University of Alberta

Caribou in Canada: Ecology and Policy

by

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Abstract

Caribou (*Rangifer tarandus* L.) populations in Canada are threatened by climate change and anthropogenic landscape disturbance, which may negatively affect caribou energetics and range occupancy, with negative consequences for vital rates. Caribou are the basis of economy and spirituality for Northern Peoples and embody numerous non-use values, but industrial incursions into caribou range are largely unchecked. Hence, the goal of this thesis was to examine broad- and fine-scale drivers of caribou population change, as well as explore the efficacy of existing management and conservation of caribou in Canada.

I investigated mechanisms by which climate change and industrial disturbance influence caribou population change. Non-migratory caribou were negatively influenced by apparent competition with predators and alternate prey facilitated by industrial landscape change. Migratory caribou body condition and reproductive capacity were negatively influenced by climate-driven changes in plant and insect phenology. Arctic island-dwelling caribou were negatively affected by starvation associated with climate-driven rain-on-snow events. I explored how summer plant productivity and winter snow conditions influenced maternal condition, fetal weight, and antler weight in barren-ground caribou. Maternal body condition and fetal weight in March were positively influenced by previous summer's plant productivity, whereas winter snow conditions did not adequately explain variation in fetal size or maternal condition. Antler weight in male and female barren-ground caribou was positively influenced by the previous summer's plant productivity as well as by snow conditions. Finally, I compared Canada's Species-at-Risk legislation to the ecological needs of threatened boreal caribou. Old growth boreal forest was emphasized as essential for the species' persistence, but the Federal Recovery Strategy did not identify critical habitat spatially. Moreover, habitat protection was a provincial/territorial, rather than federal, responsibility and there was no legal obligation for the provinces to protect caribou habitat. While there exists little means by which to mitigate the effects of climate change on caribou, anthropogenic disturbance-related population declines can be managed by limiting industrial incursions into caribou range.

Key words: body condition, caribou, ecology, landscape disturbance, management, maternal effects, population dynamics, *Rangifer tarandus*, species-at-risk

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1.0 General Introduction

1.1 Caribou and the north

Caribou and reindeer (*Rangifer tarandus* L.) are widely distributed across the circumpolar north and make among the last remaining large-scale ungulate migrations in the northern hemisphere (Berger 2004). Three ecotypes, including tundra-dwelling, forest-dwelling, and mountain-dwelling, are represented by seven subspecies (barren-ground caribou [*R. t. groenlandicus*], Grant's caribou [*R. t. granti*], woodland caribou [*R. t. caribou*], Peary caribou [*R. t. pearyi*], wild and domestic reindeer [*R. t. tarandus*], Svalbard reindeer [*R. t. platyrhynchus*], and forest reindeer [*R. t. fennicus*]), all of which may be migratory or non-migratory (Cronin *et al*. 2005). Space is central to the species' persistence; caribou and reindeer of all subspecies require spatial separation from predators, other prey species, and human activities to carry out life processes including foraging, reproducing, and predator avoidance (Bergerud 1985, Rettie & Messier 2000, Vors *et al*. 2007, Nagy *et al*. 2011).

Caribou are an important prey species for a host a predators, including wolves (*Canis lupus*), coyotes (*C. latrans*), bears (*Ursus* spp.), lynx (*Lynx* spp.), cougars (*Puma concolor*), and eagles (*Aquila* spp. and *Haliaeetus* spp.) (Bergerud & Elliott 1986, Seip 1992, Gustine *et al*. 2006, Boisjoly *et al*. 2010). Caribou, in turn, play a role in nitrogen cycling on the tundra via grazing and defecation, thereby maintaining plant and invertebrate assemblages (Jeffries *et al*. 1994, Post & Klein 1996, Suominen & Olofsson 2000).

Caribou and reindeer are an inextricable component of northern economies and socio-cultural practices (Shehee *et al*. 2013, Wray & Parlee 2013), and may have been the first domesticated animal (Geist 2003). Caribou continue to be a primary source of protein and income for Northern Peoples across the circumpolar north via hunting and herding; indeed, permanent human settlement of the Arctic may have been impossible without caribou and reindeer as a predictable source of food and other resources (Jernsletten 2002, Baskin 2003, Geist 2003, Hummel & Ray 2008).

Hence, the importance of caribou and reindeer to Northern Peoples and ecosystems cannot be overstated. Despite this, caribou and reindeer populations are far from secure. Advancing industrial activity coupled with climate warming threatens the species' future (Hummel & Ray 2009, Sharma *et al*. 2009, Festa-Bianchet *et al*. 2011). Climate change threatens to upset the tenuous balance between seasonal energy uptake/expenditure and migratory *Rangifer* vital rates (Tews 2007, Post & Forchhammer 2008). Increased summer insect activity may decrease time spent feeding by caribou (Hughes *et al*. 2009, Witter *et al*. 2012), while advanced spring green-up deprives parturitient female caribou of protein-rich forage (Post & Forchhammer 2008). Deep and crusty winter snows also increase energy expenditure during locomotion and feeding (Tews 2007). Consequences of poor body condition in females include low birth mass (Adams 2005) and reduced physical growth of calves (Weladji & Holand 2006), failure of females to conceive (Cameron *et al*. 1993), and higher mortality in all age classes (Tveraa *et al*. 2007).

The vital rates of non-migratory woodland caribou are negatively affected by apparent competition caused by anthropogenic disturbance (Wittmer *et al*. 2007, Festa-Bianchet *et al*. 2011), whereby alternate prey species (e.g., moose [*Alces alces*] and deer [*Odocoileus* spp.]) numerically increase in caribou habitat altered by forestry, roads, and petroleum infrastructure (Courbin *et al.* 2009, Whittington *et al.* 2011, Latham *et al*. 2013). Predator populations respond numerically and increase mortality of caribou that, due to low reproductive capacity, are slow to recover (Bergerud 1971).

In Canada, woodland and southern mountain caribou are recognized as Threatened, while Peary caribou are designated as Endangered (COSEWIC 2004). Northern mountain and Dolphin-Union (*R. t. groenlandicus* x *peary*i) populations are designated as Special Concern (COSEWIC 2004). Only Newfoundland and barren-ground populations are "not at risk" but both of these populations have recently declined (Humber & Doucet 2008, Gunn *et al*. 2009). Caribou and reindeer populations have also declined in Alaska (Joly *et al*. 2011), Scandinavia (Tyler 2010) and Russia (Baskin 2005). Although caribou and reindeer populations typically undergo long-term population fluctuations (Gunn 2003), the synchronicity of these declines coupled with climate warming and rapidly advanced industrial activities in the north underscore the species' vulnerability. This situation is exacerbated by political reluctance to stem industrial development within caribou range, which would entail economic losses in the billions of dollars.

1.2 Objectives

The objective of this thesis was to assess population trends and drivers of population change for caribou and reindeer herds across their circumpolar range, while also examining specific interrelationships of seasonal range quality and caribou body condition – specifically, fetal mass, maternal fat and protein reserves, and antler mass. The former three have direct implications for caribou survival and reproduction, while the latter is a visual indicator of nutritional status. Finally, I compared Canada's existing Species-at-Risk policy for threatened woodland caribou with this subspecies' habitat needs, within the greater global context of ecological-economic trade-offs.

To accomplish these goals, I relied on an extensive database of caribou body condition and reproductive status measurements taken from the Beverly caribou herd in Nunavut/NWT by Don Thomas (Canadian Wildlife Service) between 1980 and 1987. I also drew upon a large suite of caribou and reindeer population databases shared by many researchers (listed in Acknowledgements section), publicly available climate data (e.g., the North Atlantic Oscillation index and the Normalized Difference Vegetation Index), and Environment Canada's "Recovery Strategy for Woodland Caribou, Boreal Population, in Canada" (Environment Canada 2012).

Chapters in this thesis, which total five including the General Introduction, are organized into independent manuscripts (i.e., paper format thesis). Chapter Two, Global Declines of Caribou and Reindeer, has been published. The format of each chapter, excluding specific University of Alberta guidelines, follows that of the journal *Ecology*. Below I provide a brief description of each chapter.

In Chapter Two, I assessed global population trends of all caribou and reindeer subspecies across the species range and elaborate the mechanisms by which climate warming and anthropogenic landscape change can influence this species' vital rates. In Chapters Three and Four I examined the influence of summer foraging conditions and winter snow conditions on maternal body condition, fetal mass, and antler mass in barren-ground caribou. In Chapter Five I explored the disjunction between woodland caribou ecology and Canadian Species-At-Risk legislation. Taken together, these chapters addressed the population ecology and conservation of caribou, both in Canada and globally. The goal of these manuscripts was expand and improve our understanding of the intricate interrelationships of caribou body condition, population change, climate factors and industrial landscape disturbance, and encourage policy makers to limit decisively and unequivocally further caribou habitat loss.

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2.0 Global declines of caribou and reindeer[1]

2.1 Introduction

The persistence of caribou and reindeer (*Rangifer tarandus*) is threatened by global change, namely climate warming and anthropogenic landscape disturbance. Within caribou and reindeer range, forestry, mineral extraction and petroleum infrastructure have fragmented *Rangifer* habitat (Cameron *et al*. 2005) and altered floral and faunal species composition (Vors *et al*. 2007, Vistnes & Nelleman 2008). Arctic surface air temperatures have warmed at twice the global rate (Fig. 2.1a; Anisimov *et al*. 2007), accompanied by spatially erratic increases in precipitation with higher frequencies of extreme weather events, e.g., freezing rain (Fig. 2.1b; Rinke & Dethloff 2008). The adaptive capacity of northern ecosystems is limited because their spatial extent is constrained by a northward-advancing treeline and a warming Arctic Ocean. Of 43 major herds that have been monitored during the last decade at least 34 are declining. (Fig. 2.2). Herds for which census data have been gathered have declined an average of 57% from historical population maxima. The global, synchronous declines of *Rangifer* simultaneously implicate significant change to regional limiting factors and call into question the species' resilience. While dramatic fluctuations, driven by forage availability and stochastic weather events, have characterized many *Rangifer*

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herds, fluctuations were historically inconsistent because of local variation in climate, predation, and human intervention (i.e., hunting, herding).

Rangifer forms the socioecological cornerstone of circumpolar indigenous cultures, from subsistence hunting of caribou by Aboriginal peoples in Canada, Greenland and Alaska, to reindeer husbandry by Sámi in Scandinavia and numerous herding cultures across Siberia. The species' annual treks to and from summer and winter ranges are the last remaining large-scale ungulate migrations in the northern hemisphere, long after other migratory ungulate populations, e.g., bison (*Bison bison*), saiga antelope (*Saiga tatarica*), were eradicated by human activities and habitat change (Berger 2004). Like the bygone hordes of passenger pigeons (*Ectopistes migratorius*) and cod (*Gadus morhua*), the abundance and broad distribution of *Rangifer* belies its vulnerability. Caribou and reindeer hover on the precipice of major decline because of changes in plant and insect phenologies, spatiotemporal changes in species overlap, and increased frequency and intensity of extreme weather events. Here, we demonstrate how these factors influence individual fitness and hence population change, operating directly through physiology (e.g., reproductive processes) and indirectly through changes in access to forage, timing of migration, competition and predator-prey interactions.

2.2 Methods and Results

I reviewed and synthesized literature on global change, caribou and reindeer, to describe the mechanisms by which climate change and anthropogenic landscape change influence *Rangifer* population dynamics. I gathered population data for 58 major caribou and reindeer herds from published literature, government databases, wildlife management boards, and directly from researchers to create Figure 2.2, and found that 34 were reported as declining, eight were increasing, and 16 had no data. I gathered 40 time series of population estimates for smaller herds within the major herd ranges. The time series spanned an average of 21.6 years, and population estimates were available for an average of 9.9 years. I compared the population trajectories of these herds, and found that 11 were in decline for <10 years, eight were in decline for 10–19 years, and six were in decline for >20 years. Mean % decline for these herds is 57% (SE = 0.27) from known population maxima.

2.3 Discussion

2.3.1 Phenology Changes

Phenology changes are diagnostic of climate warming (Stenseth *et al*. 2002). Typical of migratory ungulates, including wildebeest (*Connochaetes taurinus*; Berger 2004) and elk (*Cervus elaphus*; Boyce 1991), the population dynamics of *Rangifer* are closely cued to plant phenology. Parturition coincides with the flush of highly nutritious plant growth in spring (Post *et al*. 2003), and subsequent calf growth depends on high-quality forage to maximize body condition before winter (Post & Klein 1999, Weladji & Holand 2006). Lower rates of conception and over-winter calf survival result from failure of adults to regain sufficient body mass lost during the previous winter and of calves to maximize their physical growth rate, respectively (Reimers 1977, Cameron *et al*. 1993, Rönnegård *et al*. 2002). Evidence from caribou in Greenland emphasizes the link between reproductive success and climate warming. Progressively earlier onset of plant green-up accompanies warmer spring temperatures, but the timing of caribou parturition has not shifted to correspond with peak forage availability (Post & Forchhammer 2008). This 'trophic mismatch' diminishes both mother and calf's ability to exploit high-quality forage during a period of high energetic requirements (i.e., lactation, replenishing winter fat reserves, calf physical growth), taxing female body condition and consequently lowering calf production (Post & Forchhammer 2008).

Changes in insect phenology – earlier emergence and increased abundance – indirectly reduce summer forage availability by reducing the amount of time *Rangifer* can spend foraging undisturbed. Oestrid flies [i.e., warble flies (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*)] activity is strongly, positively correlated with ambient temperature (Hagemoen & Reimers 2002). Larvae of these insects are endoparasites of *Rangifer*, and heavy parasite loads are associated with poor body condition (Weladji *et al*. 2003). Mosquito (Culicidae) activity is also correlated positively with air temperature, and mosquito harassment is associated with poor body condition (Helle & Kojola 1994). Caribou or reindeer subjected to oestrid fly or mosquito harassment spend significantly less time foraging, and significantly more time exhibiting panic behaviours, such as running (Toupin *et al*. 1996, Hagemoen & Reimers 2002).

Wild reindeer (*R. t. tarandus*) in southern Norway do not compensate for increased insect harassment by increasing time spent grazing (Colman *et al*. 2003). *Rangifer* calves must exploit high-quality summer forage to grow sufficiently to achieve size sufficient to ensure survival through winter (Rönnegård *et al*. 2002). Females, burdened by lactation and demands of gestation, must regain sufficient body mass and fat to conceive the following autumn (Cameron *et al*. 1993, Rönnegård *et al*. 2002). Females must also obtain sufficient forage intake to support lactation, or calves will be weaned prematurely, with negative consequences for calf survival (Kofinas *et al*. 2002). Males must regain lost winter mass to ensure prime body condition for the autumn rut, their season of highest energetic demand (Reimers 1977). Hence, the summer plane of nutrition directly affects body condition entering winter, with consequences for fertility (Reimers 1977, Cameron *et al*. 1993, Colman *et al*. 2003), and insect harassment might be the most important mechanism linking warmer summer temperatures with poor body condition in *Rangifer*.

2.3.2 Spatiotemporal Changes in Species Overlap

Changes in species range overlap, characteristic of both climate warming and anthropogenic landscape change, threaten the persistence of non-migratory woodland caribou (*R. t. caribou*). Unlike migratory caribou and reindeer, woodland caribou do not undertake long, seasonal migrations, and exist in small, scattered groups in late seral stage coniferous forest and peatlands (Bergerud 1985). These habitats, naturally low in mammalian diversity, allow caribou to spatially separate themselves from other ungulates [e.g., moose (*Alces alces*), deer (*Odocoileus* spp.), elk] and the high predator populations that accompany these alternate prey species (Seip 1992, Vors *et al*. 2007, Wittmer *et al*. 2007). Anthropogenic landscape disturbance, particularly forest harvest and petroleum infrastructure, has converted large areas of woodland caribou habitat into early-seral-stage forest, attractive to moose and deer (Seip 1992, Schaefer *et al*. 1999, Vistnes & Nelleman 2008). Predator populations, especially wolves (*Canis lupus*), respond numerically to increased prey biomass, increasing predation pressure on caribou. Consequences of this shift in predator-prey dynamics are heavily depredated woodland caribou populations that are slow to recover, given their low reproductive potential and relative ease of capture, compared with larger prey like moose, as well as ongoing industrial development within caribou range. Indeed, many populations at the southern edge of woodland caribou range, where human disturbance of landscapes is greatest, are at immediate risk of extirpation (e.g., Southern Mountain herds, British Columbia, Wittmer *et al*. 2007; Little Smoky herd, Alberta, McLoughlin *et al*. 2003).

Climate change is implicated in northward species range shifts (Parmesan and Yohe 2003) and subsequent changes in the spatial and temporal associations of species interacting on different trophic levels (Harrington *et al*. 1999). While climate change is not yet definitively implicated in the range recession of woodland caribou in North America (Vors *et al*. 2007), it is implicated in the northward expansion of alternate prey species (e.g., white-tailed deer; Thompson *et al*. 1998). This deer frequently carries the meningeal brain worm

(*Parelaphostrongylus tenuis*). Although *P. tenuis* is harmless to deer, it is lethal to caribou. Consequently, reintroductions of caribou to areas where infected deer are present have invariably failed (e.g., Cape Breton; Dauphiné 1975). As a vector for this parasite, deer range expansion threatens to exclude caribou from vast areas of forest and, as industrial development and climate warming convert mature softwood stands to early seral stage mixed or hardwood stands within the boreal forest, the wolf-caribou-moose balance may shift in favour of wolves and moose.

Predation is not currently deemed a population regulating factor for large, migratory caribou herds (Manseau *et al*. 1996), because their distribution overlaps with that of predators only during certain seasons and/or alternate prey are typically absent (Messier *et al*. 1988). However, predation may negatively affect migratory caribou abundance when forage resources are not sufficient to maintain high caribou densities to swamp predators on calving grounds (Dale *et al*. 1994) and loss of lichen as a winter food resource is likely as the treeline advances northward (Cornelissen *et al*. 2001). Repercussions of climate warming for migratory caribou thus might include increased predation pressure. Migratory caribou and reindeer typically winter within the boreal forest and, as the frontier of the boreal forest shifts northward, spatial overlap between moose and caribou on winter range will increase, given that higher moose populations support higher wolf populations than would be present if caribou were the primary prey (Ballard *et al*. 1997), and significant predation mortality occurs on the winter range of *Rangifer* (Ballard *et al*. 1997, Kojola *et al*. 2004). Vulnerability to predation also may be amplified by escalating industrial development in the Arctic, which is associated with reduced *Rangifer* movement, poor body condition and low fecundity (Cameron *et al*. 2005).

2.3.3 Extreme Weather Events

Increased frequency and intensity of extreme weather events are hallmarks of climate change (Anisimov *et al*. 2007), and changes in the frequency of rare events typically increase the variability of vital rates (Boyce *et al*. 2006). For *Rangifer*, these stochastic events are significant, even principal driving factors of population dynamics (Forchhammer *et al*. 2002, Tews *et al*. 2007, Helle & Kojola 2008, but see Tyler 2012). The indirect, density-independent effects of extreme weather events are most significant during winter, where precipitation (deep snow and/or freezing rain) creates unpredictable access to forage. Freezing rain may effectively 'lock pastures' under an impenetrable layer of ice, inaccessible to grazing *Rangifer* (Aanes *et al*. 2002). Winter forage restriction affects multiple generations simultaneously. Extreme overwinter loss of body reserves is associated with high mortality in all age classes (Tveraa *et al*. 2003). Reductions in fetal growth and birth weight can result from poor maternal condition forced by hard-packed snow cover (Forchhammer *et al*. 2002). In turn, calf mass at birth, postnatal growth and development, and calf survival may be lower (Adams 2005, Tveraa *et al*. 2007). Females that fail to recover sufficient body fat reserves may fail to conceive the following autumn (Cameron *et al*. 1993). Together, these influences result in covariance of vital rates with substantial consequences to population size (Coulson *et al*. 2005).

The influence of winter climate on ungulate population dynamics generally increases with latitude (Aanes *et al*. 2002). The *Rangifer* subspecies most at risk from increased frequency and severity of extreme winter weather events are Peary caribou (*R. t. pearyi*) found on Canadian High Arctic Islands, and Svalbard reindeer (*R. t. platyrhynchus*), which inhabit the Svalbard archipelago, north of Norway. The unpredictability of extreme weather events may be key drivers of these insular *Rangifer* population dynamics, given their limited options for dispersal. Deep snow and freezing rain have been implicated in the catastrophic loss of Peary caribou populations from many Canadian High Arctic islands (Miller & Gunn 2003, Tews *et al*. 2007). Three successive winters (1995–1997) of unfavourable winter conditions resulted in mass starvation – a 98% decline of Peary caribou on the Western Queen Elizabeth Islands (Miller & Gunn 2003). Likewise, severe winters are linked to population declines of Svalbard reindeer, which are minimally hunted and exist in a predator-free environment. A severe winter in 1993–1994 instigated an 80% decline of the Brøggerhalvøya population of Svalbard reindeer (Solberg *et al*. 2001, Aanes *et al*. 2002). Although the negative impact of extreme winter weather events may be dampened for continental caribou and reindeer populations, given their greater mobility, 'locked pastures' are implicated in past declines of continental reindeer populations (Tveraa *et al*. 2007) and are likely to cause further declines across the circumpolar north, given the range and extent of predicted winter precipitation changes (Rinke & Dethloff 2008).

2.4 Conclusion

While global attention focuses on the increasing effects of climate change in Polar Regions, caribou and reindeer have not received the international attention of other northern fauna, such as polar bears (*Ursus maritimus*). *Rangifer*, however, is the cultural and socioeconomic cornerstone of northern people throughout the circumpolar north and, through herding and hunting, permitted these cultures to survive in a harsh and unpredictable environment. Northern indigenous caribou hunters note that changes in weather patterns, increased forest fire frequency and industrial development within caribou range have negatively affected caribou body condition and have altered movements from traditional routes (Parlee *et al*. 2005, Kendrick & Manseau 2008). General consensus among scientists is that climate change is altering phenologies, the spatiotemporal overlap of species, and increasing the frequency of extreme weather events (Stenseth *et al*. 2002, Parmesan & Yohe 2003), and that these changes are most profound at northern latitudes (Rinke & Dethloff 2008).

Negative impacts on caribou and reindeer populations are apparent already and likely will continue concurrent with climate change. Changes in plant and insect phenologies directly and indirectly interfere with *Rangifer*'s ability to forage. Reindeer and caribou may not adjust their timing of migration to coincide with the onset of spring green-up; consequences of this 'trophic mismatch' include lower calf production and high calf mortality because females and their offspring are unable to fully exploit high-quality forage (Post & Forchhammer

2008). Heightened insect harassment coincident with temperature and precipitation increases further prevent *Rangifer* populations from fully exploiting summer forage; the energetic cost of escaping from biting insects is high, diverts considerable time from foraging, and occurs when the nutritional requirements of *Rangifer* are high (Messier *et al*. 1988, Toupin *et al*. 1996, Hagemoen & Reimers 2002).

Spatiotemporal changes in species overlap may alter apparent competition and disease transmission. For woodland caribou, the delicate wolf-caribou-moose balance might further shift in favour of wolves and moose, while industrial development and climate warming converts mature softwood stands to early seral stage mixed or hardwood forest, further increasing predation pressure on already declining woodland caribou populations (Vors *et al*. 2007, Wittmer *et al*. 2007). Migratory caribou and reindeer may face increased predation pressure and interspecific competition as shrubs and forest displace tundra, and the ranges of southern ungulate species expand northward. Range overlap with other ungulate species likely will increase transmission of parasites and epizootic diseases to caribou.

Extreme weather events, characteristic of climate warming, already are implicated in the catastrophic population loss of Peary caribou from many of the Canadian High Arctic islands (Miller & Gunn 2003), declines of Svalbard reindeer (Solberg *et al*. 2001), and semi-domestic Scandinavian reindeer (Tveraa *et al*. 2007). Insular populations, or those restricted to small ranges, are most at risk. Even for continental populations with large ranges, winter forage restriction resulting from freezing rain may increase mortality of animals that, because of insect harassment and changes in plant phenology, were unable to build body condition sufficiently before the onset of winter. The cumulative effects of phenology changes, spatial and temporal changes in species overlap, and extreme weather events are thus significant threats to the long-term persistence of caribou and reindeer.

The importance of caribou and reindeer to northern ecosystems and cultures cannot be overstated. Their presence is vital to nutrient cycling, northern economy and spirituality. Arctic soils are nutrient-limited, but grazing and subsequent defecation by caribou and reindeer increase content and turnover rates of nutrients, especially nitrogen (N) (Jeffries *et al*. 1994, Post & Klein 1996, Olofsson *et al*. 2004). A positive feedback loop likely exists in this situation: caribou or reindeer release N into Arctic soils, increasing both soil N and N-uptake by vegetation. In turn, caribou and reindeer are more likely to reuse these N-rich grazing areas, perpetuating the process (Post & Klein 1996). In addition, reindeer grazing in northern Scandinavia has been shown to increase species richness of both plants and invertebrate assemblages (Suominen & Olofsson 2000).

Loss of caribou and reindeer will remove a significant source of meat and income for northern peoples. The annual harvest of the Beverly and Qamanirjuaq caribou herds in northern Canada is valued at US$17.5 million annually, for example (Beverly & Qamanirjuaq Caribou Management Board 2008). Reindeer husbandry in Finland accounts for approximately €35 million annually and is significant in maintaining the economy in Finland's north (Jernsletten 2002). Yet, individual reindeer herders' incomes are generally low and, consequently, the industry is highly vulnerable to the effects of climate change (Weladji & Holand 2006). Siberian reindeer herders' salaries are typically <US$800 per year; although this is significantly below minimum subsistence levels, it is a primary source of income for many indigenous Siberian peoples and is expected to decrease further if reindeer populations continue to decline and economic conditions do not favour reindeer-herding enterprises (Jernsletten 2002).

Apart from economic value, which can be measured directly, caribou and reindeer sustain many passive values, i.e., values that cannot be measured directly. These include education in traditional ways of life, kinship and bonding, recreational enjoyment of hunting caribou or reindeer, and existence of caribou and reindeer to bequest to future generations (Beverly & Qamanirjuaq Caribou Management Board 2008). The deep cultural reverence for *Rangifer* is echoed across the circumpolar north, from Siberian reindeer herds ['If the reindeer do not come, there will be no Eveny' (Vitebsky 2005)] to Alaskan caribou hunters ['Caribou are our life. Without caribou (the Gwich'-in People) wouldn't exist' (Bass 2004)].

Despite the importance of *Rangifer* to northern cultures and economy, the species' management typically has relied on 'half-way solutions;' actions that deal with the symptoms rather than the root cause of the problem (Frazer 1992). Woodland caribou management includes wolf culls, intended to reduce predation pressure. In this situation, increased predation pressure is the 'symptom' of habitat change. While caribou survival and recruitment increases when wolf culls are initiated (e.g., British Columbia, Bergerud & Elliott 1996; Alaska, Boertje *et al*. 1996), predator control is ineffective as a long-term solution. This is because removing all wolves from an area may facilitate the increase of other prey species besides caribou, ultimately allowing more wolves to immigrate into the system and perpetuating the need for culls (Bergerud 1996). Unlike large herds of migratory caribou and reindeer, which are primarily affected by climate change, the 'root cause' (i.e., habitat change) of non-migratory boreal forest caribou decline can be addressed directly by minimizing human landscape disturbance within the species' range (Vors *et al*. 2007). Yet Canada, which hosts the world's largest woodland caribou population, continues to rely on 'half-way' solutions and has not legislated habitat protection for its remaining boreal caribou herds.

Large fluctuations in population size characterize many caribou and reindeer populations (Klein 1991, Gunn 2003) and thus, short-term studies must be interpreted with caution when drawing conclusions about the role of climate change in the current, global population declines of *Rangifer*. Regardless, it is equally dangerous to assume that past population fluctuations will ensure future recovery, given that the predicted magnitude of temperature and precipitation changes in their northern habitats and the potential of these changes to irrevocably alter the factors driving *Rangifer* population dynamics. Caribou and reindeer have been an inextricable part of the North, the substance of mythology and survival for Northern Peoples for generations. Rate and severity of climate change, pace of industrial development in the North, as well as management actions by humans will determine the fate of these migrants.

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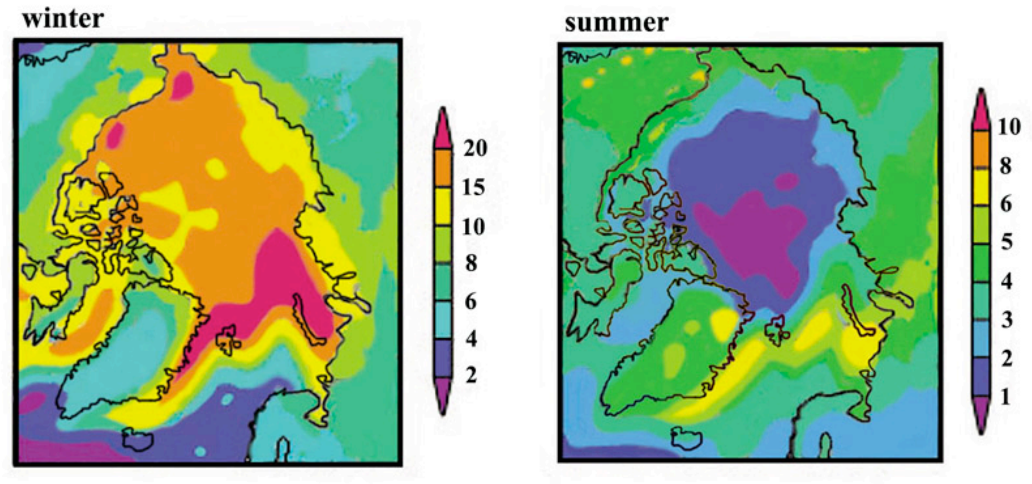

Figure 2.1a. Seasonal mean surface air temperature changes by 2099. Colours indicate differences between historical (1980–1999) and predicted (2080–2099) surface air temperatures (Rinke & Dethloff 2008).

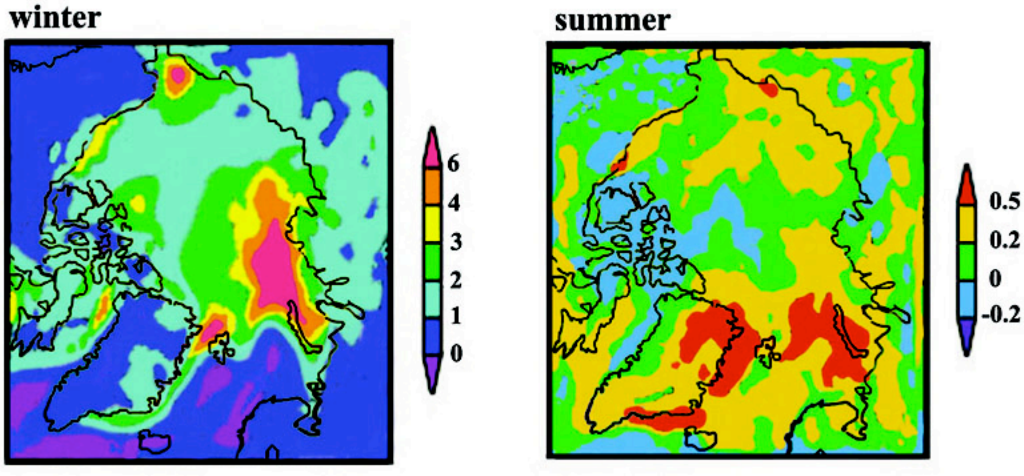

Figure 2.1b. Seasonal changes in precipitation by 2099. Colours indicate normalized changes; for example, a value of 2 indicates precipitation predicted for 2080–2099 will be twice that observed in 1980–1999 (Rinke & Dethloff 2008).

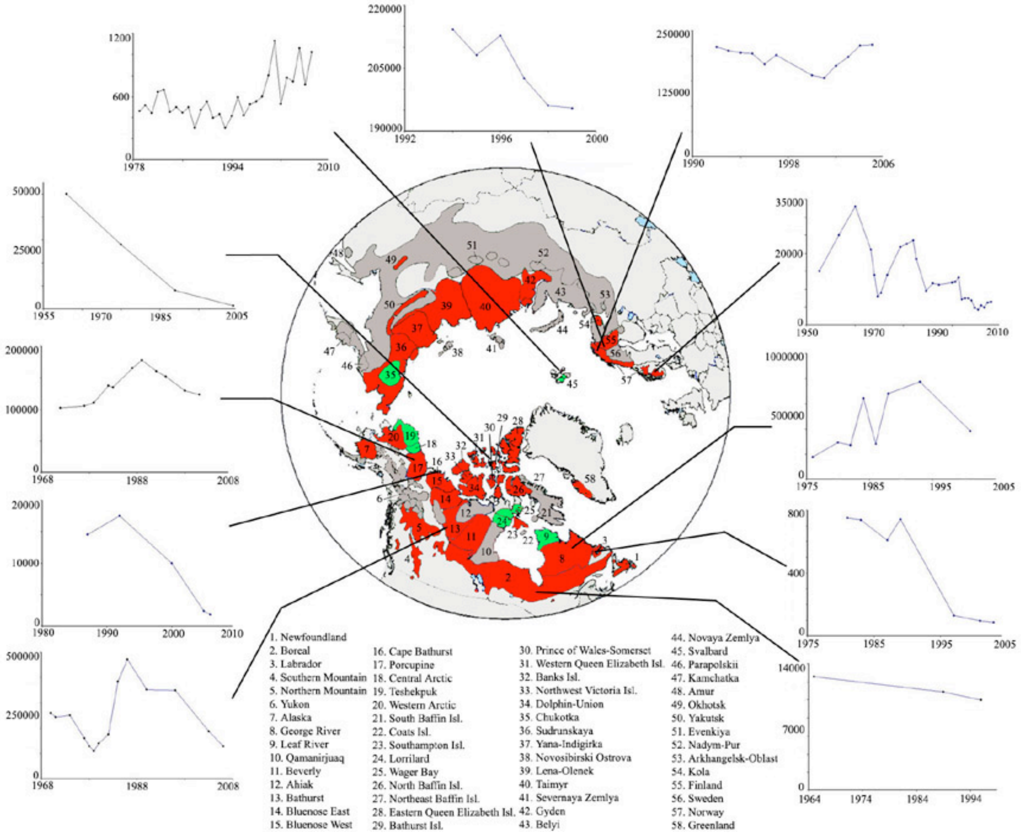

Figure 2.2. Population trajectories of 58 major caribou and reindeer herds worldwide. Herd ranges depicted in red are in population decline and ranges depicted in green are experiencing population growth. Population data are unavailable for herd ranges illustrated in grey. Time series of population estimates for 11 caribou and reindeer populations are included to illustrate historical fluctuations in population size. The *x*-axis represents year of population estimate and the *y*-axis represents estimate of population size.

3.0 Maternal and environmental effects on caribou fetus size

3.1 Introduction

In mammals, heterogeneity in individual fitness, defined as covariation in life history traits such as longevity and reproductive success (Hamel *et al*. 2009), is determined both by genetic factors (Hunt 2004) and by conditions experienced during fetal and neonatal development (Albon *et al*. 1987, Gaillard *et al*. 1993, Feder *et al*. 2008). In large mammals that are capital breeders (i.e., rely on body fat reserves to sustain a pregnancy; Stephens *et al*. 2009), maternal condition is a primary determinant of early development (Skogland 1984, Albon *et al*. 1987, Hamel *et al*. 2009). Mothers with abundant body fat reserves are better able to balance the energetic demands of pregnancy and lactation with those of body maintenance than their thinner counterparts (Cameron *et al*. 1993, Weladji *et al*. 2008, Hamel et al. 2010, Martin & Festa-Bianchet 2010). Environmental conditions experienced by the mother either pre-conception (e.g., Dauphiné & McClure 1974, Langvatn *et al*. 2004) or post-conception (e.g., Post & Stenseth 1999, Forchhammer *et al*. 2001) also influence fetal and neonatal growth, and these factors may have life-long consequences for the survival and reproductive success of offspring (Clutton-Brock *et al*. 1992, Feder *et al*. 2008).

Bottom-up influences can have significant effects on large herbivores on the tundra (Krebs *et al*. 2003); primary productivity on the tundra peaks in July and August because reduced photoperiod and cold temperatures limit photosynthetic activity before and after these months (Huemmrich *et al*. 2010).

Consequently, northern ungulates have a brief period during which to maximize fat gain before winter. Females must replenish body reserves lost to pregnancy and lactation (Langvatn *et al*. 2004, Tollefson *et al*. 2010) and achieve a minimum threshold of body fat to conceive during the upcoming rut (Cameron *et al*. 1993, Rönnegård *et al*. 2002). Inadequate nutrition before the breeding season can delay ovulation and lower female receptiveness (Tanaka *et al*. 2003, Langvatn *et al*. 2004), resulting in late-conceived fetuses that will have a shorter period to grow and gain body weight over summer prior to winter (Côté & Festa-Bianchet 2001, Dale *et al*. 2008). Plant productivity on summer range is therefore a crucial pre-conception factor that influences early development in northern ungulates.

Snow depth and hardness are important post-conception factors that can affect fetal development in northern ungulates (Forchhammer *et al*. 2001, Parker *et al*. 2009). Locomotion and foraging are energetically expensive in deep and hard snow (Fancy & White 1985, Saether & Heim 1993, Mysterud *et al*. 2008), and the metabolic costs of nourishing the growing fetus increase as winter progresses (Pekins *et al*. 1988). Maternal resources may be diverted from the developing fetus if the mother does not have sufficient body reserves to balance the energetic demands of gestation with maintenance of her own body tissues (Forchhammer *et al*. 2001). Small ungulate neonates, the product of slow fetal growth, experience high mortality during the first days following birth due to predation and adverse weather conditions (Adams *et al*. 1995) and may not gain sufficient weight to survive the following winter (Cook *et al*. 2004).

These pre- and post-conception factors may thus affect the survival and reproductive success of northern ungulates, because larger and heavier juveniles are better able to withstand harsh environmental conditions and have higher first-year survival (Loison *et al*. 1999, Côté & Festa-Bianchet 2001, Moyes *et al*. 2006) and reproduce earlier (Gaillard *et al*. 1997). The influence of pre- and post-conception environmental conditions, coupled with that of maternal effects, make it difficult to identify the primary determinant of fetal size.

Barren-ground caribou (*Rangifer tarandus groenlandicus*) are a model species with which to disentangle the effects of pre- and post-conception conditions (i.e., summer forage and winter snow depth/hardness) on fetal size. Barren-ground caribou migrate between spatially distinct seasonal ranges and there are strong maternal condition effects on fetal size (Skogland 1984, Reimers 2002, Rowell & Shipka 2009). Breeding and parturition are synchronized (Dauphiné & McClure 1974). Summer foraging conditions influence female body condition and, hence, timing of ovulation and conception (Skogland 1985, Cameron *et al*. 1993, Crête & Huot 1993, Adams & Dale 1998). Following rut, caribou migrate to their winter range south of tree line, where they forage for lichens (e.g., *Cladina* spp.). Barren-ground caribou are adapted to movement and foraging in snow (i.e., are "chionophiles;" Telfer & Kelsall 1984), but deep and/or crusty snow conditions are associated with poor body condition (Adams 2005, Kumpula & Colpaert 2003).

I investigated the effects of pre- and post-conception environmental factors on fetus size in the Beverly caribou herd (hereafter, BCH). I determined whether fetal mass in BCH varied over time, and developed a maternal body condition index from various body condition measurements from pregnant females using principal component analysis (PCA). I used this condition index as a response variable in a set of generalized linear mixed models (GLMMs) that I used to investigate the effects of primary productivity in late summer, represented by mean NDVI in August on the late summer range, when caribou are released from insect harassment and daily movements decrease, indicating time spent grazing (Nagy 2011), winter climate conditions (represented by the North Atlantic Oscillation index and snow depth on the winter range), maternal age, and fetus sex on caribou fetal weight in late March. Winter forage availability is assumed to be constant, based on Thomas & Kiliaan's (1998b) conclusion that caribou body condition – the same data used in this study – was unaffected by winter lichen availability between 1982 and 1987. I also built a set of GLMMs to investigate the effects of these environmental variables on maternal condition in March. I used Akaike Information Criterion (AIC) for model selection, and AIC weights and evidence ratios as weights of evidence that the top-ranked model best fit the data (Burnham & Anderson 2002), and I assessed model fit using Adjusted D-Squared (Guisan & Zimmerman 2000).

3.2 Methods

3.2.1 Study Area

The annual range of BCH includes much of Nunavut plus parts of northern Saskatchewan and the southeastern Northwest Territories in Canada (Fig. 3.1). The winter range is in the Taiga Shield Ecozone, stretching from Great Slave Lake in the Northwest Territories to Reindeer Lake in northeastern Saskatchewan. Dominant vegetation included black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and lichens (e.g., *Cladina* spp.). Winters are long and cold, with average temperature of -20˚ C. Precipitation is variable, but typically light, ranging from 250 – 500 mm annually. The summer range of BCH lies within the Southern Arctic Ecozone characterized by tundra shrubs, including dwarf birch (*Betula nana*) and willow (*Salix* spp.), and lichens. The summer is short and cool, with an average temperature of 10˚ C.

3.2.2 Data Collection

Fetal mass data were collected from BCH from 1982 to 1987. During this time, BCH increased from ~114,300 in 1980 to ~131,800 in 1984, and then declined to ~93,500 in 1987 coincident with declining pregnancy rates and calf recruitment, though wide confidence intervals around the population estimates indicate that population trajectory cannot be stated with certainty (Thomas & Kiliaan 1998a). Adult female caribou (n = 403) were collected in late March (mean collection date = March 19, range = March 16 – 24) from 1982 – 1987. For each individual caribou, whole body weight minus reproductive tract and rumen fill was obtained using a tripod and dial scale. Age was estimated from cementum annuli in the first incisor and first molar (Thomas & Kiliaan 1985). Kidneys and kidney fat were removed and weighed in a laboratory. Bone marrow was extracted from a 10 cm section of femur, weighed and dried to estimate water and fat content, following the methods of Nieland (1970). Fetuses were removed from the reproductive tract, weighed, measured and sexed. Collection methods are detailed in Thomas & Kiliaan (1998a).

3.2.3 Fetal sex ratio and trends in fetal mass

I tested for differences in fetal sex ratio among years using Chi-Square analysis. We also used analysis of variance (ANOVA) to determine whether average fetal weight differed among years, and regression to evaluate trend in fetal weight.

3.2.4 Maternal condition index

I used measurements of body fat (back fat depth in mm, kidney fat weight in g, and % femur marrow fat), and total body weight minus reproductive tract from 403 pregnant female barren-ground caribou ≥ 2 years old to develop an index of maternal condition. I used principal component analysis (PCA) to reduce these four variables into a single, dimensionless variable of maternal condition, and used this variable to represent maternal condition in subsequent analyses. I also examined the correlation between maternal age and body condition, because older females are often in better physical condition than younger females.

3.2.5 Model development

I used generalized linear mixed models (GLMMs) to investigate the variation in late March fetal mass as a function of late summer primary productivity, and winter climate. I pooled male and female fetuses because they respond similarly to variation in environmental conditions (Weladji & Holand 2003) and because the fetal sex ratio did not significantly differ from 1:1 during the study period, except in 1987 when the fetal sex ratio was skewed towards females. I used a remotely-sensed indicator of photosynthetic activity, the average Normalized Difference Vegetation Index (NDVI), in August for the years previous to the March collections (Fig. 3.2) on BCH's late summer range to represent primary productivity in this area. NDVI data were processed by the Global Inventory Monitoring and Modeling Systems (GIMMS) group from images captured by the Advanced Very High Resolution Radiometers (AVHRR) on NOAA satellites obtained from the NASA Land Long Term Data Record (http://ltdr.nascom.nasa.gov/cgi-bin/ltdr/ltdrPage.cgi). NDVI is widely used to quantify photosynthetic activity and to assess ecological responses to vegetation changes (Pettorelli *et al*. 2005a). BCH shows strong site fidelity to their late-summer range (Nagy 2011). Caribou are released from insect harassment in August and must maximize fat gain before rut. I overlaid a shapefile of BCH's late summer range on a grid of mean August NDVI values in northern Canada to obtain NDVI information specific to this area. I conducted this analysis in ArcMap (ESRI 2008).

I included broad- and fine-scale indicators of snow depth in our models. I used the January-March average of the North Atlantic Oscillation (NAO) index (Fig. 3.3), which describes opposing patterns of atmospheric pressure at northern latitudes (Hurrell *et al*. 2003), as a broad-scale index of snow and temperature conditions on BCH's winter range. Negative NAO values indicate low pressure over this region and, hence, warmer winters with more snowfall, whereas positive NAO values indicate high pressure and, consequently, colder and drier conditions. I obtained monthly NAO indices from the National Oceanic and Atmospheric Administration (NOAA; http://www.cpc.ncep.noaa.gov/products/precip/cwlink/pna/nao.shtml). Snow depth was measured on BCH's winter range during the study period to the nearest cm at 11 locations in areas of known caribou use between March 14 and 30 each winter (Fig. 3.4). Collection methods and sample locations are detailed in Thomas & Kiliaan (1998b).

I built a set of 13 candidate *a priori* models that portrayed plausible interrelationships of fetus weight, late summer NDVI, winter NAO, fetus sex, maternal age, and maternal condition. I included the latter two covariates because they are known to influence fetus mass. Male fetuses are typically heavier than female fetuses, while older or heavier mothers usually carry heavier fetuses (Skogland 1984, Reimers 2002). I also built a set of eight candidate models to investigate the response in maternal condition to variation in late March, late summer primary productivity, and winter conditions represented by the NAO and average snow depth on BCH's winter range. I included "Ordinal Date of Collection" and "Year" as random terms in both sets of models to account for fetal weight differences based on collection date and because individual caribou could not be regarded as full replicates with regard to environmental effects (Reimers *et al*. 2005). I conducted all statistical analyses with S-Plus (Insightful Corp., 2002).

3.2.6 Model selection

I evaluated support for the candidate models with Akaike Information Criterion (AIC), following the protocol of Burnham & Anderson (2002); the model with the lowest ΔAIC is deemed the best fitting. In addition, I calculated AIC weights (w_i), which estimate the likelihood of model *i* being correct, given the data, thus providing a way to compare the relative weight of evidence for each candidate model. I also calculated evidence ratios, which measure the evidence that a model is not the most parsimonious among the set of candidates; the larger the value, the stronger the evidence that model *i* is not the best approximating model (Crawley 2007). I assessed model fit using Adjusted D^2, which estimates the proportion of deviance explained by a model and is analogous to R^2, but takes into account the number of observations and number of parameters in a set of candidate models (Guisan & Zimmerman 2000).

Adjusted D^2 is defined as:

$$\frac{1-(n-1)}{(n-k)*\left(1-\frac{\mathit{null\ deviance}-\mathit{residual\ deviance}}{\mathit{null\ deviance}}\right)}$$

The value of Adjusted D^2 increases with an increasing number of observations (n) or a decreasing number of parameters (k).

3.3 Results

3.3.1 Maternal condition index

The first principal component captured 93 % of variation in maternal body condition and described fat reserves, and was not significantly correlated with maternal age ($R = 0.22$). Hence, I included maternal age as a covariate in the models.

3.3.2 Fetal sex and weight change among years

Fetal weight varied during the study period (Fig. 3.5), with the lightest fetuses ($\bar{x} = 1186 \pm 39.85$ g, $n = 58$) in 1982 and heaviest fetuses in 1987 ($\bar{x} = 1566 \pm 52.03$ g, $n = 28$). Analysis of variance indicated that average fetal weight varied significantly over time ($F_{5,397} = 13.73$, $p < 0.01$). Regression suggested a positive trend in fetal weight over the study ($t_4 = 3.24$, $p < 0.01$, $n = 403$). Fetal sex ratio only deviated significantly from 1:1 in 1987 when it was female-biased (Table 3.1).

3.3.3 Statistical modeling

Of the 13 candidate models describing fetal weight in late March, August NDVI, maternal condition, maternal age, and fetal sex were important predictors (Table 3.2). The w_i for this model indicated a 76 % probability that this was the best approximating model, and the Adjusted D^2 of 0.77 indicated a good fit of the model to the data. The other 12 models shared the remaining 23 % of support. Evidence ratios recapitulated these results; the model with the covariates representing August NDVI, maternal condition, maternal age, and fetal sex had the smallest evidence ratio. The evidence ratios for the remaining models were at > 3 times larger than the evidence ratio for the most parsimonious model, which indicate a strong weight of evidence that the remaining models do not adequately approximate the data.

August NDVI of the previous year was an important predictor of maternal condition in late March (Table 3.3). The w_i for this model indicated a 73 % probability that this model best approximated the data. model fit, an Adjusted D^2 of 0.61, for this model indicated a moderate proportion of deviance explained by the data. The remaining seven models share the remaining 27 % of support. Evidence ratios also indicate that August NDVI was the most parsimonious model for maternal condition in late March. There is a strong weight of evidence that the remaining models do not approximate the data, as their evidence ratios were > 3 times larger than the evidence ratio for the most parsimonious model.

3.4 Discussion

Plant productivity on BCH's late summer range positively influenced barren-ground caribou fetal weight and maternal body condition in late March. In addition, maternal condition, maternal age (i.e., older females were in better condition and had heavier fetuses), and fetal sex (i.e., males heavier than females) were positively correlated with fetal mass, consistent with patterns in other caribou and reindeer populations (e.g., Rönnegård *et al*. 2002, Couturier *et al*. 2009). Average fetal weight increased during the study period, concurrent with increasing primary productivity on BCH's late summer range, and suggested that larger fetuses were further along in gestation (Ringberg & Aakvaag 1982). These results suggest that primary productivity on BCH's late summer range provided females with sufficient nutrition to breed earlier in the rut and, consequently, maximized time for fetal growth before sampling in March.

The late summer foraging period for barren-ground caribou is bounded by seasons of high energetic expenditure and diminished photosynthetic activity. Early to mid-summer (i.e., late June and July) is characterized by harassment by parasitic (e.g., warble flies [*Hypoderma tarandi*] and nose bot flies [*Cephenemyia trompe*]) and biting (e.g., mosquitoes [Culicidae] insects (Weladji *et al*. 2003). This harassment increases energetically expensive behaviours such as running and reduces time spent feeding, often resulting in a negative energy balance (Toupin *et al*. 1996, Colman *et al*. 2003, Hughes *et al*. 2009). Colder temperatures and reduced photoperiod in autumn trigger vegetation senescence (Huemmrich *et al*. 2010), and this senesced vegetation is of lower nutritional value to caribou (Parker *et al*. 2005). In addition, ruminants digest less forage on a daily basis as forage quality declines and, hence, small differences in forage nutrient content can significantly influence body condition (Robbins 1983, White 1983, Hobbs 2003, Cook *et al*. 2004). These factors underscore the importance of the late summer range as a time and place for caribou to recover fat and lean tissue catabolized the previous winter, and as the last opportunity for rapid growth of juveniles and subadults, undisturbed by insects.

Poor body condition is correlated with unfavourable (i.e., deep and crusty) snow for many ungulate species (Mysterud *et al*. 2008), because these snow conditions require considerable energy to move through and forage in (Fancy & White 1995) and, consequently, may depress fetal size via increased maternal energy expenditure (Forchhammer *et al*. 2001). However, maternal condition in March was best explained by late summer range primary productivity, which suggests that winter snow conditions did not impact maternal condition sufficiently to influence fetal growth negatively. I also found that the addition of the NAO index or average snow depth on the winter range to the top-ranked models did not appreciably improve model fit: AIC weights suggested little support for any model that included the NAO or average snow depth.

The NAO is a broad-scale index and possibly did not adequately represent local snow conditions in feeding areas and movement corridors important to

BCH. Indeed, linking large-scale climate variables to population dynamics can be problematic because of heterogeneity in environmental variables and the difficulty in testing long-term predictions (Krebs & Berteaux 2006). Average snow condition depth on the winter range similarly did not improve model fit. The snow depth data did not represent all snow conditions encountered by BCH during the winter because snow depth sampling locations were determined subjectively (Thomas & Kiliaan 1998b). Indeed, snow depths are wind-dependent and, consequently, are highly variable within the forest-tundra transition, with significant drifting in open areas and the greatest snow accumulation around and under trees (Timoney *et al*. 1992, Auger & Payette 2010).

Conversely, these snow and climate data may not have improved model fit because barren-ground caribou mitigate harsh winter snow conditions via habitat selection. Winter snow conditions are well documented to negatively influence fetal growth and adult body condition in caribou, especially for insular populations (Adamczewski *et al*. 1987, Miller & Barry 2009) and reindeer populations on fenced winter ranges (Tveraa *et al*. 2003). I do not disagree that winter conditions may negatively impact adult body condition and fetal mass, but continental, free-ranging caribou, like BCH, move to areas where local snow conditions (i.e., shallower) facilitate ease of feeding and locomotion (Messier *et al*. 1988, Ion & Kershaw 1989, Johnson *et al*. 2001). BCH spent each winter during the study in a different part of their winter range, and these areas were frequently hundreds of kilometers from the previous winter's locus of activity (Thomas & Kiliaan 1998b).

The relationship between late summer range primary productivity, maternal condition and fetal weight emphasizes the importance of summer range conditions for caribou population dynamics, given the importance of size and nutritional condition for survival and reproductive success in northern ungulates (Saether & Heim 1993, Loison *et al*. 1999, Côté & Festa-Bianchet 2001, Moyes *et al*. 2006). In addition, late summer primary productivity best explained body condition of female caribou in March; this also attests to the influence of summer nutrition on winter body condition and supports the assertion that winter body condition is a function of body condition in autumn (Dale *et al*. 2008, Cook 2011). However, caribou population dynamics are governed by multiple factors (e.g., stochastic weather events, predation, forage availability) that undoubtedly interact and may shift in relative importance through time (Vors & Boyce 2009). Although BCH demonstrates strong site fidelity to its late summer range (Nagy *et al*., *in press*), I cannot assert that productivity on late summer range will always be the most important determinant of barren-ground caribou fetal size or maternal condition.

An additional caveat is that fetal size in late March may not always be indicative of size at birth. The fetuses in our study were collected at the end of the second trimester, and the greatest amount of fetal growth occurs in the subsequent third trimester (Dauphiné & McClure 1974). The third trimester is the most energetically taxing for the mother (Chan-McLeod *et al*. 1999) and, although my analysis indicates strong influence of summer productivity on fetal weight, nutrition and snow conditions in April and May also influence perinatal size and viability (Adams 2005).

The industrial footprint (e.g., mines, road construction) is growing in the Arctic (Young 2011), and climate warming is increasing arctic primary production (Jia *et al*. 2009). Warmer summers with higher plant productivity may improve caribou body condition (Pettorelli *et al*. 2005b, Couturier *et al*. 2009, but see Post & Forchhammer 2008), but these nutritional benefits may be counteracted by industrial activity. Encounters with industrial disturbance can increase energetic expenditures (Bradshaw *et al*. 1998), disrupt timing of migration, and lead to diminished range use or abandonment of areas surrounding industrial development (Vistnes & Nelleman 2008). In addition, compensatory growth of small caribou calves may not occur if summer foraging conditions are poor (Dale *et al*. 2008). Migratory caribou habitat must therefore be managed to conserve the areas that provide the greatest summer nutrient gain (Parker *et al*. 2009).

3.5 Conclusion

Heterogeneity in individual fitness ultimately has multiple origins, including environmental effects experienced by the fetus during gestation. Primary productivity on the late summer range positively influences size, and thus individual quality, of barren-ground caribou fetuses as well as maternal condition in late March. The relative importance of late summer range versus other seasonal environmental effects, such as snow conditions, may shift through time, but the fidelity of barren-ground caribou herds to their late summer ranges emphasizes the need to conserve these areas in the face of increasing industrial development in the Arctic.

3.6 References

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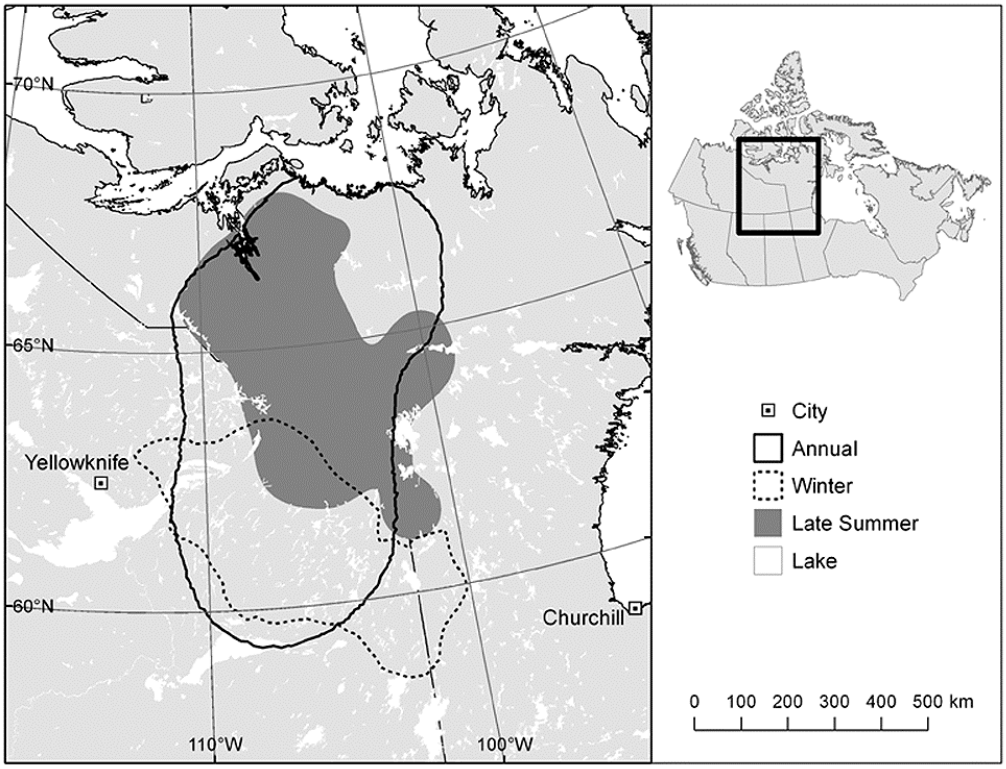

Figure 3.1. The annual range of the Beverly caribou herd in Nunavut, Northwest Territories, and Saskatchewan. The late summer range is depicted in dark grey and the winter range is designated by a dotted line.

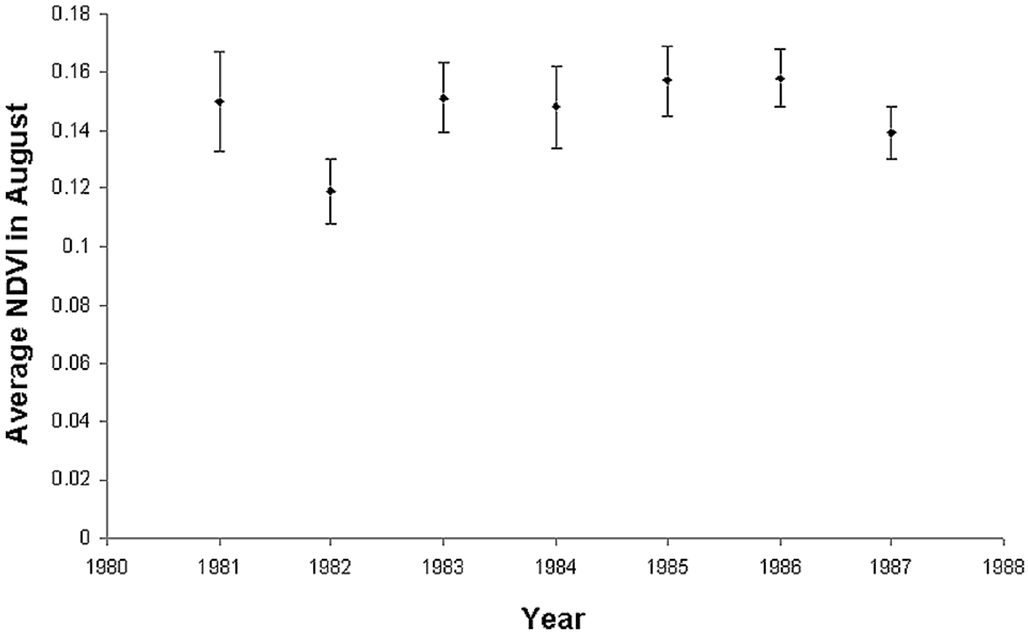

Figure 3.2. Average ± SE Normalized Difference Vegetation Index (NDVI) on the late summer (August) range of the Beverly caribou herd from 1981–1987. Higher NDVI values indicate increased photosynthetic activity.

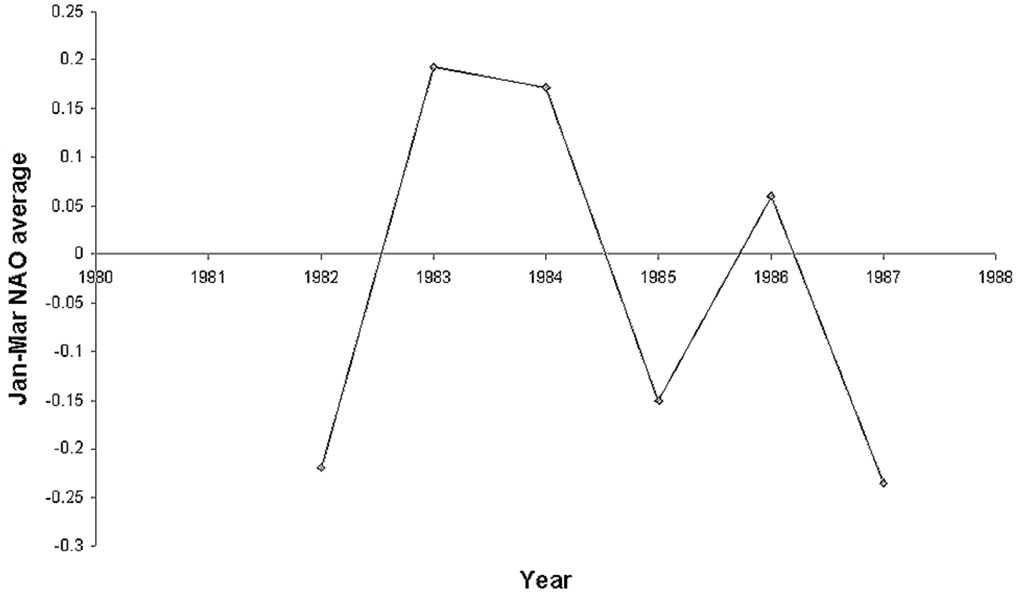

Figure 3.3. January-March average of the North Atlantic Oscillation (NAO) index from 1982 –1987. Positive values denote cold and dry winter conditions while negative values indicate warmer and wetter winter conditions.

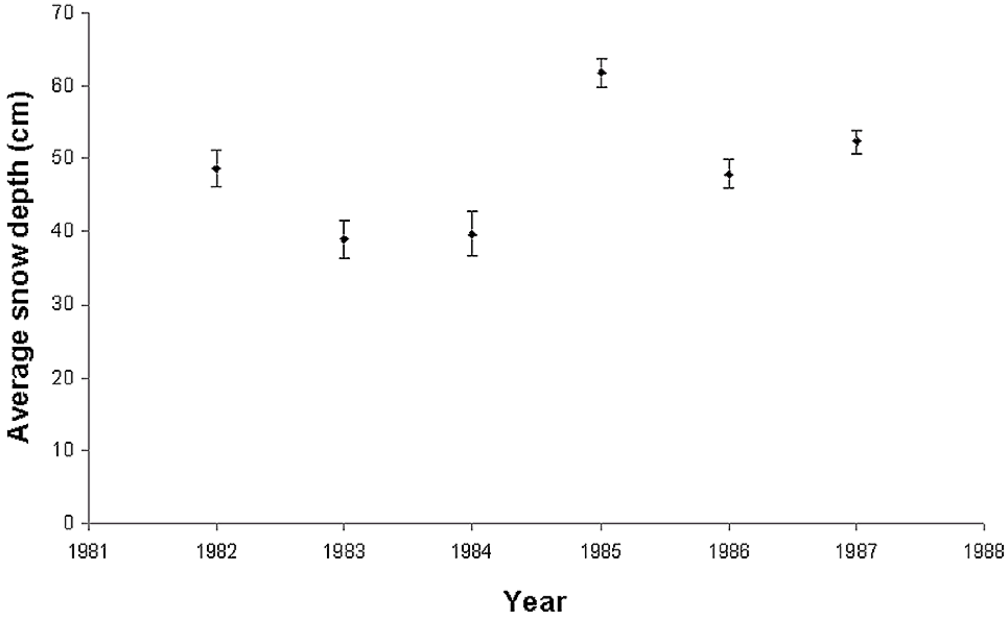

Figure 3.4. Average snow depth (cm) on the Beverly caribou herd's winter range from 1982 –1987 measured to the nearest cm at 11 locations in areas of known caribou use between March 14 and 30 each winter.

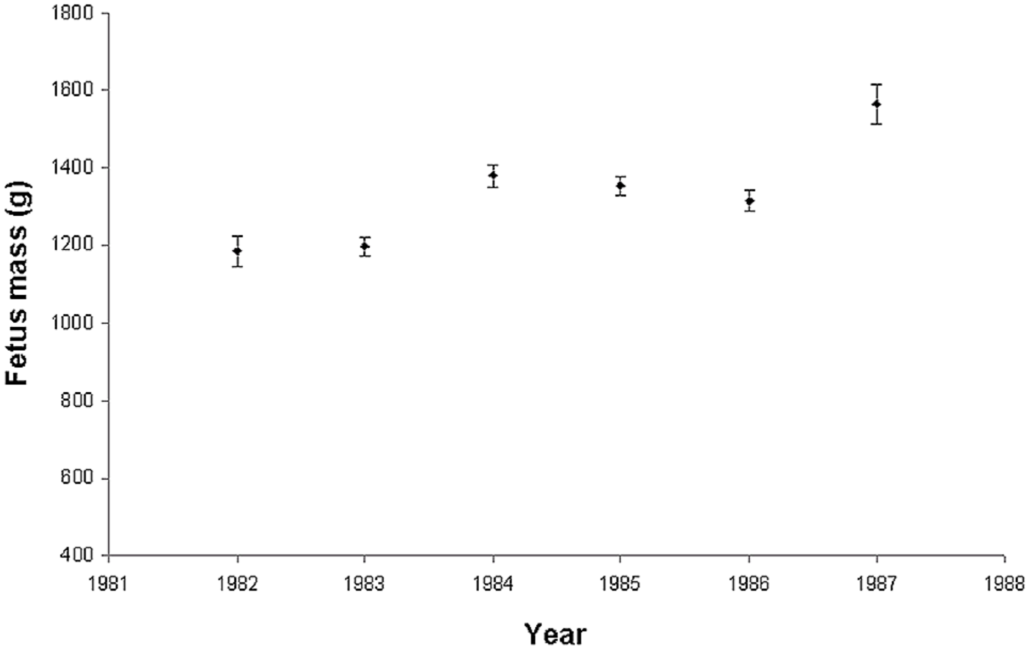

Figure 3.5. Trends in mean fetal weight (g) ± SE collected in December from the Beverly caribou herd from 1981–1987.

Table 3.1. Sex ratios of barren-ground caribou fetuses collected from the Beverly caribou herd between 1982 and 1987, and results of chi-square analysis that tested for differences in the frequency of male versus female fetuses. Significant differences at $p = 0.05$ are marked with an asterisk.

Year	**# Male Fetuses**	**# Female Fetuses**	**X^2**	**df**
1982	26	32	0.62	1
1983	31	27	0.27	1
1984	47	42	0.28	1
1985	48	48	0	1
1986	36	38	0.1	1
1987	8	20	5.1*	1

Table 3.2. Akaike Information Criterion (AIC) weights (w_i), evidence ratios, and proportion of variance explained (Adjusted D^2) for a set of 13 candidate models depicting relationships between barren-ground caribou fetal weight in March, maternal body condition (Maternal condition), maternal age (Age), fetal sex (Sex) primary productivity on the late summer range (NDVI), January-March average of the North Atlantic Oscillation (NAO), and average snow depth in cm (Snow depth) on the winter range (snow depth).

Model	**k**	**ΔAIC**	**w_i**	**evidence ratio**	**adjusted D^2**
Maternal condition + Age + Sex + NDVI	4	0	0.76	1.00	0.78
Maternal condition + Age + Sex + NDVI + NAO	5	2.28	0.24	3.12	0.75
Maternal condition + Age + Sex + NDVI + Snow	5	10.40	< 0.01	181.27	0.74
Maternal condition + Age + Sex + NDVI + NAO + Snow	6	11.37	< 0.01	294.41	0.74
Maternal condition + Age + Sex + NAO + Snow	5	14.53	< 0.01	1429.38	0.73
Maternal condition + Age + Sex + NAO	4	17.18	< 0.01	5377.61	0.33
Maternal condition + Age + Sex + Snow	4	25.64	< 0.01	$3.6*10^5$	0.32
Maternal condition + Age + Sex	3	26.77	< 0.01	$6.5*10^5$	0.25
NDVI	1	42.87	< 0.01	$2.0*10^9$	0.05
NAO	1	48.87	< 0.01	$4.1*10^{10}$	<0.01
Maternal condition	1	53.58	< 0.01	$4.3*10^{11}$	<0.01
Age	1	53.64	< 0.01	$4.4*10^{11}$	<0.01
Snow	1	57.46	< 0.01	$3.0*10*^{12}$	<0.01

Table 3.3. Akaike Information Criterion (AIC) weights (w_i), evidence ratios and proportion of variance explained (Adjusted D^2) for a set of candidate models depicting relationships between maternal body condition of barren-ground caribou in March, maternal age (Age), NDVI on the late summer range (NDVI), average snow depth in cm on the winter range (Snow depth), and the January-March average of the North Atlantic Oscillation (NAO).

Model	**k**	**ΔAIC**	w_i	**evidence ratio**	**adjusted D^2**
Age	1	0	0.73	1.00	0.61
Age + NDVI	2	2.63	0.19	3.72	0.54
Age + NAO	2	5.94	< 0.01	19.49	0.29
Age + NDVI + Snow	3	6.91	< 0.01	31.65	0.28
Age + NDVI + NAO + Snow	4	8.00	< 0.01	54.59	0.28
Age + NDVI + NAO	3	11.45	< 0.01	306.43	0.29
Age + NAO + Snow	3	13.82	< 0.01	1002.24	0.27
Age + Snow	2	14.23	< 0.01	1230.28	0.27

4.0 Age, reproductive status, and environment effects on caribou antler mass

4.1 Introduction

Antlers, which are conspicuous of and unique to the family Cervidae, are shed and regrown annually, are costly to grow and, consequently, reflect environmental conditions during the time in which they grow (e.g., white-tailed deer [*Odocoileus virginianus*], Ashley *et al*. 1998, elk [*Cervus elaphus*], Smith 1998, roe deer [*Capreolus capreolus*], Pelabon & Van Breukulen 1998). Allocation of body resources to somatic growth takes precedence over antler growth (Putnam & Sullivan 2000, Mysterud *et al*. 2005, Eggeman *et al*. 2009) and, hence, a strong relationship typically exists between antler size/mass and environmental conditions that affect summer forage quality (Putnam & Sullivan 2002, Kruuk *et al*. 2002, Torres-Porras *et al*. 2009).

Caribou and reindeer (*Rangifer tarandus*) are unique among cervids in that both males and females grow antlers. Antlers on males are the most morphologically elaborate of any cervid, function as symbols of social rank and male vigor, and serve as weapons for intrasexual combat (Geist 1998, Smith 1998). Presence of antlers on females is positively correlated with snow depth and duration, because deep snow results in more competition for winter food resources (Schaefer & Mahoney 2001). Antlered females can oust larger but unantlered males from feeding sites (Schaefer & Mahoney 2001) but, unlike males, antler size plays only a minor role in establishing social rank compared to age and body size (Holand *et al*. 2004). Barren-ground caribou (*R. t.*

groenlandicus) reside in an arctic to subarctic, strongly seasonal environment where food resources are discontinuous in both space and time, and body resources can be depleted by insect avoidance in summer (Colman *et al*. 2003, Hughes *et al*. 2009) and travel through deep snow in winter (Fancy & White 1985, Saether & Heim 1993, Mysterud *et al*. 2009).

I investigated the effects of age, reproductive status, and environmental factors on antler mass in male and female caribou of the Beverly caribou herd (hereafter, BCH). I characterized variation in weight between male and female antlers and, for females, determined whether antler mass differed between pregnant and non-pregnant caribou. I also determined how antler mass varied with age, as well as among years. I used generalized linear models (GLMs) to investigate the effects of primary productivity in summer (represented by mean July NDVI on the mid-summer range), and both broad- and fine-scale snow conditions (represented by the North Atlantic Oscillation index and snow depth on the winter range, respectively), age of the animal, reproductive status (females only), and whole body weight (minus rumen fill and reproductive tract) on caribou antler mass in December. I used Akaike Information Criterion (AIC) for model selection, and AIC weights and evidence ratios as weights of evidence that the top-ranked model best fit the data.

4.2 Methods

4.2.1 Study Area

The BCH's annual range encompasses much of Nunavut, northeastern Saskatchewan and the southeastern Northwest Territories in Canada (Fig. 3.1). The herd's winter range stretches from Great Slave Lake in the Northwest Territories to Reindeer Lake in Saskatchewan, and falls within the Taiga Shield Ecozone. Black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and lichens (e.g., *Cladina* spp.) are dominant vegetation in this ecozone. Winters are long and cold, with an average temperature of -20˚ C. Precipitation ranges from 250 – 500 mm annually. The BCH summer range lies within the Southern Arctic Ecozone in Nunavut, which is characterized by tundra shrubs that include dwarf birch (*Betula nana*) and willow (*Salix spp.*), as well as lichens. Summers in this ecozone are short and cool, with an average temperature of 10˚ C.

4.2.2 Data Collection

I used antler weights collected from adult (*i.e.*, ≥ 2 years old) male (*n* = 110) and female (*n* = 155 pregnant; *n* = 68 non-pregnant) caribou collected during organized hunts in December from 1982 through 1986 (mean collection date = December 9, range = December 2 – 15). Antler growth does not occur during this period. Caribou were shot randomly with the exception of avoiding calves. Each individual caribou was weighed using a tripod and dial scale to determine whole body weight (minus reproductive tract and rumen fill). Age was estimated from cementum annuli in the first incisor and first molar (Thomas & Kiliaan 1985). Pregnancy status was recorded for females. Kidneys and kidney fat were removed and weighed in a laboratory. Antlers were sawed off at the pedicel and weighed on an electronic scale in a laboratory. Collection methods are detailed in Thomas & Kiliaan (1998).

4.2.3 Statistical Analysis

I calculated mean antler mass for males and for females of both reproductive classes. I used t-tests to characterize antler weight differences between males and females (pregnant and non-pregnant females pooled), and also to determine whether average antler weight differed between pregnant and non-pregnant females. I used linear regression to ascertain whether antler weight varied with age within the sex and reproductive classes, as well as to determine if antler weight within these groups varied among years.

4.2.4 Model development

I used generalized linear models (GLMs) to investigate the interrelationships of antler weight in December, early summer primary productivity, previous winter's snow conditions, age, reproductive status, and whole body weight. I used whole body weight because it is positively correlated with antler mass in cervids and is a composite of skeletal frame size, fat and protein reserves (Markusson & Folstad 1997). I included age as an independent variable because older animals tend to have heavier antlers than younger animals

(Bubenik & Bubenik 2011); once asymptotic body mass is achieved, a greater portion of body resources may be allocated to antler growth (Stewart *et al*. 2000, Yoccoz *et al*. 2002, Schmidt *et al*. 2007). I analyzed male and female caribou separately, but pooled pregnant and non-pregnant females because I included reproductive status as an independent variable in the set of candidate models for females.

I used average Normalized Difference Vegetation Index (NDVI), which is a remotely sensed indicator of photosynthetic activity, in July on BCH's mid-summer range to represent primary productivity in this area. NDVI is widely used to quantify plant photosynthetic activity and to assess ecological responses to vegetation changes (Pettorelli *et al*. 2005). NDVI data were processed by the Global Inventory Monitoring and Modeling Systems (GIMMS) group from images captured by the Advanced Very High Resolution Radiometers (AVHRR) on NOAA satellites obtained from the NASA Land Long Term Data Record (http://ltdr.nascom.nasa.gov/cgi-bin/ltdr/ltdrPage.cgi). I overlaid a shapefile of BCH's early summer range, using ArcMap (ESRI 2008), on a grid of mean July NDVI values in northern Canada to obtain NDVI information specific to this area.

I included broad- and fine-scale indicators of snow depth in the models. I used the January-March average of the North Atlantic Oscillation (NAO) index as a broad-scale measurement of the previous winter's snow and temperature conditions on BCH winter range. The NAO describes opposing patterns of atmospheric pressure at northern latitudes, and strongly influences winter climate in northeastern Canada (Hurrell *et al*. 2003). Negative NAO values indicate warmer and wetter winters in this region, while positive NAO values indicate colder and drier winters. I obtained monthly NAO indices from the National Oceanic and Atmospheric Administration (NOAA; http://www.cpc.ncep.noaa.gov/products/precip/cwlink/pna/nao.shtml). I also included fine-scale snow depth on BCH's winter range, which was measured to the nearest cm at 11 locations in areas of known caribou use between March 14 and 30 each winter. Sample locations are described in Thomas & Kiliaan (1998).

I subsequently built two sets of *a priori* candidate models, one for males and one for females, that portrayed plausible interrelationships of antler weight, age, reproductive status, body weight, coarse- and fine-scale winter snow conditions, and early summer plant productivity. All models were built and evaluated with S-Plus (Insightful Corp., 2002).

4.2.5 Model selection

I evaluated support for each set candidate models with Akaike Information Criterion (AIC), where the model with the lowest AIC is deemed the most parsimonious; the best fitting model will have the smallest w_i (Burnham & Anderson 2001). I calculated AIC weights (w_i) to estimate the likelihood of model *i* being correct, given the data, thereby comparing the relative weight of evidence for each candidate model. I also calculated evidence ratios, which measure the evidence that a model is not the most parsimonious among the set of candidates; the larger the value, the stronger the evidence that model *i* does not adequately explain the data (Crawley 2007). Finally, I assessed model fit using

Adjusted D^2; this is analogous to R^2 wherein it estimates the amount of deviance explained by a model, but also takes into account the number of observations and number of parameters in a set of candidate models (Guisan & Zimmerman 2000). Adjusted D^2 is estimated as:

$$\frac{1-(n-1)}{(n-k)*\left(1-\frac{null\ deviance - residual\ deviance}{null\ deviance}\right)}$$

where the value of Adjusted D^2 increases with an increasing number of observations (n) or a decreasing number of parameters (k).

4.3 Results

4.3.1 Variation in Antler Mass

The antlers of male caribou ($\bar{x}$ = 685 g, 95% CI = 562 – 810) were, as expected, substantially heavier than those of female caribou ($\bar{x}$ = 184 g, 95% CI = 159 – 208) ($t = 11.02$, $df = 319$, $p < 0.01$). The antlers of males were, on average, four times as heavy as those of females. Pregnant females ($\bar{x}$ = 240 g, 95% CI = 219 – 260) also had significantly heavier ($t = -6.16$, $df = 221$, $p < 0.01$) antlers than non-pregnant females ($\bar{x}$ = 127 g, 95% CI = 99 – 155). The antlers of pregnant females were, on average, twice the weight of non-pregnant females' antlers.

Antler weight in males was positively related to age (Figure 1; $F_{1,108}$ = 194.80, $p < 0.01$, $R^2 = 0.64$). Antler weight in both pregnant ($F_{1,153}$ = 2.68, $p <$ 0.01, $R^2 = 0.11$) and non-pregnant ($F_{1,66}$ = 6.95, $p < 0.01$, $R^2 = 0.10$) females also was significantly, positively related to age (Fig. 4.1).

Antler weight did not vary among years (Fig. 4.2) for male ($F_{1,108}$ = 0.77, $p = 0.38$), pregnant female ($F_{1,153}$ = 2.68, $p = 0.10$), or non-pregnant female caribou ($F_{1,66}$ = 1.38, $p = 0.24$).

4.3.2 Model Selection

Of 13 candidate models for male caribou, age, body weight, July NDVI and the previous winter's NAO index were important predictors of antler weight in December (Table 4.1). The w_i for the highest-ranked model indicated an 86% probability that this model best approximated the data, and the remaining 12 models shared 14% of support. Model fit for the top-ranked model indicated a high proportion of deviance explained; adjusted D^2 for this model was 0.72. Of the 16 candidate models for female caribou, age, body weight, reproductive status, the previous winter's NAO, and July NDVI were the best approximating model for antler weight (Table 4.2). This model possessed a w_i of 97%; the other 15 models shared the remaining 3% of support. Age, reproductive status, body mass, or environmental variables alone did not adequately explain variation in the data. However, model fit was poorer, and the top-ranked model for female antler weight had an adjusted D^2 of 0.58, indicating a large proportion of unexplained variance in the data. Evidence ratios supported these results; the models containing the covariates representing age, body weight, July NDVI, previous winter's NAO and, for females, reproductive status, possessed the smallest evidence ratio for both males and females. For the remaining models in each set of candidates, the evidence ratios were at least > 6 and > 49 times larger for males and females, respectively, which indicate a strong weight of evidence that these models do not adequately fit the data.

4.4 Discussion

Antler weight in male and female barren-ground caribou is influenced by a combination of factors, including body size and age, as well as environmental factors that influence energy intake and expenditure, such as the previous winter's broad-scale snow conditions and primary productivity in early summer. These factors may have implications for social status, fighting and breeding success in males, and defense of winter food resources in females (Barrette & Vandal 1986, Geist 1998, Kruuk *et al*. 2002, Holand *et al*. 2004), but, the relative contributions of each of these factors to antler weight could not be ascertained.

The NAO was included in top-ranked models for both male and female antler weight, which implies a lag effect of the previous winter's snow conditions on antler growth. Antlers are not an energetic priority when somatic requirements are not met; under unfavourable (i.e., deep) snow conditions, less energy is available for antler growth (Putnam *et al*. 2000, Eggeman *et al*. 2009, Torres-Porras *et al*. 2009). Indeed, late winter is frequently a time of energetic stress for caribou, because locomotion and foraging in deep snow uses considerable energy

(Fancy & White 1985, Saether & Heim 1993, Mysterud *et al*. 2009) and available food resources are nitrogen-poor (Parker *et al*. 2005). Many females are in the later, most energetically demanding stage of pregnancy (Adams *et al*. 1995) and males have spent much of their fat reserves during the rut (Geist 1998).

The NAO, though it is an imperfect representation of "on the ground" snow conditions, perhaps best represented conditions encountered by BCH because it is a general index of broad-scale conditions. The finer scale snow depth measurements ("snow" in the models) may not have adequately captured variation in snow depth on the herd's winter range because caribou mitigate unfavourable snow conditions via habitat selection, i.e., moving to areas where shallower and softer snow is more amenable to foraging (Messier *et al*. 1988, Ion & Kershaw 1989, Johnson *et al*. 2001).

Primary productivity in July was also included in the top-ranked model for male and female caribou. The bulk of antler growth occurs in early summer, coincident with the peak in primary productivity (Bubenik & Bubenik 2011). However, early summer is also characterized by insect harassment, which increases energetically expensive behaviours like running and shaking, and caribou may spend less time foraging during this season (Colman *et al*. 2003, Hughes *et al*. 2009). No direct measures of insect abundance exist for BCH during the study period, which precludes inclusion of an insect harassment index. Severity of insect harassment is positively correlated with ambient temperature and cloud cover, and is negatively correlated with wind speed (Weladji *et al*. 2003), but these data were either non-existent (i.e., cloud cover) or sparse (i.e., temperature and wind speed) because weather stations on the Canadian tundra are spaced hundreds of kilometers apart and, during the study period, none existed within the BCH summer range.

4.5 Conclusion

Age, body size, summer nutrition and winter snow conditions all contribute to antler weight in caribou, but other data insufficiencies limit our conclusions. Each individual caribou in this study is a "snapshot in time" of conditions particular to that year. Each individual was sampled only once and, consequently, it is impossible to assess how the same individual invests body resources into antler weight from year to year. In addition, prime bulls were all but absent from this study. Collections occurred in December, but prime bulls shed their antlers after the rut in October and November (Lincoln 1992). Data from prime bulls would have added an insightful component to this study, because these animals have the largest and heaviest antlers (Geist 1998).

Genetic contributions cannot be ruled out, because antler size is heritable (e.g., white-tailed deer, Lukefahr & Jacobson 1998; red deer, Kruuk *et al*. 2007; roe deer, Vanpé *et al*. 2010). Nutritional effects mediated through environmental conditions are presumed to override genetic contributions to antler size; captive feeding experiments with white-tailed deer demonstrated that antler size decreased with suboptimal nutrition irrespective of genetic potential for large antlers (Lockwood *et al*. 2007). Teasing apart genetic and environmental contributions to any physical trait is challenging, even under controlled conditions

(Postma 2006), though the genetic contributions to both antlers and horns may be greatly overstated (Lockwood *et al*. 2007, Webb *et al*. 2012). Indeed, Loehr *et al*. (2010) indicated little potential for selection to produce a change in horn size for thin horn sheep (*Ovis dalli*) because of a negligible individual effect. Rather, local weather variables and the Pacific Decadal Oscillation (PDO) best predicted variance in horn volume. Although similar studies have not been conducted for caribou, our analysis suggested a similar pattern – winter weather variables (i.e., snow conditions) as mediated through the NAO and summer foraging conditions influenced antler size for caribou of the Beverly herd.

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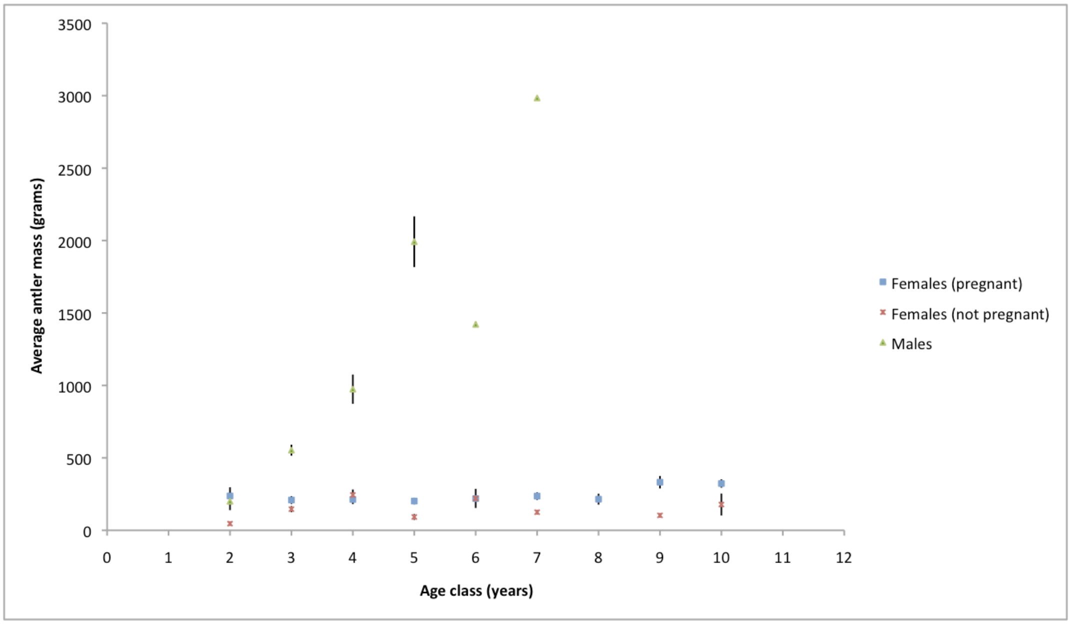

Figure 4.1 Mean antler weight (g) ± SE for barren-ground caribou of different age classes (range 2 – 10 years old) from the Beverly herd collected in December between 1982 and 1986.

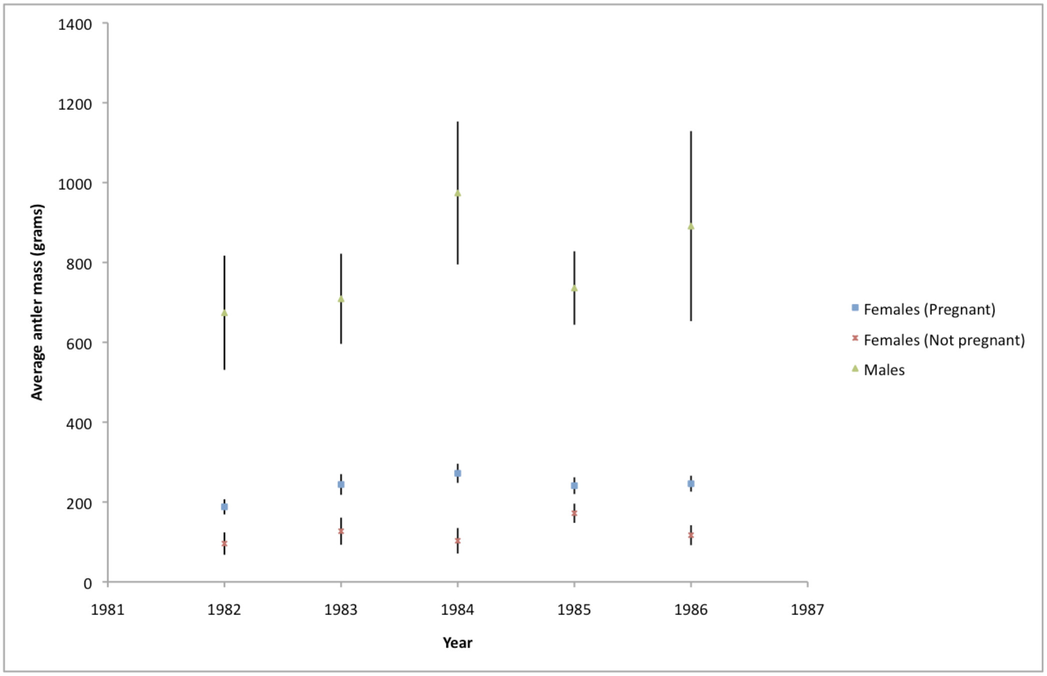

Figure 4.2 Interannual variation in mean antler weight (g) ± SE for barren-ground caribou of different sex and reproductive classes from the Beverly herd between 1982 and 1986.

Table 4.1. Akaike Information Criterion (AIC) weights (w_i), evidence ratios, and proportion of variance explained (Adjusted D^2) for a set of candidate models depicting relationships between antler weight of male barren-ground caribou, whole body weight (Weight), NDVI on the early summer range (NDVI), previous winter's average snow depth (Snow) in cm on the winter range (snow), and previous winter's January-March average North Atlantic Oscillation (NAO).

Model	***k***	**ΔAIC**	***w***	**evidence ratio**	**adjusted D^2**
Age + Weight + NAO + NDVI	4	0	0.86	1.00	0.72
Age + Weight + NAO + NDVI + Snow	5	3.65	0.13	6.20	0.70
Age + Weight + NDVI + Snow	4	12.83	< 0.01	610.94	0.68
Age + Weight + NAO + Snow	4	16.89	< 0.01	4651.75	0.68
Age + Weight + NDVI	3	19.54	< 0.01	17500.76	0.68
Age + Weight + NAO	3	20.74	< 0.01	31888.47	0.66
Age + Weight + Snow	3	28.91	< 0.01	$18.95*10^5$	0.64
Age + Weight	2	35.03	< 0.01	$40.42*10^6$	0.54
Weight	1	58.52	< 0.01	$50.98*10^{11}$	<0.01
Age	1	73.35	< 0.01	$84.67*10^{14}$	<0.01
NDVI	1	175.45	< 0.01	$12.54*10^{37}$	<0.01
NAO	1	180.28	< 0.01	$14.03*10^{38}$	<0.01
Snow	1	188.52	< 0.01	$86.41*10^{39}$	<0.01

Table 4.2 Akaike Information Criterion (AIC) weights (w_i), evidence ratios, and proportion of variance explained (Adjusted D^2) for a set of candidate models depicting relationships between antler weight of female barren-ground caribou, whole body weight (Weight), reproductive status (Preg), NDVI on the early summer range (NDVI), previous winter's average snow depth in cm on the winter range (Snow), and previous winter's January-March average North Atlantic Oscillation (NAO).

Model	**k**	**ΔAIC**	**w_i**	**evidence ratio**	**adjusted D^2**
Age + Weight + Preg + NAO + NDVI	5	0	0.97	1.00	0.58
Age + Weight + Preg + NAO + NDVI + Snow	6	7.81	0.01	49.65	0.49
Age + Weight + Preg + NDVI + Snow	5	9.65	< 0.01	124.58	0.47
Age + Weight + Preg + NAO + Snow	5	10.83	< 0.01	224.75	0.47
Age + Weight + Preg + NDVI	4	11.10	< 0.01	257.23	0.29
Age + Weight + Preg + NAO	4	13.06	< 0.01	685.39	0.27
Age + Weight + Preg + Snow	4	23.08	< 0.01	102744.43	0.27
Age + Weight + Preg	3	25.00	< 0.01	268337.28	0.27
Age + Weight	2	35.22	< 0.01	$44.46*10^{6}$	0.26
Age	1	36.22	< 0.01	$73.29*10^{6}$	0.16
Age + Preg	2	48.18	< 0.01	$28.98*10^{9}$	0.13
NAO	1	49.38	< 0.01	$52.81*10^{9}$	<0.01
Preg	1	71.93	< 0.01	$41.62*10^{14}$	<0.01
Weight	1	75.81	< 0.01	$28.96*10^{15}$	<0.01
Snow	1	106.32	< 0.01	$12.22*10^{22}$	<0.01
NDVI	1	115.11	< 0.01	$99.04*10^{23}$	<0.01

5.0 Boreal caribou in Canada: policy versus ecology

5.1 Introduction

Human land use has been in conflict with boreal woodland caribou (*Rangifer tarandus caribou*; hereafter boreal caribou) since early European settlement of Canada. They have highly specific habitat requirements coupled with naturally low population density and low reproductive potential. They were hunted heavily during the late 19th century and early 20th century and faced direct habitat loss to land clearing for human settlement, agriculture and forestry (Moisan 1958, Bergerud 1974, Schaefer 2003). The role of human harvest in caribou population declines was recognized, and recreational hunting was banned as early as 1929 in parts of Ontario (De Vos & Peterson 1951). However, habitat loss has not been directly addressed in government policies, procedure, and protocols. Widespread landscape change caused by industrial development has eroded and fragmented boreal caribou range across Canada and altered how boreal caribou interact with predators via apparent competition mediated by ungulate species that flourish in human-modified landscapes (Festa-Bianchet *et al.* 2011). Some boreal caribou populations are now confined to "islands" of suitable habitat that are isolated from continuous boreal caribou habitat (e.g., Pukaskwa National Park herd, Ontario [Bergerud 1985]; Charlevoix herd, Québec [Duchesne *et al*. 2000], and other populations have declined to the point of being at immediate risk of extirpation (e.g., Little Smoky herd, Alberta [Schneider *et al.* 2010]).

The inverse relation between anthropogenic landscape disturbance and caribou habitat occupancy and population size is well-studied, and research has addressed caribou habitat selection (e.g., Rettie & Messier 2001, Brown *et al.* 2003, Hins *et al.* 2009, Moreau *et al.* 2012, Pinard *et al.* 2012), behavioural reactions (including avoidance) to disturbance (e.g., James & Stuart-Smith 2000, Dyer *et al.* 2002, Courtois *et al.* 2007, Dussault *et al.* 2012, Leblond *et al.* 2012), redistribution following disturbance (e.g., Smith *et al.* 2000), and spatiotemporal lags between disturbance and caribou range loss (e.g., Vors *et al.* 2007, Faille *et al.* 2010). Predator-prey interactions facilitated by industrial landscape disturbance, the most important proximate factor linking landscape disturbance with caribou population decline, have also been studied (e.g., Courbin *et al.* 2009, Whittington *et al.* 2011).

Decline of boreal caribou, given the species' elusive nature and secluded habitat, is a "hard-to-perceive, slow-motion crisis" (Schaefer 2003). Boreal caribou were recognized by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as "threatened" (i.e., likely to become endangered if limiting factors are not reversed) in 2000. Environment Canada's "Recovery Strategy for Woodland Caribou, Boreal Population, in Canada" was released in 2012, nearly four years behind schedule. The Recovery Strategy, under Canada's Species at Risk Act (SARA), obliges Canada to prevent caribou from becoming extirpated or extinct, but provides no legal recourse if Canadian provinces and territories do not implement protection of caribou habitat (M. Gorrie, *pers. comm.*). SARA's "Safety Net" Clause would permit the federal government to mandate boreal caribou habitat protection, but boreal caribou habitat co-occurs with natural resources (e.g., energy, forestry) that are significant, even primary, drivers of provincial and national economies. Boreal caribou have little direct use, and use of other natural resources has taken priority over caribou and their habitats. Hence, boreal caribou in Canada face a "perfect storm" of factors linked to their decline: high sensitivity to habitat change and lack of political will to instigate habitat protection and restoration that would inevitably interfere with extraction of natural resources.

5.2 Boreal Caribou Ecology

Boreal caribou spend their entire life cycle in the boreal forest and typically select >80 years old black spruce (*Picea mariana*) or jackpine (*Pinus banksiana*) stands with abundant lichen (e.g., *Cladina* spp.) growth (Schaefer & Pruitt 1991, Rettie & Messier 2001, Brown *et al*. 2003, Whittington *et al*. 2011). These habitats satisfy all life processes, including foraging, reproduction and predator avoidance. Unlike the long-distance seasonal migrations of migratory barren-ground caribou (*R. t. groenlandicus*), boreal caribou undertake movements of tens to hundreds of kilometers between seasonal ranges within their larger annual home ranges (Rettie & Messier 2001, Ferguson & Elkie 2004, Briand *et al*. 2009, Nagy *et al*. 2011, Basille *et al*. 2013).

Parturitient females isolate themselves from conspecifics during calving to minimize predation of highly vulnerable neonates (Bergerud 1985, Carr *et al*. 2011). Unlike barren-ground caribou that form herds of 1,000s to 100,000s of individuals, boreal caribou occur as a continuous distribution of solitary individuals during early spring to late summer, and in small groups of two to 25 during the rest of the year (Nagy *et al.* 2011). This "spacing out" strategy, coupled with low productivity habitat, minimizes contact with other ungulates (e.g., moose [*Alces alces*] and white-tailed deer [*Odocoileus virginianus*]) and predators (e.g., wolves [*Canis lupus*], coyotes [*C. latrans*] and bears [*Ursus* spp.]; Bergerud *et al*. 1984, Rettie & Messier 2000, Latham *et al*. 2011).

5.3 Limiting Factors for Boreal Caribou

Although disturbances, e.g., wildfires and wind-throw, are natural components of the boreal forest life cycle and improve caribou habitat over long temporal scales by regenerating lichen patches (Schaefer & Pruitt 1991), conversion of old-growth boreal forest to young, mixed-wood stands may change how boreal caribou interact with predators. Early seral stage forests, as well as edge created by cut blocks, roads and other linear features are attractive for moose and deer (Seip 1992, Wittmer *et al*. 2005, Latham *et al*. 2011). Predator populations respond numerically to this increased concentration of prey, thereby resulting in higher predation on boreal caribou (Bergerud & Elliott 1986, Wittmer *et al*. 2005, Courbin *et al*. 2009, Whittington *et al*. 2011). Heavily depredated boreal caribou populations are slow to recover because they have low reproductive rates and are relatively easier for predators to capture than larger ungulates like moose, and there is no numerical feedback mechanism between caribou density and predator density. This situation exemplifies "apparent competition," where an increase of one prey species population correlates with the decline of another, not because of direct competition for a shared food resource, but because of a shared predator (Holt 1977).

Additional and, often, additive threats to boreal caribou persistence include linear features (i.e., roads, seismic lines, trails and utility corridors) that can facilitate predator mobility, speed of travel, access to once-secluded boreal caribou habitat, and provide barriers to boreal caribou movement (James & Stuart-Smith 2000, Dyer *et al*. 2002, Nagy 2011, Whittington *et al*. 2011). Early successional stands within caribou habitat also can decrease the spatial separation of caribou and moose and, consequently, increase predation risk (Peters *et al.* 2013). Illegal human harvest, though data are scarce, is a significant cause of mortality for some boreal caribou populations (e.g., Labrador; Schmelzer *et al.* 2004). The effects of climate change on boreal caribou are not well-understood (Vors & Boyce 2009), but the northward range expansion of white-tailed deer is linked to climate warming (Côté *et al*. 2004). White-tailed deer in boreal caribou range may be an additional alternate prey and further influence wolf-caribou dynamics (Latham *et al*. 2011). White-tailed deer in eastern Canada can be vectors of the meningeal brainworm (*Parelaphostrongylus tenuis*; Dumont & Crête 1996). This endoparasite is harmless to deer but lethal to caribou and, consequently, coexistence of these two species is deemed impossible when this parasite is present (Dauphiné 1975, Pitt & Jordan 1994).

5.4 Boreal Caribou and the Species-at-Risk Act

Canada bears the legal obligation, under the Canadian Species at Risk Act (SARA), to "...prevent wildlife species from being extirpated or extinct...as a result of human activity" (p. 7, SARA 2012). For a federally listed species, the Department of Environment must develop a recovery strategy that provides the "...identification of species' critical habitat" (p. 21, SARA 2012), the latter of which is defined as, "habitat necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species." Boreal caribou were listed as "threatened" by COSEWIC in 2000 and, subsequently, by SARA in response to nation-wide population decline. Environment Canada released the "Recovery Strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada" in 2012 (hereafter, Recovery Strategy). The Recovery Strategy defines critical habitat for caribou as, "the area within the boundary of each boreal caribou range that provides an overall condition that will allow for an ongoing recruitment and retirement cycle of habitat which maintains a perpetual state of a minimum of 65% of the area as undisturbed habitat [and possesses the] biophysical attributes required by boreal caribou to carry out life processes" (Environment Canada 2012).

SARA mandates development of an "action plan" based on the recommendations of the Recovery Strategy. This plan would, among other things, identify critical habitat, identify portions of critical habitat that have not been protected, state the measures being implemented to achieve population and distribution objectives, and evaluate the socio-economic costs and benefits derived from the action plan's implementation (p. 25, SARA 2012). Although the Recovery Strategy and Action Plan are developed at the federal level, implementation of "range plans," i.e., detailed management strategies for individual caribou population ranges, is the responsibility of the provincial governments.

5.5 Big Oil versus Caribou

Lack of political will to limit industrial development in the boreal forest is the greatest threat to boreal caribou. Research on boreal caribou has increased sharply over the past decade, but directing attention and funding to research, as opposed to limiting industrial incursions into caribou habitat, is unlikely to improve the likelihood of long-term caribou persistence. Management decisions are invariably based on incomplete knowledge, but deferring decisions for the sake of more research is risky when habitat loss is ongoing (Grantham *et al.* 2009). A sizeable body of research identifies intact, old-growth coniferous forests and peatlands as low predation-risk habitats in which boreal caribou carry out life processes (e.g., Bergerud & Elliott 1986, Stuart-Smith *et al*. 1997, Rettie & Messier 2000, Courbin *et al*. 2009, Nagy 2011) and the vast space needs of caribou have been apparent for decades (e.g., Bergerud *et al.* 1984).

This sizeable body of knowledge is well-referenced in the Recovery Strategy, but considerable political will is needed to translate this knowledge base into effective policies, policies and protocols. The Recovery Strategy proposes that 65 % undisturbed habitat within a boreal caribou range is needed for the population's long-term persistence. This amount of undisturbed habitat was obtained by regressing the probability that population growth rate for a given caribou population was stable or increasing with total area within caribou ranges disturbed by 500 m-buffered wildfires ≤ 40 years old and all 500 m-buffered anthropogenic disturbances (Environment Canada 2012, Appendix E).

The Recovery Strategy did not designate the entire range of boreal caribou as critical habitat, nor did it define the location of undisturbed habitat spatially, i.e., "critical habitat," within boreal caribou ranges. The Recovery Strategy's description of critical habitat, as opposed to a map, is acceptable under SARA, but this lack of spatial specificity provides little impetus for practical application of this concept, unless the primary focus is to mitigate, rather than limit, disturbance within caribou habitat. Identification of critical habitat can be deferred to the Action Plan, which is slated for release by December 31, 2015 (Environment Canada 2012). Although the federal government may invoke the "Safety Net" clause, which would permit the federal, rather than provincial/territorial, government to protect caribou, there are no legal consequences if release of the Action Plan is postponed, nor if the provinces and territories do not protect caribou critical habitat. This is a far graver issue: further postponing of legislated caribou habitat protection while habitat loss is ongoing.

The lack of caribou critical habitat spatial delineation, timeline for an Action Plan or legal incentive to protect caribou critical habitat, reflect the current Canadian government's valuation of boreal caribou. Economic values appear to drive current decision making, but assigning monetary value to boreal caribou is extremely difficult because boreal caribou have little direct value, i.e. that which can be quantified with market data and economic transactions (Kotchen & Reiling 2000). The non-use values of boreal caribou include existence value (i.e., the satisfaction people derive from knowing caribou exist) and bequest value (i.e., the bequest of caribou to future generations) are not measurable by market data. While boreal caribou are legally harvested by Aboriginal peoples in Canada, they tend to be hunted opportunistically and do not comprise large parts of traditional diets in most parts of Canada. This is a stark contrast to migratory barren-ground caribou, upon which tens of thousands of northern Aboriginal people depend for protein. For example, the meat value alone of the Beverly and Qamanirjuaq caribou herds, which reside primarily in Nunavut, exceeds US$17.5 million annually (Beverly and Qamanirjuaq Caribou Management Board 2008). Guided recreational hunts for barren-ground caribou often cost in excess of US$8000 per person and comprise an important source of income and employment for northern peoples. By comparison, few Canadians have ever seen boreal caribou, given that these animals are sparsely distributed and cryptic even within their preferred habitat, and most people now reside in urban centres far from intact boreal forest.

Canada has a poor track record for protecting caribou. Boreal caribou in Canada's Maritime region were all but extirpated until the creation of Gaspésie National Park in 1937 (Moisan 1958). The Gaspésie caribou herd, the only remaining boreal caribou population south of the St. Lawrence River, is threatened by ongoing industrial landscape disturbance surrounding the park and, consequently, is recognized by SARA as endangered. The last five remaining mountain-dwelling caribou in Banff National Park were wiped out by an avalanche in spring 2009; this marked the first time that a large mammal species vanished from a Canadian national park in over a century (Gurd and Nudds 1999). The fact that southern mountain caribou herds were shrinking was apparent well before they were granted "threatened" status by COSEWIC in 2000 and by SARA in 2002. Despite these designations, concerns raised by scientists (e.g., Kinley 2009), and that small populations are at greater risk to stochastic events (Lande *et al*. 2003), no recovery planning or habitat protection took place prior to the Banff herd's demise. Indeed, the disappearance of caribou from Banff National Park starkly illustrates the consequences of delaying legislation to protect caribou.

Alberta's caribou program epitomizes the disjunction between research and legislation for boreal caribou. This petroleum-rich province is home to the most damaged boreal caribou ranges in Canada; percent industrial disturbance within caribou ranges approaches 95 % for some populations (mean = 57 %, range = 21–95 %, *n* = 12 local populations; Environment Canada 2012) and all are classified as "not self-sustaining." Significant research from this province has elucidated boreal caribou reactions to disturbance (e.g., Smith *et al.* 2000, Dyer *et al.* 2002) and changes in predator-prey interactions resulting from disturbance (e.g., James *et al.* 2004, Latham *et al.* 2011), but this research has not prompted the Alberta provincial government to place limits on industrial development in caribou ranges. Rather, Alberta continued to sell oil and gas leases even within the most disturbed caribou ranges (e.g., Little Smoky) until the Alberta Energy

Department announced in May 2013 that further sale of leases within both the Little Smoky and A La Peche caribou ranges would be suspended until range plans are completed (*Edmonton Journal* 2013).

Alberta has directed management actions to "half-way" solutions, such as predator culls (Schneider *et al.* 2010, Boutin *et al.* 2012) and penning of pregnant females (Smith & Pittaway 2011), which focus on "symptoms" rather than underlying causes of caribou population loss (*sensu* Frazer 1992). Wolf culls often produce short-term improvements in vital rates (e.g., Bergerud & Elliott 1986, Boertje *et al*. 1996, Hayes *et al*. 2003), but this management prescription overlooks the ecosystem-level consequences of predator culls. In boreal caribou ranges with high populations of alternate prey species, culls could instigate "predator release" of these prey which, in turn, could profoundly alter plant species composition, increase disease transmission among prey species, and incite high-amplitude predator-prey oscillations (Wasser *et al*. 2011). Wolf populations rebound quickly once predator culls cease perpetuating the need for predator control (Bergerud 1996, NRC 1997). Pregnant female caribou in the Little Smoky range were herded into corrals in late March and released once their calves were three weeks old and less vulnerable to predation. However, survival of corral-born calves did not differ significantly from that of wild-born calves (Smith & Pittaway 2011). These intensive management interventions cost millions of dollars and, with ongoing industrial development in Alberta's caribou ranges, will only serve to delay extirpation.

5.6 The Challenge of Effective Management

Boreal caribou persistence depends on space for predator avoidance and foraging. Neither predator culls nor calf protection addresses these spatial needs. Rather, directing management efforts away from habitat protection underscores the reluctance of the Canadian government and provinces to limit extraction of commercially valuable natural resources from caribou range. Although boreal caribou are listed as “threatened” or vulnerable” in seven out of nine Canadian provinces, and all nine have released provincial recovery strategies (Table 5.1), none have implemented the range plans mandated by SARA.

Protected areas are present within existing boreal caribou range. Prince Albert National Park (3,874 km^2) in Saskatchewan includes boreal caribou range (Arlt & Manseau 2011), but little is known of boreal caribou population trends or distribution in this province (Environment Canada 2012). In Ontario, boreal caribou occur within Wabakimi Provincial Park (8,920 km^2) and Woodland Caribou Provincial Park (4,500 km^2) but forest harvest and road networks are widespread outside these protected areas. The 5,500 km^2 range of the Charlevoix herd in Quebec spans three protected areas that total 1,205 km^2, but intensive forest harvest occurs outside these protected areas (St-Laurent & Dussault 2012). Proposed protected areas in Labrador, Québec, Ontario and the Northwest Territories would protect 10,000 km^2 of boreal caribou range, which is about the same size as individual home ranges of female boreal caribou in the Northwest Territories (Nagy 2011), but these are still in the planning stages (Badiou *et al.* 2011) and population fragmentation is likely if habitat between these protected areas is impacted by industry. In 2012, forestry companies, conservation groups and the Ontario provincial government pledged to exclude over 8,000 km^2 of caribou habitat near the Abitibi River from logging; this was the first such proposal to advance under the Canadian Boreal Forest Agreement (CBFA), which is a multi-stakeholder group of forestry companies and conservation groups that seeks to protect at least 50% of Canada's boreal forest (CBFA 2012).

Boreal caribou population ranges range from 752 km^2 to 621,562 km^2 (average = 47,956 km^2, n = 51 population ranges; Environment Canada 2012). Given the small size and number of protected areas within caribou range, these alone are unlikely to maintain caribou within the boreal forest. Moreover, protected areas are at risk to becoming islands of suitable caribou habitat embedded in a highly modified landscape, leading to population fragmentation. Risks of this "island effect" include functional habitat loss within the protected areas due to spillover effects from disturbance (Vors *et al*. 2007) and loss of gene flow between caribou populations, with negative consequences for genetic diversity (Boulet *et al.* 2007). Thus, the efficacy of protected areas as strongholds for boreal caribou will be compromised if industrial disturbance in adjacent areas is not limited. Land-use planning, if configured properly, could lessen the consequences of industrial disturbance. A direct, positive relationship exists between patch size of low predation risk (i.e., intact boreal forest) habitat and population growth rate of boreal caribou (Nagy 2011). Large blocks of intact, mature coniferous forest would minimize contact with other ungulates and predators, thereby maintaining spatial separation of caribou, predators and alternate prey (Briand *et al.* 2009, Courbin *et al.* 2009, Peters *et al.* 2013).

5.7 A Global Issue

The conflict of interest between boreal caribou and economic gain reflects a greater, global issue; namely, when a threatened or endangered species conflicts with economic interests, conservation priorities are often compromised. This situation is exacerbated when the direct use value of the threatened species and communities or countries would forego economic gain by limiting exploitation of their habitat (Nantha & Tisdell 2009). This scenario repeats itself worldwide with many taxa.

Orangutans (*Pongo* spp.) in Indonesia and Malaysia are critically endangered and face ongoing conversion of their lowland rainforest habitat to oil palm (*Elaeis guineensis*) plantations (Wich *et al.* 2008). Palm oil is the world's most consumed vegetable oil and is a cornerstone of local economies in these countries (Carter *et al.* 2007). Orangutans, conversely, have almost no direct use value, and these two countries would forego billions of dollars of lost oil palm revenue by conserving orangutan habitat instead of expanding oil palm cultivation (Nantha & Tisdell 2009). White-backed woodpeckers (*Dendrocopos leucotos*) require old-growth deciduous forests with abundant dead trees in which to forage and reproduce, but widespread logging has extirpated this species from much of Europe (Tomiałojc 2000). White-backed woodpeckers are thus critically endangered and largely confined to residual pockets of intact deciduous forest in

Poland’s Białowieża Forest (Czeszczewik & Walankiewicz 2006). The Polish government has not prevented logging within this forest, only 100 km^2 of which is protected by a national park, despite assertions by scientists that cessation of harvest in this area is needed for the woodpeckers’ persistence (Czeszczewik & Walankiewicz 2006). Mangrove (Family Rhizophoraceae) swamps, one of the world’s most threatened ecosystems (Duke *et al*. 2007), have been cleared in favour of aquaculture ponds, especially shrimp cultivation (Barbier & Cox 2003). Despite ecosystem services and, hence, long-term economic benefits provided by these plants (e.g., protecting human settlements from storms and erosion), the immediate economic value of intact mangroves is difficult to compare to the short-term economic returns of shrimp aquaculture (Polidaro *et al.* 2010). Indeed, shrimp aquaculture increased over 400% between the late 1980s and late 1990s (Anderson & Fong 1997), and mangroves continue to be cleared in coastal tropical areas to increase capacity for shrimp aquaculture (Polidaro *et al.* 2010).

The value of revenue lost by ceasing industrial incursions into these species’ habitats increases with the rising profitability of natural resource extraction and cultivation (Nantha & Tisdell 2009). Striking commonalities link these scenarios: low direct use value of the species and habitat in question, the foregoing of long-term ecosystem services provided by intact habitats in favour of short-term economic gain, and high direct value of and increasing global demand for the natural resources being extracted. Boreal caribou habitat protection is thus a direct competitor for economic revenue for Canada. Though significant opportunities for protection of boreal caribou habitat still exist where the industrial footprint is minimal, such as the Yukon, NWT, northern Ontario and Quebec's intact boreal forest, caribou are unlikely to persist where the industrial footprint is greatest (e.g., Alberta) and priority for natural resource extraction dictates land use.

The "perfect storm" of disconnect between research and management, recovery planning, and legislation is unlikely to improve, given the importance of boreal resources to Canada's economic growth. Boreal caribou are caught in an "analysis paralysis" where research effort is high, but the political drive to translate this research into meaningful management actions is low. The future of boreal caribou in Canada is, consequently, uncertain (Festa-Bianchet *et al*. 2011). Unless the Canadian government restricts the industrial footprint in caribou habitat, which would allow for sustainable boreal caribou populations, further population loss is inevitable. Canadian society has a choice between economic growth and maintaining caribou within the boreal forest, but there is unwillingness in government to admit that money is more important than caribou. The choice, clearly, has been made.

5.8 References

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Table 5.1. Boreal caribou conservation status, population estimates, number of local populations delineated, and existing recovery plans for the Canadian provinces.

Jurisdiction	**Status (year recognized)**	**Boreal caribou population estimates**[a]	**# Local populations delineated (# surveyed)**[b]	**Recovery plan (year released)**
Canada	Threatened (2002)	24,722 – 25,513	51 (40)	Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada (2012) ec.gc.ca/publications
Alberta	Threatened (2001)	2074 – 2315	12 (12)	Alberta Woodland Caribou Recovery Plan 2004/05–2013/14 (2005) srd.alberta.ca/FishWildlife/WildlifeManagement/CaribouManagement/
British Columbia	Imperiled (2006)	1040 – 1110	5 (3)	Implementation Plan for the Ongoing Management of Boreal Caribou (Rangifer tarandus caribou) in British Columbia (2011) env.gov.bc.ca/wld/speciesconservation/bc/
Labrador	Threatened (2002)	2983	3 (3)	Recovery Strategy for Three Woodland Caribou Herds (Rangifer tarandus caribou; Boreal Population) in Labrador (2004) env.gov.nl.ca/env/wildlife/endangeredspecies/mammals.html
Manitoba	Endangered (1994)	1063 – 1543	13 (10)	Manitoba's Conservation and Recovery Strategy for Boreal Woodland Caribou (Rangifer tarandus caribou) (2005) manitobamodelforest.net/publications.html#woodlandcaribou
Northwest Territories	Not listed	6500	1	Implementation Plan for the Action Plan for Boreal Woodland Caribou in the Northwest Territories: 2010–2015 (2010) nwtspeciesatrisk.ca/tiki/tiki-index.php?page=WoodlandCaribou
Ontario	Threatened (2007)	1284	9 (3)	Recovery Strategy for Woodland Caribou (Forest-dwelling, Boreal Population) in Ontario (2008) mnr.gov.on.ca/en/Business/Species/2ColumnSubPage/249504.h

				tml
Québec	Vulnerable (2005)	9778	6 (6)	The Forest-Dwelling Caribou (Rangifer tarandus) Recovery Plan in Québec – 2005-2012 (2008) collections.banq.qc.ca/ark:/52327/bs1935969
Saskatchewan	Not listed	No data	No data	Draft Recovery Strategy for Boreal Woodland Caribou in Saskatchewan (2007) not available online

[a] Environment Canada (2012)

[b] Local populations have not been delineated in Saskatchewan, and additional local population ranges likely exist within continuous boreal caribou range in the Northwest Territories, Ontario and Québec, but have not yet been delineated (Environment Canada 2012).

6.0 Conclusion

Renowned population ecologist Graham Caughley posited, “I strongly suspect that the deepest insight into a population comes from studying how survival and fecundity are influenced by the conditions in which the animals live. Such an approach cuts deeper into the problem of population ecology than do any of the others” (Sinclair *et al*. 2006). Caughley’s assertions ring true as much for caribou as they do for any species; a capacious body of research spanning both decades and subspecies veritably “cuts into the problem” of how caribou vital rates are shaped by their surroundings. Caribou management, to a great extent, has not emulated this research. This is largely the result of inability, in the case of climate change, or unwillingness, in the case of anthropogenic landscape disturbance, to protect caribou habitat from destruction.

For this thesis, I examined the ecology and policy of caribou in Canada. The overriding conclusion of this work is that caribou management will only be effective if it limits disruption of habitats, be they summer range for barren-ground caribou or old growth coniferous forest for boreal caribou, that are key to caribou survival and reproduction.

In Chapter Two, I examined global trends of caribou and reindeer populations and documented a 57% decline from previous population maxima. I elaborated upon three main mechanisms of decline: plant and insect phenology changes, spatio-temporal changes in overlap between caribou, predators and alternate prey species, and increased frequency of extreme weather events. These are not mutually exclusive and may shift in importance through time, but comprise three main drivers of global *Rangifer* decline.

Chapters Three and Four challenge the long-held paradigm that winter is the primary limiting season for caribou and assert that late summer, via its influence on fetal mass and adult caribou body condition, is an important limiting season. Indeed, I found that primary productivity on the migratory Beverly caribou herd's late summer range best predicted both fetal mass and maternal body condition in late winter, whereas winter snow conditions had little bearing on these indices. I also found that antler mass in both male and female caribou, which is highly sensitive to foraging conditions, was positively related to summer primary productivity.

The late summer range is virtually the only place in which migratory caribou can forage undisturbed and maximize weight gain before autumn. Insect harassment is low (Weladji *et al*. 2003), vegetation has not yet senesced (Huemmrich *et al*. 2010) and, consequently, migratory caribou exhibit strong fidelity to their late summer range (Nagy 2011). Fidelity to the late summer range rivals that of the calving range, the latter of which is used for a comparatively shorter time period (Nagy 2011). Yet management efforts for migratory caribou remain calving ground-centric (e.g., Porcupine caribou herd and the Arctic National Wildlife Refuge in Alaska, Kotchen & Burger 2013), even though herds may switch calving grounds (Nagy 2011).

Instead, management attention should shift to protecting late summer ranges. Industrial activities are rapidly increasing in the arctic (Young 2011) and some, such as diamond mines in the Northwest Territories, are within caribou summer ranges. Even small changes in forage uptake can instigate comparatively large changes in body condition and, hence, vital rates (Robbins 1983, White 1983, Hobbs 2003, Cook *et al*. 2004), underscoring the need to limit disturbance of these vital areas. Protection of caribou late summer ranges is especially urgent in the face of a warming arctic. While a warmer arctic with greater primary productivity (Jia *et al*. 2009) may improve caribou body condition (Couturier *et al.* 2009 but see Post & Forchhammer 2008), these gains may be negated by increased insect harassment (Witter *et al*. 2012) and increased industrial disturbance.

Chapter Five discusses the disjunction between “the conditions in which the animals live” and caribou management, which is further exemplified by lack of implementation of the Species-at-Risk Act (SARA) for boreal caribou. Research (e.g., Rettie & Messier 2000, Courbin *et al*. 2009, Latham *et al*. 2011) identifies anthropogenic disturbance-mediated apparent competition as the chief driver of boreal caribou population loss. Despite release of the Federal recovery strategy for boreal caribou in 2012, and legal mandate under SARA to protect what is deemed “critical habitat,” no boreal caribou habitat has been protected from development.

Our heightened understanding of how caribou survival and reproduction are influenced by the conditions in which they live has not actuated sound management actions. Attempts to directly limit caribou mortality have largely been restricted to reducing hunter harvest for some migratory herds (e.g., Bathurst herd, NWT) or predator culls for boreal herds (e.g., Little Smoky herd, AB). Neither of these actions directly addresses the spatial needs of caribou. Addressing the spatial needs of boreal caribou would entail limiting extraction of commercially valuable natural resources and, consequently, billions of dollars of lost revenue.

Caribou and industry can coexist if large enough areas – tens of thousands of km^2 – are left free from anthropogenic disturbance (Vors *et al.* 2007), and substantial swaths of relatively undisturbed boreal forest still span parts of the NWT, Ontario and Québec. Such a trade-off seems unlikely, given society’s insatiable demand for boreal forest products. Societal priorities must shift from maximizing economic gain from the boreal forest to retaining undisturbed areas for caribou and other species, or else caribou may not be present for future generations. Thus, despite Caughley’s paradigm and the summation of this thesis, it is up to Canadian society to decide if and how caribou will persist on this landscape.

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