain caribou critical habitat will ultimately depend on a political calculation. On one hand, the willingness of the courts to scrutinize ministerial discretion exercised under section 80 of SARA, together with the opinion from the Minister's 2018 assessment that southern mountain caribou are experiencing imminent threats to their recovery (Government of Canada 2018b), lends support to the view that the Minister may recommend that the federal government issue an emergency order to protect critical habitat for the southern mountain caribou on provincial lands. Recent judicial decisions interpreting section 80 of SARA have scrutinized ministerial reluctance to recommend issuing emergency protection orders for boreal woodland caribou in Alberta and western chorus frog in Quebec (Adam v. Canada 2011, Centre québécois du droit de l’environnement v. Canada 2015). In both cases, the court ordered the Minister to reconsider their refusal to recommend that the federal government issue an emergency order. The Minister responded by declining to recommend issuing an emergency order in the boreal woodland caribou case but recommended issuing the order in the western chorus frog case (Government of Canada 2016). For southern mountain caribou, the federal government has indicated its preference to negotiate a solution for critical habitat protection with BC provincial and Indigenous governments using section 11 conservation agreements rather than by using its discretionary power to issue a section 80 order that would override provincial authority (Stueck 2019). Federal overreach, along with potentially negative effects on recreation and forestry, may be politically unpalatable, and the federal government appears reluctant to exercise its discretionary power to protect southern mountain caribou critical habitat on BC provincial lands.

SARA section 11 conservation agreements for southern mountain caribou

The federal government and the Province of BC finalized a bilateral section 11 conservation agreement (hereafter, "Bilateral Agreement") for southern mountain caribou in February 2020. The Bilateral Agreement establishes a framework for intergovernmental cooperation and outlines several measures and strategies intended to recover all three groups of southern mountain caribou. The agreement does not explicitly propose prohibiting any activities, such as timber harvest, that have the potential to destroy critical habitat (Government of Canada 2020b). The parties to the agreement for southern mountain caribou in BC to date do not include timber companies, which hold long-term licenses (usually 20–25 years) to harvest timber on provincial Crown land. It is unclear how this agreement will affect timber harvest for companies with licenses that cover thousands of square kilometers within identified critical habitat and that provide exclusive rights to forest management and harvest for decades.

In addition to the Bilateral Agreement, the federal and provincial governments finalized a Partnership Agreement under SARA section 11 with the West Moberly and Saulteau First Nations in February 2020 that complements the Bilateral Agreement by providing additional protections for the Central Group of southern mountain caribou. The Partnership Agreement goes further than the Bilateral Agreement by establishing moratoria on industrial disturbance in specific areas and providing concrete details on measures to protect and restore habitat (Government of Canada et al. 2020). Specifically, the Partnership Agreement formalized a set of BC Government interim moratoria from June 2019 on new permits logging and road construction permits within a 7,551-km^2 area of provincial Crown land. These moratoria overlap portions of seven subpopulations, four LPUs and 5,217 km^2 (10%) of existing high/low elevation critical habitat (7% of all southern mountain caribou critical habitat). All parties agreed to review and reassess the moratoria every two years over the duration of the 30-year agreement. The Partnership Agreement provides an example of how engaging Indigenous governments can strengthen critical habitat protection through SARA. However, the creation of similar agreements involving Indigenous governments in BC is not without significant challenges, including uncertainty over territorial sovereignty. Large portions of BC's provincial Crown land are on unceded traditional territory claimed by First Nations, who retain Aboriginal title to these lands and their resources along with the provincial government (Rossiter and Wood 2016).

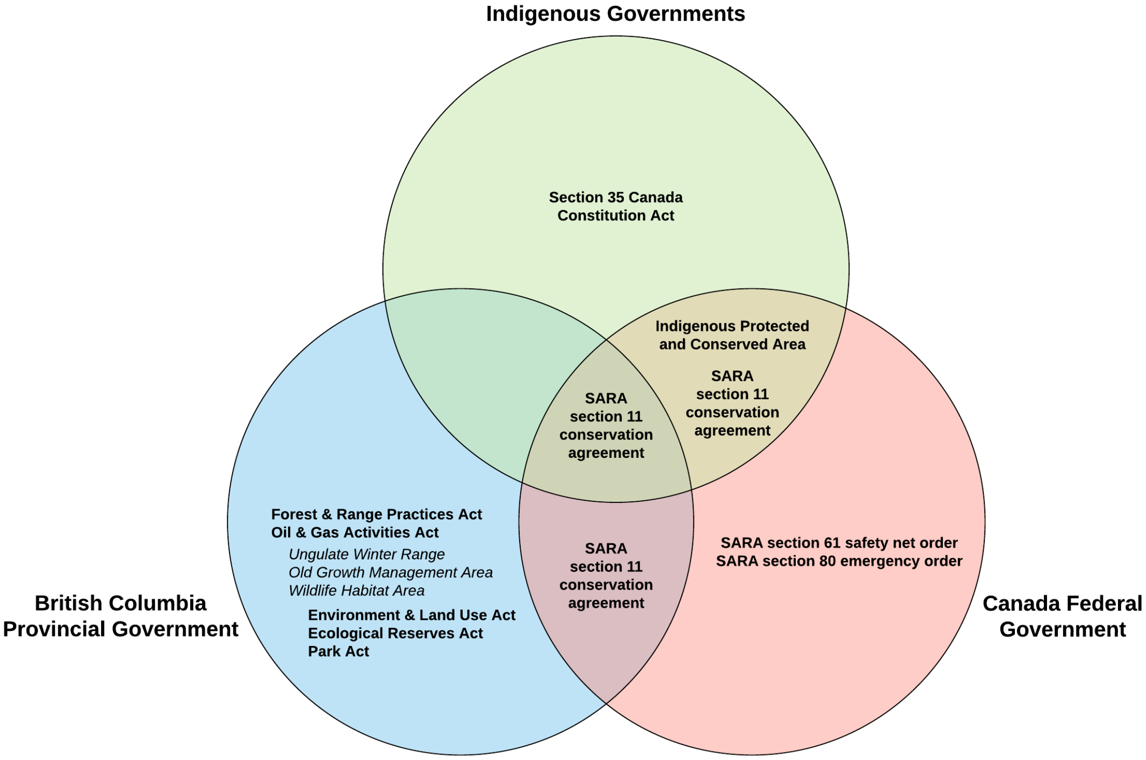

Figure 4-3. Legislative tools and agreements that can potentially protect southern mountain caribou (*Rangifer tarandus caribou*) critical habitat in British Columbia by restricting and prohibiting timber harvest and road construction.

Southern mountain caribou critical habitat protection via BC provincial legislation and policy

Because BC does not have dedicated SAR legislation, the province relies on other mechanisms to protect critical habitat for southern mountain caribou. A 2017 study conducted by the federal and BC governments listed 15 “legislative instruments” that could prohibit destruction of caribou critical habitat, five of which focus on restriction or prohibition of timber harvest and road construction (Figure 4-3; Government of Canada 2017). Below, we briefly highlight three instruments administered under the Forest and

Range Practices Act (FRPA) and the Oil and Gas Activities Act (OGAA), as well as a policy approach through the Cumulative Effects Framework.

Both FRPA and OGAA include regulations that implement management and protection for environmental values in BC, yet the spatial distribution and degree of protection for southern mountain caribou critical habitat offered by FRPA and OGAA is highly variable and depends on the critical habitat category. Regulations under FRPA and OGAA allow the BC Minister of Environment and Climate Change to establish Ungulate Winter Ranges (UWRs) and Wildlife Habitat Areas (WHAs). UWRs and WHAs established to protect southern mountain caribou either prohibit forest harvesting activities in high elevation winter areas (‘no harvest zones’) or allow for harvest with some restrictions in low elevation winter areas and corridor areas (‘conditional harvest zones’). FRPA and OGAA also allow the Minister to establish Old Growth Management Areas (OGMAs), which prohibit tree cutting except for cases of insect infestation and disease. Together, OGMAs and no harvest zones within UWRs and WHAs administered through FRPA or both FRPA and OGAA overlap 51% of high/low elevation range critical habitat (BC Data Catalogue 2019b, 2019c, 2019d). These legislative tools appear to have been successful in protecting high/low elevation range critical habitat, as < 7 km^2 of areas covered by their protections were logged in the five years after June 2014. BC provincial parks, protected areas, and ecological reserves increase the total area receiving full protection to 47% of all southern mountain caribou critical habitat and 63% of high/low elevation range critical habitat. However, conditional harvest zones within UWRs and WHAs administered through FRPA or both FRPA and OGAA do not offer effective protection of critical habitat, as 80% of logged high/low elevation range critical habitat in the five years following its identification overlaps these areas.

Unlike high/low elevation range critical habitat, matrix range critical habitat overlaps very few areas with existing provincial legislation that could provide protection. Less than 19% of matrix range critical habitat is protected by a combination of parks (14%) and OGMAs (4%), and none overlaps UWRs or WHAs. Nearly 100% of matrix range critical habitat logged in the five years after its identification is not protected by provincial legislation (Figure 4-4). The lack of legislation protecting matrix range critical habitat may reflect a reluctance of the BC provincial government to limit timber harvest in these areas. Notably, 50% of matrix range critical habitat and 47% of logged matrix range critical habitat overlaps the low elevation interior cedar-hemlock biogeoclimatic zone, which is among the most productive and economically valuable forest types for BC’s forestry industry (Meidinger and Pojar 1991). In comparison, 9% of high/low elevation critical habitat and logged high/low elevation critical habitat overlaps the interior cedar hemlock zone. The discrepancy in protection between high/low elevation range and matrix range critical habitats for southern mountain caribou suggests that the discretionary measures in provincial law and policy can, but do not necessarily, amount to effective and enforceable critical habitat protection.

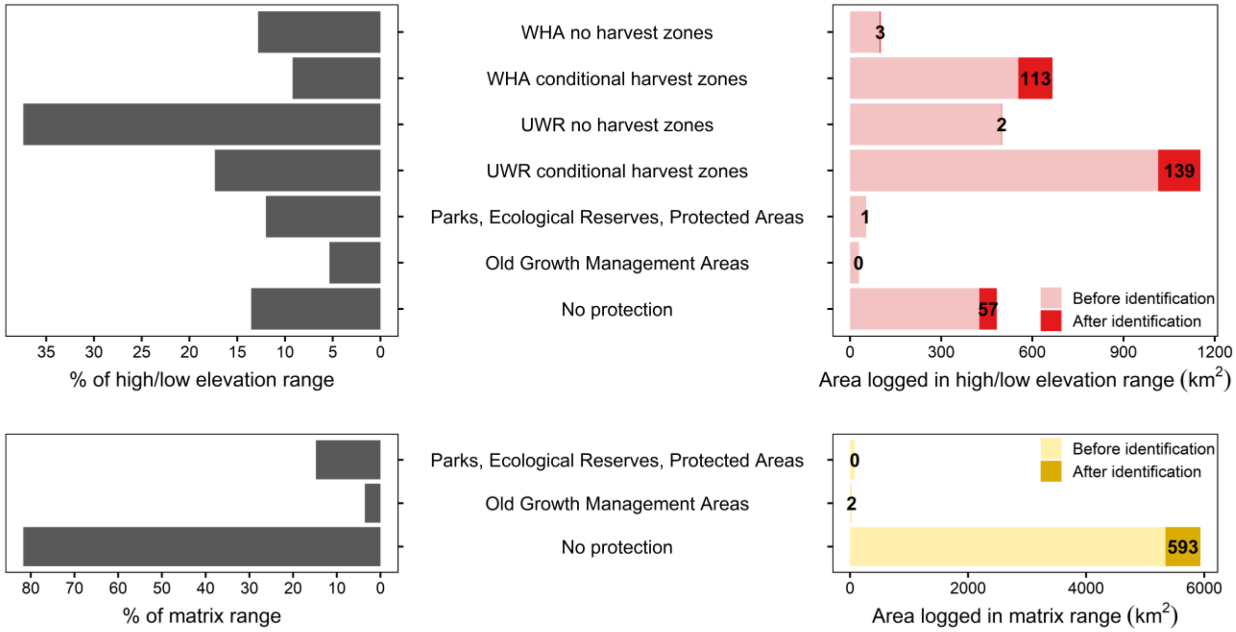

Figure 4-4. Percent of area in southern mountain caribou (*Rangifer tarandus caribou*) high/low elevation range (left, top) and matrix range (left, bottom) critical habitat covered by British Columbia provincial legislative tools that restrict timber harvest and road construction, and area logged before and after critical habitat identification in June 2014 within these same areas (right). Areas logged after critical habitat identification labeled in bold. Some areas of critical habitat are covered by more than one legislative tool.

Complementary and alternative mechanisms to protect critical habitat

Continued declines in southern mountain caribou numbers and ongoing destruction of their critical habitat underscore the need for alternative mechanisms to protect these areas and recovery the species. In addition to the legislation outlined above, BC is implementing a provincial Cumulative Effects Framework (CEF) that could influence the authorizations of future development projects that have the potential for adverse effects on identified critical habitat. The CEF is a policy instrument intended to complement existing provincial legislation, assessing and managing effects that accumulate from multiple sources across the landscape on different “values” such as old growth forests. The CEF stems in part from criticism of the province’s environmental assessment process, which fails to consider the interacting effects of multiple development projects over space and time, and for southern mountain caribou, rarely rejects projects based on their potential for negative effects (Collard et al. 2020). A test assessment protocol under the CEF for old growth forests includes specific forest tracts based on the presence of identified critical habitat and Land Act reserves for southern mountain caribou (BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2017). The CEF offers a unified framework for provincial decision-makers across different ministries to follow when considering whether to approve authorizations and renewals for permits and licenses (e.g., for road construction and forest harvest), environmental assessments for development projects, and potential effects of proposed activities on established or asserted Aboriginal or treaty rights (Government of BC 2016, Vlasschaert 2016). Once implemented, the CEF may provide an opportunity to engage Indigenous people and local stakeholders in developing assessments, providing an avenue for transparent, participatory decision making that builds trust and public support for mitigating cumulative effects on critical habitat.

Indigenous Protected and Conserved Areas

Under section 35 of Canada's Constitution Act, the governments of Canada and BC each have a statutory obligation to consult with Indigenous people when they consider actions that may adversely affect Aboriginal or treaty rights (Newman 2014). Further, the right to hunt in perpetuity, as if they had not entered into treaty, is a common treaty right for many Indigenous people in Canada (Laird et al. 1899). A 2011 decision by the BC Court of Appeals found that the BC Ministry of Energy and Mines' decision to approve an environmental assessment for coal mining exploration in southern mountain caribou critical habitat failed to consult with the West Moberly First Nations and infringed on their treaty rights to hunt caribou (West Moberly First Nations v. B.C. 2011).

Establishment of Indigenous Protected and Conserved Areas (IPCAs) in regions where Indigenous people seek to assert their treaty rights may prove to be an effective and complementary policy tool to protect critical habitat, recognize treaty rights, and address reconciliation with Indigenous people. IPCAs incorporate Indigenous values and traditional ecological knowledge into planning, stewardship, and management processes, which are shared between federal and Indigenous governments. Although both western science approaches and traditional ecological knowledge and can inform critical habitat identification (Polfus et al. 2014), the latter has been overlooked in the identification of critical habitat for southern mountain caribou. The concept of IPCAs marks an important shift from the colonial model of protected areas (Zurba et al. 2019). It adopts a more holistic approach to conservation that explicitly includes Indigenous people and cultural practices and supports the implementation of the 2015 Truth and Reconciliation Commission’s Calls to Action and the United Nation’s Declaration on the Rights of Indigenous Peoples (Indigenous Circle of Experts 2018).

IPCAs are being increasingly used in Canada as a holistic tool that both affirms indigenous rights and protects caribou by explicitly recognizing cultural practices while working to conserve critical habitat for caribou. For example, in late 2018, the Decho First Nations, the federal government and the Government of the Northwest Territories established the Edéhzhíe Indigenous Protected Area (14,218 km^2) in the Northwest Territories, which protects critical habitat for boreal woodland caribou. Farther south, the Kaska Dena First Nation recently received federal funding to pursue a proposed 40,000 km^2 Kaska IPCA in northern BC that would overlap large portions of six herds of northern mountain woodland caribou, which are listed under SARA as a Species of Special Concern. While conservationists can provide political leverage and information to support establishing IPCAs, it is important to note that IPCAs may have different objectives than traditional protected areas, such as enabling Indigenous land management towards self-determination and facilitating economic development. Further, IPCAs cannot be relied upon as the only means of protecting southern mountain caribou critical habitat.

International treaties and agreements

Protecting critical habitat of imperiled species is consistent with and supports Canada's international commitments to conserve biodiversity and recognize the unique rights of Indigenous peoples. Canada is attempting to work with Indigenous people to help fulfill its commitments to protect at least 17% of terrestrial and inland fresh water areas by 2020 through Aichi Target 11 of the Convention on Biodiversity and Target 1 of the 2020 Biodiversity Goals and Targets for Canada (Government of Canada 2018c). Recent research showed that within Canada, Brazil and Australia, indigenous-managed lands support more vertebrate species than traditional protected areas (Schuster et al. 2019). IPCAs and agreements between Indigenous and Crown governments affirm Canada's commitment to the United Nations Declaration on the Rights of Indigenous Peoples, which articulates the rights of Indigenous peoples to exercise rights to their lands, territories and resources and the maintenance of their cultures. Caribou conservation and critical habitat protection also help Canada meet its long-term commitments under the 2015 Paris Agreement on climate change to reduce emissions and increase carbon storage, because late-successional forests store huge amounts of carbon in live biomass and in soils (Yona et al. 2019). International treaties and agreements, over which the federal government has constitutional jurisdiction, may serve to increase political pressure on federal and provincial governments to protect southern mountain caribou habitat.

CONCLUSION AND RECOMMENDATIONS

Even after the extirpation of several subpopulations since the 2014 Recovery Strategy, and despite existing tools to fully protect critical habitat, logging and road construction continue to destroy southern mountain caribou critical habitat in BC. There are many political reasons for the federal government's reluctance to use orders under sections 61 and 80 of SARA for protecting southern mountain caribou critical habitat, yet these actions would provide the strongest immediate habitat protection. Instead, the federal government has entered a section 11 conservation agreement, but it is unclear whether the agreement will provide effective protection for critical habitat located outside the moratoria areas defined in the accompanying Partnership Agreement. Further, there appears to be no strategic framework guiding decisions on which southern mountain caribou subpopulations receive concrete habitat protections, such as moratoria on resource development, in any future agreements under section 11.

Dedicated BC SAR legislation implementing non-discretionary critical habitat protection could effectively prevent habitat destruction but has yet to receive strong consideration from the BC legislature. In the absence of these approaches, alternative and complementary approaches are necessary to protect southern mountain caribou critical habitat. These include using tools under existing BC provincial legislation, collaborating with Indigenous peoples to develop and implement conservation agreements and IPCAs to recover caribou, and facilitating assessments and public engagement under the provincial CEF. In an era where conservation is riddled with challenges including lack of funding, irreversible consequences for failure, and opposition from billion-dollar industry groups (Boan et al. 2018), saving imperiled species requires solutions that make gains across multiple objectives, thereby increasing the potential political benefits of conservation.

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APPENDIX 4A

Detailed methods for spatial analyses

We used the ‘sf’ package (Pebesma 2018) in Program R (R Core Team 2019) to perform spatial intersections between polygon shapefiles of southern mountain caribou critical habitat identified in the Recovery Strategy, harvested areas in British Columbia, and legal boundaries for provincial legislative tools restricting timber harvest and road construction. We considered all timber harvest polygons with a disturbance start date later than 3 June 2014 to be logged after critical habitat identification. The harvest dataset includes areas harvested from 1915 through June 2019, but nearly all (99.7%) data are from after 1959.

Table 4A-1. Summary of southern mountain caribou (*Rangifer tarandus caribou*) critical habitat categories and associated minimum undisturbed habitat management thresholds from the federal Recovery Strategy, shown by subpopulation group. Dark shading indicates critical habitat that is likely to be destroyed by any resource extraction activity. Light gray shading indicates critical habitat likely to be destroyed if it increases the likelihood of increased predator density or reduces effectiveness of predator management. Adapted from Government of Canada 2017.

Critical habitat category	Minimum undisturbed habitat management thresholds		
	Northern group	Central group	Southern group
High elevation winter range	Minimal disturbance	Minimal disturbance	Minimal disturbance
High elevation summer range	Minimal disturbance	Minimal disturbance	Minimal disturbance
Low elevation winter range	≥ 65% undisturbed	≥ 65% undisturbed	n/a
Low elevation summer range	Minimal disturbance	n/a	n/a
Low elevation early winter and/or spring range	n/a	n/a	Minimal disturbance
Type 1 matrix range: *other areas within LPU annual range, including seasonal migration areas and lower use areas*	≥ 65% undisturbed*	≥ 65% undisturbed*	Wolf densities < 3/1000 km^2
Type 2 matrix range: *areas surrounding annual ranges, areas of trace occurrences, and dispersal zones between subpopulations and LPUs*	Wolf densities < 3/1000 km^2	Wolf densities < 3/1000 km^2	Wolf densities < 3/1000 km^2

Incomplete mapping of critical habitat in the Recovery Strategy did not include type 1 or type 2 matrix range for the northern or central groups.

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