Boreal Caribou Conceptual Ecological Model Technical Report (*DRAFT*)

Submitted to:

Environment and Climate Change Canada's National Boreal Caribou Knowledge Consortium Secretariat

Submitted by:

Habitat Restoration Working Group of the National Boreal Caribou Knowledge Consortium

National Boreal Caribou Knowledge Consortium

Executive Summary

Habitat restoration is expected to play a key role in the recovery of boreal woodland caribou (*Rangifer tarandus caribou*) in Canada. Population declines are correlated with the proportion of ranges affected by anthropogenic and natural disturbances and reversing these impacts is expected to benefit caribou populations. However, there are various mechanisms that lead from habitat stressors to caribou declines, and the effects of these mechanisms differ among ranges. Understanding the ecological pathways driving observed relationships can inform restoration planning by: 1) directing treatments towards the most critical, range-specific mechanisms; 2) identifying possible confounding factors that need to be addressed; and, 3) supporting adaptive management by generating testable hypotheses and clarifying monitoring needs.

Here we present a conceptual Boreal Caribou Conceptual Ecological Model developed by the Habitat Restoration Working Group of the National Boreal Caribou Knowledge Consortium. The model is composed of 14 factors and associated relationships that generate pathways leading from a variety of landscape disturbance stressors. The model does not capture all possible factors in the system, but only those that are likely exerting significant effects. Nor does it address specific restoration treatment options but it can inform the design of treatments by identifying the functional effects that treatments should be addressing.

Caribou survival and recruitment are affected directly by predation, nutrition, disease and hunting. All of these link back to one or more habitat stressors that drive the national disturbance model (i.e., fire, insect pests, forest alteration/clearing and linear development). The pathways are interacting and are also affected by external factors (e.g., climate change). The habitat stressors alter forage available to caribou and to other primary prey, the distribution and abundance of primary prey, associated predators and of humans, and ultimately cause population declines via lower caribou survival and reproductive success.

A key next step for the conceptual model is the development of appropriate response metrics to monitor. This would provide the means to compare the relative effects of different drivers among ranges and would highlight key knowledge gaps. The model would then provide a complete framework for adaptive management as habitat restoration is implemented.

Acknowledgements

The Boreal Caribou Ecological Model was developed by the Habitat Restoration Working Group (HRWG) of the National Boreal Caribou Knowledge Consortium under the direction of Tatyana Flick (Environment and Climate Change Canada, Government of Canada) and Katalijin MacAfee (Natural Resources Canada, Canadian Forest Service). The HRWG is a composition of representatives from government, industry, Indigenous communities and organizations, ENGOs, and consultants with a working knowledge of habitat restoration. Contributors to the development of the conceptual model include: Amanda Dookie (Environment and Climate Change Canada, Canadian Wildlife Service), Amanda Martin (Environment and Climate Change Canada, Science & Technology Branch), Art Rodgers (Government of Ontario), Cynthia Chand (Government of Alberta), Dani Degenhardt (Natural Resources Canada), Dennis Brannen (Government of Manitoba), Elston Dzus (Alberta-Pacific Forest Industries Inc.), George Duffy (Government of Alberta), Jaime Pinzon (Natural Resources Canada), James Hodson (Government of Northwest Territories), Jason Dicker (Nunatsiavut Government), Jérôme Rioux (Gouvernement du Québec), John Pisapio (Government of Newfoundland & Labrador), Katalijn MacAfee (Natural Resources Canada, Canadian Forest Service), Katherine Mehl (Government of Saskatchewan), Katherine Wolfenden (Fort Nelson First Nation), Kelli Cote (Matrix Solutions), Kristy Burke (FUSE Consulting / Alberta Regional Caribou Knowledge Partnership), Laura Finnegan (Foothills Research Institute), Lisa Worthington (Government of Northwest Territories), Maria Ciancio (Government of Northwest Territories), Mark Boulton (Suncor), Melanie Dickie (Alberta Biodiversity Monitoring Institute, Caribou Monitoring Unit), Michael Cody (Cenovus Energy Inc.), Nadia Skokun (Government of British Columbia), Paula Bentham (Golder Associates Inc.), Peter Friedrichsen (Prince Albert Model Forest), Robin Steenweg (Environment and Climate Change Canada, Canadian Wildlife Service), Scott Schilds (Government of British Columbia), Steven Wilson (EcoLogic Research), Susan Leech (The Firelight Group), Tatyana Flick (Environment and Climate Change Canada, Science & Technology Branch), Tom Habib (Alberta-Pacific Forest Industries Inc.), Vern Doell (Government of Saskatchewan), Walter Andreeff (Métis Nation of Alberta).

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1 INTRODUCTION

The *Amended Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada* (Environment and Climate Change Canada, 2020) identifies habitat restoration as a key requirement. While considered critical in highly disturbed ranges, there is currently limited information available to guide the planning, treatment selection and monitoring of restoration activities to maximize the effectiveness of treatments. The recovery strategy provides a clear definition of "disturbed" habitat, but conditions that may be accelerated through habitat treatments to create ecologically functional "undisturbed" habitat are less clear.

Caribou population growth is correlated with both natural and anthropogenic disturbance (Johnson et al., 2020). However, the mechanisms that lead from various habitat stressors, to habitat disturbance, to changes in prey and predator dynamics, and finally to caribou populations are less well-defined and variable among caribou ranges. Understanding the ecological pathways driving the relationship between habitat disturbance and caribou decline can inform restoration programs by identifying range-specific pathways to decline and how they may interact or be confounded by other factors. With this information, restoration programs can be designed to maximize the likelihood of a positive population response by caribou.

Here we present a conceptual Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group of the National Boreal Caribou Knowledge Consortium (hereafter HRWG). The HRWG is a composition of representatives from government, industry, Indigenous communities and organizations, ENGOs, and consultants with a working knowledge of habitat restoration. The intent of the conceptual model is to depict key ecosystem processes, pathways and interactions among factors - directly outlining the mechanistic pathways in which habitat disturbance precipitates through the boreal forest to impact caribou populations. The conceptual model is informed by the well-established national relationship between percent (%) area disturbed and caribou recruitment at the population range scale. The Boreal Caribou Ecological Model (the model) illustrates how the national disturbance-recruitment relationship is mediated through several interacting pathways that are causing caribou population decline, which vary in strength regionally. It attempts to integrate evidence currently available in the scientific and management literature, along with the working knowledge of HRWG members from across Canada, into comprehensive working hypotheses that can guide the development and implementation of habitat restoration treatments and experiments, inform monitoring programs, and identify knowledge gaps.

2 GOALS

The goals of the Boreal Caribou Ecological Model are to:

1. Develop a **common, shared language** to facilitate communication among diverse groups regarding boreal caribou recovery across Canada;
2. Form a **foundation for synthesizing** what is currently known about the boreal caribou system and the role of habitat restoration within it; and,
3. Develop **testable hypotheses** regarding habitat restoration [and other management] actions.

Additionally, future development could:

1. Provide a means for **defining appropriate response metrics** to monitor;
2. Provide a means by which to **compare the relative effects** of system drivers on boreal caribou survival and recruitment at the range scale;
3. Allow for **knowledge gaps to be clearly identified** and addressed; and,
4. Support an **adaptive management** approach.

The model does not address specific restoration treatment options but it can inform the design of treatments by identifying the functional effects that treatments should be addressing and, additionally, by providing the theoretical basis for effectiveness monitoring.

3 APPROACH

The model was developed iteratively via meetings of the HRWG held between March 2019 and June 2020. Formally, the model is a directed acyclic graph, where boxes represent factors important to the caribou system. Direct causal relationships are represented by a single arrow between factors while indirect causes involve chains of more than one arrow and factors. Arrows can represent either positive (solid) or negative (dashed) relationships. Because the arrows represent causal relationships and a temporal ordering, loops are not allowed (otherwise the future could cause the past; hence, an “acyclic” graph). Management actions are not included in the graph, only the factors that could change as a result of management actions, including habitat restoration.

This document was developed to provide technical guidance based on the current state of scientific knowledge. It does not explicitly incorporate Traditional Ecological Knowledge, which will play a critical role in successful habitat restoration and species recovery.

4 MODEL STRUCTURE

The model is composed of 14 factors and associated relationships that generate pathways leading from a variety of landscape disturbance stressors. These affect the distribution and abundance of components of suitable caribou habitat, the distribution and abundance of primary predators and prey, and ultimately caribou survival and recruitment (Figure 1). Climate change is included as a stressor that can alter rates of landscape disturbance, affect important components of caribou and primary prey habitat, and can also affect the predator-prey system directly.

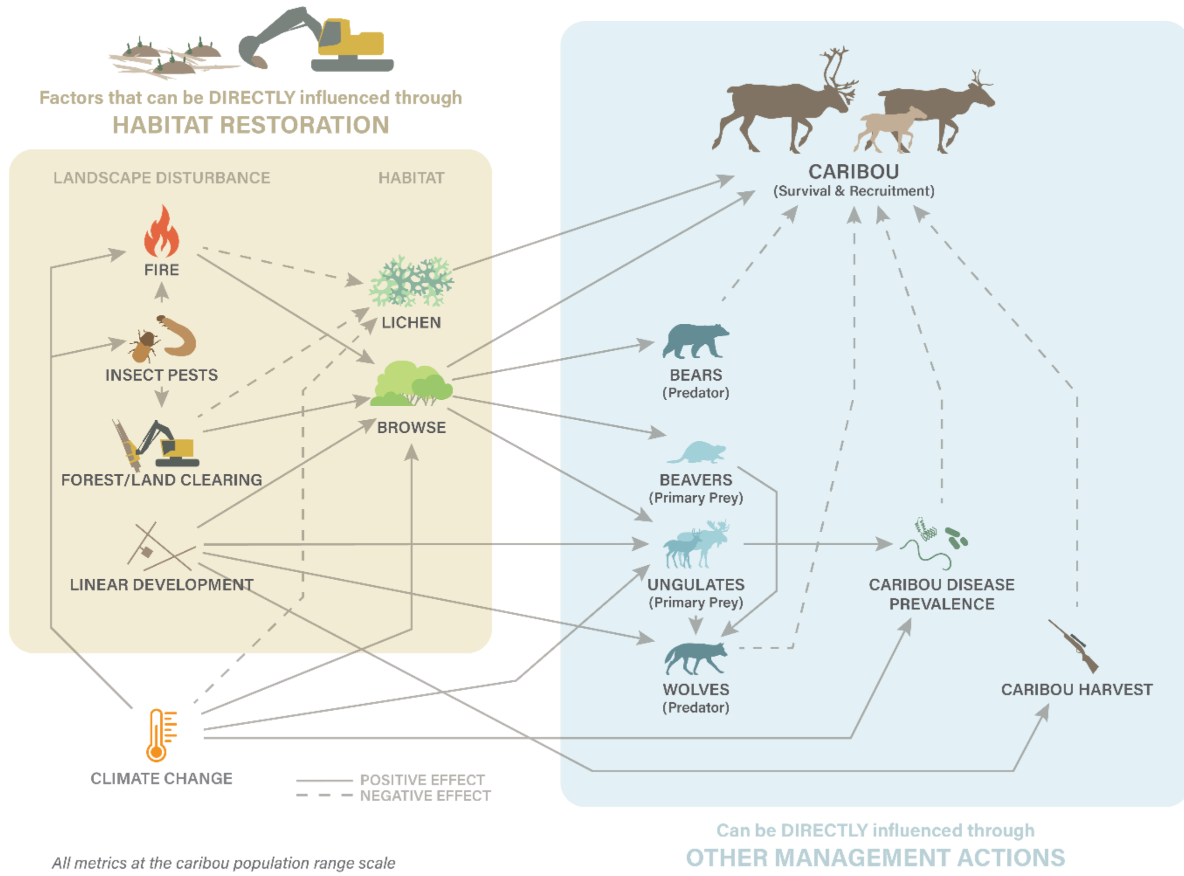


Figure 1: Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group. Solid arrows represent positive effects and dashed arrows indicate negative effects.

The model is not intended to capture all possible factors in the system, but only those that are likely exerting significant effects. Like the original national disturbance model, it is intended to be applied aspatially at the scale of caribou ranges. The relative strength of each of these pathways likely varies across time and space, and as such those weightings are not depicted here. Additionally, these pathways typically function through four key types of factors (predation, nutrition, disease and hunting) which are depicted Appendix A.

4.1 Landscape Disturbance

The scientific review for boreal caribou critical habitat provided a probabilistic evaluation of critical habitat for boreal caribou relative to the set of conditions (demographic and environmental) within each range (EC, 2011). Meta-analysis of population recruitment in relation to disturbance was undertaken and the combined disturbance (fire and 500 m buffered anthropogenic disturbance) model explained approximately 70 percent of the variation in boreal caribou recruitment across Canada (EC, 2011). Contributions to landscape disturbance are recognized as both natural (fire, insect pests) and of anthropogenic origin (forest alteration/clearing, linear disturbance). The relative contribution of different disturbances varies among ranges across Canada. For example, the effect from fire has been documented as lower than the effect from forest cutovers (Vors et al., 2007).

4.1.1 Fire

Fire results in a mosaic of burned and unburned (residual) habitat patches. The total area burned by wildfires each year is extremely variable and is affected by weather. Some caribou in Canada have evolved within areas of relatively short fire-return intervals (EC, 2011). Caribou demonstrate ambivalent responses to burn, rarely abandoning areas at the home range scale (Silva et al., 2020) but selecting unburned residual patches such as old-growth forest stands or bogs and fens rather than early-stage regenerating forests (Skatter et al., 2017; Konkolics 2019). Burns (< 50 years since disturbance) during the snow-free period offer access to herbaceous shrubs and vegetation, insect relief and predator avoidance (Nagy, et al., 2005 *as cited within* Culling & Culling, 2006). Recent evidence suggests that increased use of burned habitats does not affect female survival (Konkolics, 2019).

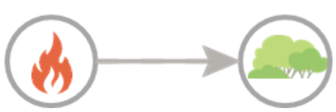
The following direct pathways are captured in the model to characterize the expected consequences of fire:

1. **Decreased lichen abundance.**

   The alteration by wildfire of mature to old growth coniferous forests with extensive terrestrial lichen forage can reduce the condition of habitat suitable for caribou (Russell, 2018). In the first few decades following disturbance, fire strongly affects the abundance and distribution of terrestrial lichens (Coxson & Marsh, 2001) when mature forests burn.

2. **Increased browse abundance.**

   As conditions worsen for terrestrial lichens they generally improve for shrubs and herbaceous vegetation (Coxson & Marsh, 2001; Heggberget et al., 2002). As noted above, while fire initially reduces the availability of winter lichen forage for caribou, it can provide an increase in herbaceous forage important to meet energetic demands during calving and summer seasons (Nagy et al., 2005), facilitate natural regeneration of coniferous trees (i.e., jack pine) and prevent replacement of lichens by inedible feather mosses in mature forest (COSEWIC, 2012).

4.1.2 Insect Pests

Impacts from insect pests include widespread tree mortality or creating trunk defects, reduction in tree vigor and growth rates, trees more susceptible to secondary insects and diseases (Alfaro, 1988). Pests, or the mitigation measures to control pests, may change stand structure by selectively killing particular tree species (e.g., mature pine) or by changing species composition to favour more browse (e.g., Chagnon et al., 2021).

The following direct pathways are captured in the model to characterize the expected consequences of forest pest epidemics or spread:

1. **Increased forest / land clearing.**

   Use of timber harvesting and prescribed burns to control pests (Nobert et al., 2020) results in forest/tree clearing. Even in the absence of these treatments, tree mortality caused by pests such as mountain pine beetle can thin stands and result in changes in light penetration and forest floor conditions, specifically moisture and temperature (Cichowski & Williston, 2005). In Québec, spruce budworm outbreak contributes to a change in forest structure with a resultant increase in deciduous shrubs (Chagnon et al., 2021). The increase in deciduous shrub has a positive numerical response on moose and a higher mortality risk of boreal caribou in winter (Labadie et al., 2021).

2. **Increased fire prevalence.**

   Rate of fire spread and fire intensities have been predicted (e.g., Page and Jenkins, 2007) and documented in experimental fires and wildfires in recent mountain pine beetle-killed stands (Perrakis et al., 2014). Although very little fire behaviour has been documented in mountain pine beetle-killed stands and fire spread is a complex process, overall evidence exists for more rapid crown fire behaviour and very rapid spread of fire given fuel conditions in the first few years following mountain pine-beetle attack (Perrakis et al., 2014). Fire hazard varies depending on red-attack stage or gray-attack (post-epidemic) stage. Spruce budworm-killed balsam fir also creates conditions of intense and rapidly spreading fire behaviour (Wotton et al., 2009 as cited within Perrakis et al., 2014), although the effect is likely short-term.

4.1.3 Forest Alteration/Clearing

Forest and land clearing occurs within caribou range through natural processes (pests), forest cutovers, mining, wellsites, linear/road development, peat harvesting and agricultural conversion at varying scales across jurisdictions. Forest alteration/clearing resulting in the conversion of mature coniferous stands have led to the loss of spatial separation of caribou with other ungulates and their predators (Latham et al., 2011b; Peters et al., 2013; c.f., Mumma et al., 2018).

There are a large number of studies that have correlated forest alteration/clearing with negative effects on caribou, although most do not disentangle direct effects such as direct disturbance and habitat use changes with forage availability, from indirect effects such as behavioural changes due to predation risk and higher predation rates.

Specifically, caribou may respond negatively to forest alteration/clearing by not using areas of otherwise suitable habitat or changing their selection of habitat, because of its proximity to disturbance (Carr et al., 2011; Courtois et al., 2008; Dyer et al., 2001; Johnson et al., 2015; Leblond et al., 2011, 2013; Moreau et al., 2012; Nagy 2011; Smith et al., 2000; Weclaw & Hudson, 2004; Weir et al., 2007; Vors et al., 2007). Although forest harvest may represent a temporary disturbance, empirical evidence has demonstrated its negative effects on caribou (e.g., Courtois et al., 2008; Fortin et al., 2013; Johnson et al., 2015; Schaefer and Mahoney, 2007; Smith et al., 2000). In particular, Vors et al. (2007) identified forest cutovers as the strongest predictor of caribou extirpation in Ontario, above other anthropogenic landscape disturbances considered (including fires, roads, utility corridors, mines, pits and quarries, lakes, trails, and rail lines).

Caribou are negatively associated with logged landscapes, while moose, deer and wolves are positively associated (Bowman et al., 2010). The harvesting of forests within entire wintering areas has led to the demise of local caribou herds in Ontario (Cumming, 1992; Vors et al., 2007).

The following direct pathways are captured in the model to characterize the expected consequences of forest alteration/clearing:

1. **Decreased lichen abundance.**

   Forest alteration/clearing of mature coniferous forests reduces lichen abundance within these previously mature stands.

2. **Increased early seral browse abundance.**

   Forest alteration/clearing or alteration (e.g., due to pests) within, or adjacent to critical boreal caribou habitats increases the amount of early seral browse which is demonstrated in a numerical response by primary prey (e.g., deer; Dawe, 2011) (e.g., moose; Labadie et al. 2021).

4.1.4 Linear Development

Linear development including roads, pipeline, transmission lines, seismic lines and other cutlines contribute to anthropogenic disturbances within caribou ranges. There is an abundance of research on how linear developments alter the space-use of caribou (Faille et al., 2010; Nellemann & Cameron, 1998; Pinard et al., 2012), other ungulates and predators (Dickie et al., 2019; Finnegan et al., 2018a; Fisher and Burton 2018; Tigner et al., 2014). The avoidance of these features may decrease available habitat to caribou. Despite the mounting evidence that linear developments modify the space-use of caribou, moose, deer, wolves and bears, there remains limited evidence that directly ties linear developments to population demographics of these species (Dickie et al., 2020; but see Whittington et al., 2011).

The following direct pathways are captured in the model to characterize the expected consequences of linear development:

1. **Increased browse abundance.**

   Early seral browse suitable for ungulates and bears is abundant on seismic lines (Finnegan et al., 2018b; Dawe et al., 2017). An unsupported hypothesis is that this increase in browse is sufficient to indirectly influence ungulate movements or increase the density of primary prey in caribou habitat.

2. **Increased wolf and bear predation**.

   Linear disturbances are preferentially being selected for predator travel (Latham et al., 2011; Whittington et al., 2011; DeCesare et al., 2012) and linear developments have been associated with increased predator mobility as compared to surrounding forests (James, 1999; Dickie et al., 2017; Dickie et al., 2019; DeMars and Boutin, 2017). Wolves and their kill sites have been documented closer to linear developments than random (James, 1999; James & Stuart-Smith, 2000).

3. **Increased human harvest**.

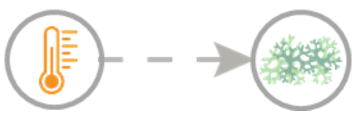
   Linear developments increase the efficiency of people to access caribou range and human-caused caribou mortalities have been documented closer to linear corridors (James and Stuart-Smith, 2000). Linear developments, particularly roads, can facilitate hunting and poaching by increasing human access (Edmonds 1988; Leblond et al., 2007). While this negatively affects caribou, increased hunter harvest access may also reduce the abundance of primary prey through the same mechanism; although this is not captured in the model.

4.2 Climate Change

Environment and Climate Change Canada (2020) assigns a *medium* level of concern to climate change as a threat to boreal caribou but notes that long-term impacts are largely unknown. Barber et al. (2018) forecasted the effects of climate change on boreal caribou in Alberta using three general circulation models, focusing on changes in upland vegetation cover and wildfire that are expected to result in changes to nutritional resources and predation risk.

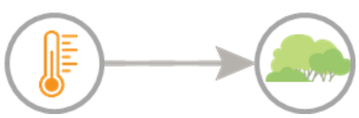
The following direct pathways are captured in the model to characterize the expected consequences of climate warming:

1. **Decreased lichen abundance**.



With warming temperatures, water tables in lowland boreal habitats are predicted to drop, drying out peatlands and increasing fire frequency (Camill & Clark, 2000; Heggberget et al., 2002; Kettridge et al., 2015). Fire strongly affects the frequency and distribution of terrestrial lichens (Coxson & Marsh, 2001; Lewis et al., 2019). Icing events, caused by more-frequent freeze-thaw cycles, can significantly reduce the lichen biomass accessible to caribou during the critical winter season (Mallory and Boyce 2018).

2. **Increased browse abundance**.



As conditions worsen for terrestrial lichens they generally improve for shrubs and herbaceous vegetation (Coxson & Marsh, 2001; Heggberget et al., 2002).

3. **Increased ungulate abundance**.

Mortality associated with severe (i.e., very cold and deep snow) winters, particularly among juveniles, is a key limiting factor in ungulate populations (e.g., Ballard et al., 1981; Bartmann et al., 1992; Singer et al., 1997; Garrott et al., 2003). Climate, particularly the severity of the winters, has been associated with range expansion of white-tailed deer in Alberta (Dawe, 2011; Fisher et al., 2020; Laurent et al., 2020). The northern expansion of white-tailed deer has also been documented in Ontario (MNR, 2009; Racey and Armstrong, 2000). This expansion has been facilitated by a combination of landscape change (i.e., habitat conversion resulting in higher suitability deer habitat) and climate change (MNR, 2009; Racey and Armstrong, 2000). Warmer temperatures are expected to reduce the frequency of severe winters and therefore increase over-winter survival of ungulates, leading to higher densities of primary prey species.

4. **Increased caribou disease prevalence**.

Warmer temperatures may make conditions more favourable for various disease vectors in caribou (Festa-Bianchet et al., 2011; Hoberg et al., 2008). and, anecdotally, prevalence among caribou in western Canada seems to be increasing.

5. **Increased fire prevalence**.

Fire ignition and growth are strongly dependent on weather conditions; consequently, a warming climate is expected to increase fire activity in the boreal forest. Models predict increases in fire occurrence of 75-140% by 2100 (Wotton et al., 2010). Evidence of increases in fire activity in the boreal forest is already evident (van Lierop et al., 2015).

6. **Increased insect pest eruptions**.

Forest insects and pathogens have a much larger footprint in forests than fire, although their effects are often less severe and sometimes even benign. However, all aspects of insect outbreak behaviour are expected to increase as the climate warms (Cichowski & Williston, 2005; Logan et al., 2003; Jactel et al., 2019). Climate warming is causing increases in severity of large infestations or outbreaks and range expansion in a number of insect pests such as those of the spruce budworm or mountain pine beetle causing tree mortality and reducing tree growth (Fuentealba et al., 2013). Expected temperature increases and changes in precipitation patterns may cause increased severity of spruce budworm outbreaks (Logan et al., 2003) and contribute to the ongoing expansion of the geographical range of mountain pine beetle north and east of its historical range within Canada; together, these could trigger epidemic infestations eastward through the boreal forest (Fuentealba et al., 2013; Nealis & Peter, 2008; Safranyik et al., 2010).

4.3 Habitat

In general, caribou survival is highest where use of productive upland habitats, which are selected by other ungulates and their predators, is limited (Anderson, 1999; Bradshaw et al., 1995; Thomas et al., 1996; Stuart-Smith et al., 1997; Schneider et al., 2000; McLoughlin et al., 2005; Tracz, 2005). As disturbance increases and habitats become more suitable for primary prey, spatial separation becomes more difficult to maintain (Courtois et al., 2007).

Behavioural responses to disturbance may further reduce available habitat for caribou (Dyer et al., 2001, 2002; Oberg 2001; Rettie & Messier 2001; Weclaw & Hudson, 2004; Leblond et al., 2011; Polfus et al., 2011; Moreau et al., 2012; Apps et al., 2013; CPAWS Wildlands League, 2013; Leblond et al., 2013; possibly increasing detection rates by predators (Smith, 2004; Beauchesne et al., 2014) or contracting caribou range (Vors, 2006).

Landscape disturbance directly affects the distribution and abundance of forage available to caribou and to other species important to the broader predator-prey system. As landscape disturbance increases, lichen resources generally decline while other forages generally (but not always; Neufeld et al., 2021) benefit, generally fragmenting areas of suitable habitat for caribou into smaller patches.

Nagy (2011) found a positive correlation between population growth rates and access to secure unburned habitat, particularly where most of the habitat was in patches greater than 500 km². Refuge from predation is critical for caribou, and larger patches of intact habitat reduce the likelihood that caribou will be found within the search radius of predators travelling linear features or hunting in nearby, suitable primary prey habitat. Some linear features (e.g., above-ground pipelines [ABMI and Alberta Innovates, 2012; Jalkotzy et al., 1997]; roads [[Dyer et al., 2002]) are also hypothesized to form a semipermeable barrier to the free movement of caribou between patches of suitable habitat (Dyer et al., 2001; Dyer et al. 2002). These effects contribute to an increase in overlap (and reduced spatial separation) between ungulates (moose, deer) and predators into caribou habitats (James et al., 2004; Latham et al., 2011b).

Where suitable habitat has been reduced and fragmented as a result of wildfire, caribou do not appreciably alter their distribution or range fidelity (Dunford, 2003; Culling and Culling, 2006; Silva, 2020), instead focusing their use on residual patches within the burns, remaining forest stands, bogs and fens (Dunford, 2003; Kansas et al., 2016, Skatter et al., 2017).

Habitat arrangement metrics, such as patch size distribution, patch isolation, barrier effects, etc., are all generally correlated with levels of disturbance within a range. The effect of habitat arrangement on caribou, independent of the overall level of disturbance in a range, has not been clearly demonstrated and is not addressed in this model.

4.3.1.1 Lichen

Terrestrial, and to a lesser extent, arboreal lichens comprise the majority of the winter diet of boreal caribou throughout Canada (e.g., Thomas et al., 1996; Arseneault et al., 1997; Newmaster et al., 2013; Thompson et al. 2015). Winter being a critical season for ungulates, an abundant supply of lichen forage is considered critical for caribou populations. As a result, in the model an increase in the abundance of lichen is expected to **directly increase caribou survival and recruitment**. This effect will not be significant where caribou populations are not limited by available lichen or other forage, but rather are limited by other factors (e.g., unsustainable predation).

4.3.1.2 Browse

"Browse" in the model refers primarily to boreal trees, shrubs, forbs and other plants that comprise the year-round forage of moose (e.g., Renecker and Hudson, 1988; Timmermann and McNichol, 1988; Routledge and Roese, 2004) and deer (e.g., Lefort et al., 2007).

The following direct pathways are captured in the model to characterize the expected consequences of more abundant browse:

1. **Increased caribou survival and recruitment.**

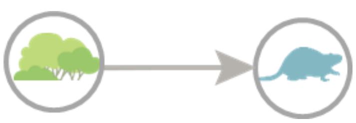
   While a diet dominated by lichens sustains caribou through the winter months, a high-quality diet in the summer is essential for the accumulation of fat and protein reserves necessary for overwinter survival and successful reproduction (e.g., Parker et al., 2009).

2. **Increased bear predation.**

   Black and grizzly bears make use of many of the same early seral forage species used by ungulates, and their populations can respond positively when the distribution and abundance of suitable forage increases (e.g., Brodeur et al., 2008).

3. **Increased beaver abundance.**

   As an abundant and generalist herbivore, beavers also appear to respond positively to more abundant, early seral forage (Potvin et al., 2005).

4. **Increased ungulate abundance.**

   Like caribou, other ungulates depend on high-quality and abundant forage resources available during the growing season to maximize their condition before entering the stressful winter and subsequent calving seasons (e.g., Parker et al., 2009). Conversion of older forests to early seral habitat or to agriculture areas through forest and land clearing has increased the abundance of deer, their reproductive success, and are sources for immigration of deer into caribou ranges (Charest, 2005; Dawe et al., 2014; Fisher and Burton, 2021). This increase in ungulate abundance can "spill over" into adjacent habitats where browse remains relatively unchanged (Latham, 2011b).

4.4 Population Dynamics

4.4.1 Predator-Prey

Predation has been identified as the largest source of mortality of caribou, limiting both adult female and calf survival (Apps et al., 2013; Bergerud & Elliot, 1986; Festa-Bianchet et al., 2011; Lewis et al., 2016; McLoughlin et al., 2003; Rettie & Messier, 1998; Seip, 1992; Wittmer et al., 2005). Increased predation is a combination of density ("numerical response") and per capita kill rates ("functional response"). Increased predation on caribou is hypothesized to result from increased ungulate abundance within and surrounding caribou range, which therefore increases predation on caribou via apparent competition (Serrouya et al., 2020). Increased moose density and the expansion of deer, particularly white-tailed deer, is thought to increase the density of predators (Latham et al., 2011b).

The dominant predator species are variable across Canada. Predation by wolves, black and grizzly bears and cougars is common in western Canada (Edmonds 1988; Stuart-Smith et al., 1997; Rettie and Messier 1998), whereas in eastern Canada where wolves have been extirpated, predation by coyotes and black bears is common (Frenette et al., 2020; Lewis et al., 2016; St. Laurent et al., 2020). Here we have focussed on the role of wolves and bears (both grizzly bears and black bears).

4.4.1.1 Wolves

1. **Decreased caribou survival and recruitment**.

Increased wolf densities within caribou range (Bergerud and Elliot, 1986; Frenette et al., 2020) is hypothesized to increase the incidental predation of caribou by wolves. Facilitated movement on linear disturbances (DeCesare, 2012; Dickie et al., 2017; Latham et al., 2011a) and increased encounter rates via increased spatial-overlap (DeMars & Boutin, 2017; Mumma et al., 2018; Whittington et al., 2011) are hypothesized to increase the per capita kill rate of caribou by wolves (McKenzie et al., 2012). The functional response of wolves is further tied to the numerical response, such that increased hunting efficiency can increase reproductive output (Serrouya et al., 2020).

4.4.1.2 Bears

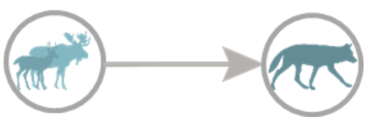
1. **Decreased caribou survival and recruitment**.

The role of bears in caribou mortality is variable across Canada. Black bear predation is common in eastern Canada (Dussault et al., 2012; Frenette et al., 2020; Lewis et al., 2016; St. Laurent et al., 2020). Grizzly bear predation on ungulate calves has been shown to be high in some systems (Brockman et al., 2017). In western Canada, black and grizzly bears do not appear to be significant predators of caribou adults or calves, but do depredate some calves (Gustine et al., 2006). Linear features are hypothesized to increase encounter rates between black bears and calves (DeMars & Boutin, 2017; Tigner et al., 2014).

4.4.1.3 Ungulates

The following direct pathways are captured in the model to characterize the expected consequences of increased ungulates:

1. **Increased wolf and bear predation.**



Increased primary prey density on the landscape results in increased predator density, and thus increased incidental predation on caribou - a process termed "apparent competition" (Holt, 1977; Peters et al., 2013). Other ungulates such as moose and deer make up a large component of wolf diet, especially in winter, thereby increasing wolf density (Frenette et al., 2020; Latham et al., 2011; Latham et al., 2013).

2. **Increase caribou disease prevalence**.

By increasing ungulate contact rates with caribou (Festa-Bianchet et al., 2011; Barber et al. 2018). Deer and moose are susceptible to a number of diseases, such as *Onchocera* spp., (Verocai et al., 2012; McFrederick et al., 2013), *Rumerfalaria andersoni* (Grunenwald et al., 2016), and many others that can transfer to caribou via direct or environmental contact (Tryland and Kutz, 2017). Winter tick infestations have been implicated in moose die-offs (Samuel, 2007). There is concern about disease transference from other ungulates (e.g., deer) as their populations increase and contact with caribou becomes more likely (Festa-Bianchet et al., 2011; B arber et al. 2018; MNRF, 2014).

4.4.1.4 Beavers

1. **Increase wolf and bear predation.**

Beavers can make up a large component of wolf diet, especially in summer, thereby increasing wolf density (Fuller and Keith, 1980; Gable et al., 2018; Latham et al., 2013). The role of beavers in bear diet is not well understood; black and grizzly bear diets are predominantly made up of plants, but animal protein is eaten opportunistically and can vary by season and reproductive status (Hatler et al., 2008; Nielsen et al., 2016). In some systems bears have been found to depredate beavers, though it is believed that bears are less significant beaver predators than wolves (Smith et al., 1994). While beavers have the potential to increase wolf and bear density, as well as increase predator use of caribou habitat while searching for beavers, this remains a knowledge gap in Canada's boreal forest.

4.4.2 Caribou Harvest

1. **Decreased caribou survival and recruitment**.

Harvest no longer occurs in many caribou ranges, either via hunter harvest mandates or voluntary moratoriums on hunting by Indigenous Peoples. However, the degree to which poaching and Indigenous harvest occurs is not well documented and likely varies across ranges.

4.4.3 Caribou Disease Prevalence

1. **Decreased caribou survival and recruitment.**

Caribou are susceptible to a number of diseases including parasites, bacterial infections, viruses, and prions (Tryland and Kutz, 2013). Chronic Wasting Disease is of particular concern (Arifin et al., 2020), though the susceptibility of caribou is not fully understood (Cheng et al., 2017). The majority of information on caribou disease prevalence comes from research related to domesticated and semi-domesticated reindeer populations, though research in North America is increasingly available (BCIP 2014, Finnegan et al., 2016).

4.4.4 Caribou Survival and Recruitment

Many caribou populations have low adult female survival and low calf recruitment despite high pregnancy rates (McLoughlin et al., 2003; St. Laurent et al., 2020; Pinard et al., 2012). The relationship between cumulative habitat disturbance and boreal woodland caribou population demography are well established (EC 2011, 2012; Johnson et al., 2020). Boreal caribou living in areas with higher densities of linear features and other human disturbances have reduced recruitment (EC, 2011), lower survival rates (Johnson et al., 2020), and overall lower population growth rates (Sorensen et al., 2008; Serrouya et al., 2020). Caribou survival and recruitment is a function of the pathways described above.

4.5 Knowledge Gaps

The model captures the major pathways leading from climate and habitat stressors to caribou decline; however, the relative strength of pathways is uncertain and varies among ranges. This has obvious management implications because recovery actions that target weak pathways are unlikely to generate significant benefits.

Research to date has largely focused on either single, direct pathways or effects (e.g., effect of fire on lichen, effect of wolf control on caribou survival and recruitment) or on indirect and multiple pathways (e.g., effect of composite measures of landscape disturbance on caribou demography). Some direct pathways have yet to be estimated (e.g., effect of browse on bear distribution and abundance in caribou range, role of beavers in driving predator populations and distribution, independent patch size effects). Furthermore, a large body of literature focuses on behavioral responses, but does not explicitly address how these changes in behaviour influence the abundances of primary prey, predators or caribou.

The following are priority knowledge gaps that are relevant to the design and implementation of restoration treatments:

1. The effect of linear development on browse abundance and subsequently on primary-prey abundance. Linear features are common but cover only a small portion of the landbase. The extent to which they are driving the numerical response of primary prey through habitat enhancement is unclear.

2. The degree to which linear development increases wolf and bear predation. While the link between linear developments and predator behaviour are well established, there is currently little

direct evidence linking increased selection for, and movement on, these features to predator density or kill rates of caribou.

3. The relative effects of 1 and 2, above - how linear development increases wolf abundance via prey-enrichment versus access-enhancement pathways (i.e., wolf numerical versus wolf functional responses). The relative strength of these pathways, as well as their interactive effects, informs the expected benefit of management actions to reduce ungulate browse versus blocking predator access.
4. The relative effect of habitat change versus climate change on primary prey abundance, and what the relevant retrospective and prospective timescales are. Restoration efforts to reduce primary prey populations via browse abundance may have limited effect if primary populations are expanding primarily due to the decreasing frequency of severe winters.
5. The relative effects of habitat patch size, habitat configuration and other landscape metrics independent of range-wide levels of habitat disturbance amount (total % area). While the relationship between range-wide disturbance metrics and elements of the caribou systems are relatively well-understood, the independent effects of spatial arrangement are not.
6. Role of terrestrial lichen transplants in lichen establishment. The literature indicates that terrestrial lichen fragment and mat transplants can be used to establish terrestrial lichen communities, however, it remains unclear which technique is best for restoring terrestrial lichen (Rapai & McMullin, 2017) and impact to caribou overall.
7. The spatio-temporal scale at which habitat restoration must occur to mitigate the effect of each stressor on caribou populations via each of the causal mechanisms identified. While this report highlights the current state of knowledge of each of the pathways or mechanisms, testing the efficacy of habitat restoration trials at scale to mitigate the effects identified remain in their infancy.

4.6 Intended Application

The Boreal Caribou Ecological Model is intended to inform planning and implementation of habitat restoration activities, either independently or in conjunction with other recovery actions. Given limited resources it is important to direct effort towards actions that are most likely to generate significant benefits to caribou survival and recruitment. While habitat disturbance is broadly correlated with caribou declines, the types of disturbances, and therefore the significance of their associated pathways, vary from range to range, suggesting that different mixes of recovery actions might be warranted.

For example, recent studies have concluded that anthropogenic disturbance is a more significant driver of caribou declines than fire (ECCC, 2020; Johnson et al., 2020). This suggests that treatments directed at restoring anthropogenic disturbance are likely to generate greater benefits to caribou than attempting to accelerate recovery from fire. But even within the anthropogenic disturbance footprint, restoration effort needs to be allocated between linear and polygonal disturbance and benefits to caribou are likely to vary depending on the particular mix of primary prey and predators and other circumstances characteristic of different ranges.

The model also identifies potentially confounding factors along pathways that could reduce the effectiveness, or the ability to measure the effectiveness, of habitat restoration. For example, actions to reduce primary prey and/or predators will confound the ability to measure the benefit to caribou of habitat restoration treatments focused on reducing browse or disrupting wolf movements. Similarly, climate change may limit the benefits of habitat restoration treatments if fire frequency and over-winter survival of ungulates increases. These possible confounders need to be acknowledged and tested to ensure informed decision-making regarding the allocation of recovery effort.

This work is intended to inform the design and implementation of restoration treatments by identifying the pathways to caribou decline that could/should be disrupted by treatments. The selection of treatments and their spatial deployment requires range-specific operational planning.

5 NEXT STEPS

1. Define metrics that can be used to assess the condition of each factor in the model.
2. Estimate the current condition of metrics within caribou range, where possible or through case studies.
3. Identify key relationships to be tested/monitored via adaptive management trials or modelling.
4. Link to range planning to frame restoration treatment selection, project planning and effectiveness monitoring.

6 APPENDIX A

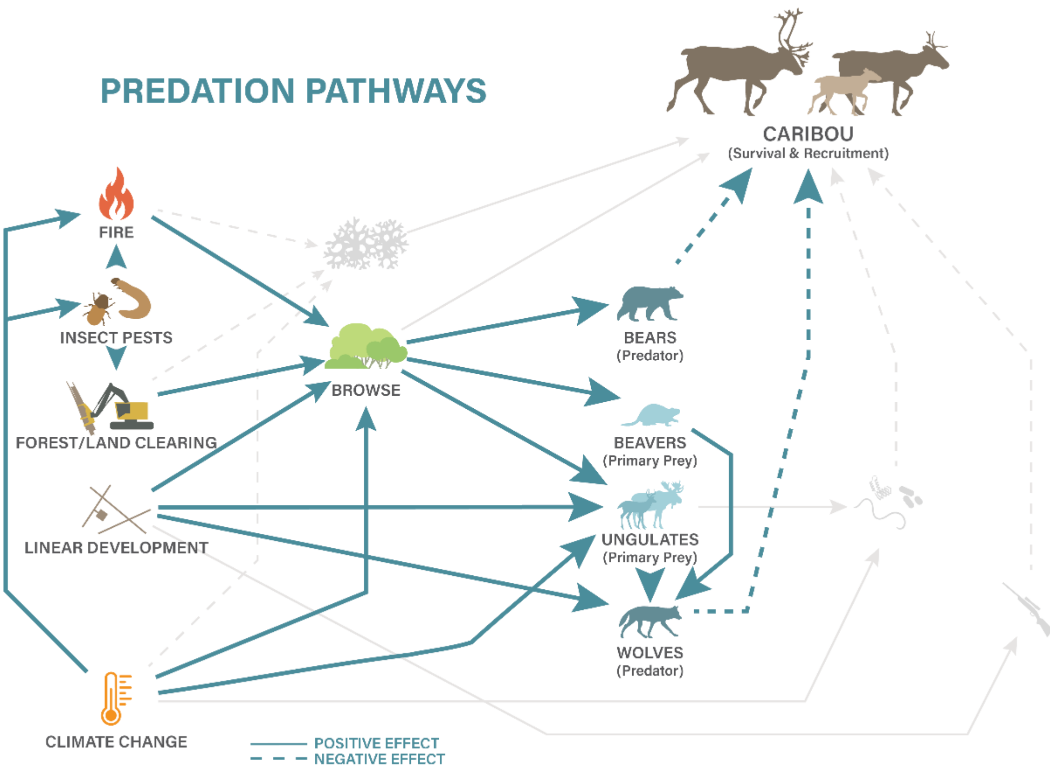


Figure A2: Highlighted 'predation pathways' in the Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group. Solid arrows represent positive effects and dashed arrows indicate negative effects.

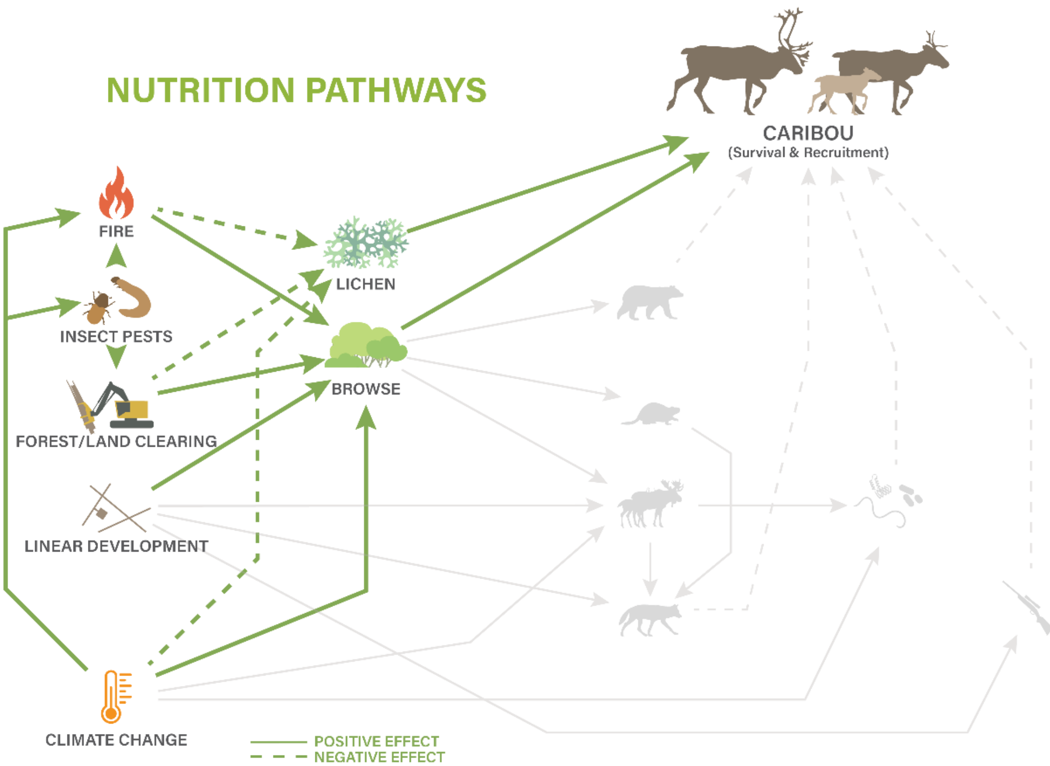


Figure A2: Highlighted 'nutrition pathways' in the Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group. Solid arrows represent positive effects and dashed arrows indicate negative effects.

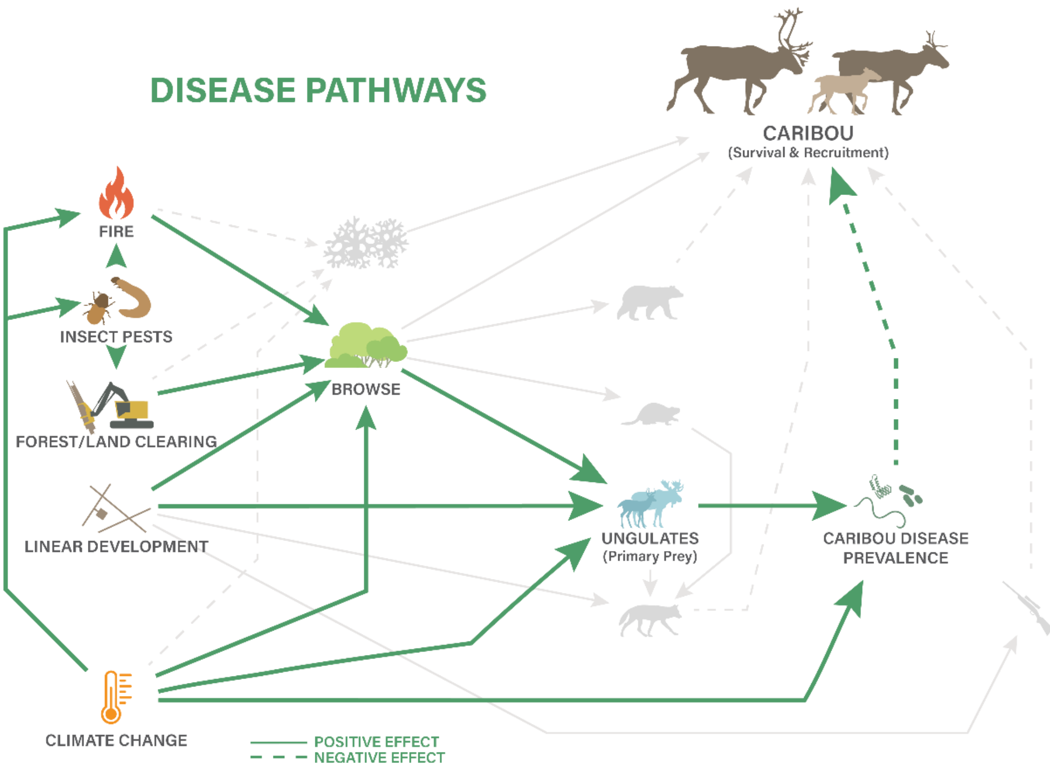


Figure A3: Highlighted 'disease pathways' in the Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group. Solid arrows represent positive effects and dashed arrows indicate negative effects.

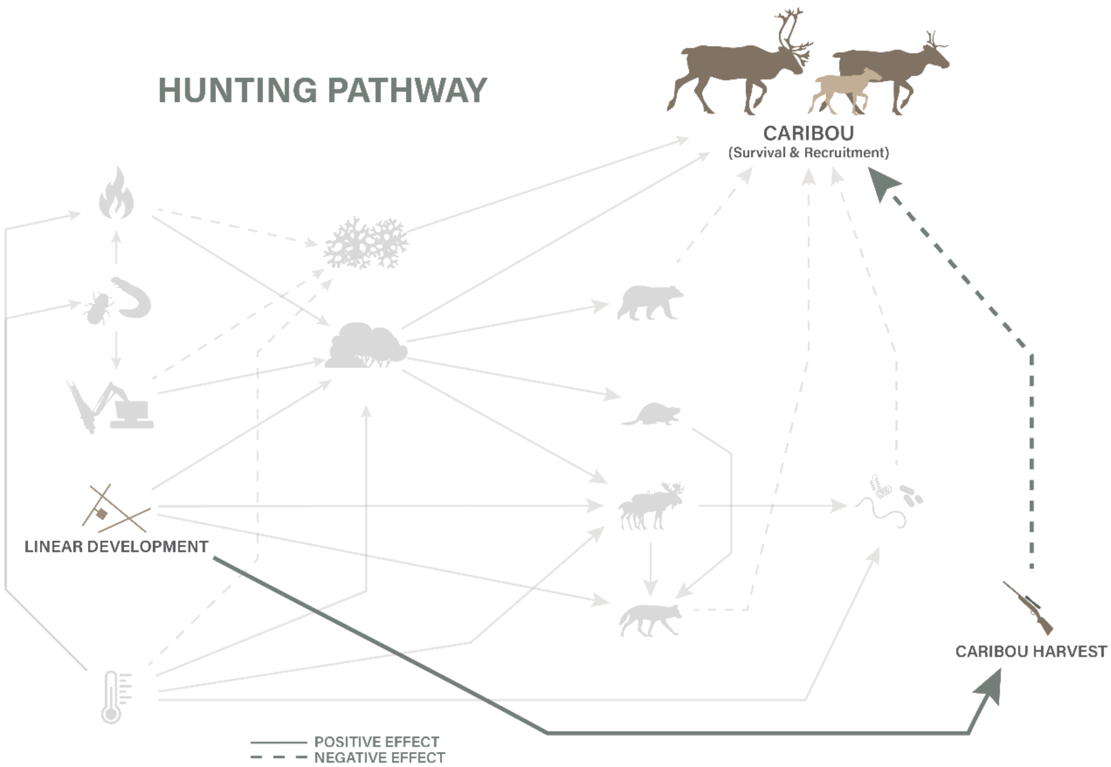
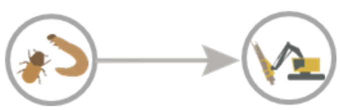
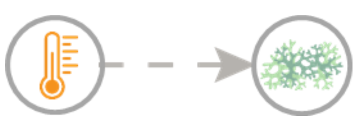
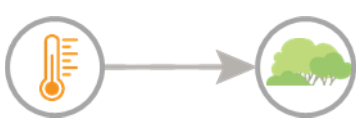


Figure A4: Highlighted 'hunting pathway' in the Boreal Caribou Ecological Model developed by the Habitat Restoration Working Group. Solid arrows represent positive effects and dashed arrows indicate negative effects.

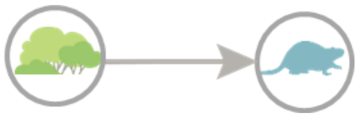
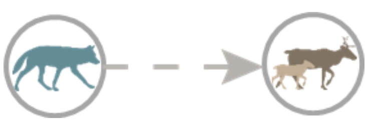
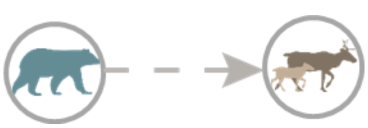
7 APPENDIX B

Table B1: References for pairwise model mechanisms.

4.1 LANDSCAPE DISTURBANCE		
4.1.1 FIRE		
	↑ FIRE = ↓ LICHEN ABUNDANCE	Coxson & Marsh, 2001 Russell, 2018
	↑ FIRE = ↑ LICHEN ABUNDANCE	COSEWIC, 2012 Coxson & Marsh, 2001 Heggberget et al., 2002 Nagy et al., 2005
4.1.2 INSECT PESTS		
	↑ INSECT PESTS = ↑ FOREST / LAND CLEARING	Chagnon et al., 2021 Cichowski & Williston, 2005 Labadie et al., 2021 Nobert et al., 2020
	↑ INSECT PESTS = ↑ FIRE PREVALENCE	Page and Jenkins, 2007 Perrakis et al., 2014 Wotton et al., 2009
4.1.3 FOREST ALTERATION / CLEARING		
	↑ FOREST ALTERATION / CLEARING = ↓ LICHEN ABUNDANCE	

	↑ FOREST ALTERATION / CLEARING = ↑ EARLY SERAL BROWSE ABUNDANCE	Dawe, 2011 Labadie et al. 2021
4.1.4 LINEAR DEVELOPMENT		
	↑ LINEAR DEVELOPMENT = ↑ BROWSE ABUNDANCE	Dawe et al., 2017 Finnegan et al., 2018b
	↑ LINEAR DEVELOPMENT = ↑ WOLF AND BEAR PREDATION	DeCesare et al., 2012 Dickie et al., 2017; Dickie et al., 2019; DeMars and Boutin, 2017 James, 1999; James & Stuart-Smith, 2000 Latham et al., 2011 Whittington et al., 2011
	↑ LINEAR DEVELOPMENT = ↑ HUMAN HARVEST	Edmonds 1988; James & Stuart-Smith, 2000 Leblond et al., 2007
4.2 CLIMATE CHANGE		
	↑ CLIMATE CHANGE = ↓ LICHEN ABUNDANCE	Camill & Clark, 2000 Coxson & Marsh, 2001 Heggberget et al., 2002 Kettridge et al., 2015 Lewis et al., 2019 Mallory and Boyce 2018
	↑ CLIMATE CHANGE = ↑ BROWSE ABUNDANCE	Coxson & Marsh, 2001 Heggberget et al., 2002

	↑ CLIMATE CHANGE = ↑ UNGULATE ABUNDANCE	Ballard et al., 1981 Bartmann et al., 1992 Dawe, 2011 Fisher et al., 2020 Laurent et al., 2020 MNR, 2009 Racey and Armstrong, 2000 Singer et al., 1997 Garrott et al., 2003
	↑ CLIMATE CHANGE = ↑ DISEASE PREVALENCE	Festa-Bianchet et al., 2011 Hoberg et al., 2008
	↑ CLIMATE CHANGE = ↑ FIRE PREVALENCE	van Lierop et al., 2015 Wotton et al., 2010
	↑ CLIMATE CHANGE = ↑ INSECT PEST ERRUPTIONS	Cichowski & Williston, 2005 Logan et al., 2003 Fuentealba et al., 2013 Jactel et al., 2019 Nealis & Peter, 2008 Safranyik et al., 2010
4.3 HABITAT		
	↑ LICHEN = ↑ CARIBOU SURVIVAL AND RECRUITMENT	Thomas et al., 1996 Arseneault et al., 1997 Newmaster et al., 2013 Thompson et al. 2015
	↑ BROWSE = ↑ CARIBOU SURVIVAL AND RECRUITMENT	Parker et al., 2009

	↑ BROWSE = ↑ BEAR PREDATION	Brodeur et al., 2008
	↑ BROWSE = ↑ BEAVER ABUNDANCE	Potvin et al., 2005
	↑ BROWSE = ↑ UNGULATE ABUNDANCE	Charest, 2005 Dawe et al., 2014 Fisher and Burton, 2021 Latham, 2011b Parker et al., 2009
4.4 POPULATION DYNAMICS		
4.4.1 PREDATOR-PREY		
	↑ WOLVES = ↓ CARIBOU SURVIVAL AND RECRUITMENT	Bergerud and Elliot, 1986 DeCesare, 2012 DeMars & Boutin, 2017 Dickie et al., 2017 Frenette et al., 2020 Latham et al., 2011a McKenzie et al., 2012 Mumma et al., 2018 Serrouya et al., 2020 Whittington et al., 2011
	↑ BEARS = ↓ CARIBOU SURVIVAL AND RECRUITMENT	Brockman et al., 2017 DeMars & Boutin, 2017 Dussault et al., 2012 Frenette et al., 2020 Lewis et al., 2016 Gustine et al., 2006 St. Laurent et al., 2020 Tigner et al., 2014

	↑ UNGULATES = ↑ WOLF AND BEAR PREDATION	Frenette et al., 2020 Holt, 1977 Latham et al., 2011 Latham et al., 2013 Peters et al., 2013
	↑ UNGULATES = ↑ CARIBOU DISEASE PREVALENCE	Barber et al. 2018 Festa-Bianchet et al., 2011 McFrederick et al., 2013 Tryland and Kutz, 2017 Tryland and Kutz, 2017 Verocai et al., 2012
	↑ BEAVERS = ↑ WOLF AND BEAR PREDATION	Fuller and Keith, 1980 Gable et al., 2018 Hatler et al., 2008 Latham et al., 2013 Nielsen et al., 2016 Smith et al., 1994
4.4.2 CARIBOU HARVEST		
	↑ CARIBOU HARVEST = ↓ CARIBOU SURVIVAL AND RECRUITMENT	
	↑ CARIBOU DISEASE PREVALENCE = ↓ CARIBOU SURVIVAL AND RECRUITMENT	BCIP 2014 Cheng et al., 2017 Finnegan et al., 2016 Tryland and Kutz, 2013

8 LITERATURE CITED

Air Pollution Information System (APIS). N.d. Acid deposition Montane habitats. Website: http://www.apis.ac.uk/node/933

Alberta Biodiversity Monitoring Institute (ABMI) and Alberta Innovates-Technology Futures. 2013. Assessing the influence of in situ industrial development on caribou (*Rangifer tarandus*) movement in the Lower Athabasca Planning Region of Alberta. 2012 Final Report. Prepared for the Ecological Monitoring Committee of the Lower Athabasca, 32 pp.

Alfaro, R. I., 1988. Pest damage in forestry and its assessment. Northwest Environmental Journal 4: 279-300.

Anderson, R.B. 1999. Peatland Habitat Use and Selection by Woodland Caribou (*Rangifer tarandus tarandus*) in Northern Alberta. Master of Science Thesis, University of Alberta. Edmonton, AB.

Apps, C.D., McLellan, B.N., Kinley, T.A., Serrouya, R., Seip, D.R., Wittmer, H.U., 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. J. Wildl. Manage. 77, 1409–1419.

Arifin, M.I., Staskevicius, A., Shim, S.Y., Huang, Y.H., Fenton, H., McLoughlin, P.D., Mitchell, G., Cullingham, C.I., Gilch, S., 2020. Large-scale prion protein genotyping in Canadian caribou populations and potential impact on chronic wasting disease susceptibility. Mol. Ecol. 29, 3830–3840. https://doi.org/10.1111/mec.15602

Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y., Deshaye, J., 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: An application of fire history and Landsat data. The Journal of Applied Ecology 34, 65–78. https://doi.org/10.2307/2404848

Ballard, W.B., Spraker, T.H., Taylor, K.P., 1981. Causes of neonatal moose calf mortality in south central Alaska. The Journal of Wildlife Management 45, 335–342. https://doi.org/10.2307/3807916

Barber, Q.E., Parisien, M.-A., Whitman, E., Stralberg, D., Johnson, C.J., St-Laurent, M.-H., DeLancey, E.R., Price, D.T., Arseneault, D., Wang, X., Flannigan, M.D., 2018. Potential impacts of climate change on the habitat of boreal woodland caribou. Ecosphere 9, e02472. https://doi.org/10.1002/ecs2.2472

Bartmann, R.M., White, G.C., Carpenter, L.H., 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 3–39.

Beauchesne D., J.A.G. Jaeger, and M.H. St- Laurent. 2014*. Thresholds in the capacity of boreal caribou to cope with cumulative disturbances: Evidence from space use patterns*. Biological Conservation 172: 190- 199.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566–1575.

Bergerud, A., and Elliot, J., 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64, 1515–1529.

Bowman, J., J.C. Ray, A.J. Magoun, D. Johnson and F.N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Canadian Journal of Zoology. 88:454-467.

Bradshaw, C.J.A. and D.M. Hebert. 1996. Woodland Caribou Population Decline in Alberta: Fact or Fiction? *Rangifer* Special Issue No. 9:223-234.

Brockman, C.J., Collins, W.B., Welker, J.M., Spalinger, D.E., Dale, B.W., 2017. Determining kill rates of ungulate calves by brown bears using neck-mounted cameras. Wildl. Soc. Bull. 41, 88–97. https://doi.org/10.1002/wsb.733

Brodeur, V., Ouellet, J.-P., Courtois, R., Fortin, D., 2008. Habitat selection by black bears in an intensively logged boreal forest. Can. J. Zool. 86, 1307–1316. https://doi.org/10.1139/Z08-118

Camill, P., Clark, J.S., 2000. Long-term perspectives on lagged ecosystem responses to climate change: permafrost in boreal peatlands and the grassland/woodland boundary. Ecosystems 3, 534–544. https://doi.org/10.1007/s100210000047

Carr, N.L., A.R. Rodgers, S.R. Kingston, and D.J. Lowman. 2011. Use of Island and mainland shorelines by woodland caribou during the nursery period in two northern Ontario parks. *Rangifer* 19:49 62.

Chagnon, C., M. Bouchard and D. Pothier. 2021. Impacts of spruce budworm outbreaks on the understory of boreal forest in eastern Canada: implications for woodland caribou. Submitted article.

Charest, K.S. 2005. Changes in moose and white-tailed deer abundance in northeastern Alberta and the relationship to cumulative impacts. M.Sc. Thesis, University of Alberta, Edmonton, Alberta.

Cheng, Y.C., Musiani, M., Cavedon, M., Gilch, S., 2017. High prevalence of prion protein genotype associated with resistance to chronic wasting disease in one Alberta woodland caribou population. Prion 11, 136–142. https://doi.org/10.1080/19336896.2017.1300741

Cichowski, D. and P. Williston. 2005. Mountain pine beetles and emerging issues in the management of woodland caribou in Westcentral British Columbia. *Rangifer* Special Issue No. 16.

COSEWIC, 2012. Woodland caribou (*Rangifer tarandus caribou*) COSEWIC assessment and status report. https://www.canada.ca/en/environment-climate-change/services/species -risk-public-registry/cosewic-assessments-status-reports/woodland-caribou.html

Courtois, R., J.P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience 14(4): 491 498.

Courtois, R., Gingras A., Fortin D., Sebbane A., Rochette B., Breton L. 2008. Demographic and behavioural response of woodland caribou to forest harvesting. Canadian Journal of Forest Research 38: 2837 2849.

Coxson, D.S., Marsh, J., 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Can. J. Bot. 79, 1449–1464. https://doi.org/10.1139/cjb-79-12-1449

CPAWS Wildlands League (Canadian Parks and Wilderness Society Wildlands League). 2013. Crossing Caribou Country: A special report assessing the impacts of new transmission line routes on threatened caribou in NW Ontario. Toronto, ON, 55 p. + 3 App.

Culling, D.E., and B. A. Culling. 2006. Ecology and Seasonal Habitat Selection of Boreal Caribou in the Snake-Sahtaneh Watershed, British Columbia 2000 to 2004. Technical Report. Prepared for: Canadian Forest Products Ltd., Fort Nelson, BC. Prepared by: Diversified Environmental Services, Fort St. John, BC. 80 pp.

Cumming, H.G. 1992. *Woodland Caribou: facts for forest managers*. Forestry Chronicle 68:481-492.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, *Odocoileus viginianus*, in the boreal forest of northern Alberta, Canada. Ph.D. thesis. University of Alberta, Edmonton, Alberta.

Dawe, K. L., E. M. Bayne, and S. Boutin. 2014. Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. Canadian Journal of Zoology 92: 353-363.

Dawe, C.A., Filicetti, A.T., Nielsen, S.E., 2017. Effects of linear disturbances and fire severity on velvet leaf blueberry abundance, vigor, and berry production in recently burned jack pine forests. Forests 8, 1–14. https://doi.org/10.3390/f8100398

DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K.G., Hervieux, D., Neufeld, L., 2012. Estimating ungulate recruitment and growth rates using age ratios. J. Wildl. Manage. 76, 144–153. https://doi.org/10.1002/jwmg.244

DeMars, C.A., Boutin, S., 2017. Nowhere to hide: Effects of linear features on predator-prey dynamics in a large mammal system. J. Anim. Ecol. 274–284. https://doi.org/10.1111/1365-2656.12760

DeMars, C.A., Breed, G.A., Potts, J.R., Boutin, S., 2016. Spatial patterning of prey at reproduction to reduce predation risk: what drives dispersion from groups? Am. Nat. 187, 678–687. https://doi.org/10.1086/685856

Denryter, K.A., Cook, R.C., Cook, J.G., Parker, K.L., 2017. Straight from the caribou's (*Rangifer tarandus*) mouth: detailed observations of tame caribou reveal new insights into summer–autumn diets. Can. J. Zool. 95, 81–94. https://doi.org/10.1139/cjz-2016-0114

Dickie, M., McNay, R.S., Sutherland, G.D., Cody, M., Avgar, T., 2019. Corridors or risk? Movement along, and the use of, linear features vary predictably among large mammal predator and prey species. J. Ecol. 1–32. https://doi.org/10.2307/2256210

Dickie, M., Serrouya, R., McNay, R.S., Boutin, S., 2017. Faster and farther: Wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. 53, 253–263. https://doi.org/10.1111/1365-2664.12732

Dickie, M., N. Love, R. Steenweg, C. Lamb, J. Polfus, A. Ford. 2020. The Effects of Linear Features on Woodland Caribou: A review to inform management thresholds. Technical Report prepared for the Technical Working Group of the Intergovernmental Partnership Agreement for the Conservation of the Central Group of the Southern Mountain Caribou.

Dunford, J.S. 2003. Woodland Caribou-Wildfire Relationships in Northern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta.

Dussault, C., Pinard, V., Ouellet, J.P., Courtois, R., Fortin, D., 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: Fitness rewarding or maladaptive behaviour? Proc. R. Soc. B Biol. Sci. 279, 4481–4488. https://doi.org/10.1098/rspb.2012.1700

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Can. J. Zool. 80, 839–845. https://doi.org/10.1139/z02-060

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. J. Wildl. Manage. 65, 531–542.

Dzus, E., 2001. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta. Edmonton, AB. https://doi.org/10.5962/bhl.title.115174

Edmonds, E.J. 1988. Population Status, Distribution and Movements of Woodland Caribou in West-Central Alberta. Canadian Journal of Zoology, 66:817-826.

Environment and Climate Change Canada (ECCC), 2020. Amended Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada. Species at Risk Act Recovery Strategy Series. Environment and Climate Change Canada, Ottawa. xiii + 143pp.

Environment and Climate Change Canada (ECCC), 2012. Boreal ecosystem anthropogenic disturbance vector data for Canada based on 2008 to 2010 Landsat imagery.

Environment Canada, 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada: 2011. Ottawa, Ontario, Canada, p. 102 pp plus appendices.

Faille G., Dussault C., Ouellet J.P., Fortin D., Courtois R., St Laurent M.H., Dussault C. 2010. Range fidelity: The missing link between caribou decline and habitat alteration? Biological Conservation 143(11): 2840 2850.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., Gunn, A., 2011. Conservation of caribou (*Rangifer tarandus*) in Canada : an uncertain future. Can. J. Zool. 89, 419–434. https://doi.org/10.1139/Z11-025

Finnegan, L.A., Macbeth, B., MacNearney, D., Pigeon, K., Larsen, T., Schwantje, H., Kutz, S.J., 2016. Caribou mortality and disease prevalence in west-central Alberta. Final Report. Hinton, AB.

Finnegan, L., Pigeon, K.E., Cranston, J., Hebblewhite, M., Musiani, M., Neufeld, L., Schmiegelow, F., Duval, J., Stenhouse, B., 2018a. Natural regeneration on seismic lines influences movement behaviour of wolves and grizzly bears. PLoS One 13. https://doi.org/e0195480

Finnegan, L., MacNearney, D., Pigeon, K.E., 2018b. Divergent patterns of understory forage growth after seismic line exploration: Implications for caribou habitat restoration. For. Ecol. Manage. 409, 634–652. https://doi.org/10.1016/j.foreco.2017.12.010

Fisher, J.T., Burton, A.C., 2018. Wildlife winners and losers in an oil sands landscape. Frontiers. 16, 323–328. https://doi.org/10.1002/fee.1807

Fisher, J.T., Burton, A.C. 20201. Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. Ecology and Evolution 11:900–11.

Fisher, J.T., Burton, A.C., Nolan, L., Roy, L., 2020. Influences of landscape change and winter severity on invasive ungulate persistence in the Nearctic boreal forest. Sci Rep 10, 8742. https://doi.org/10.1038/s41598-020-65385-3

Fortin, D., P. L. Buono, A. Fortin, N. Courbin, C.T. Gingras, P.R. Moorcroft, R. Courtois, and C. Dussault. 2013. Movement Responses of Caribou to Human induced Habitat Edges Lead to their Aggregation near Anthropogenic Features. The American Naturalist 181(6):827 836.

Frenette, J., Pelletier, F., St-Laurent, M.H., 2020. Linking habitat, predators and alternative prey to explain recruitment variations of an endangered caribou population. Glob. Ecol. Conserv. 22. https://doi.org/10.1016/j.gecco.2020.e00920

Fuentealba A, R. Alfaro and É. Bauce. 2013. Theoretical framework for assessment of risks posed to Canadian forests by invasive insect species. Forest Ecology and Management 302 (2013) 97–106. http://dx.doi.org/10.1016/j.foreco.2013.03.023

Fuller, T.K., Keith, L.B., 1980. Wolf Population Dynamics and Prey Relationships in Northeastern Alberta. J. Wildl. Manage. 44, 583–602.

Gable, T.D., Windels, S.K., Romanski, M.C., Rosell, F., 2018. The forgotten prey of an iconic predator: a review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp. Mamm. Rev. 48, 123–138. https://doi.org/10.1111/mam.12118

Garrott, R.A., Eberhardt, L.L., White, P.J., Rotella, J., 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Can. J. Zool. 81, 33–45.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., Heard, D.C., Gustine, D.D., Resources, N., Studies, E., British, N., 2006. Calf Survival of Woodland Caribou in a Multi-Predator Ecosystem Linked references are available on JSTOR for this article : Calf Survival of Woodland Caribou in a Multi-Predator Ecosystem Sobrevivencia de Crais de Caribu de Bosque en un Ecosistema con Depredadores Multiples 1–32.

Grunenwald, C.M., Carstensen, M., Hildebrand, E., Elam, J., Laaksonen, S., Oksanen, A., Gerhold, R.W., 2016. Epidemiology of the lymphatic-dwelling filarioid nematode *Rumenfilaria andersoni* in free-ranging moose (*Alces alces*) and other cervids of North America. Parasites and Vectors 9. https://doi.org/10.1186/s13071-016-1740-x

Hatler, D., 1972. Food habits of black bears in anterior Alaska. Can. F. Nat. 86, 17–31.Heggberget, T.M., Gaare, E., Ball, J.P., 2002. Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. Ran 22, 13–31. https://doi.org/10.7557/2.22.1.388

Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S., Boutin, S., 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Can. J. Zool. 91, 872–882.

Hoberg, E.P., Polley, L., Jenkins, E.J., Kutz, S.J. 2000. Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. Revue scientifique et technique (International Office of Epizootics) 27, 511–528.

Holt, D., 1977. Predation, apparent competition, and the structure of prey communities. Theor. Popul. Biol. 12, 197–229.

Jactel, H., Koricheva, J., Castagneyrol, B., 2019. Responses of forest insect pests to climate change: not so simple. Current Opinion in Insect Science 35, 103–108. https://doi.org/10.1016/j.cois.2019.07.010

Jalkotzy, M.G., P.I. Ross, and M.D. Nasserden. 1997. The effects of linear developments on wildlife: a review of selected scientific literature. Prep. For: Canadian Association of Petroleum Producers (CAPP). Prep. By: Arc Wildlife Services Ltd. Calgary, AB. 115 pp.

James, A., Boutin, S., Hebert, D., Rippin, A., 2004. Spatial separation of caribou from moose and its relation to predation by wolves. J. Wildl. Manage. 68, 799–809.

James, A., Stuart-Smith, A., 2000. Distribution of caribou and wolves in relation to linear corridors. J. Wildl. Manage. 64, 154–159.

James, A.R.C., 1999. Effects of Industrial Development on the Predator-Prey Relationship Between Wolves and Caribou in Northeastern Alberta. University of Alberta.

Johnson, C.A., Sutherland, G.D., Neave, E., Leblond, M., Kirby, P., Superbie, C., McLoughlin, P.D., 2020. Science to inform policy: Linking population dynamics to habitat for a threatened species in Canada. J. Appl. Ecol. 57, 1314–1327. https://doi.org/10.1111/1365-2664.13637

Johnson, C.J., Ehlers, L.P.W., Seip, D.R., 2015. Witnessing extinction - Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. Biol. Conserv. 186, 176–186. https://doi.org/10.1016/j.biocon.2015.03.012

Kansas, J., Vargas, J., Skatter, H.G., Balicki, B., and McCullum, K. 2016. Using Landsat imagery to backcast fire and post-fire residuals in the Boreal Shield of Saskatchewan: implications for woodland caribou management. Int. J. Wildland Fire, 25(5): 597–607. doi:10.1071/WF15170s.

Konkolics S. M. 2019. A burning question: The spatial response of woodland caribou to wildfire in northeastern Alberta. MSc Thesis, University of Alberta: Calgary, AB. 58 pp.

Kettridge, N., Turetsky, M.R., Sherwood, J.H., Thompson, D.K., Miller, C.A., Benscoter, B.W., Flannigan, M.D., Wotton, B.M., Waddington, J.M., 2015. Moderate drop in water table increases peatland vulnerability to post-fire regime shift. Sci Rep 5, 8063. https://doi.org/10.1038/srep08063

Labadie, G., P.D. McLoughlin, M. Hebblewhite and D. Fortin. 2021 Insect-mediated apparent competition between mammals in a boreal food web. Submitted article.

Latham, A., 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in Northeastern Alberta. University of Alberta.

Latham, A., Latham, M.C., Boyce, M.S., 2011a. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. Can. J. Zool. 89, 267–277. https://doi.org/10.1139/Z10-115

Latham, A., Latham, M.C., McCutchen, N.A., Boutin, S., 2011b. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. J. Wildl. Manage. 75, 204–212.

Latham, A.D.M., Latham, M.C., Knopff, K.H., Hebblewhite, M., Boutin, S., 2013. Wolves, white-tailed deer, and beaver: Implications of seasonal prey switching for woodland caribou declines. Ecography (Cop.). 36, 1276–1290. https://doi.org/10.1111/j.1600-0587.2013.00035.x

Leblond M., C. Dussault, J.P. Ouellet, M. Poulin, R. Courtois and J. Fortin, 2007. Electric fencing as a measure to reduce moose-vehicle collisions. Journal of Wildlife Manage. 71(5):1695-1703

Leblond M., Dussault C., Ouellet J.P. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. Journal of Zoology 289(1): 32 40.

Leblond, M., Frair J., D. Fortin, C. Dussault, J. P. Ouellet, and R. Courtois. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest dwelling caribou faced with intensive human activity. Landscape Ecology 26(10): 1433 1446.

Lee, P., Boutin, S., 2006. Persistence and developmental transition of wide seismic lines in the western Boreal Plains of Canada. J. Environ. Manage. 78, 240–250. https://doi.org/10.1016/j.jenvman.2005.03.016

Lefort, S., Tremblay, J.-P., Fournier, F., Potvin, F., Huot, J., 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range. Ecoscience 14, 109–116. https://doi.org/10.2980/1195-6860(2007)14[109:IOBFAW]2.0.CO;2

Lewis K.J., C. J. Johnson, and M. D. Nayeem Karim. 2019. Fire and lichen dynamics in the Taiga Shield of the Northwest Territories and implications for barren- ground caribou winter forage. Journal Veg Sci. 30:448–460.

Lewis, K.P., Gullage, S.E., Fifield, D.A., Jennings, D.H., Mahoney, S.P., 2016. Manipulations of black bear and coyote affect caribou calf survival. J. Wildl. Manage. 81, 122–132. https://doi.org/10.1002/jwmg.21174

Logan, J.A., Régnière, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1, 130–137. https://doi.org/10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2

Mallory, C.D., Boyce, M.S. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews 26, 13-25.

McFrederick, Q.S., Haselkorn, T.S., Verocai, G.G., Jaenike, J., 2013. Cryptic Onchocerca species infecting North American cervids, with implications for the evolutionary history of host associations in Onchocerca. Parasitology 140, 1201–1210. https://doi.org/10.1017/S0031182012001758

McKenzie, H., Merrill, E., Spiteri, R., Lewis, M., 2012. How linear features alter predator movement and the functional response. Interface Focus 2, 205–216.

McLoughlin, P., Dzus, E., Wynes, B., Boutin, S., 2003. Declines in populations of woodland caribou. J. Wildl. Manage. 67, 755–761.

McLoughlin, P.D., J.S. Dunford and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74:701-707.

McLoughlin, P. D., C. Superbie, K. Stewart, P. Tomchuk, B. Neufeld, D. Barks, T. Perry, Greuel, C. Regan, A. Truchon-Savard, S. Hart, J. Henkelman, and J. F. Johnstone. 2019. Population and habitat ecology of boreal caribou and their predators in the Saskatchewan Boreal Shield. Final Report. Department of Biology, University of Saskatchewan, Saskatoon. 238 pp.

MNR (Ministry of Natural Resources). 2009, Ontario's Woodland Caribou Conservation Plan. Queen's Printer for Ontario, Toronto, ON, Canada.

MNRF. 2014. Range management policy in support of woodland caribou conservation and recovery. Available at: https://www.ontario.ca/document/range management policy support woodland caribou conservation and recovery. Accessed November 2015.

Moreau, G., D. Fortin, S. Couturier and T. Duchesne. 2012. Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. Journal of Applied Ecology 49:611-620.

Mumma, M.A., Gillingham, M.P., Parker, K.L., Johnson, C.J., Watters, M., 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. Biol. Conserv. 228, 215–223. https://doi.org/10.1016/j.biocon.2018.09.015

Nagy, J.A., W. Wright, T. Slack, I. Ellsworth and M. Kienzler. 2005. Ecology of boreal woodland caribou in the Lower Mackenzie Valley, NT: work completed in the Inuvik Region April 2003 to November 2004. Dept Resources, Wildlife and Economic Development, Inuvik, NT. 54 pp.

Nagy J.A.S. 2011. Use of space by caribou in northern Canada. PhD Dissertation, University of Alberta, Edmonton, AB, 164 pp.

Nealis V.G., Peter, B., 2008. Risk Assessment of the Threat of Mountain Pine Beetle to Canada's Boreal and Eastern Pine Forests. Nat. Res. Canada, Can. For. Serv., Pac. For. Centre Inf. Rep. BC-X-417. 31pp.

Nellemann C., and R.D. Cameron. 1998. Cumulative impacts of an evolving oil field complex on the distribution of calving caribou. Canadian Journal of Zoology 76(8): 1425 1430.

Neufeld, B. T, C. Superbie, R. J. Greuel, T. Perry, P.A. tomchuk, D. Fortin and P.D. McLoughlin, 2021. Disturbance- Mediated Apparent Competition Decouples in a Northern Boreal Caribou Range. Journal of Wildlife Management 1–17; 2020; DOI: 10.1002/jwmg.21982

Newmaster, S.G., Thompson, I.D., Steeves, R.A.D., Rodgers, A.R., Fazekas, A.J., Maloles, J.R., McMullin, R.T., Fryxell, J.M., 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. Can. J. For. Res. 43, 897–900. https://doi.org/10.1139/cjfr-2013-0108

Nielsen, S.E., Larsen, T.A., Stenhouse, G.B., Coogan, S.C.P., 2017. Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. Oikos 126, 369–380. https://doi.org/10.1111/oik.03144

Nobert, B. R., T. A Larsen, K. E Pigeon and L. Finnegan, 2020. Caribou in the cross-fire? Considering terrestrial lichen forage in the face of mountain pine beetle (*Dendroctonus ponderosae*) expansion. PLoS ONE 15(4): e0232248. https://doi.org/10.1371/journal.pone.0232248

Oberg, P., 2001. Responses of Mountain caribou to linear features in a west central Alberta landscape. University of Alberta.

Page, W. and Jenkins, M. (2007). Predicted fire behavior in selected mountain pine beetle-infected lodgepole pine. Forest Science, 53(6): 662-674.

Parker, K.L., Barboza, P.S., Gillingham, M.P., 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23, 57–69. https://doi.org/10.1111/j.1365-2435.2009.01528.x

Perrakis, D.D.B., Lanoville, R.A., Taylor, S.W. et al. Modeling Wildfire Spread in Mountain Pine Beetle-Affected Forest Stands, British Columbia, Canada. fire ecol 10, 10–35 (2014). https://doi.org/10.4996/fireecology.1002010

Peters,W., M. Hebblewhite, N. Decesare, F. Cagnacci, and M. Musiani. 2013. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. Ecography 36(4): 487- 498.

Pinard V., Dussault C., Ouellet J.P., Fortin D., Courtois R. 2012. Calving rate, calf survival rate, and habitat selection of forest dwelling caribou in a highly managed landscape. Journal of Wildlife Management 76(1): 189 199.

Polfus, J.L., Hebblewhite, M., Heinemeyer, K., 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biol. Conserv. 144, 2637–2646.

Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. Can. J. For. Res. 35, 151–160.

Racey, G.G., and T. Armstrong. 2000. Woodland caribou range occupancy in northwestern Ontario: Past and present. Rangifer Special Issue 12: 173 184.

Rapai SB, McColl D, McMullin RT. 2017. Examining the role of terrestrial lichen transplants in restoring woodland caribou winter habitat. THE FORESTRY CHRONICLE. VOL. 93, No 3.

Renecker, L.A., Hudson, R.J., 1988. Seasonal quality of forages used by moose in the aspen-dominated boreal forest, central Alberta. Ecography 11, 111–118. https://doi.org/10.1111/j.1600-0587.1988.tb00788.x

Rettie, J.W. and F. Messier. 2001. Range Use and Movement Rates of Woodland Caribou in Saskatchewan. Can. J. Zool. 79:1933-1940.

Rettie, W.J., Messier, F., 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Can. J. Zool. 76, 251–259.

Routledge, R.G., Roese, J., 2004. Moose winter diet selection in central Ontario. Alces 40, 95–101.

Rughetti, M., Toïgo, C., Von Hardenberg, A., Rocchia, E., Festa-Bianchet, M., 2011. Effects of an exceptionally snowy winter on chamois survival. Acta Theriol. (Warsz). 56, 329–333. https://doi.org/10.1007/s13364-011-0040-2

Russell K. L. M. 2018. Close encounters of a burned kind: Spatiotemporal effects of fire on habitat selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter. MSc Thesis, University of Northern British Columbia: Prince George, BC. 135 p.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W., 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Canadian Entomologist 142, 415–442

Samuel, W.M., 2007. Factors affecting epizootics of winter ticks and mortality of moose. Alces 43, 39–48.

Schaefer, J.A., and S.P Mahoney. 2007. Effects of progressive clearcut logging on Newfoundland caribou. Journal of Wildlife Management 71(6): 1753 1757.

Schaefer, J. A., & Pruitt, W. O. (1991). Fire and woodland caribou in southeastern Manitoba. Wildlife Monographs, 116, 1–39.

Schneider, R.R., B. Wynes, S. Wasel, E. Dzus and M. Hiltz. 2000. Habitat Use by Caribou in Northern Alberta, Canada. Rangifer. 20(1):43-50.

Schwantje, H., Macbeth, B., Kutz, S.J., Elkin, B.T., 2014. British Columbia Boreal Caribou Health Program Year 2 Final Report. Victoria, BC.

Seip, D.R., 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Can. J. Zool. 70, 1494–1503.

Serrouya, R., Dickie, M., DeMars, C., Wittmann, M.J., Boutin, S., 2020. Predicting the effects of restoring linear features on woodland caribou populations. Ecol. Modell. 416. https://doi.org/10.1016/j.ecolmodel.2019.108891

Serrouya, R., Dickie, M., Lamb, C.T., van Oort, H., Kelly, A.P., DeMars, C., McLoughlin, P.D., Larter, N.C., Hervieux, D., Ford, A.T., Boutin, S., 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. Proc. R. Soc. B 288. https://doi.org/https://doi.org/10.1098/rspb.2020.2811

Silva J. A. 2020. Fire, lichens, and woodland caribou (*Rangifer tarandus caribou*) in Canada's Boreal Shield. MSC Thesis, University of Alberta: Calgary, AB. 107 pp.

Silva J.A., S. E. Nielsen, P. D. McLoughlin, A. R. Rodgers, C. Hague, S. Boutin. 2020. Comparison of pre-fire and post-fire space use reveals varied responses by woodland caribou (*Rangifer tarandus caribou*) in the Boreal Shield. Can. J. Zool. 98: 751–760.

Singer, F.J., Harting, A., Symonds, K.K., Coughenour, M.B., 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. The Journal of Wildlife Management 61, 12–25. https://doi.org/10.2307/3802410

Skatter H.G., M. L. Charlebois, S. Eftestøl, D. Tsegaye, J. E. Colman, J. L. Kansas, K. Flydal, and B. Balicki. 2017. Living in a burned landscape: woodland caribou (*Rangifer tarandus caribou*) use of postfire residual patches for calving in a high fire – low anthropogenic Boreal Shield ecozone. Can. J. Zool. 95: 975–984.

Smith, K.G. 2004. Woodland Caribou Demography and Persistence Relative to Landscape Change in West-central Alberta. M.Sc. Thesis, Department of Biological Sciences, University of Alberta, Edmonton, AB. 112 pp.

Smith, K.G., E.J. Ficht, D. Hobson, T.C. Sorensen and D. Hervieux. 2000. Winter Distribution of Woodland Caribou in Relation to Clear-cut Logging in West-central Alberta. Canadian Journal of Zoology, 78:1433-1440.

Smith, D.W., Trauba, D.R., Anderson, R.K., Peterson, R.O., 1994. Black bear predation on beavers on an island in Lake Superior. Am. Midl. Nat. 132, 248–255. https://doi.org/10.2307/2426580

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., Boutin, S., 2008. Determining Sustainable Levels of Cumulative Effects for Boreal Caribou. J. Wildl. Manage. 72, 900–905. https://doi.org/10.2193/2007-079

St. Laurent, M., Dickie, M., Becker, M., Serrouya, R., Boutin, S., 2020. Evaluating the mechanisms of landscape change on white-tailed deer populations. J. Wildl. Manage. 1–14. https://doi.org/10.1002/jwmg.21979

Stuart-Smith, A.K., C.J.A. Bradshaw, S. Boutin, D.M. Hebert and A.B. Rippin. 1997. Woodland Caribou Relative to Landscape Patterns in Northeastern Alberta. Journal of Wildlife management, 61:622-633.

Thomas, D.C., Edmonds, E.J., Brown, W.K., 1996. The diet of woodland caribou populations in west-central Alberta. Ran 16, 337–342. https://doi.org/10.7557/2.16.4.1275

Thompson, I.D., Wiebe, P.A., Mallon, E., Rodgers, A.R., Fryxell, J.M., Baker, J.A., Reid, D., 2015. Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario. Can. J. Zool. 93, 87–98. https://doi.org/10.1139/cjz-2014-0140

Tigner, J., Bayne, E.M., Boutin, S., 2014. Black bear use of seismic lines in Northern Canada. J. Wildl. Manage. 78, 282–292. https://doi.org/10.1002/jwmg.664

Timmermann, H.R., McNicol, J.G., 1988. Moose habitat needs. The Forestry Chronicle 64, 238–245. https://doi.org/10.5558/tfc64238-3

Tracz, B.V. 2005. Woodland caribou (*Rangifer tarandus caribou*) home range and habitat-use relationships to industrial activity in northeastern Alberta. M.Sc. Thesis, Department of Biological Sciences, University of Alberta, Edmonton, AB. 99 pp.

Tryland, M., Kutz, S., 2019. Reindeer and Caribou Health and Diseases. Taylor and Francis Group, Boca Raton, Florida.

van Lierop, P., Lindquist, E., Sathyapala, S., Franceschini, G., 2015. Global forest area disturbance from fire, insect pests, diseases and severe weather events. Forest Ecology and Management 352, 78–88. https://doi.org/10.1016/j.foreco.2015.06.010

Verocai, G.G., Lejeune, M., Beckmen, K.B., Kashivakura, C.K., Veitch, A.M., Popko, R.A., Fuentealba, C., Hoberg, E.P., Kutz, S.J., 2012. Defining parasite biodiversity at high latitudes of North America: New host and geographic records for *Onchocerca cervipedis* (Nematoda: *Onchocercidae*) in moose and caribou. Parasites and Vectors 5, 1. https://doi.org/10.1186/1756-3305-5-242

Vors, L.S. 2006. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. M.Sc. thesis, Trent University, Peterborough, Ontario, Canada. 146 pp.

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.., Patterson, B.., 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. J. Wildl. Manage. 71, 1249–1256. https://doi.org/10.2193/2006-263

Vors, L.S. and M.S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626-2633.

Weclaw, P. and R.J. Hudson. 2004. Simulation of Conservation and Management of Woodland Caribou. Ecological Modelling 177 (2004):75-94.

Weir, J.N, S.P. Mahoney, B. McLaren, and S.H. Ferguson. 2007. Effects of mine development on woodland caribou Rangifer tarandus distribution. Wildlife Biology 13(1): 66 74.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J., Musiani, M., 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. J. Appl. Ecol. 48, 1535–1542. https://doi.org/10.1111/j.1365-2664.2011.02043.x

Wittmer, H.U., Sinclair, A.R.E., Mclellan, B.N., 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144, 257–267. https://doi.org/10.1007/s00442-005-0055-y

Wotton, B.M., M.E. Alexander, and S.W. Taylor. 2009. Updates and revisions to the 1992 Canadian Forest Fire Behavior Prediction System. Information Report GLC-X-10, Natural Resources Canada, Great Lakes Forestry Centre, Sault Ste. Marie, Ontario, Canada

Wotton, B.M., Nock, C.A., Flannigan, M.D., 2010. Forest fire occurrence and climate change in Canada. Int. J. Wildland Fire 19, 253–271. https://doi.org/10.1071/WF09002