Responses of Arctic Caribou (*Rangifer tarandus*) to Changing Climate Conditions

by

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Abstract

The ability of species to adapt to the shifting environmental conditions associated with climate change will be a key determinant of their persistence in the coming decades. This is a challenge already faced by species in the Arctic, where rapid environmental change is well underway. Caribou and reindeer (*Rangifer tarandus*) play a key role in Arctic ecosystems and provide irreplaceable socioeconomic value to many northern peoples. Recent decades have seen declines in many *Rangifer* populations, and there is strong concern that climate change is threatening the viability of this iconic Arctic species. Here, I investigated several ways through which climate and climate change either affect or are predicted to affect caribou in the Arctic.

First, I reviewed the existing literature to provide a broad synthesis of the environmental factors that limit caribou and reindeer populations and how these might be affected by a warming climate. My review suggested that the response of *Rangifer* populations to climate change is, and will continue to be, varied in large part to their broad circumpolar distribution. Next, I investigated the relationships between broad climate patterns, summer-range quality, and population dynamics in three barren-ground caribou herds in northern Canada. Large-scale climate oscillations might contribute to the observed dramatic fluctuations and regional synchrony in *Rangifer* abundance, and I tested this hypothesis using long-term barren-ground caribou abundance and physical condition datasets. I found that positive intensities of the Arctic Oscillation (AO) in the summer were associated with warmer temperatures, improved growing conditions for vegetation, and better body condition of caribou. Over this same period, the body condition of female caribou was positively related to fecundity, and population trajectories of caribou herds followed the direction of the AO. These findings suggest that broad climate patterns can influence barren-ground caribou population dynamics through effects on summer-range quality, and that caribou might benefit from increased plant productivity during warmer summers associated with climate change.

However, the effects of climate change are complex and do not occur in isolation. For example, phenological shifts are occurring in many ecosystems around the world. Failure to adjust migratory and reproductive timing to keep pace with the earlier onset of spring has led to negative demographic effects for populations of species across a variety of taxa. I investigated the response of barren-ground caribou in the Qamanirjuaq herd to changing spring phenology from 2004 to 2016, and found that despite the advancing onset of spring, there was no evidence for the development of a trophic mismatch because the advancing green-up was outpaced by earlier migration and calving by caribou. Changing snow cover on the late winter and migratory ranges was the most-supported driver of advancing migratory behaviour. I next explored the effect of snow conditions on barren-ground caribou movement during spring migration and used a mechanistic movement model, integrated step-selection analysis, to estimate barren-ground caribou habitat selection across 194 individual spring migrations. I found that warmer mean spring temperatures leading to the earlier onset of spring snow melt negatively influenced caribou movement, and caribou travelled slower in years with highly variable melting and patchy spring snow conditions which led to longer time spent in migration.

Lastly, I used least-cost path analysis and circuit theory to model the effects of sea-ice loss on habitat connectivity for Peary caribou (*R. t. pearyi*), a subspecies that is widely dispersed across the islands of the Canadian Arctic Archipelago and relies on sea ice to move seasonally between island habitats. My results highlighted the critical role that some islands play in facilitating connectivity between Peary caribou populations, and that without rigorous greenhouse gas emission reductions my projections indicated that by 2100 all connectivity

between the more southern Peary caribou populations will be lost for important spring and early-winter movement periods. Although mitigating climate change at regional levels is challenging due to its global causes, climate change impacts to species might be moderated through conservation areas that allow species to adapt or adjust to changing conditions. My work used data-driven approaches to identify important areas for both the Qamanirjuaq migration and Peary caribou connectivity, and by permitting caribou to continue to use these areas undisturbed we might provide them with a better opportunity to adjust to rapid environmental change.

Preface

Some chapters in this thesis have been previously published. Chapter 2 has been published as “Mallory, C. D., & Boyce, M. S. (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews*, *26*(1), 13–25. https://doi.org/dx.doi.org/10.1139/er-2017-0032”. Conor Mallory performed the review and wrote most of the manuscript, and Mark Boyce provided advice and manuscript revisions.

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Chapters 4 and 5 have been submitted and currently undergoing peer review. The author list for both chapters is Mallory, C. D., Williamson, S. N., Campbell M.W., & Boyce, M.S. For both chapters Conor Mallory performed analysis and wrote most of the manuscripts. Scott Williamson performed analysis and provided advice and manuscript revisions. Mitch Campbell and Mark Boyce provided advice and manuscript revisions.

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Table of Contents

List of Tables

List of Figures

1 Introduction

Caribou (*Rangifer tarandus*), usually called reindeer in Europe, is a species of deer distributed broadly across the circumpolar world (Vors and Boyce 2009). Within the *R. tarandus* species there are several subspecies including barren-ground caribou (*R.t. groenlandicus*), boreal caribou (*R.t. caribou*), Peary caribou (*R.t. pearyi*), and Svalbard reindeer (*R.t. platyrhynchus*), which can be typically distinguished through combinations of morphology, behaviour, and ecology (Naughton 2012). In North America, caribou once ranged across most of Canada and Alaska but have been extirpated from large areas of their historic southern range, primarily due to habitat loss and degradation from industrial activity (McLoughlin et al. 2003; Vors et al. 2007; Festa-Bianchet et al. 2011).

Caribou and reindeer are an important part of northern boreal and tundra ecosystems (Festa-Bianchet et al. 2011). They are the most abundant large herbivore across their Arctic range and as such affect vegetation communities through herbivory (van der Wal 2006) and provide biomass for predator populations (Bergerud 1988; Dale et al. 1994). *Rangifer* are also significant socioeconomically, with subsistence harvesting by indigenous peoples and the herding of semi-domesticated reindeer providing food and income to communities across the north (Rees et al. 2008; Vors and Boyce 2009; Festa-Bianchet et al. 2011). Global declines in *Rangifer* abundance have given rise to concerns regarding how a changing climate might be affecting caribou and reindeer populations, and whether it might destabilize historically cyclical caribou population dynamics (Vors and Boyce 2009). The overall objective of this thesis was to improve our understanding of potential current and future impacts of climate change on Arctic caribou, with specific focus on several populations in Nunavut, Canada.

The relationships between environmental conditions, climate, and *Rangifer* populations have been the subject of many studies and in some cases offer conflicting projections for how *Rangifer* might respond to changing climate. For example, some of the most well documented effects of Arctic and global change on terrestrial ecosystems have been "greening" and shrubification of the tundra (Myers-Smith et al. 2011; Yu et al. 2017), along with advancement in the phenology of plants and animals (Parmesan and Yohe 2003; Cleland et al. 2007; Post et al. 2018). Changes in climate that lead to higher productivity of tundra plants could benefit caribou by increasing forage the biomass available in summer, however these warmer temperatures could also increase biting fly harassment (Witter et al. 2012b) and reduce forage quality (Turunen et al. 2009). The first objective of my research was to review and synthesize existing literature on relationships between climate conditions and *Rangifer* to provide a thorough exploration of the many environmental factors that limit and regulate caribou and reindeer populations, and how these might be affected by a warming climate.

Although there is broad agreement that historically barren-ground caribou populations have fluctuated cyclically over decadal timescales, the drivers of these cycles remain unclear (Bergerud 1996; Gunn 2003). Both bottom-up and top-down mechanisms, as well as stochastic weather events, have been suggested to limit and regulate Arctic *Rangifer* populations (Klein 1991; Bergerud 1996; Solberg et al. 2001; Miller and Gunn 2003a; Tveraa et al. 2007). The observed synchrony between abundance trends in some populations across large geographic areas has implicated broad climate patterns such as the Arctic Oscillation, North Atlantic Oscillation, and Pacific Decadal Oscillation as important factors in caribou population dynamics (Aanes et al. 2002; Joly et al. 2011; Mallory et al. 2018a). These climate patterns have been suggested to influence regional vegetation productivity and availability and thus affect caribou fecundity and calf survival (Gunn 2003; Festa-Bianchet et al. 2011; Joly et al. 2011). Regional climate oscillations also might temper climate change effects and the associated responses of caribou populations (Joly et al. 2011). The Bathurst, Beverly, and Qamanirjuaq are three migratory barren-ground caribou herds that have exhibited relatively synchronous population trends from the 1980s to present (Mallory et al. 2018a). The second objective of my research was to assess whether large-scale climate patterns, in this case the Arctic Oscillation, can be linked to the synchrony in population dynamics of these three herds.

The third objective of my research was to test whether certain climate change signals could be identified on the range of the Qamanirjuaq herd, and if so, determine if and how these changes might be affecting reproductive, migratory, and movement behaviours. Altered phenology is one of the most frequently observed consequences of climate change (Parmesan 2006), and one of the key concerns regarding changing phenology is the development of phenological or trophic mismatches. A trophic mismatch can occur when species at different trophic levels have unequal responses to changing environmental conditions, resulting in a loss of synchrony between the peak resource requirements of the higher trophic level and peak availability of the lower level (Durant et al. 2007). Post and Forchhammer (2008) reported that the development of a trophic mismatch between caribou parturition and spring green-up had reduced the reproductive success of a caribou population in Greenland. In contrast, several other studies of caribou in Alaska (Gustine et al. 2017) and reindeer in Norway (Tveraa et al. 2013; Veiberg et al. 2017) have found no evidence for the development of a trophic mismatch between *Rangifer* parturition and spring green-up. Due to the broad circumpolar distribution of *Rangifer* and the variety of habitats and environmental conditions different populations inhabit, it is reasonable to expect variable responses to climate change across populations (Mallory and

Boyce 2018). In chapters four and five of this thesis I analyse spring green-up and snow melt to investigate changing spring phenology on the Qamanirjuaq herd's range, and use telemetry from tracked caribou to determine how changing phenology affects caribou movement behaviours.

Peary caribou, North America's most northerly ranging *Rangifer* subspecies, are thought to be particularly vulnerable to climate change. These caribou experience occasional population crashes resulting from starvation following icing or heavy snow events that render forage inaccessible under a thick layer of ice (Miller and Gunn 2003b). Extreme weather events, including those that lead to icing, are anticipated to become more frequent with climate change (Tews et al. 2007a). Another concern for Peary caribou is that declining sea ice coverage and a longer ice-free season will reduce connectivity between island habitats, with consequences for genetic variability and the ability of individuals to escape extreme weather events (Jenkins et al. 2016). In chapter 6, I used sea ice projections, least-cost path analysis, and circuit theory to model landscape connectivity across the Canadian Arctic Archipelago under several future climate scenarios. These models were then used to identify islands and sea ice corridors that contribute most to maintaining connectivity across Peary caribou range.

2 Observed and predicted effects of climate change on Arctic caribou and reindeer

2.1 Introduction

Caribou and reindeer (both *Rangifer tarandus*) have great ecological and socioeconomic importance. *Rangifer* is the most abundant large terrestrial herbivore across the circumpolar world, playing a key role in northern ecosystems through grazing effects on plant communities and by supporting predator populations (van der Wal 2006; Musiani et al. 2007; Bernes et al. 2015). Socioeconomically, caribou and reindeer are a major component of the subsistence harvest by indigenous peoples (Wolfe and Walker 1987; Wolfe 2004; Kendrick et al. 2005). Indigenous and local people also herd domesticated and semi-domesticated reindeer across northern Eurasia (Moen 2008; Rees et al. 2008; Turunen et al. 2016) and North America (Lantis 1950; Klein 1970), and *Rangifer* populations provide socioeconomic means to at least 20 indigenous peoples across the circumpolar world (Uboni et al. 2016).

Many *Rangifer* populations are reported to be in decline globally (Vors and Boyce 2009; Festa-Bianchet et al. 2011), although there are exceptions (Gunn et al. 2009; Joly et al. 2011; and see Uboni et al. 2016 for long-term trends in Eurasian reindeer populations). Though large-scale fluctuations in *Rangifer* abundance are characteristic of the species (Gunn 2003), the decline of many populations concurrent with Arctic warming has precipitated concern for the future status of the species and for the associated socioeconomic consequences. At the same time, substantial research effort has developed to study the global effects of climate change, with considerable work going into Arctic species and ecosystems. The current effects of climate change in the Arctic have been well documented (Post et al. 2009) and future projections anticipate continued and dramatic changes (Lawler 2009; IPCC 2014).

Climate change is predicted to affect *Rangifer* populations both positively and negatively through a variety of mechanisms, including increased wildfire activity on winter ranges, increased summer insect harassment, changing forage quality and quantity in the summer and winter, increased icing events in winter, changing spring phenology, and changes to distributions and migratory behaviour (Sharma et al. 2009; Joly et al. 2012; Witter et al. 2012b; Loe et al. 2016; Albon et al. 2017; Le Corre et al. 2017). The extensive distribution of *Rangifer* globally (Fig. 2.1), with different subspecies occupying a relatively diverse range of habitats, presents difficulty in generalizing how climate change effects will be realized across populations. On top of this, variability and complexity in climate patterns further serve to complicate the observed heterogeneity in climate change effects (e.g., Joly et al. 2011).

Here, we review the observed and predicted effects of climate change on Arctic caribou and reindeer. Previous work has reviewed some specific aspects of climate change and *Rangifer* (Heggberget et al. 2002; Weladji et al. 2002; Moen 2008; Joly et al. 2009; Tyler 2010), or discussed climate change among other threats to *Rangifer* (Vors and Boyce 2009; Festa-Bianchet et al. 2011), and our intent is to build and expand on these previous reviews with recent studies and a discussion of climate change impacts on *Rangifer* as a whole.

Rangifer tarandus is the sole species of the genus, but there are numerous subspecies and ecotypes. Subspecies found in North America are typically referred to as caribou, and those found in Eurasia as reindeer. We term Arctic caribou and reindeer populations as those that spend part or all of the year above 60°N. In particular, we focus on barren-ground caribou (*R.t. groenlandicus, R.t. granti*), Peary caribou (*R.t. pearyi*), Svalbard reindeer (*R.t. platyrhynchus*), reindeer (*R.t. tarandus, R. tarandus*) in Scandinavia and northern Eurasia, and caribou (*R.t. caribou*) in northern Quebec and Labrador, Canada. We divide our review into five categories: i) summer range conditions, ii) parasites and disease, iii) movement, migration, and distribution, iv) extreme weather and icing events, and v) winter range quality. Finally, we provide discussion of how these effects may interact.

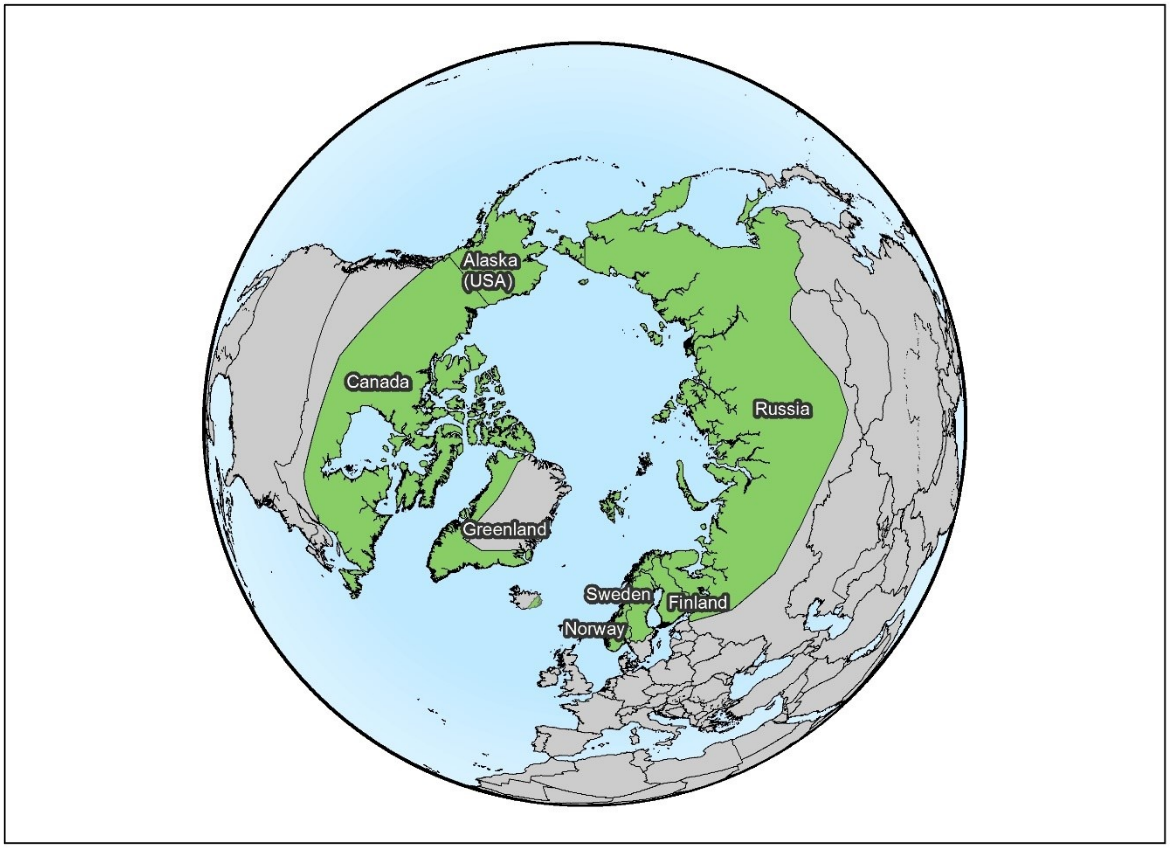

Fig 2.1 Approximate global distribution of caribou and reindeer (*Rangifer tarandus*).

2.2 Summer range conditions

Summer is a critical foraging period for *Rangifer* populations. During the brief period of high-quality green vegetation in the Arctic summer, caribou and reindeer must forage effectively to recover from the nutritional stress of the previous winter (Gerhart et al. 1996; Parker et al. 2009; but there are some examples of caribou gaining fat over winter, e.g., Couturier et al. 2009) and to build fat reserves and body condition in anticipation of upcoming food constraints over the next winter (Mörschel and Klein 1997). During the summer, lactation by females places additional energetic demands on cows (Parker et al. 1990, 2009; Barboza and Parker 2008) that must be met through adequate nutrition (Gerhart et al. 1996). Males must also be able to forage sufficiently to build the necessary body reserves for the fall rut (Skoog 1968; Barboza et al. 2004). Availability of quality summer forage has been linked, through improved body condition, to positive effects on fecundity for *Rangifer* (Reimers 1983; Cameron et al. 1993; Gerhart et al. 1997; Pachkowski et al. 2013). Conversely, poor summer forage conditions are associated with reductions in life-history traits and increased overwinter mortality (Crête and Huot 1993; Gerhart et al. 1996; Sharma et al. 2009). Anticipating how climate change might influence summer vegetation quality and the access of *Rangifer* populations to it is central to conceptualizing how the effects of a changing climate may be realized in caribou and reindeer.

The life histories of many species have evolved such that the timing of high energetic or nutritional requirements, such as parturition and lactation in *Rangifer*, coincide with the timing of peak nutrient availability in forage species (Klein 1990; Post and Klein 1999; Stenseth and Mysterud 2002; Post et al. 2003). A disruption in synchronous events across trophic levels can result from incongruent responses to environmental changes between these trophic levels. Specifically for the case of herbivores, a trophic mismatch could arise should the annual timing of plant emergence advance with warming temperatures and earlier snowmelt while the timing of calving remains consistent or advances at a slower rate. This divergence from phenological synchrony is often referred to as a trophic mismatch, phenological mismatch, or a match-mismatch (Stenseth and Mysterud 2002; Parmesan 2006; Durant et al. 2007; Doiron et al. 2015). These mismatches decouple the association between the availability of highly nutritious stages of forage plants and the timing of high-nutritional demands for lactation, hypothetically leading to negative effects on animal body condition and with accompanying influences on reproduction and survival (Parmesan 2006; Post and Forchhammer 2008). Phenological mismatches, and their resultant negative consequences for reproduction, have been reported in a wide range of species (Donnelly et al. 2011) and are predicted to be more likely to develop and have more severe effects in long-distance migrants (Both et al. 2010). Post and Forchhammer (2008) first reported evidence of a trophic mismatch in a *Rangifer* population and its apparent negative impact on reproduction. They described a decline in reproductive success in a West Greenland caribou population that occurred concurrently with a divergence in timing of calving and the emergence of forage species (the period of peak nutrient availability as defined by in plant nitrogen concentration). These findings led to consideration of whether the developments of trophic mismatches between the parturition of caribou populations and the phenology of vegetation on their calving grounds might be contributing to the global decline in *Rangifer* populations (Vors and Boyce 2009).

However, further explorations into the development of phenological mismatches for caribou and reindeer have not supported the generality of this phenomenon. Studies from Tveraa et al. (2013), Veiberg et al. (2017), and Gustine et al. (2017) found no evidence of a trophic mismatch between the onset of spring vegetation and *Rangifer* reproductive success in reindeer populations in northern Norway, Svalbard, or Alaskan caribou, respectively. In fact, it is characteristic of Arctic *Rangifer* populations to calve before spring green-up occurs. Tveraa et al. (2013) noted that the reindeer they studied calved two to four weeks before the onset of spring.

Gustine et al. (2017) reported that growing season had not begun in 1977 or in 2011-2013 at the timing of parturition and that key forage species did not emerge until 4-11 days after parturition dates of the Central Arctic Herd. A number of other studies further corroborate the timing of parturition as occurring well before the emergence of vegetation (Fleck and Gunn 1982; Reimers et al. 1983; Crête and Huot 1993; Veiberg et al. 2017).

Both Veiberg et al. (2017) and Gustine et al. (2017) noted that because caribou and reindeer are capital breeders (Taillon et al. 2013), it is expected that the influence of spring phenology should be less important than that of maternal winter body condition on reproductive success. Reliance on maternal body stores for foetal development rather than dietary income may mitigate negative effects of changing phenologies (Stephens et al. 2009; Gustine et al. 2017; Veiberg et al. 2017). As previously noted, it has been well documented that many *Rangifer* populations calve before the onset of vegetation growth, reinforcing the importance of maternal capital for reproduction (Barboza and Parker 2008) and in some ways curtailing the conceptual potential for spring phenological mismatches. Gustine et al. (2017) suggested that due to the reliance of *Rangifer* on maternal capital, it might be more useful to consider potential mismatches arising in the late summer and fall when cows build nutritional stores to finance reproduction (Thompson and Barboza 2014), rather than at parturition.

In contrast to the original concern surrounding the negative effects on caribou and reindeer stemming from phenological mismatches, a growing number of studies indicate that early onset of spring could benefit some *Rangifer* populations by providing earlier access to high-quality forage (Cebrian et al. 2008), which can supplement the high nutritional costs of parturition and lactation and positively affect calf body condition (Pettorelli et al. 2005; Helle and Kojola 2008; Couturier et al. 2009b; Tveraa et al. 2013).

Changes to the onset of spring also serve to increase the length of the growing season. Predicted increases in growing season length and primary productivity in the Arctic are expected to generally benefit *Rangifer* (Tews et al. 2007b; Sharma et al. 2009; but see also notes on forage quality in Turunen et al. 2009), owing to the previously examined relationship between body condition and reproduction. Changes to Arctic primary productivity are anticipated to be dramatic. Epstein et al. (2000) predicted climate warming to result in large increases in plant biomass in high and low Arctic regions, along with altered plant community composition. More recent studies also predict dramatic changes, with Pearson et al. (2013) suggesting increases of 29-68% in above ground biomass in the Arctic by 2050 and an expansion of woody cover in the Arctic of up to 52%. This increase in productivity results from warming temperatures, as well as lengthened growing seasons and greater nutrient availability from faster decomposition rates (van der Kolk et al. 2016; Yu et al. 2017). Along with predicted effects of climate change, many studies have documented current increasing trends in primary productivity in the Arctic (e.g., Fraser et al. 2011; Elmendorf et al. 2012; Ju and Masek 2016) occurring in parallel to changing plant community composition. Shrub species, such as birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.) are expanding the northern extent of their range (Sturm et al. 2001; Hallinger et al. 2010; Myers-Smith et al. 2011; Naito and Cairns 2011; Frost and Epstein 2014) and reducing species richness on the tundra (Pajunen et al. 2012). However, increases in shrub cover have thus far not been uniform, with substantial heterogeneity in the local response to warming across the Arctic (Myers-Smith et al. 2015). Further, grazing pressure can affect local variation in shrub expansion, and so local and regional densities of ungulates may influence patterns of shrub expansion (Pajunen et al. 2012; Ravolainen et al. 2014; Christie et al. 2015; the potential influence of shrub expansion on the abundance of other ungulate and predator species will be discussed in a later section).

Increased productivity has documented positive effects for caribou and reindeer. From 1994 to 2015 October body mass in Svalbard reindeer increased as a result of greater plant productivity (Albon et al. 2017), which can be linked to warmer summer temperatures (van der Wal and Stien 2014). The benefit of increased summer plant productivity on *Rangifer* condition and reproduction is substantiated by studies from across their pan-Arctic range, correlating summer forage availability to body condition, fecundity, and population growth (Crête and Huot 1993; Gerhart et al. 1996; Pettorelli et al. 2005; Couturier et al. 2009b; Tveraa et al. 2013). The effects of changing plant community composition may add complexity to these observed relationships by altering the typical quality of *Rangifer* summer diets. Woody plants (e.g., shrubs) have greater chemical and structural defenses against herbivory and lower available protein than other typical summer forage, such as grasses, forbs, and sedges (Thompson and Barboza 2014). Higher concentrations of secondary metabolites, such as phenols and tannins, can reduce digestible energy (Lawler and White 2006) and protein availability (McArt et al. 2009) in forage. Hence, increasing abundance of woody plants in Arctic environments might have negative nutritional consequences for *Rangifer* (Lawler and White 2006; Bryant et al. 2014; Thompson and Barboza 2014), and this changing resource availability might necessitate altered habitat selection by animals to address dietary requirements (Thompson and Barboza 2014).

Beyond changes in forage quality related to plant community composition, warmer summers may also have impacts to the nutritional quality of *Rangifer* forage. Increased summer temperatures have been reported to decrease nitrogen concentration in forage species (Bø and Hjeljord 1991; Michelsen et al. 1996; Lenart et al. 2002; Hansen et al. 2006) through dilution effects within plants caused by increased net carbon production (Turunen et al. 2009). This relationship is not consistent across studies, however, as other experiments have reported increased nitrogen concentration in forage species when grown in warmer conditions (Richardson et al. 2002). There are several potential reasons for these discrepancies, including diverse responses across species, and different soil and bedrock conditions where the experiments were conducted (Turunen et al. 2009). In addition to the effects of temperature on forage quality, rising atmospheric greenhouse gas concentrations are predicted to increase surface UV-B radiation (Taalas et al. 2000) with a broad array of potential effects for organisms (Callaghan et al. 2004). For *Rangifer* forage species, increases in UV-B radiation can reduce forage quality by increasing concentrations of phenolics and other secondary compounds (Soppela et al. 2006; Rinnan et al. 2008; see review by Turunen et al. 2009), thereby reducing digestible energy and available protein (Lawler and White 2006; McArt et al. 2009; Turunen et al. 2009). Changes in forage quality are expected to vary regionally (Hansen et al. 2006; Turunen et al. 2009), and this variation will likely be significant for how well *Rangifer* populations are able to cope with other environmental changes due to the multiplier effects of forage quality on *Rangifer* condition and populations (White 1983; Cebrian et al. 2008).

2.3 Parasites and disease

Harassment by parasitic insects is a key driver of Arctic caribou behaviour, movement, and body condition during summer. Warble flies (*Hypoderma tarandi*) and nose botflies (*Cephenemyia trompe*), both of the family *Oestridae*, are the predominant source of harassment for Arctic caribou (Downes et al. 1986) and reindeer (Anderson et al. 2001; Hagemoen and Reimers 2002), though mosquitoes (*Culicidae*), blackflies (*Simuliidae),* and horseflies (*Tabanidae*) also are known to attack *Rangifer* (Hagemoen and Reimers 2002). The response of

Rangifer to oestrid harassment is dramatic, with individuals often exhibiting panicked and violent movements. Spontaneous running and jumping by individuals can disrupt the behaviour of herds, which may travel erratically for long periods to seek refuge from the fly harassment (Hagemoen and Reimers 2002). In Norway, Hagemoen and Reimers (2002) observed reindeer running for hours seeking relief from harassment, with only occasional and brief pauses to forage. On days with severe oestrid harassment, the authors observed reindeer running from harassment in the morning until late in the evening. *Rangifer* seek relief from insect harassment on windy hilltops, on snow patches, and in other unproductive areas (Downes et al. 1986; Ion and Kershaw 1989; Walsh et al. 1992; Toupin et al. 1996). The deleterious effects of parasitic insects are twofold. There are, of course, the direct effects of the parasitic burden that results from successful parasite attacks, with increasing parasite load in an individual associated with decreasing body condition and reproduction (Thomas and Kiliaan 1990; Albon et al. 2002; Hughes et al. 2009; Ballesteros et al. 2012; Cuyler et al. 2012; Pachkowski et al. 2013). Second, the behavioural response of *Rangifer* to insect harassment is detrimental to individuals through a reduction in time spent foraging and increased energy expenditure (Downes et al. 1986; Ion and Kershaw 1989; Mörschel and Klein 1997; Hagemoen and Reimers 2002; Skarin et al. 2010; Witter et al. 2012a). These behavioural responses can result in reduced body condition going into the winter (Helle and Tarvainen 1984; Helle and Kojola 1994; Weladji et al. 2003), with negative implications for survival and fecundity (Thomas and Kiliaan 1998a).

The period of intense insect harassment in the Arctic is limited by environmental conditions, such as temperature, wind, and precipitation (Downes et al. 1986). Historically, this has meant that there are periods of the Arctic summer and fall that have little to no parasitic insect harassment, due to the brief period of temperatures conducive to activity of parasitic species. As the climate changes and annual temperatures warm, the period of insect harassment is predicted to increase (Brotton and Wall 1997; Callaghan et al. 2004; Witter et al. 2012b), perhaps with serious costs to caribou. Studies have suggested that observed links between warmer summers and poorer body condition of caribou is related to the increased level of insect harassment associated with warmer temperatures (Helle and Tarvainen 1984; Klein 1991; Mörschel and Klein 1997; Hagemoen and Reimers 2002; Weladji et al. 2003). Longer and warmer summers could then produce a negative response in caribou condition because the season would have more abundant and active parasitic insects. However, there is also some suggestion that increased summer precipitation and cloudier weather resulting from climate change could reduce insect harassment of caribou and reindeer (Heggberget et al. 2002), at least in some areas. This again identifies the importance of the local and regional effects of climate change.

Caribou and reindeer may compensate for foraging time lost due to insect harassment by increasing grazing behaviour during times when harassment is low (i.e., in the evening), or later in the summer when the insect season has ended (Skogland 1984; Downes et al. 1986). However, when Colman et al. (2003) tested this idea, they found that reindeer did not increase grazing time in the evening to compensate for reduced grazing on days when insect harassment was greater. Similarly, Witter et al. (2012b) found no compensatory grazing by caribou after days when foraging opportunities were lost to insect harassment.

Over seasonal time scales, the potential for *Rangifer* to compensate for the lower food intake and increased energy expenditure resulting from insect harassment by increasing the time spent grazing later in the season is contingent on adequate time and forage quality following the termination of the insect season. Longer periods of insect activity resulting from a warming climate will have consequences for the length of time *Rangifer* can spend foraging unhindered by parasitic flies.

Climate change is also predicted to increase parasitism of *Rangifer* by other taxa, such as protozoans and helminths. Warming temperatures are predicted to alter the geographic distribution, transmission rates, host-parasite assemblages, and life-cycle phenologies of pathogens (Harvell et al. 2002; Kutz et al. 2004, 2005; Polley and Thompson 2009; Simard et al. 2016), and in some cases, the northern expansion of parasitic species have already been observed (Laaksonen et al. 2010; Kutz et al. 2013). Arctic ecosystems are vulnerable to invasions by exotic species, including parasites, due to a number of factors. In comparison to more southerly regions, biodiversity is typically low, which increases the susceptibility of the ecosystem to invasions, and cold-adapted Arctic species may lose their competitive advantage to potential invaders as the climate warms (Kutz et al. 2009; Polley and Thompson 2009; Davidson et al. 2011).

Parasitic burdens influence wildlife species at the individual and population levels, and parasites have been reported to regulate *Rangifer* population densities (Albon et al. 2002; but see Tompkins et al. 2011). Epizootics have been observed in both wild caribou and domesticated reindeer populations (Ball et al. 2001), and the climate-mediated introduction of novel parasites to naïve wildlife populations could present conditions for epidemic disease outbreaks (Davidson et al. 2011). Changes to the intensity of parasitic infection, along with the potential introduction of novel parasites and pathogens, have the prospect to cause serious individual and population effects to vulnerable *Rangifer* populations. The possibility for environmental conditions to increase the abundance and diversity of *Rangifer* pathogens, in concert with the reduced physical condition of *Rangifer* caused by the other mechanisms discussed herein, may have a compounding detrimental effect on populations. Animals in poorer condition tend to be more susceptible to parasitic infection, and the physiological costs of infection can further deteriorate body condition, creating a cycle of infection (Beldomenico and Begon 2009; Tompkins et al. 2011).

2.4 Movement, migration, and distribution

The movement patterns and behaviour of animals are fundamental characteristics of life that shape features of populations and ecosystems (Nathan et al. 2008). Many caribou populations undertake annual long-distance movements between summer and winter ranges to avoid predation during the calving period (Bergerud 1988, 1996; Heard et al. 1996), and to take advantage of emergent vegetation on the tundra (Klein 1970, 1992; Skogland 1984; Heard et al. 1996). The value and purpose of this migratory behaviour, developed over evolutionary timescales, is at risk because of a rapidly changing environmental baseline (Robinson et al. 2009). We have previously discussed the implications of phenological mismatches on forage availability and nutrition, but potential impacts of climate change on *Rangifer* migratory behaviour exist beyond the calving ground.

Many migratory (and non-migratory) caribou populations use ice for movement during the winter (Miller and Gunn 1986; Miller et al. 2005). Some, such as the Dolphin and Union population and Peary caribou, migrate across the sea ice between seasonal ranges (Miller et al. 1977; Poole et al. 2010), while others prefer moving across frozen lakes and rivers for ease and directional persistence of movement, and increased visibility of predators (Pruitt 1959; Sharma et al. 2009; Leblond et al. 2016). Warming surface temperatures will, and already are, changing the annual timing of both sea ice (Poole et al. 2010) and freshwater ice (Latifovic and Pouliot 2007; Sharma and Magnuson 2014) formation and break-up. A reduction in the availability of ice suitable for movement (i.e., ice that can support the weight of caribou or reindeer) along the migratory paths of *Rangifer* populations, or conversely an increase in thin ice and open water, could have deleterious consequences for migratory behaviour. For example, Leblond et al. (2016) studied the influence of ice on the movements of caribou of the Rivière-aux-Feuilles herd in northern Québec, Canada. They reported that caribou tended to select ice and avoid water when crossing or moving near large water bodies, and further that ice increased caribou movement rates. Simulations predicted that for the Rivière-aux-Feuilles herd, as much as 36% of ice crossings during the spring and fall migrations could be lost by 2070 (Leblond et al. 2016). Loss of ice crossings would likely increase the distance travelled during migrations because the migratory path would skirt water bodies rather than cross them (Leblond et al. 2016), thereby increasing the energetic cost of migration.

Although they tend to avoid water during migration (Leblond et al. 2016; Fullman et al. 2017), caribou are adept swimmers (Miller 1995; Avgar et al. 2013). Based on behavioural observations, they are likely familiar with breaking through thin ice and are certainly able to survive these events (Miller and Gunn 1986). Nonetheless, breaking through the ice still presents a fatal risk to caribou (Miller and Gunn 1986; Miller et al. 2005) and increased frequency of these events caused by changes in the phenology of ice formation and break-up due to climate change enhances the risk of mortality.

Other conditions along the migratory route that affect the timing and duration of caribou migrations are also subject to the influence of climate change. The energetic cost of locomotion of an animal is dependent on the characteristics of the surface over which they are travelling.

Deep snow increases the energetic cost of locomotion and slows movement (Fancy and White 1987a; Nicholson et al. 2016), and caribou tend to select areas with lower snow depth for ease of movement and better access to forage (Duquette 1988; Johnson et al. 2001). The migratory patterns of caribou are integral to their life history and show substantial flexibility in response to environmental conditions, particularly respecting snow conditions and temperature (Nicholson et al. 2016; Le Corre et al. 2017). Le Corre et al. (2017) reported earlier spring migration departure dates following mild winters and delayed migrations when snowfall was abundant in April. They suggested that caribou might begin migrations early following mild winters to avoid poor snow conditions (i.e., melting snow that may be more difficult to move through) during migration, and that caribou may use cues from the weather (e.g., mild winters, amount of precipitation) to predict conditions along the migration route and adjust their departure dates accordingly. Although this offers some indication that caribou are able to modify their migratory behaviour in response to climate change (see also Post and Forchhammer 2008), variable conditions along the migratory route may limit the usefulness of this ability because earlier departure dates in winter did not necessarily correspond to earlier spring arrival (Le Corre et al. 2017).

For those *Rangifer* populations that move across sea ice, the challenges associated with altered ice phenologies could be greater. The Dolphin and Union herd migrates from its summer and fall range on Victoria Island to the Canadian Arctic mainland as sea ice forms in the early winter and back across the sea ice again in the late winter or early spring (Poole et al. 2010). Because the movement of the Dolphin and Union herd to their winter range is contingent upon ice formation, significant changes to ice phenology in this area would be directly reflected in changes to migratory behaviour. Sea ice between Victoria Island and the mainland formed 8 to 10 days later over the period from 1982 to 2008 (Poole et al. 2010). The short-term effects of delayed sea ice formation are largely limited to mortality associated with caribou trying to cross ice that is too thin (Miller and Gunn 1986; Miller et al. 2005; Poole et al. 2010). Over the longer term, however, a lengthened ice-free season (Comiso 2002; Comiso et al. 2008) could disrupt the migratory behaviour of *Rangifer* populations that cross sea ice during seasonal migrations associated with life history events, such as calving (Joly 2012). Longer-term implications for range degradation also are possible, by restricting grazing pressure to a smaller portion of the annual range (Miller et al. 2005; Poole et al. 2010).

Peary caribou populations range near the northern edge of viability for herbivores because their habitat approaches the climatic limits for plant growth (Miller and Gunn 2003b). Peary caribou rely on seasonal movements between High Arctic islands to reduce grazing pressure during periods of high caribou density and to maintain an adequate supply of forage on islands that serve as both summer and winter range (Miller et al. 1977). These movements between islands allow individuals to optimize grazing opportunities by selecting the best seasonal ranges during periods of poor environmental conditions and possibly to reduce predation risk from wolves (Miller 2002). Changes in ice phenology could reduce the connectivity of the Peary caribou inter-island range, and thus diminish their ability to use this range flexibly to mitigate the effects of their harsh environment. This could effectively reduce the size of Peary caribou range, limiting population growth and raising vulnerability to extreme weather events. The loss of range connectivity may also increase the genetic isolation of Peary caribou, with implications for population viability (Jenkins et al. 2016).

Climate change also can influence the range and distribution of other *Rangifer* subspecies. Changes to habitat, whether from anthropogenic (e.g., industrial development, roads) or natural disturbances (e.g., fire) can lead to distributional or range shifts in wildlife populations. Similarly, changes to habitat resulting from altered climate regimes can cause animals to modify their distributions, often northward (Parmesan and Yohe 2003). *Rangifer* populations, particularly those that are migratory, may be susceptible to these types of climate effects because their seasonal distributions take advantage of traditional climate gradients that may be substantially transformed in the future. Using climate and habitat models, Sharma et al. (2009) predicted the future distributions of two migratory caribou populations (the Rivière George herd and the Rivière-aux-Feuilles herd) in Quebec and Labrador, Canada. They found that the range of both herds is anticipated to shift northward, but the Rivière George herd, except during the fall, is likely to experience significant range contraction throughout the year, while the range of the Rivière-aux-Feuilles herd might expand under climate change. These distributional shifts could have a compounding effect on caribou populations because changes to herd ranges could lead to changes in abundance (Sharma et al. 2009), and range contraction has also been observed to coincide with decreases in population size (Bergerud et al. 2008).

Changes to snow patterns in southern Norway may lead to range shifts of reindeer populations and a transition to more sedentary behaviour (Heggberget et al. 2002). *Rangifer* populations that typically display sedentary behaviour also might exhibit distributional shifts resulting from a reduction in habitat quality, as has been described for a population of caribou on Baffin Island, Canada (Ferguson and Messier 2000; Ferguson et al. 2001). Although the distributional changes of *Rangifer* populations can have demographic effects, these populations also might be affected by the range expansions of other species. The northern expansion of ungulate species, such as moose (*Alces alces*) (Norment et al. 1999) and white-tailed deer (*Odocoileus virginianus*) (Veitch 2001; Dawe and Boutin 2016) could increase interspecific competition for certain forage species and introduce novel pathogens to *Rangifer* populations

(Kutz et al. 2009). For example, increases in productivity on the tundra and more frequent wildfire activity (which increases the proportion of immature to mature forests) on migratory caribou winter ranges (see section below) is predicted to improve habitat quality for moose and resultantly increase their abundance on caribou ranges (Sharma et al. 2009; Joly et al. 2012).

Though other ungulates might not directly compete for forage species, the greater range overlap between these species could also support higher-density predator populations. Increases in alternate prey has on caribou ranges been shown to increase predator abundance resulting in apparent competition (Latham et al. 2011; Boutin et al. 2012). Wolves (*Canis lupus*) that follow and prey on migratory barren-ground caribou typically den near the tree line and give birth to pups in late May and early June (Heard and Williams 1992). During the denning period wolf movements are limited because pups cannot travel long distances from their dens (Klaczek et al. 2016). Reduction of predation risk from wolves, particularly to vulnerable calves, has thus been suggested as one of the drivers of caribou migrations to calving grounds on the tundra (Bergerud 1988, 1996). The changing habitat composition and northern advance of non-migratory ungulates could sustain increased resident wolf populations farther north, potentially reducing the effectiveness of caribou migratory strategies to avoid predation during calving (Bergerud 1988, 1996; Sharma et al. 2009).

2.5 Extreme weather and icing events

Many studies have investigated the relationship between winter conditions and *Rangifer* populations. Of particular interest have been extreme weather events leading to icing, or "locked-pastures", on the winter range. Restricted or total loss of access to forage through icing of the winter range can have severe fitness consequences and sometimes be fatal for herbivores. Hansen et al. (2011, 2014) and Tyler (2010) provided thorough discussions of the relationship between climate, snow, ice, and *Rangifer* population dynamics and declines, and so we will only review this topic briefly to provide context for a more holistic consideration of the suite of potential climate change effects on *Rangifer* populations.

Basal ice layers in the snowpack during winter can result from several mechanisms, including rain-on-snow events, cyclical thawing and freezing of the snowpack, and meltwater running through the snowpack and freezing against the ground (Tyler 2010 and references therein). In the winter, *Rangifer* often dig, or crater, in snow to access the forage beneath, the energetic cost of which is dependent upon the depth and physical characteristics of the snow (Fancy and White 1985). The formation of these basal ice layers encases the vegetation below the snowpack in ice, rendering it inaccessible to *Rangifer*. Icing events, which result in malnutrition and starvation, have been associated with catastrophic die-offs of *Rangifer* (but see Tyler 2010) and other ungulates (Forchhammer and Boertmann 1993; Putkonen and Roe 2003). These events have particular significance in the High Arctic among Peary caribou (Miller and Gunn 2003b; Tews et al. 2007a; Miller and Barry 2009; Langlois et al. 2017) and Svalbard reindeer (Kohler and Aanes 2004; Hansen et al. 2014), but have also been observed in semi-domesticated reindeer populations in Scandinavia (Heggberget et al. 2002; Putkonen and Roe 2003) and Russia (Bartsch et al. 2010; Forbes et al. 2016). Non-catastrophic rain-on-snow and icing events have negative associations with body condition (Bartsch et al. 2010; Loe et al. 2016) and reproductive success (Helle and Kojola 2008; Stien et al. 2012) in caribou and reindeer. Increased rainy and icy conditions in winter have also been linked to changes in the adult sex ratio of Svalbard reindeer (Peeters et al. 2017), due to the differential effects of these winter conditions on the survival of the adult male and female segments of the population.

An increased frequency of extreme weather events, such as rain-on-snow, is an anticipated outcome of climate change and is predicted to negatively affect many Arctic species (Putkonen and Roe 2003; Rennert et al. 2009). The population dynamics of Peary caribou and Svalbard reindeer are driven by a combination of stochastic weather events and density-dependent effects (Aanes et al. 2000; Solberg et al. 2001; Tews et al. 2007b; Miller and Barry 2009; Tyler 2010), and greater frequency of extreme weather events could dramatically alter the normal dynamics of these populations. Svalbard reindeer have been reported to adapt behaviourally to icing events by moving from their ice-locked home range in search of more favourable foraging conditions (Hansen et al. 2010; Stien et al. 2010), and this behaviour appears to provide benefits to fitness correlates (Loe et al. 2016). However, more numerous rain-on-snow and thaw and refreeze events during the winter could result in both longer periods of forage inaccessibility, but also larger areas being affected, potentially reducing available forage refugia for *Rangifer* and the effectiveness of observed behavioural plasticity (Stien et al. 2010; Wilson et al. 2013a).

2.6 Winter range conditions

The migratory behaviour of many barren-ground caribou populations is characterized by large-scale movements between summer to winter ranges. Some populations have both summer and winter ranges on the tundra, while others migrate from summer ranges on the tundra to winter ranges in the boreal forest (Festa-Bianchet et al. 2011). During the winter months, caribou forage primarily on terricholous lichen mats (Scotter 1967; Thomas and Hervieux 1986; Jandt et al. 2008), which are readily digested by caribou and are high in energy relative to other available forage (Thomas and Hervieux 1986). These lichen mats are generally considered to be highly flammable (Sylvester and Wein 1981), presenting a susceptibility of this important forage to destruction from wildfire.

Communities and researchers have long raised concerns regarding the negative effects of forest fires on the winter ranges of barren-ground caribou (Klein 1982; Thomas and Kiliaan 1998b), and many studies have investigated fire-caribou relationships. Over time, research has led to opposing views on the significance of the effects of fire on migratory caribou (Bergerud 1974; Klein 1982), although at present there is general agreement in the literature that wildfire is detrimental to caribou winter range. At the population level, caribou tend to avoid recently burned areas (Thomas et al. 1996; Joly et al. 2003, 2009; Barrier and Johnson 2012; Anderson and Johnson 2014), with selection by caribou primarily determined by the reduction in mature habitat and available lichen forage. Caribou tend to select mature stands (> 40 years old) containing relatively abundant lichen cover (Joly et al. 2003) and avoid immature stands, although recent studies have found that there may be more individual variation in the use of these areas than previously thought (Anderson and Johnson 2014), and some individuals may take advantage of these areas for increased vascular forage (Joly et al. 2003). Caribou may also use immature stands as habitat for movement (Rickbeil et al. 2017) or possibly to reduce predation risk through enhanced visibility (Anderson and Johnson 2014). The effects of fire on caribou winter habitat, and associated avoidance by individuals, extend well beyond the short-term loss of vegetation due to the recovery time of lichen species. Most forage lichens require in excess of 50 years to reach relevant biomass for consumption (Maikawa and Kershaw 1976), with 60 to 80 years post-fire necessary to achieve the largest abundance of forage lichens (Thomas 1998;

Anderson and Johnson 2014). In some cases, only 180 years after burning do primary forage lichen species (e.g., *Cladina rangiferina*, *Cladina stellaris*) reach maximum biomass (Collins et al. 2011). This slow recovery rate of forage lichens means that once an area is burned, it may remain low-quality winter-forage habitat that is unattractive for caribou grazing for decades (Collins et al. 2011).

Fire is a natural and important component of many ecosystems (Rowe and Scotter 1973; Bonan and Shugart 1989) and is a keystone ecosystem process of the boreal forest, driving its physical and biological organization (Weber and Flannigan 1997). Although caribou and other species may be adapted to traditional fire cycles in the boreal forest (Klein 1982), there has been a significant and increasing trend in burned area across Canada and Alaska over the past four decades (Gillett and Weaver 2004; Kasischke and Turetsky 2006). Beyond this recent trend, climate warming is predicted to further increase the frequency of and area burned by forest fires (Flannigan et al. 2009). Results from Flannigan et al. (2005) predicted that the area burned in Canada could increase by 74-118% by the end of the century, and Wotton and Flannigan (1993) suggested that the length of the fire season could increase by around 30 days annually. Some studies have predicted less extreme changes in fire activity, with projections being near the upper limit of the historical range of fire occurrence (Girardin and Mudelsee 2008), though predicted future fire activity remains higher than the long-term average. This increase in the frequency of wildfire above historical levels has also been predicted for Arctic and northern biomes (Joly et al. 2012), with an associated predicted reduction in quality and availability of preferred winter barren-ground caribou habitat (Rupp et al. 2006; Gustine et al. 2014). Decreasing availability of quality winter forage can reduce the nutritional status of individuals during the winter (White 1983), and food limitation can lead to density-dependent effects, such as a decline in recruitment and female body size (Skogland 1986). Reduced quality of winter forage and body condition of individuals has implications for population demography, as it influences survival and reproductive rates (Couturier et al. 1990, 2009b; Cameron et al. 1993; Crête and Huot 1993; Cameron 1994; Mahoney and Schaefer 2002).

Lichens are low in protein and because caribou subsist primarily on lichen over the winter, they develop a negative protein balance (Gerhart et al. 1996; Parker et al. 2005) even when winter range quality is high. As typically observed in temperate and northern ungulates, the body condition of some caribou populations has been shown to decline over winter (Dauphiné 1976; Adamczewski et al. 1993), however reduced body condition following winter is not ubiquitous. Couturier et al. (2009a) provided examples of caribou populations gaining fat through the winter and suggest that some caribou populations may gain fat over winter as a result of poor summer range forage conditions. This potential for winter forage to compensate for a poor-quality summer (Schmelzer and Otto 2001; Dale et al. 2008; Couturier et al. 2009a) highlights the importance of winter-range quality for caribou.

Winter habitat quality also may be affected under climate change scenarios by altered plant community composition. As predicted under climate warming scenarios (e.g., Chapin et al. 1995; Walker et al. 2006), the cover extent of graminoids and shrubs is increasing in some northern areas (Cornelissen et al. 2001; Sturm et al. 2001; Joly et al. 2007; Olthof et al. 2008b) at the expense of lichen-rich communities. Warming temperatures improve growing conditions for vascular plants, which can begin to occupy areas previously more suitable for lichen (Cornelissen et al. 2001; Olthof et al. 2008). Transitions from lichen-dominated to vascular plant-dominated communities likely stem from increased competition and shading from vascular plants, along with warmer and drier conditions (Olthof et al. 2008).

The notion that climate change will negatively affect barren-ground caribou by reducing high-quality winter habitat through increasing forest fire activity or changes in plant community composition hinges largely on the assumption that lichen-rich diets are required by caribou in winter. Bergerud (1974) argued that caribou do not require lichens in the winter, citing several studies when caribou had been observed to subsist on winter forage other than lichens (Kelsall 1968; Skoog 1968; Bergerud 1972). He further argued against the claims of earlier studies that forest fires on the winter range of barren-ground caribou had led to population declines (e.g., Scotter 1964), stating that there was little evidence to substantiate a link between winter range destruction and caribou abundance. More recently, authors have suggested that winter diets predominantly consisting of graminoids rather than lichens may not be detrimental to *Rangifer* populations (Heggberget et al. 2002; van der Wal 2006), with van der Wal (2006) proposing that from the caribou perspective the disappearance of lichens does not necessarily constitute habitat destruction. However, Joly et al. (2009) contrasted this assertion with examples from the Western Arctic Herd (WAH), noting that increased graminoids and decreased lichens have been observed in the winter diet of WAH caribou, concurrent with a decline in recruitment and abundance in the herd. The authors stated that WAH caribou avoid recently burned areas in the winter even though graminoids return quickly post-fire (Jandt et al. 2008), implying that increased graminoids do not make these areas appealing and do not easily replace lichen as primary winter forage. Joly et al. (2009) suggested that the specialized, and non-lichen, winter diets of the High Arctic *Rangifer* populations described by Heggberget et al. (2002) and van der Wal (2006) might reflect the specific environmental and ecological conditions of their ranges, such as low density populations and few predators, and may not be applicable to other populations. Thus, the ability of *Rangifer* to subsist on non-lichen forage species over the winter may depend on the specific *Rangifer* subspecies, ecotype, and range characteristics of the population in question.

Regardless of whether caribou populations rely on forage species other than lichens in the winter, what is supported by both recent (Joly et al. 2009; Anderson and Johnson 2014) and older studies (Scotter 1964) is that during the winter barren-ground caribou select for mature forest stands with productive lichen communities and avoid immature and recently burned stands. We believe that it is therefore a reasonable and precautionary approach to consider it likely that the reduction of abundant lichen forage on the winter range, whether through increased fire activity or altered community composition, can lead to negative effects on barren-ground caribou populations through changes in habitat use and behaviour, or abundance.

2.7 Conclusions

The predicted consequences of climate change on *Rangifer* populations are complex and varied. How these environmental changes might interact remains unclear and will undoubtedly differ across the circumpolar *Rangifer* range. On summer ranges, increasing temperatures will likely lead to longer growing seasons, increases in plant productivity, and an earlier onset of spring, all of which could increase *Rangifer* body condition and reproductive success by shortening the winter period of food limitation, providing earlier access to forage (and thus offsetting the costs of parturition and lactation), and generally increasing the quantity and period of available forage (Tews et al. 2007a; Cebrian et al. 2008; Helle and Kojola 2008; Tveraa et al. 2013; Veiberg et al. 2017). However, this same increase in temperature will also likely increase insect harassment, provide opportunity for predators, potential competitor species, parasites, and diseases that have historically been restricted to more southerly ranges to expand northward, and alter plant community composition to be dominated by potentially less nutritious species (Sharma et al. 2009; Witter et al. 2012b; Kutz et al. 2013; Thompson and Barboza 2014; Simard et al. 2016). Additionally, all *Rangifer* populations may not respond positively to the advancement of spring (Post and Forchhammer 2008; Kerby and Post 2013).

The interplay of potential effects in the winter is similarly convoluted. Although increased temperatures and shorter winters may benefit *Rangifer* by improving access to forage, warm weather also produces more frequent icing events, which can lead to mass starvation, or at least displacement from preferred habitat, in populations (Hansen et al. 2014; Loe et al. 2016; Langlois et al. 2017). Increases in wildfire activity on winter ranges of caribou populations can degrade habitat quantity and quality, while improving it for other ungulate species whose ranges could then expand (Joly et al. 2012; Anderson and Johnson 2014).

Confounding the understanding of the interaction between the various impacts of climate change is the potential for distributional shifts of *Rangifer* populations, and changes in migratory behaviour. Though we may predict the effects of climate change on populations where they currently exist, over the longer term, changing environmental conditions may result in the northward shift of population ranges (Sharma et al. 2009). Warmer temperatures may force caribou to alter their migratory routes to avoid open water that was historically frozen (Le Corre et al. 2017), or become more sedentary (Heggberget et al. 2002). Changing sea ice conditions may restrict inter-island movements of Peary caribou in the High Arctic (Jenkins et al. 2016) as well as the migratory behaviour of some other *Rangifer* populations (Poole et al. 2010; Joly 2012). The possibility of range shifts further muddles the already complex business of making predictions.

So, how might these factors play out? Albon et al. (2017) suggested that increases in summer forage will lead to higher autumn body mass, but increased frequency of winter icing events could result in more frequent years with low body mass coming out of winter. Albon et al. (2017) further predicted that although higher plant productivity in the Arctic could allow for larger *Rangifer* populations, these populations might exhibit greater fluctuations in abundance resulting from more frequent food restrictions in winter. Tews et al. (2007b) used simulations to compare the effects of greater forage availability in summer with the effects of increased icing events in the winter for Peary caribou. They reported that the net effects of climate change on Peary caribou rely on the intensity of the two mechanisms they modelled. Increasing forage biomass will be beneficial to Peary caribou, with climate change providing a net positive effect only so long as winter forage inaccessibility (through icing events) does not increase by more than 30% (Tews et al. 2007a). Gustine et al. (2017) suggested that, independent of insect harassment, increases in forage biomass and earlier springs should benefit caribou. They also commented that they expect a varied response to climate change in *Rangifer* populations across their circumpolar range. This varied response, and the importance of local and regional environmental change, appear evident when we consider that although warmer, longer summers and earlier springs are being observed, many *Rangifer* populations in the Arctic are declining (Vors and Boyce 2009; Uboni et al. 2016; Albon et al. 2017; Fauchald et al. 2017), highlighting the difficulty in reconciling predicted effects with reality.

With all due caution, we note the relative adaptability of *Rangifer* as a species to differing environmental conditions as a possible source of resilience to climate change. *Rangifer* subspecies and ecotypes are distributed across the circumpolar world at varying latitudes, from the relatively southern populations of woodland caribou (*R. t. caribou*) in Canada to Peary caribou and Svalbard reindeer in the High Arctic. This distribution illuminates the ability of *Rangifer* to excel in an assortment of ecosystems and habitats. Previous authors have noted the difficulty in generalizing the effects of climate change for *Rangifer* populations considering their broad distribution across a diverse range of environmental conditions (Tyler 2010). Perhaps this difficulty in itself provides some indication of the potential resilience of *Rangifer* to climate change. Of course, the capacity for success across a range of habitats results from behaviours and adaptations developed over evolutionary time scales and within the bounds of historic environmental variation. Rapid environmental change may well compromise the ability of Arctic species to adapt (Parmesan 2006; Loe et al. 2016).

Nonetheless, some evidence suggests that behavioural plasticity in *Rangifer* might help to mitigate certain impacts of climate change. The effects of changing plant communities could be alleviated somewhat because *Rangifer* is known to be versatile in their feeding habits, and the diet composition of caribou and reindeer varies across the species' range (Bergerud 1974; Thompson and Barboza 2013). Nicholson et al. (2016) suggested that the observed flexible use of winter ranges by caribou may be beneficial in a changing climate, allowing them to adjust range use in response to environmental conditions. Similarly, reindeer appear to be able to adjust behaviour and space use in response to icing events, and this provides some ability to minimize negative impacts of extreme weather (Stien et al. 2010; Loe et al. 2016). Plasticity in reproductive strategies also might help to buffer the effects of climate change. The environmental conditions of early life can influence survival and reproductive success of entire cohorts (Lindström and Kokko 2002). Female Svalbard reindeer born after experiencing high rain-on-snow events *in utero* adjusted their reproductive strategy to breed at lower body mass than those females that did not experience high rain-on-snow *in utero* (Douhard et al. 2016). This strategy resulted in cohorts born under poor environmental conditions having similar levels of reproductive success and mean fitness as those born under good environmental conditions, thereby minimizing potential demographic consequences of higher levels of rain-on-snow *in utero*.

Our review highlights the mixed effects of climate change on various *Rangifer* populations. Much of the literature indicates that caribou and reindeer could have some resilience to climate warming, however, given the current state of *Rangifer* populations globally we should maintain a precautionary view when anticipating any positive effects of climate change on *Rangifer*. We also hasten to emphasize that our review has not considered any effects from anthropogenic disturbance, and that in many cases anthropogenic disturbance presents a much more immediate threat to *Rangifer* populations than does climate change (Rees et al. 2008; Vors and Boyce 2009; Festa-Bianchet et al. 2011; Uboni et al. 2016). Habitat loss and fragmentation have been key contributors to the declines of more southerly caribou populations (McLoughlin et al. 2003; Vors et al. 2007; Faille et al. 2010; Festa-Bianchet et al. 2011). Although development pressure is generally lower on the ranges of Arctic *Rangifer* than those found further south, a warming climate is anticipated to improve access to resources in the north, and likely increase industrial activity in the Arctic (Prowse et al. 2009). The effects of anthropogenic disturbance on *Rangifer* have been well documented (Johnson et al. 2005; Reimers and Colman 2006; Vistnes and Nellemann 2008; Polfus et al. 2011; Boulanger et al. 2012; Wilson et al. 2013b, 2016), and the potential for habitat loss, fragmentation, and degradation from increased human activity in the Arctic could impair the ability of *Rangifer* to adjust to a rapidly changing environment (Vistnes and Nellemann 2008).

3 Climate influences body condition and synchrony of barren-ground caribou abundance in northern Canada

3.1 Introduction

Dramatic fluctuations of barren-ground caribou (*Rangifer tarandus groenlandicus*) populations have been well documented, but remain poorly understood (Gunn 2003). These fluctuations have been linked to variation in summer- and winter-range quality and availability (Adamczewski et al. 1988; Manseau et al. 1996), predation (Bergerud and Ballard 1988), extreme weather events (Chan et al. 2005), parasites (Weladji et al. 2003; Hughes et al. 2009), and forage exploitation (Messier et al. 1988). A global decline in *Rangifer* populations has occurred across the species' range with climate change and anthropogenic disturbance implicated as potential mechanisms (Vors and Boyce 2009). While various factors contribute to the abundance trajectory of each herd, regional synchrony in abundance has been observed across proximate caribou herds (Klein 1991; Gunn et al. 2011; Fauchald et al. 2017) although this synchrony is not consistent (Bergerud 1996). Regional variation in caribou population trends can be partly attributed to the effects of broad-scale climate patterns, such as those represented by Arctic Oscillation (AO), the North Atlantic Oscillation (NAO), and the Pacific Decadal Oscillation (PDO) (Joly et al. 2011).

The AO is a broad climate index derived from surface atmospheric pressure patterns that track the strength of the polar vortex (Thompson and Wallace 1998). The AO has positive and negative phases that influence broad weather patterns across the northern hemisphere (Thompson et al. 2000). For example, during the positive phase of the AO, atmospheric pressure over the Arctic is lower than average, which tends to result in warmer and wetter winters in northern regions as warmer air is able to move further north (Thompson et al. 2000; Aanes et al. 2002).

Negative values of the AO indicate high pressure in the Arctic region, allowing greater southward penetration of cold Arctic air. However, the effects of the AO on weather patterns can vary markedly across the north (Joly et al. 2011). The AO can and does fluctuate between positive and negative phases daily, but often will remain primarily in one phase or the other for prolonged periods. Similar indices, such as the NAO and PDO, influence weather patterns in a comparable way, though in different regions of the world (Hurrell 1995; Mantua et al. 1997).

Several studies have found links between broad climate patterns, represented by climate indices, and *Rangifer* populations around the circumpolar world. Relationships have been identified between the intensity of the AO and reindeer population growth rates on Svalbard (Aanes et al. 2002), similarly for the AO and PDO and caribou growth rates and calf recruitment in Alaska and the Yukon Territory (Hegel et al. 2010; Joly et al. 2011), and again for the AO and Porcupine herd abundance (Griffith et al. 2002), the NAO and caribou population dynamics (Post and Stenseth 1999; Forchhammer et al. 2002; Post and Forchhammer 2002), and the NAO and caribou calf body mass (Couturier et al. 2009b). In contrast, Zalatan (2006) examined a 100-year period and found an inconsistent relationship between the intensity of the AO and reported dynamics of the Bathurst population.

Here, we examine the relationship between the AO and three barren-ground caribou herds in northern Canada: the Bathurst, Beverly, and Qamanirjuaq (Nagy et al. 2011). These three herds have undergone relatively synchronous population trajectories (Fig. 3.1) over the past several decades, increasing through the 1980s, reaching peak abundance in the late 1980s to mid 1990s, and then declining at varying rates to present (Gunn et al. 2011). These declines, and particularly that of the Bathurst herd, have generated substantial concern among researchers, wildlife managers, and communities across the herds' ranges. Recent studies have investigated potential mechanisms for these declines (Boulanger et al. 2011; Adamczewski et al. 2015), but have not explored whether the similar trends in abundance might be related to broad climate patterns. We hypothesize that the relative synchrony of population trajectories of the Bathurst, Beverly, and Qamanirjuaq caribou herds over the last 35 years is in part related to the effects of the intensity of the AO, and further that long-term abundance fluctuations of barren-ground caribou are linked to broad climate indices. We expect that this relationship acts through the influence of climate patterns on environmental conditions that affect forage quality, quantity, and availability on the caribou range (e.g. Aanes et al. 2002), and thus on the physical condition of individual animals. To test these hypotheses, we use long-term datasets on the physical condition and fecundity of the Beverly herd, and estimates of abundance of each herd over the past 35 years. First we describe how the AO is related to local weather patterns on the range of these herds. We then test for a relationship between the AO and physical condition of Beverly caribou from 1982 – 1987, and demonstrate that this can be linked to herd productivity. Lastly, we further investigate the relationship between the AO and barren-ground caribou by comparing the intensity of the AO to the direction of population growth for these three barren-ground caribou herds.

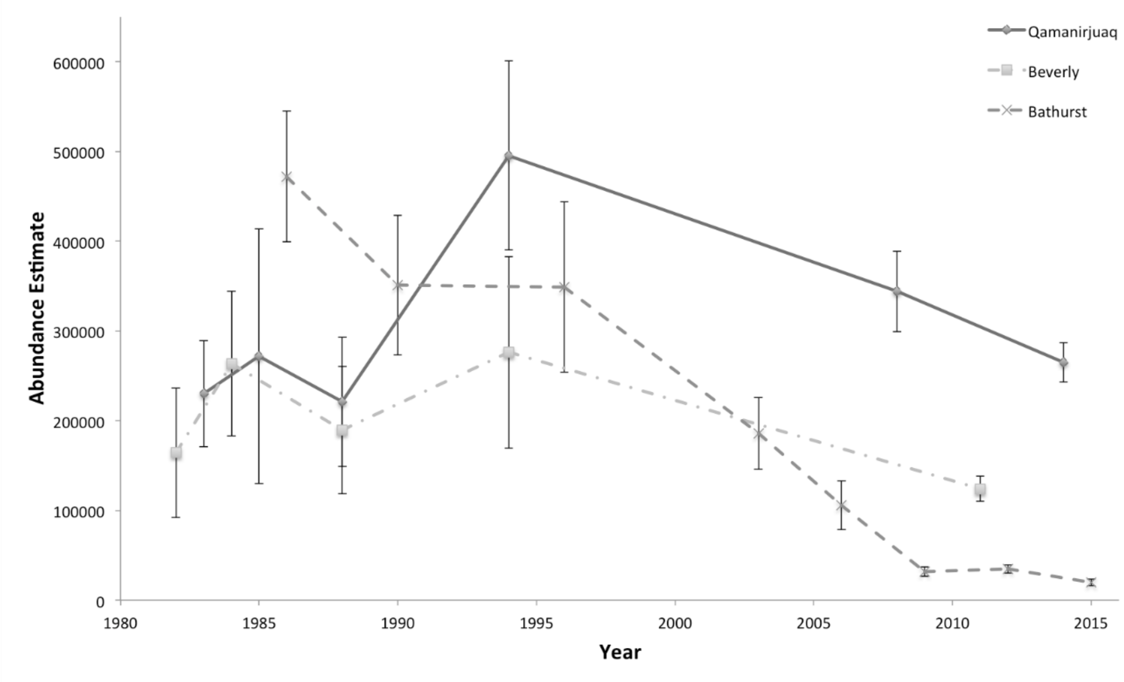

Fig 3.1 Abundance estimates for the Qamanirjuaq, Beverly, and Bathurst barren-ground caribou herds (*Rangifer tarandus groenlandicus*) from 1982 to 2015. Error bars show ± standard error.

3.2 Materials and Methods

Barren-ground caribou can be classified into several ecotypes based on their level of sociality, spatial tenure, and migratory behaviour (Nagy et al. 2011). The Bathurst, Beverly, and Qamanirjuaq herds are mainland migratory barren-ground caribou, an ecotype characterized by large aggregations of animals and collective long-distance migrations from winter ranges near or below the tree line to calving grounds and summer ranges on the tundra (Banfield 1954). Nagy et al. (2011) provided annual ranges for these three herds, among others, delineated by utilization distributions calculated from satellite telemetry locations of satellite-collared female caribou collected by the Governments of Nunavut and the Northwest Territories (Fig. 3.2). The summer ranges that we present represent the utilization distributions of satellite-collared female caribou from June 1 to August 31.

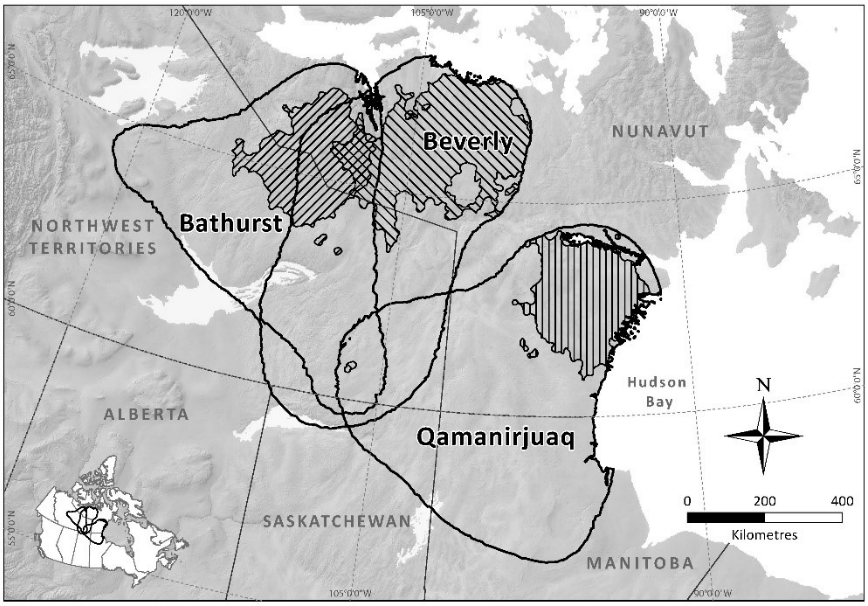

Fig 3.2 Annual ranges (solid outline) adapted from Nagy et al. (2011), and June – August (hatched) ranges of the Bathurst, Beverly, and Qamanirjuaq barren-ground caribou (*Rangifer tarandus groenlandicus*) herds. Note that June - August range extents have been clipped to conform to Nagy et al. (2011) annual range extents.

We used linear regression to identify associations between the intensity (positive or negative) of the AO and local climate variables. Annual, summer, and winter values of the AO index from 1979 to 2016 were calculated from data provided by the National Oceanic and Atmospheric Administration (<https://www.ncdc.noaa.gov/teleconnections/ao>, accessed 11 December 2016). Annual AO values were determined as the mean AO value for all months, winter values from the mean AO intensity of January, February, and March, and summer values from the AO intensities of June, July, and August. Climate data for the Beverly range was accessed from the CircumArctic *Rangifer* Monitoring and Assessment (CARMA) network's caribou range climate database (Russell et al. 2013). The CARMA database is derived from NASA's Modern Era Retrospective Analysis for Research and Applications (Rienecker et al. 2011).

Multiple regression was used to identify associations between the body condition of male and female Beverly caribou in March and the intensity of the AO during winter, the previous summer, and throughout the previous year. Information on the physical condition of Beverly caribou from 1980 to 1987 was reported in Thomas and Kiliaan (1998a), who calculated a number of body condition indices from data that they collected from 856 female and 402 male Beverly caribou. Dissectible fat (DFAT), estimated by an equation developed for barren-ground caribou by Adamczewski et al. (1987), was found to be the best condition index among those that they calculated (Thomas and Kiliaan 1998b). We used mean values of DFAT calculated for age and sex classes to approximate body condition each year over the study period. Similar data on body condition for the other two herds were not available for our analysis.

Population estimates for the Beverly, Bathurst, and Qamanirjuaq caribou herds were taken from previous publications (Beverly: Campbell et al. 2012; Qamanirjuaq: Campbell et al. 2010; Campbell et al. 2016; Bathurst: Heard and Williams 1991a, b; Gunn et al. 1997; Boulanger et al. 2014; Boulanger et al. 2017). The abundance of each of these herds has been estimated periodically for over 40 years by different researchers, although over time survey methods for estimating herd abundance have changed and improved (e.g. visual calving ground surveys to photographic calving ground surveys). This creates challenges in using early abundance estimates to make direct comparisons. For these reasons, the earliest population estimate that we considered in our analysis was from 1982 when calving ground photo surveys became the standard survey method. Although this restricted the temporal scope of our study the number of estimates across herds over 35 years provided a large enough sample for our analyses.

For each intervening period between herd population estimates, we compared the average value of the summer intensity of the AO (only summer intensity was significantly related to caribou physical condition, see Results) to the direction of population growth (positive, stable, or negative) for that period. We acknowledge that a linear trend over these periods, particularly the longer ones, is unlikely, and we did not think that the available data allowed for meaningful estimates of growth rates between population estimates. Herd abundance was designated as stable if no statistically significant trend was observed between consecutive population estimates. For example, the mean abundance estimate for the Qamanirjuaq herd declined from 495 665 (±105 426 SE) in 1994 to 348 661 (±44 861 SE) in 2008, however due to overlapping confidence intervals, the authors were not able to decisively determine a trend (Campbell et al. 2010) and we identify the population trend over this period as "stable." We performed an exact binomial test to determine whether the number of observed periods where the direction of the AO (positive or negative) was equivalent to the direction of population growth was greater than would be expected by chance. All statistical analyses were performed in Program R (R Core Team 2016).

3.3 Results

3.3.1 Arctic Oscillation and local climate

The average intensity of the AO during the summer (1 June – 31 Aug) was significantly positively associated with summer temperatures on the Beverly range (Fig. 3.3; $R^2 = 0.20$, $F_{29} = 7.13$, $p = 0.01$), meaning that summers with a positive AO value tended to be warmer. The average annual intensity of the AO during the summer also was positively associated with cumulative growing degrees (Russell et al. 2013) above 5°C (Fig. 3.4; $R^2 = 0.21$, $F_{29} = 7.53$, $p = 0.01$), an indicator of the length of a growing season. We did not find a relationship between the intensity of the AO in the summer and precipitation, although higher precipitation tended to occur in cooler years on the Beverly summer range ($R^2 = 0.10$, $F_{29} = 3.41$, $p = 0.07$). There was no consistent trend in average summer temperature on the Beverly summer range over our study period (Fig. 3.5).

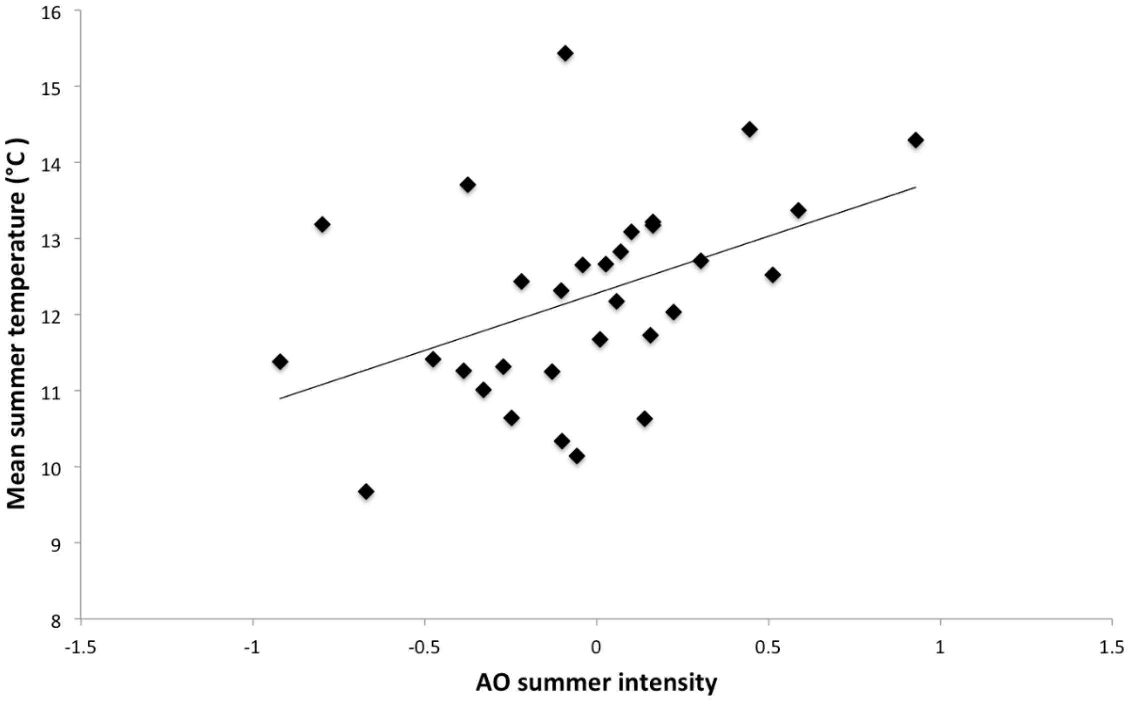

Fig 3.3 Significant ($R^2 = 0.20$, $F_{29} = 7.13$, $p = 0.01$) relationship between the annual mean summer temperature on the Beverly summer range (data from CARMA caribou range climate database) and the summer (June, July, August) intensity of the Arctic Oscillation (AO), 1981-2011 (National Oceanic and Atmospheric Administration).

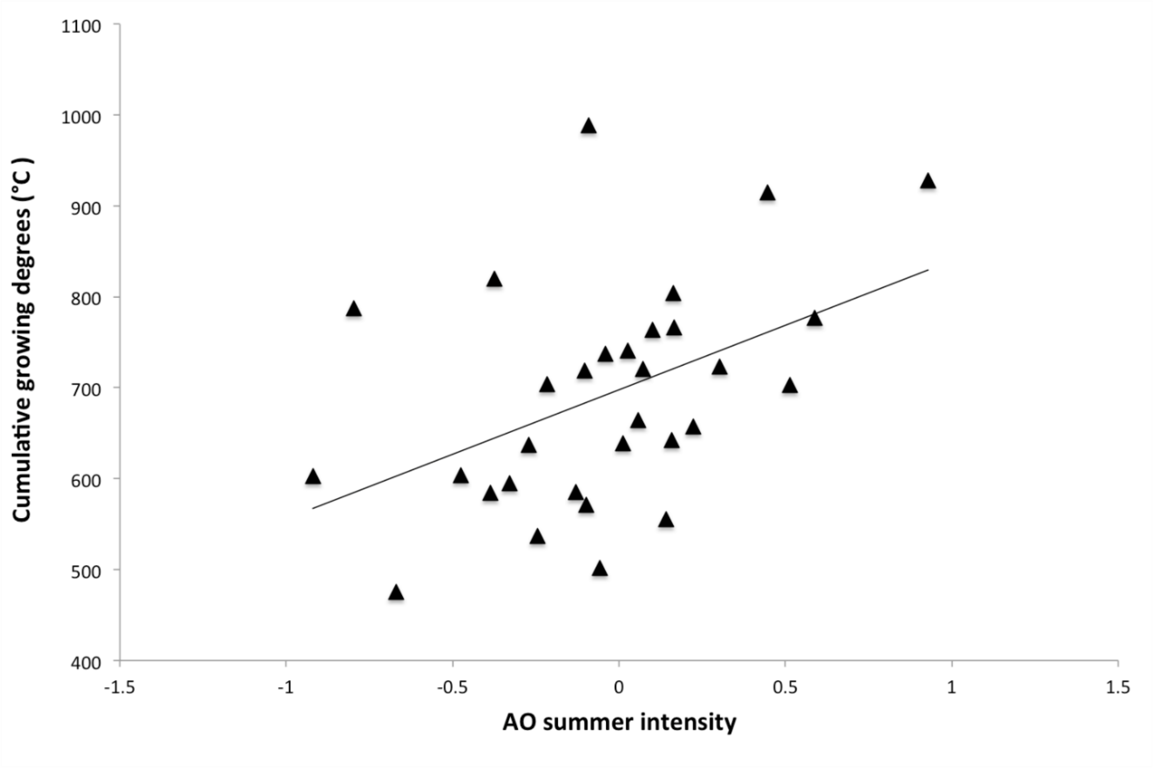

Fig 3.4 Significant relationship between the cumulative growing degrees above 5°C ($R^2 = 0.21$, $F_{29} = 7.53$, $p = 0.01$) on the Beverly summer range (data from CARMA caribou range climate database) and the summer (June, July, August) intensity of the Arctic Oscillation (AO), 1981-2011 (National Oceanic and Atmospheric Administration).

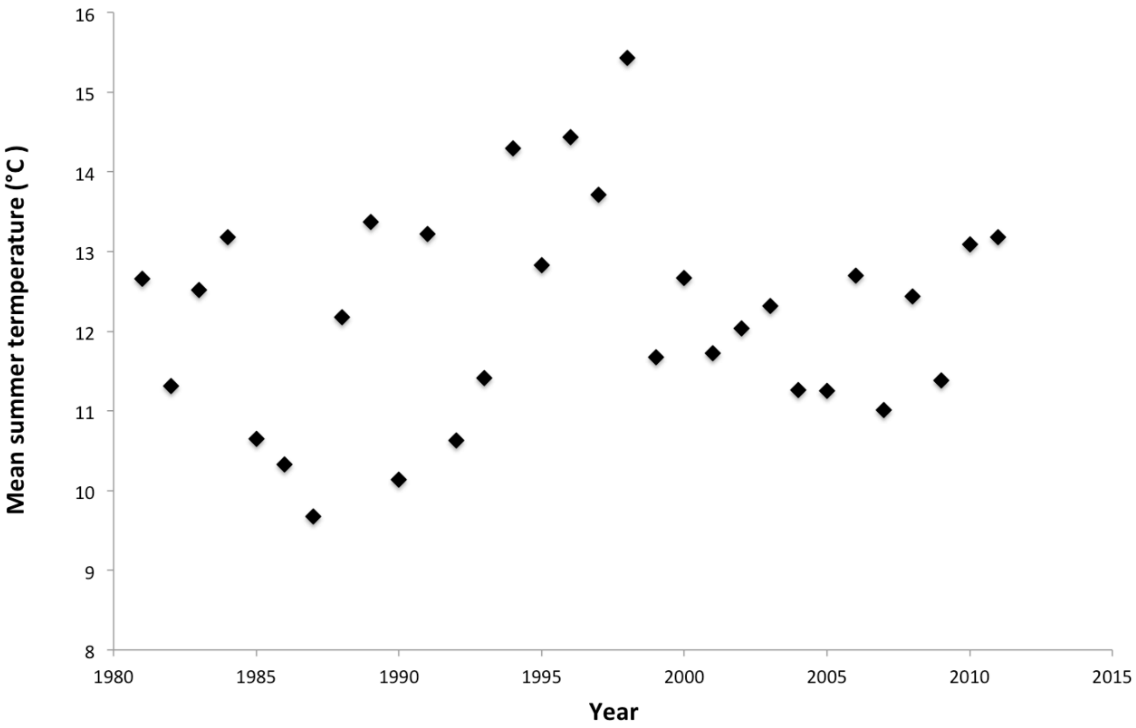

Fig 3.5 No significant relationship was found between the mean summer temperature (June, July, August) on the Beverly summer range (data from CARMA caribou range climate database) and year.

3.3.2 Beverly herd body condition

We constructed linear models of DFAT for each sex by age with the intensity of the AO (either in the winter, previous summer, or previous year) as predictor variables. The intensities of the AO in the winter and previous year were not significantly related to DFAT. However, DFAT increased with age in years with larger, positive intensities of the previous summer AO in both male (Table 3.1; $R^2 = 0.65$, $F_{25} = 23.04$, $p < 0.0001$) and female (Table 3.1; $R^2 = 0.43$, $F_{36} = 13.50$, $p < 0.0001$) caribou. To test the independent effect of the previous summer intensity of the AO, we also constructed a linear model of DFAT as predicted by age only for both male (Table 3.1; $R^2 = 0.42$, $F_{26} = 18.83$, $p < 0.001$) and female (Table 3.1; $R^2 = 0.23$, $F_{37} = 11.17$, $p = 0.002$)

caribou. For both male and female caribou, models that included the previous summer intensity of the AO explained approximately 20% more variation in DFAT than models considering age of the animals alone. To test whether the relationship between climate and DFAT was not more parsimoniously explained by summer temperature rather than intensity of the AO, we constructed a linear model of DFAT for each sex with age and the mean temperature in the previous summer as predictor variables. For both sexes, models including intensity of AO rather than mean summer temperature explained greater variation in DFAT (Table 3.1). The intensity of the AO explained a greater amount of the variance in DFAT in male caribou than female caribou.

Table 3.1 Results of multiple regression analysis of dissectible fat (DFAT) of male and female Beverly caribou (*Rangifer tarandus groenlandicus*) as predicted by age and intensity of the summer Arctic Oscillation (AOS) from 1982-1987, DFAT of male and female caribou as predicted by age and mean summer temperature (Temp) from 1982-1987, and simple regression analysis of DFAT of male and female Beverly caribou as predicted by age only from 1982-1987. All β and R^2 values significant ($p<0.01$) unless otherwise indicated.

					β (SE)	
Model	**R^2**	**Adj. R^2**	**F statistic**	**Age**	**AOS**	**Temp**
$\text{DFAT}_{\text{male}} \sim \text{Age} + \text{AOS}$	0.65	0.62	$F_{25} = 23.04$	0.50 (0.09)	1.87 (0.46)	-
$\text{DFAT}_{\text{male}} \sim \text{Age} + \text{Temp}$	0.50	0.45	$F_{25} = 12.26$	0.52 (0.11)	-	0.33 (0.17)*
$\text{DFAT}_{\text{male}} \sim \text{Age}$	0.42	0.40	$F_{26} = 18.83$	0.47 (0.11)	-	-
$\text{DFAT}_{\text{female}} \sim \text{Age} + \text{AOS}$	0.43	0.40	$F_{36} = 13.50$	0.26 (0.07)	2.53 (072)	
$\text{DFAT}_{\text{female}} \sim \text{Age} + \text{Temp}$	0.35	0.31	$F_{36} = 9.63$	0.25 (0.07)	-	0.53 (0.21)**
$\text{DFAT}_{\text{female}} \sim \text{Age}$	0.23	0.21	$F_{37} = 11.17$	0.26 (0.08)	-	

* p = 0.06, ** p = 0.02

3.3.4 Arctic Oscillation and barren-ground caribou abundance

We identified a significant, positive association between the average summer intensity of the AO and the direction of population growth of the Bathurst, Beverly, and Qamanirjuaq herds (Table 3.2; exact binomial test, $p = 0.0074$). We demonstrate this relationship during both positive and negative phases of the AO, as well as through periods of low and high caribou abundance. Warmer temperatures and longer growing seasons corresponded to stable or increasing population growth across years and herds. Note that our analysis considered only the direction of population growth between abundance estimates and the signature (positive or negative) of the summer AO and did not take into account possible variation in growth rates during the period between survey estimates. We did not attempt to estimate specific growth rates between abundance estimates.

Table 3.2 Comparison of the signature of the average annual summer intensity of the Arctic Oscillation (AOS) and population growth between population estimates of the Bathurst, Beverly, and Qamanirjuaq barren-ground caribou (*Rangifer tarandus groenlandicus*) herds. Positive values of the AOS corresponded to stable or increasing population growth, and negative values of the AOS corresponded to decreasing population growth in 13 of 15 observations, constituting a significant trend (exact binomial test, $p = 0.0074$).

Year	Population Estimate	Population growth	AOS trend
		Bathurst herd	
1986	472 000		

1990	351 000	Negative	Negative
1996	349 000	Stable	Positive
2003	186 000	Negative	Positive*
2006	128 000	Negative	Negative
2009	31 895	Negative	Negative
2012	34 690	Stable	Negative
2015	19 769	Negative	Negative
Beverly herd			
1982	164 338		
1984	263 691	Positive	Positive
1987	93 546	Negative	Negative
1994	276 000	Positive	Positive
2011	124 189	Negative	Negative
Qamanirjuaq herd			
1983	230 000		
1988	221 000	Stable	Positive
1994	495 665	Positive	Positive
2008	348 661	Stable	Positive
2014	264 718	Negative	Negative

*However, the summer AO trend from 1997 – 2003 is negative.

3.4 Discussion

We found a significant relationship between broad climate patterns and the population trajectories of three barren-ground caribou herds, consistent with previous studies of climate patterns and *Rangifer* population dynamics (Aanes et al. 2002; Joly et al. 2011; Post and Stenseth 1999; Forchhammer et al. 2002; Post and Forchhammer 2002). From 1988 to 1996, the summer intensity of the AO was largely in the positive phase, with a mean value of 0.207 (±0.135 SE), and this was a period of population stability or growth for each of the three herds that we examined here. In contrast, from 1997 to 2016 the summer AO has remained largely in the negative phase, with a mean value of -0.154 (±0.077 SE), and over this period the Bathurst, Beverly, and Qamanirjuaq herds declined in abundance. We found that a greater proportion of the variation in body condition was explained for male caribou compared to females. This is likely because our model did not account for pregnant cows that tend to have higher body fat than non-pregnant cows (Thomas and Kiliaan 1998b).

Our results suggest that during periods of positive AO intensity, warmer temperatures on the summer range result in improved growing conditions for vascular plants that benefits foraging caribou. Conversely, negative summer AO intensity is associated with cooler temperatures with associated shorter growing seasons and increased precipitation on the Beverly summer range. Though we do not have direct measures of forage quality or quantity, previous studies have found that cooler and shorter summers tend to result in reduced vascular plant growth (Chapin and Shaver 1985; Rachlow and Bowyer 1998; Lenart et al. 2002; van der Wal and Stien 2014), and therefore reduced forage quantity and availability (although climate can also affect forage species quality e.g., Turunen et al. 2009; Mallory and Boyce 2018; Zamin et al. 2017). We did not investigate relationships between the AO and climate variables on the Bathurst or Qamanirjuaq ranges and have made the assumption that similar trends exist as on the

Beverly range. We justify this assumption with the evidence of some range overlap (Fig. 3.2) between the three herds during the winter, spring, summer, and late summer periods (Campbell et al. In prep.).

From 1982 to 1987, differences in the physical condition of Beverly caribou corresponded with changes in the intensity and signature of the summer AO. We again reason that this can be explained by the effect of climate on the availability of forage (Chapin and Shaver 1985; Lenart et al. 2002; van der Wal and Stien 2014) because caribou body condition is necessarily influenced by the availability of nutritious forage in summer (Reimers 1983; Crête and Huot 1993; Gerhart et al. 1996; Couturier et al. 2009b; Tveraa et al. 2013; Albon et al. 2017). Caribou spend 7 months of the year with a negative protein balance, stemming from the low protein content of lichen, the primary constituent of their late-winter diet (Gerhart et al. 1996). Protein stores developed during the summer are not only necessary for caribou to maintain body condition over winter, but also for fetal growth and development in pregnant females. Fetal protein is synthesized from maternal tissues (Gerhart et al. 1996), and up to 80% of fetal mass is deposited in late winter, when caribou diet provides little protein (Côté et al. 2012).

In addition to the relationships between female nutrition and fetal development, the physical condition of pregnant cows also has been shown to affect calf survival (Bergerud 1996), and reduced body condition of individuals can lead to changes in population demography through effects on survival and reproduction (Crête and Huot 1993; Mahoney and Schaefer 2002; Albon et al. 2017). The physical condition of female caribou is positively linked to their reproductive success (Cameron et al. 1993; Gerhart et al. 1997; Tveraa et al. 2013), a relationship that has been documented at the population level in Beverly caribou (Thomas and

Kiliaan 1998a). Between 1980 and 1987, years with fatter female caribou corresponded to higher fecundity across the herd (Thomas and Kiliaan 1998b). These findings allow us to propose a mechanism where positive AO intensity in the summer corresponds to warmer average temperatures and a longer growing season and improved foraging conditions for caribou. This leads to caribou in better physical condition going into winter, perhaps reducing adult winter mortality, and increasing rates of fecundity and late-winter calf survival. Conditions during periods of positive AO intensity then contribute to stable or increasing population growth in these caribou herds. During periods of negative AO intensity, summers are cooler and growing seasons shorter, which then contributes to reduced quality, quantity and availability of preferred forage species, poorer condition of caribou, lower rates of fecundity, and negative population growth. We note that this proposed mechanism assumes that a similar relationship exists between the AO and condition of Bathurst and Qamanirjuaq caribou to the one observed with Beverly caribou between 1982-1987. We support this assumption with the relative proximity of the herd summer ranges (i.e., in terms of broad climate patterns), and the well-documented relationships between climate, growing season length, availability of summer forage, and caribou condition (Reimers 1983; Chapin and Shaver 1985; Crête and Huot 1993; Lenart et al. 2002; Cebrian et al. 2008; Couturier et al. 2009b; Tveraa et al. 2013; van der Wal and Stien 2014; Albon et al. 2017).

The dynamics of barren-ground caribou populations are the result of many factors, both density-dependent and stochastic (Bergerud 1996; Sæther 1997; Gunn 2003). Due to the limited data that are available for the Qamanirjuaq, Beverly, and Bathurst herds, we were unable to incorporate factors such as predation and insect harassment in our analysis. Although no substitute for these and other important factors, broad climate indices provide useful proxies that can be used to approximate a variety of environmental conditions that are important to caribou, such as forage quality and availability, temperature, snow depth, and precipitation. Caribou population fluctuations have now been linked to large-scale climate patterns across their circumpolar range, from the PDO in Alaska (Joly et al. 2011), the AO in the central Canadian Arctic (Zalatan 2006; this study), and the NAO in the Greenland and Norway (Post and Stenseth 1999; Aanes et al. 2002). This collective evidence suggests that the effects of broad climate patterns could play an important role as a driver of cyclical fluctuations in caribou populations. Other mechanisms, such as density-dependent forage exploitation, have been identified as important contributors to these fluctuations for some herds (Messier et al. 1988), but could be less important for other caribou populations (Rickbeil et al. 2015). The growing number of studies identifying a link between climate patterns and fluctuations in caribou abundance provide compelling support for climate as an important driver of barren-ground caribou cycling, a link that helps to explain global patterns (Vors and Boyce 2009), but also allows for larger scale local and regional differences in caribou population trends (Joly et al. 2011). The observed synchrony among adjacent herds is consistent with the well-documented influence of climate-caused perturbations on population synchrony (Moran 1953; Ranta et al. 1997; Post and Forchhammer 2002; Liebhold et al. 2004). Although we have insufficient data to rule out alternative hypotheses, if we can assume comparable mechanisms of population regulation among herds, we speculate that a Moran effect could contribute a theoretical underpinning to our results.

We suggest that the effects on forage of these climate patterns contribute to long-term fluctuations in caribou abundance and are of crucial importance to caribou population dynamics because they likely increase the vulnerability or resilience of caribou to other mechanisms affecting population decline and growth such as predation, insect harassment, and disease (Bergerud 1996). However, we acknowledge the potential significance of other mechanisms, including anthropogenic disturbance, which through modifications of caribou behaviour and range can overwhelm other drivers and lead to less-predictable effects on caribou condition, productivity, and ultimately abundance. Although the intensity of the summer AO has been predominantly negative over the past 20 years, long-term fluctuations of the AO are such that it will again return to a predominantly positive phase, and this could be beneficial to barren-ground caribou by affording conditions that support improved forage productivity, and in turn, reproductive productivity. However, we caution that the effects of a changing climate and warming Arctic on the relationships that we identify here are unclear. Climate change is likely to significantly alter the baseline environmental conditions to which this species is adapted, and the oscillations of broad-scale climate patterns around this baseline might further disrupt ecosystems. For example, increasingly warm summers are predicted to increase the prevalence of parasitic insects in Arctic regions and allow other parasitic species to expand the northern extent of their range (Callaghan et al. 2004; Kutz et al. 2013). Harassment by insects is a major energetic cost to caribou (Helle and Tarvainen 1984; Hagemoen and Reimers 2002; Witter et al. 2012a; Mallory and Boyce 2018), and one that might outweigh the benefits of potential increases in forage productivity associated with warmer summers. Further, improved forage associated with positive intensities of the summer AO might shift should climate change alter caribou summer range quality through changing plant community composition (e.g., increased abundance of shrubs; Sturm et al. 2001; Myers-Smith et al. 2011; Frost and Epstein 2014) and reduced forage quality (Turunen et al. 2009; Thompson and Barboza 2014; Zamin et al. 2017). In fact, under a changing environmental baseline we speculate that the relationships we identified here might be altered, even reversed, and summers with negative AO intensity that are cooler than average could potentially correlate positively to caribou life-history traits. In light of this, while we suggest that wildlife managers could consider using the AO as an index of the vulnerability of the Bathurst, Beverly, and Qamanirjuaq herds, this must be done carefully and in consideration of the implications of a changing climate and other potential mechanisms affecting caribou and their habitats.

4 Response of barren-ground caribou to advancing spring phenology

4.1 Introduction

For caribou and other migratory species, the purpose of migration is at least in part to increase fitness by moving to more suitable habitat for birthing and rearing young (Fryxell and Sinclair 1988; Heard et al. 1996; Alerstam et al. 2003). Factors that reduce the quantity and effectiveness of these important habitats or that disrupt important life history stages, such as migration or calving, can have severe negative consequences for wildlife (Brooks et al. 2002; Bolger et al. 2008; Hanski 2011). Although the most imminent threat for many caribou (*Rangifer tarandus*) populations remains anthropogenic disturbance (McLoughlin et al. 2003; Vors et al. 2007; Festa-Bianchet et al. 2011; Uboni et al. 2016), rapid environmental change also can modify habitat and disrupt species behaviours and interactions (Walther et al. 2002; Parmesan and Yohe 2003). A key concern regarding the effects of climate change on ecosystems is the alteration of ecological phenology, or the timing of life history events (Parmesan and Yohe 2003). In many species, the timing of high energetic or nutritional requirements, such as peak lactation in caribou, has evolved to coincide with peak nutrient availability in forage (Klein 1990; Stenseth and Mysterud 2002; Post et al. 2003; Williams et al. 2017). In particular, the loss of life history synchrony across trophic levels can result from the unequal response of species to environmental changes. The deviation from phenological synchrony is often referred to as trophic mismatch (Durant et al. 2007). For caribou, it has been suggested that trophic mismatches could arise if the annual timing of green-up, corresponding to peak nitrogen concentration in forage species (Klein 1970, 1990; Chapin 1980), advances with increasing temperatures and snowmelt while the timing of parturition remains consistent or advances more slowly. These mismatches could reduce the temporal overlap between the availability of highly nutritious stages of forage plants and the timing of high-nutritional demands for lactation, potentially resulting in negative effects on body condition and calf survival (Post and Forchhammer 2008). Trophic mismatches, and their negative effects on productivity, have been reported in a wide range of species (Donnelly et al. 2011), including caribou. Post and Forchhammer (2008) reported a trophic mismatch in a caribou population in Greenland and its apparent adverse effects on reproductive success. However, recent studies on Alaskan caribou and reindeer populations in northern Norway and Svalbard have found no evidence of trophic mismatches or negative effects on recruitment and calf survival from earlier springs (Tveraa et al. 2013; Gustine et al. 2017; Veiberg et al. 2017).

In addition to changes in plant community composition and phenology (Myers-Smith et al. 2011; Pearson et al. 2013), climate change is affecting ice formation and break-up (Sharma and Magnuson 2014) and terrestrial snow cover patterns (Barnett et al. 2005; Kunkel et al. 2009; Brown et al. 2010; Kapnick and Hall 2012). Although regional trends are highly variable, earlier spring melt and altered regional snowfall trends are occurring in many locations across the circumpolar world (Xie et al. 2015), and the migratory behaviour of species such as caribou might be sensitive to these environmental changes. For example, the amount, duration, and hardness of snow cover affect caribou through reduced access to forage (Collins and Smith 1991; Johnson et al. 2001) and effects on movement. Thick and soft snow requires more time and energy to move through (Fancy and White 1985; Nicholson et al. 2016), and ice crusts can slow caribou and damage their legs when broken through. These factors lead caribou to select areas with less snow for ease of movement and forage accessibility (Duquette 1988; Johnson et al. 2001). However, caribou also benefit from a certain amount of snow and ice along their migratory route, particularly to move across frozen water bodies (Leblond et al. 2016). Although photoperiod is an important cue for migration in many species (Visser et al. 2010), there is evidence to suggest that animals also use local conditions to adjust migratory behaviour (Gordo et al. 2005; Caro et al. 2013). Thus, we could expect caribou to time migration in the spring with snow and ice conditions that remain conducive to movement. This reasoning is supported by Le Corre *et al.* (2017), who reported earlier spring migration departure dates following mild winters and delayed migrations when snowfall was abundant in the late winter and early spring.

The Qamanirjuaq barren-ground caribou herd is presently the largest population of caribou in Nunavut, Canada (Campbell et al. 2010). Each year, the herd migrates from its winter range to calving grounds near Qamanirjuaq Lake in Nunavut (Fleck and Gunn 1982). As with many other caribou populations, the Qamanirjuaq herd has recently declined, with surveys indicating that herd abundance has decreased from ~496 000 animals in 1994 to ~348 000 animals in 2008, and ~288 000 animals in 2017 (Boulanger et al. 2018). In this study, we analyzed 12 years of Qamanirjuaq barren-ground caribou telemetry data along with snow and vegetation covariates to investigate whether vegetation and snow phenology are changing on the Qamanirjuaq range, and if so, whether the migratory and calving behaviour of the herd is responding to these changes. We further sought to test if there is any evidence to support the development of a trophic mismatch between resource availability and Qamanirjuaq caribou parturition. Based on reports of advancing Arctic vegetation and snowmelt in the literature (Cleland et al. 2007; Brown et al. 2010), we expected to observe some advancement in green-up and snowmelt trends. Recent studies have indicated the *Rangifer* populations can adjust reproductive and migratory behaviour in response to environmental conditions (Le Corre et al. 2017; Paoli et al. 2018, 2019), and so we anticipated that some metrics of Qamanirjuaq caribou reproductive and migratory phenology would respond to changes in green-up and snow conditions. Additionally, our own observations during aerial surveys and reports in the literature (Fleck and Gunn 1982) indicate that the Qamanirjuaq herd typically calves before green-up, and so we did not predict that a trophic mismatch, in the sense of vegetation green-up advancing earlier with respect to parturition (e.g., Post & Forchhammer 2008), would have occurred over the study period.

4.2 Materials and Methods

4.2.1 Study Area

The annual Qamanirjuaq barren-ground caribou range covers approximately 310 000 km^2 of Canada across two provinces and two territories. Their range extends from northeastern Saskatchewan and the southeastern portion of the Northwest Territories into northern Manitoba and proceeds north along the coast of Hudson Bay into the Kivalliq region of Nunavut, ending near the southern shores of Baker Lake (approximately 56.5° to 64°N, 91° to 106°W). The calving and summer ranges are entirely within the Nunavut territory. During the late spring and summer, areas of continuous permafrost, bedrock outcrops, sandy granitic tills, eskers, and large tracts of wetland characterize the Qamanirjuaq herd's range. The dominant land cover is shrub tundra, with *Betula nana*, *Salix* spp., and *Alnus crispa* occurring in warmer and drier areas, and *Salix* spp., *Sphagnum* spp. and *Carex* spp. found in wetter areas (Campbell et al. 2010).

4.2.2 Caribou movement behaviour and range use

We used an individual-based movement method to estimate key changes in movement behaviour for 115 GPS-collared female caribou. For each individual in the years 2004, and from

2006 to 2016, we estimated the beginning and end of spring migration, and the date of peak calving. We considered the end of spring migration equivalent to the beginning of the calving period. Collar data from 2005 were insufficient for our analysis and are not included here. In some years animal captures were performed along the migratory route, which reduced our sample size in those years for the start of migration. Some animals were collared for multiple years, providing a total of 228 estimated caribou calving periods and 165 estimated spring migrations. The number of animals tracked over this period changed annually. For the calving period estimate, we analyzed a minimum of 5 animals in 2004 and a maximum of 41 animals in 2013 (mean = 19, SD = 10). For the start of migration, we analyzed a minimum of 4 animals in 2004 and 32 in 2011 (mean = 14, SD = 9). The fix rate of collars changed over the study period, and included frequencies of 1-day (57 individuals), 12-hour (7 individuals), 6-hour (13 individuals), and 4-hour (50 individuals).

Consistent changes in daily movement rates were used to determine changes in movement behaviour (e.g., from migration to calving), and to identify key phenological traits. Following the typically low daily movements of the more sedentary winter period, caribou movement rates increase dramatically at the beginning of migration. Our method estimates the start of migration as the first of three consecutive days of movement rates above 10 km per day. Similarly, movement rates decline at the end of migration when caribou reach their calving area and we estimated the end of migration as the first of three consecutive days with movement rates below 10 km per day. Peak calving is typically defined for caribou as the date at which 50% of calves have been born. We did not have calving survey data to identify this date for most years, and so instead we estimated peak calving as the date with the lowest daily movement rate after migration but before the increased movement of the post-calving period (Chen et al. 2018).

A three-day window was chosen to minimize the likelihood that short bursts of high or low movement rates would be identified as the beginning or end of migration. The threshold of 10 km per day was chosen after considering previous work on Qamanirjuaq movement behaviour that found average late winter movement rates of 4.17 km/day, average spring migration movement rates of 11.98 km/day, average calving movement rates of 8.67 km/day, and average post-calving movement rates of 14.65 km/day (Nagy 2011). After estimating the dates of changes in movement behaviour, each individual's movement pattern was visually inspected to assess whether the algorithm had selected unrealistic or erroneous dates. If our method could not clearly identify the changes in movement behaviour for an individual in a given year, the individual was excluded from that year's analysis ($n = 19$). We note that we were unable to validate our estimates of calving dates or confirm whether an individual was parturient due to a lack of corroborating physical or observational data. However, we suggest that the timing of minimum movement rates provides an approximation of calving behaviour across collared females, particularly in barren-ground caribou where calving is usually highly synchronized. As with other cervid species (e.g., moose (*Alces alces*): Bowyer *et al.* 1999; white-tailed deer (*Odocoileus virginianus*): Carstensen *et al.* 2003; mule deer (*O. hemionus*): Long *et al.* 2009), changes in the movement behaviour of parturient cows can be used to estimate the timing of calving. Following parturition caribou cows slow for several days when newborn calves restrict movement (Griffith et al. 2002; Nagy 2011; DeMars et al. 2013; Chen et al. 2018), and so this period of depressed movement rates estimates the timing of parturition across pregnant cows within a group. Our experience using collar movement rates to infer parturition to facilitate aerial abundance surveys suggests this method works well and has been successfully deployed during modern mainland migratory calving ground surveys in Nunavut and the

Northwest Territories (Campbell et al. 2010; Boulanger et al. 2017). Due to the aggregation of females during this period, a relatively small proportion of collared females represents remarkably well the calving behaviour of the herd as a whole (Couturier et al. 1996; Campbell et al. 2010; Nagy and Campbell 2012).

To define the spatial extent of the calving range, we extracted the telemetry locations pooled across individual caribou each year during the estimated calving period. We then calculated the 90% contour of the utilization distribution from these points and used its extent to define an annual calving polygon for each year. For trend analysis we required a standard area over which to analyze environmental covariates, and so all annual polygons from 2004-2016 were combined to determine a total calving range across years. Utilization distributions were calculated using the adehabitatHR package (Calenge 2006) in R (R Core Team 2016). To delineate a winter range polygon we pooled caribou winter locations across years, with previous work on the Qamanirjuaq herd informing the dates delineating the winter period (Nagy 2011). The 90% contour of the utilization distribution calculated from these locations defined the winter range polygon. The spring migration polygon was defined similarly by the 90% contour of the utilization distribution of caribou locations during the month of May. The average migratory period over the study duration was from the 122nd to the 158th day of the year (~May 1 to June 6 depending on whether a leap year).

4.2.3 Vegetation phenology

The onset of vegetation green-up is typically associated with peak nitrogen concentration in Arctic plants (Klein 1970, 1990; Chapin 1980). To estimate the beginning of green-up annually on the Qamanirjuaq calving area from 2004 to 2016, we used a documented relationship between remotely sensed normalized difference vegetation index (NDVI) and maximum nitrogen concentration of tundra vegetation, whereby the date at which NDVI reaches half its annual maximum reasonably predicts peak nitrogen concentration, and by association, green-up (Doiron et al. 2013, 2015). NDVI values were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery from the Terra and Aqua platforms (MOD13Q1 and MYD13Q1 version 5) at 250-m spatial and 16-day temporal resolution. The 16-day resolution is offset between Terra and Aqua, allowing an 8-day resolution when combining the data streams. We used cubic spline interpolation to estimate daily NDVI. A snow cover mask was applied when deriving NDVI values. We chose MODIS imagery for analysis because previous studies have identified it as a preferred data source compared to others such as the Advanced Very High Resolution Radiometer for vegetation phenology at northern latitudes (Zeng et al. 2013). To test for relationships between spring temperature and green-up, we accessed daily temperature data for the Qamanirjuaq range from the CircumArctic Rangifer Monitoring and Assessment network's caribou range climate database (Russell et al. 2013). This database is derived from NASA's Modern Era Retrospective Analysis for Research and Applications (Rienecker et al. 2011).

4.2.4 Snow cover trends

Snow cover data from 2004-2016 were produced through the interpretation of MODIS fractional snow cover originating from daily MODIS Terra MOD10A1 version 6, produced at 500-m grid cells. The study area is contained within four MODIS tiles, h12_v02, h12_v03, h13_v02 and h13_v03, which were mosaicked to form single daily snow cover images from April 1 to June 30. Snow cover in MODIS is derived from an algorithm based on the normalized difference snow index (NDSI), NDVI for forested areas, a thermal mask, and a cloud mask (Hall et al. 2002). Fractional snow cover is determined through regression equations for NDSI (Salomonson and Appel 2004) and are reported as values of 0-100% (i.e., the fraction of area covered by snow within a grid cell). MOD10A1 is a semi-classified product, so for grid cells not assigned a fractional snow amount, an ancillary numerical classification between 101 and 254 was assigned for properties such as inland lakes or cloud cover. Fractional snow cover for the study area was determined daily and produced as the average of grid cells, each of which has a snow cover value of 0-100%. We derived snow cover metrics over the winter range polygon in late April (last two weeks) and migratory corridor polygon in early May (first two weeks). All spatial manipulations were conducted with ESRI's ArcGIS 10.5 and database manipulation and arithmetic averaging were conducted with R version 3.4.1 using R Studio (R Core Team 2016).

4.2.5 Influence of phenology on caribou calving

To investigate the influence of climate and environmental conditions on the timing of caribou calving and migration, we built models using snow cover and vegetation covariates collected from satellite imagery (Table 1). We fitted linear mixed effects models using individual as a random effect to account for inherent differences in movement behaviour between individuals that we could not capture otherwise. Model selection was performed with Akaike's Information Criterion corrected for small sample size (AICc), and models within 2 ΔAICc were considered competitive (Burnham and Anderson 2002). To test for potential bias from different radio collar fix rates, we also tested whether including the fix rate of collared individuals improved model fit.

We defined the annual mismatch between caribou and their forage as the number of days between peak nitrogen concentration (green-up) and peak parturition dates for the herd. We calculated the geodesic distance between an individual's location at the beginning and end of their estimated migration. The temporal length of migration was determined by the number of days between the estimated start and end of migration.

We tested models with both the standard deviation in snow cover and mean snow cover to represent snow conditions across the study area. Through our exploratory analysis we found that standard deviation, reflecting variability in snow cover across the study area, typically performed better than mean snow cover values in our models. Because of this, most of our models include variability in snow cover to provide an index of snow conditions for a given area and time series, where higher variability (standard deviation) reflected patchy or melting snow conditions (increased standard deviation in snow cover was inversely correlated with mean snow cover [$r = -0.88$, $P << 0.01$]). In our context of deriving snow cover metrics from satellite imagery, the use of variability (through standard deviation) over mean values is intuitive for two main reasons. A small amount of snow in terms of thickness might still provide a relatively high snow cover measure, and remote measures of snow cover are likely to be more variable during periods when snow is melting and bare ground is becoming visible.

We plotted the autocorrelation functions for all time series to identify any significant temporal autocorrelation in the data. We tested for multicollinearity between predictor variables with variance inflation factors. All statistical analyses were performed with R version 3.4.1 (R Core Team 2016).

4.3 Results

4.3.1 Vegetation and snow phenology

No significant temporal autocorrelation was detected in any of the time series analyzed, and so we report the trends identified using linear regression for statistical inference. Annual estimates of green-up on the Qamanirjuaq calving ground were temporally advanced over the study period by approximately 7.25 days (year: β= -0.60, *SE* = 0.54, 95% *CI* = [-1.80:0.59]) (Fig. 4.1). In several years of the study period (e.g., 2006, 2014), estimated green-up occurred much earlier (~10 days) than would be predicted by our linear model fit. As would be expected, earlier green-up was strongly correlated with June temperature on the calving range ($r = 0.84$, $P < 0.01$) (temperature data from NASA's Modern-Era Retrospective Analysis for Research and Applications; Rienecker *et al.* 2011; Russell *et al.* 2013)..

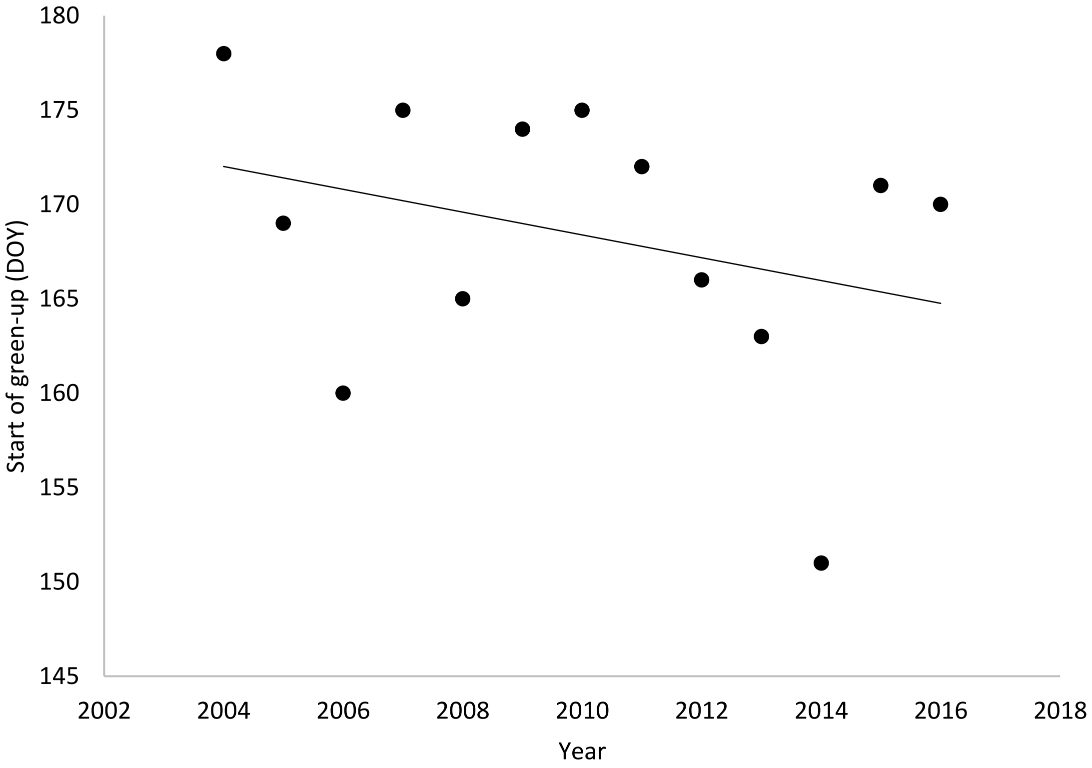

Fig 4.1 Estimated start of green-up on the Qamanirjuaq barren-ground caribou calving range from 2004 – 2016 (year: β= -0.60, *SE* = 0.54, 95% *CI* = [-1.80:0.59]). DOY: day of year.

We did not find any meaningful trends in mean snow cover on the three seasonal ranges analyzed (Fig. 4.2). However by examining statistics other than the mean, it appears that some changes in snow phenology have occurred. During half of the calving periods between 2004 and 2011, mean snow cover on the calving ground was greater than 30%, whereas from 2012 to 2016 the highest mean snow cover was 13.76%. Increased snow cover on the Qamanirjuaq calving range during the calving period was related to later green-up ($r = 0.67$, $P = 0.01$). Over the study period, we also found an increase in snow cover variability during migration (year: β= 0.94, *SE* = 0.49, 95% *CI* = [-0.15:2.02]), particularly from 2011 onward. From 2004 to 2010 average standard deviation in snow cover during migration was 10.3%, while from 2011 to 2016 it doubled to 20.6%.

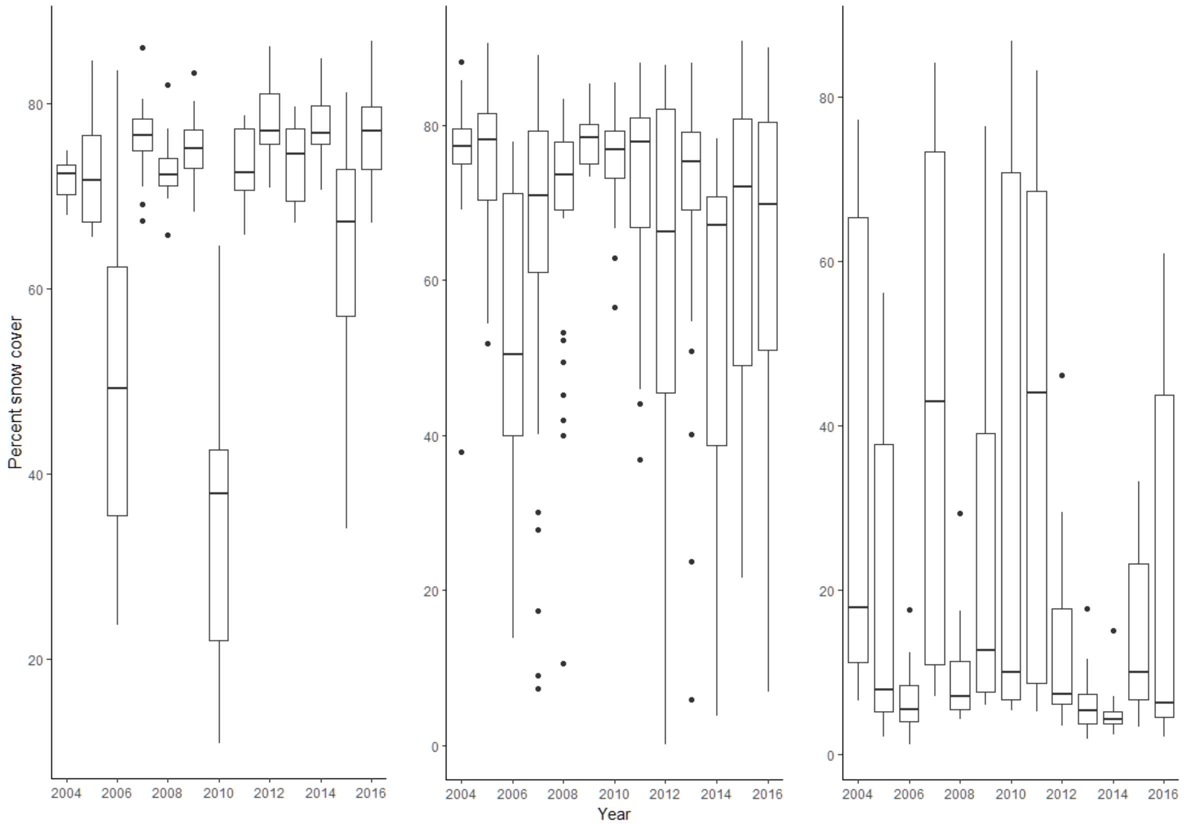

Fig 4.2 Percent snow cover from 2004 to 2016 for three seasonal ranges of the Qamanirjuaq caribou herd. Left: Late April (DOY 105 – 120) winter range. Mid: May (DOY 121 – 153) migratory range. Right: Early June (DOY 158-177) calving range. No significant linear trends exist in the mean values, however there was an increase in standard deviation of May migratory range snow cover (year: β= 0.94, *SE* = 0.49, 95% *CI* = [-0.15:2.02]) DOY: day of year.

4.3.2 Migratory and calving phenology

All measures of caribou phenology that we estimated (migration start, end, and peak calving) advanced temporally over the study period, although the trends were weak. The average start of spring migration advanced by 13.64 days from 2004 to 2016 (Fig. 4.3, year: β = -1.14, *SE* = 0.25, 95% *CI* = [-1.62:-0.65]), the average end of spring migration advanced by 6.02 days (Fig. 4.3, year: β = -0.50, *SE* = 0.12, 95% *CI* = [-0.75:-0.26]), and the average date of peak calving advanced by 9.42 days (Fig. 4.3, year: β = -0.79, *SE* = 0.09, 95% *CI* = [-0.96:-0.61]).

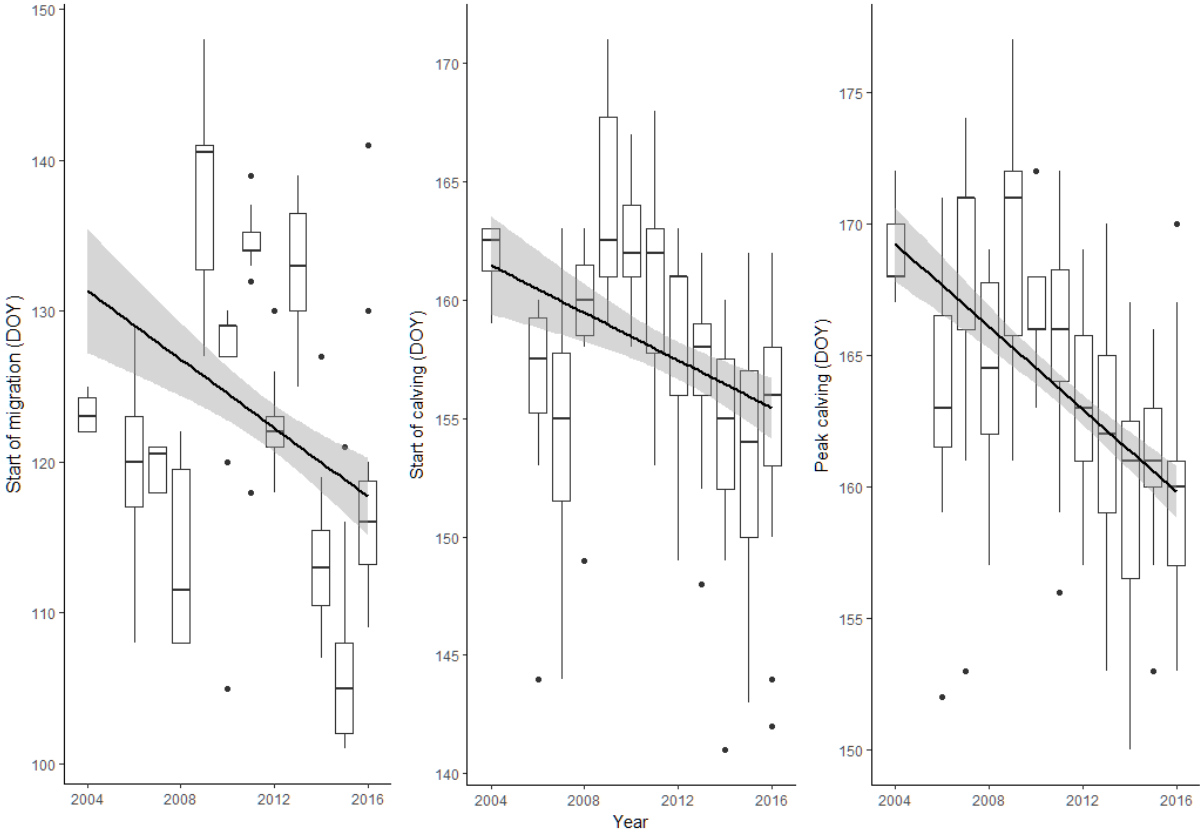

Fig 4.3 Annual estimates of three key changes in movement behaviour of Qamanirjuaq caribou in 2004 and from 2006 to 2016 with fitted trends and 95% confidence intervals. Start of migration (year: β = -1.14, *SE* = 0.25, 95% *CI* = [-1.62:-0.65]), start of calving (year: β = -0.50, *SE* = 0.12, 95% *CI* = [-0.75:-0.26]), peak calving (year: β = -0.79, *SE* = 0.09, 95% *CI* = [-0.96:-0.61]). DOY: day of year.

4.3.3 Influence of environmental phenology on caribou calving

Based on weight of evidence, our models suggested that snow conditions on the Qamanirjuaq winter range provide a cue for the start of migration, and snow conditions during migration influence the time taken to reach the calving ground (Table 4.1, Fig. 4.4). Our most supported models indicated that increasing variability in late April snow cover on the winter range, and in May snow cover along the migratory route resulted in earlier arrival on the calving range (Table 4.2, Fig. 4.5). The date of peak calving was best explained by snow conditions in May along the migratory route and snow cover on the calving ground during the average calving period (Table 4.1, Fig. 4.6). The most supported model for the length of the migration included the distance migrated, snow conditions along the migratory route in May, and late April snow conditions on the winter range (Table 4.2). Caribou took longer to migrate further distances, and more variable snow conditions increased the length of migration (Fig. 4.7).

Table 4.1 Comparison of models for the start of migration, end of migration, peak calving dates, and length of migration in 2004, and 2006 - 2016 of the Qamanirjuaq barren-ground caribou herd using Akaike's Information Criterion corrected for small sample size (AIC_c). SC: snow cover, MSC: migration snow cover, WSC: winter snow cover, SD: standard deviation.

Behaviour	**Model**	**ΔAICc**	**ωi**
Start of migration	Early May MSC SD + Late April WSC SD + Migration distance + (1|individual)	0.00	1.00
	Late April WSC SD + Migration distance + (1|individual)	35.50	0.00
	Early May MSC SD + Migration distance + (1|individual)	40.56	0.00
	Late April WSC + Migration distance + (1|individual)	61.33	0.00
	Migration distance + (1|individual)	78.22	0.00
	(1|individual)	130.25	0.00
End of migration	May MSC SD + Migration distance	0.00	0.53
	May MSC SD + Migration distance + Calving SC	1.35	0.27
	May MSC SD + Migration distance + Green-up	2.06	0.19
	May MSC SD + Green-up	8.58	0.01
	Green-up	46.43	0.00
	Intercept only	58.24	0.00
	Migration distance	59.50	0.00

Peak calving	May MSC SD + Calving SC + (1|individual)	0.00	1.00
	May MSC SD + Green-up + (1|individual)	11.45	0.00
	May MSC SD + (1|individual)	18.88	0.00
	Calving SC + (1|individual)	23.89	0.00
	Green-up + (1|individual)	28.16	0.00
	(1|individual)	63.73	0.00
Migration length	May MSC SD + Late April WSC SD + Migration distance	0.00	0.79
	Late April WSC SD + Migration distance	2.65	0.21
	May MSC SD + Migration distance	39.95	0.00
	Migration distance	41.16	0.00
	May MSC SD + Late April WSC SD	56.27	0.00
	Intercept only	94.25	0.00

Table 4.2 Parameter estimates of most supported linear and linear mixed-effects models for the timing of spring movement behaviour of the Qamanirjuaq barren-ground caribou herd. SC: snow cover, MSC: migration snow cover, WSC: winter snow cover, SD: standard deviation.

Behaviour modelled		**β**	**SE**
Start of migration	Intercept	149.67	2.01
	Early May MSC SD	-0.47	0.07
	Late April WSC SD	-0.80	0.11
	Migration distance	-0.40	0.03
End of migration*	Intercept	163.86	1.11
	May MSC SD	-0.52	0.06
	Migration distance	0.07	0.02
Peak calving	Intercept	166.20	1.16
	May MSC SD	-0.27	0.05
	Calving SC	0.10	0.02
Migration length*	Intercept	10.85	2.23
	May MSC SD	0.21	0.10
	Late April WSC SD	0.90	0.13
	Migration distance	0.33	0.04

*Fixed effects only

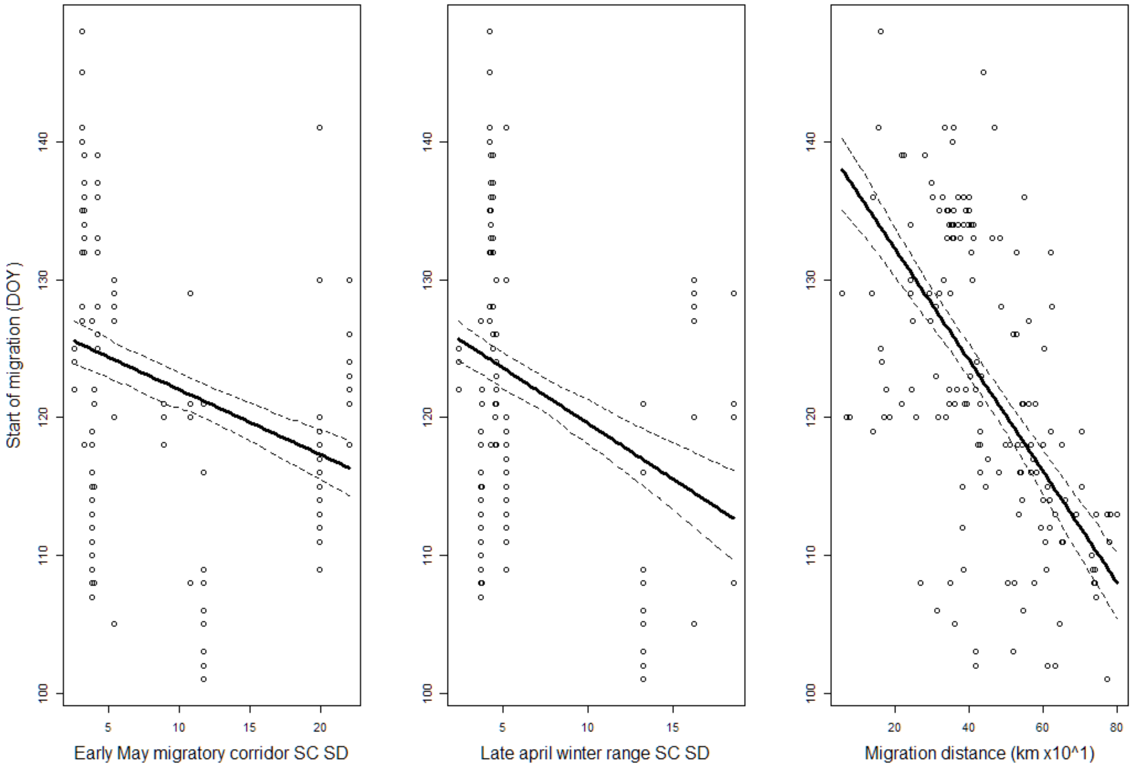

Fig 4.4 Predicted linear mixed-effects relationships for covariates in the most supported caribou migration start date model. Dotted lines represent bootstrapped 95% confidence intervals. SC: snow cover, SD: standard deviation, DOY: day of year.

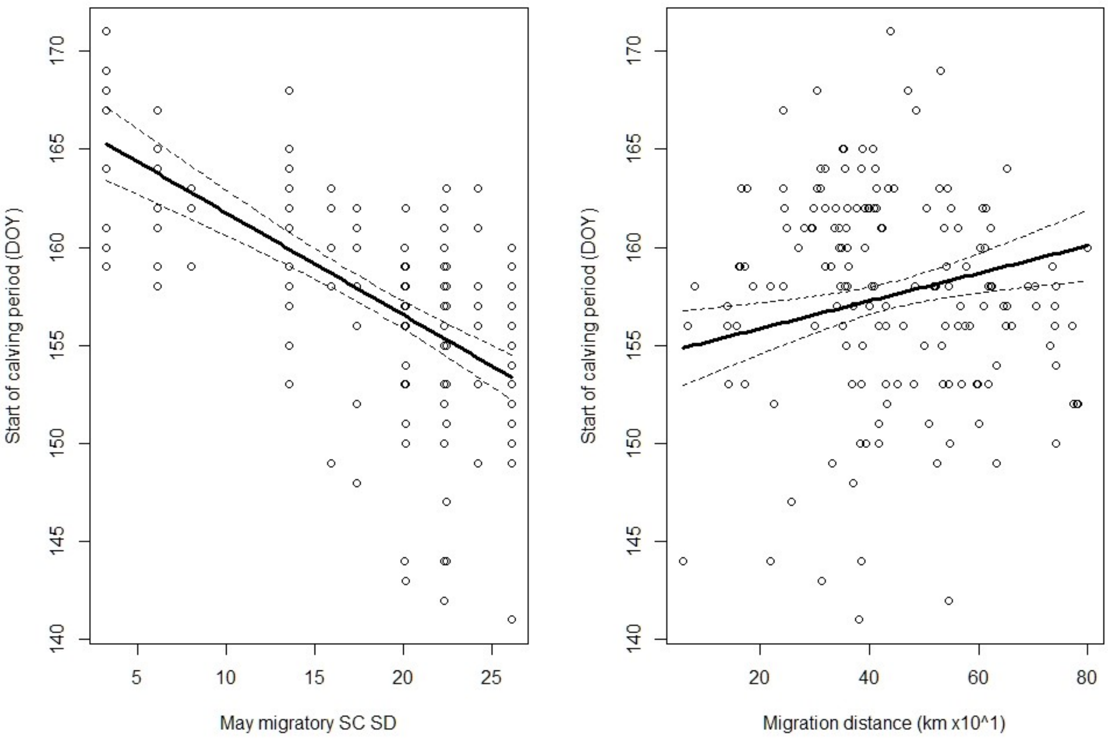

Fig 4.5 Predicted linear relationships for covariates in the most supported caribou calving start date model. Dotted lines represent 95% confidence intervals. SC: snow cover, SD: standard deviation, DOY: day of year.

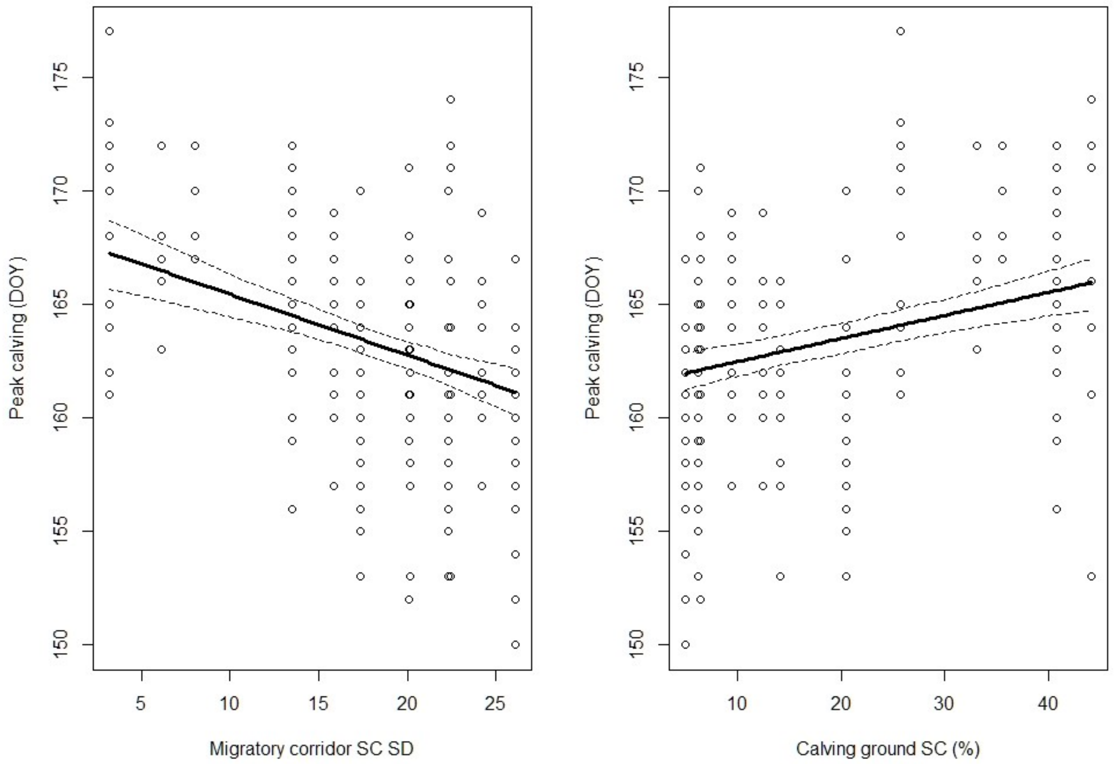

Fig 4.6 Predicted linear mixed-effects relationships for covariates in the most supported caribou peak calving date model. Dotted lines represent bootstrapped 95% confidence intervals. SC: snow cover, SD: standard deviation, DOY: day of year.

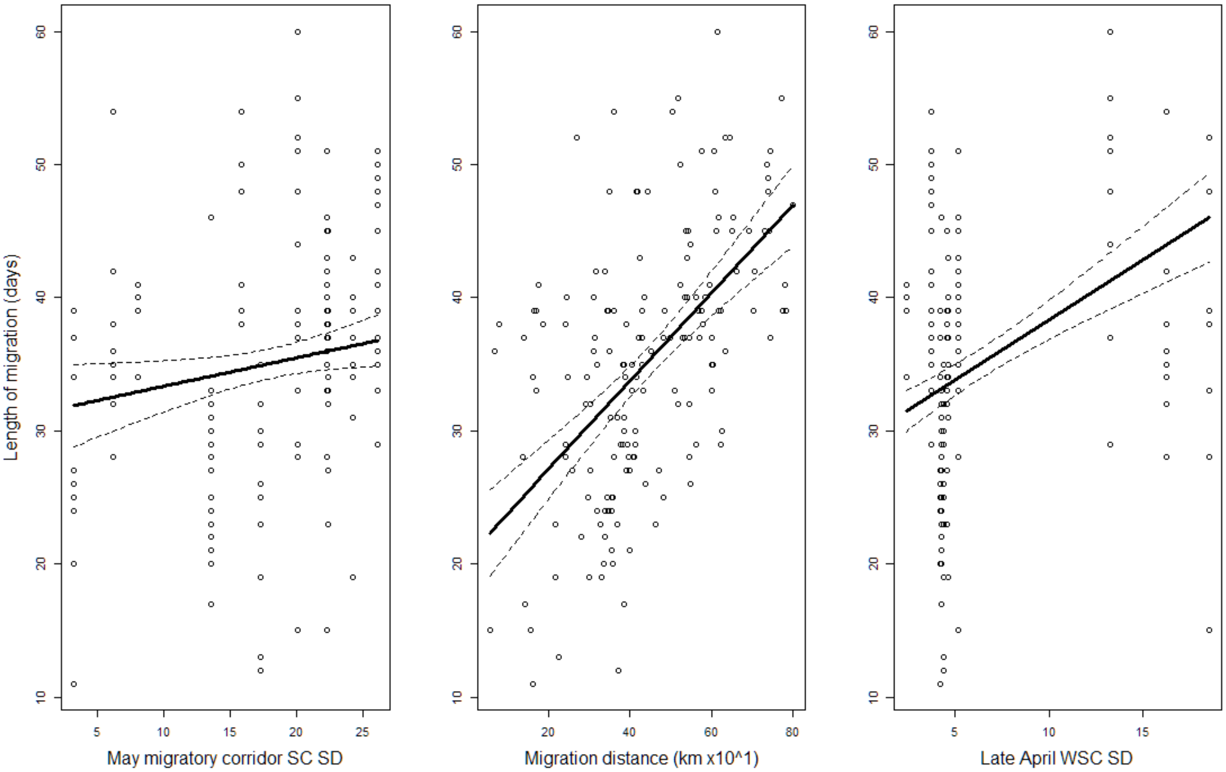

Fig 4.7 Predicted linear relationships for covariates in the most supported caribou migration length model. Dotted lines represent 95% confidence intervals. SC: snow cover, WSC: winter snow cover, SD: standard deviation.

There was no discernable trend in the “mismatch” between estimated dates of parturition and green-up over the study period (Fig. 4.8). Mean peak parturition occurred an average of 3.32 days (*SE* = 0.45, 95% *CI* = [-4.20:-2.44]) before the start of green-up and the herd typically arrived at the calving area 9.42 days (*SE* = 0.49, 95% *CI* = [-10.11:-8.19]) before green-up began. Green-up began before the median date of peak parturition in only two of the twelve years considered (2006 and 2014).

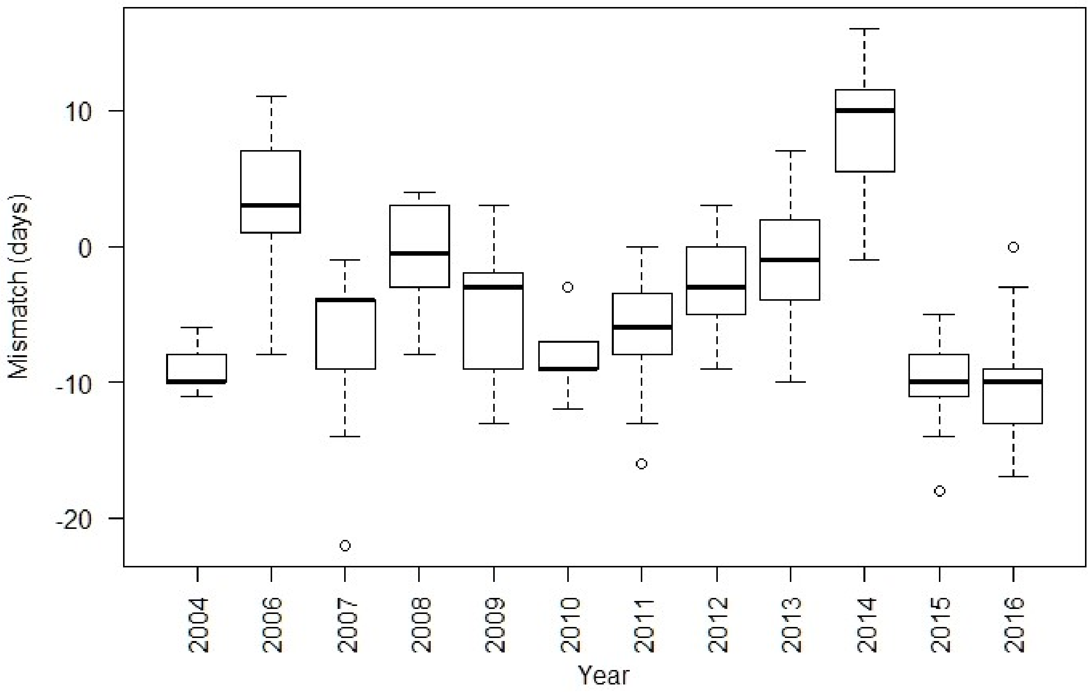

Fig 4.8 Estimated mismatch, defined as the difference (in days) between the date of caribou peak parturition and estimated start of green-up on the Qamanirjuaq calving range in 2004 and from 2006 – 2016. Peak parturition occurred an average of 3.32 days (*SE* = 0.45, 95% *CI* = [-4.20:-2.44]) before the start of green-up over this period.

Two of our final models (end of migration/start of calving and length of migration) did not include random effects because they explained little variability in the response (Table 4.1). For the end of migration, two of the models we compared were within 2 AICc, and so could be considered as competing (Table 4.1). However, these models differed only by an additional parameter, with the larger model having a ΔAICc of 1.35 over the smaller. Following Arnold (2010), we dismissed the potentially competitive model as containing an additional uninformative (in this case) parameter. Including a fix rate covariate did not improve the fit of any of our models.

4.4 Discussion

We evaluated temporal trends in a number of phenological indicators for barren-ground caribou and their habitats. We aimed to understand how barren-ground caribou spring migratory and calving behaviour might respond to phenological changes in the environment and to assess the evidence for trophic mismatch development in our study system. From 2004 to 2016, we found advancement in the annual timing of the start and end of migration, and of peak calving. We also found evidence for declining snow cover along the migratory corridor (Fig. 4.2) and for earlier green-up on the calving ground. These results provided several potential environmental drivers for the observed advancement in migratory and calving behaviour, which we evaluated for support using a weight of evidence modeling approach. Our results suggested that snow conditions on the winter range and along the migration route were the primary driver for advancing migratory behaviour.

Caribou appeared to use winter-range snow conditions as an environmental cue for migration. Late-winter and early-spring conditions seemed to provide some information about the likely conditions of the calving ground because there was moderate correlation between standard deviation in snow cover along the migratory route and date of green-up on the calving ground ($r = -0.61$, $P < 0.05$). Thus, by timing migrations to conditions that remain amenable to movement, at least at the proximal end of the migratory corridor, caribou might coarsely predict the conditions of their destination. Our findings agree with those of other recent publications in which milder winter conditions were correlated with earlier migration departures (Le Corre et al.

2017). However, Le Corre *et al.* (2017) found that mild spring conditions delayed arrival on the calving range, while in our study declining snow cover during migration advanced arrival on the calving range (end of migration), although caribou took a longer time to migrate in years with less snow. In our study system, caribou appear to have compensated for the slower pace of migration with earlier departure dates.

Consistent with some studies on long-distance avian migrants (Cotton 2003; Gordo et al. 2005), our results support the importance of winter range conditions as a driver for the timing of spring migration and ultimately arrival on the calving or breeding grounds. Snow conditions, icing conditions, and lake and river ice formation and quality are critical to barren-ground caribou migration. Ease of movement and energy expenditure during this period are largely determined by snow conditions, with thick soft snow, ice crusts, and slush hindering movement (Fancy and White 1987b; Nicholson et al. 2016). Sufficient ice thickness on water bodies along the migratory route allows caribou to make crossings safely (Miller and Gunn 1986). Caribou are known to wait for adequate ice conditions before making crossings (Poole et al. 2010) and to skirt or avoid water bodies with thin or no ice (Leblond et al. 2016). Sharp ice crusts from rain-on-snow or thaw-freeze events also can cause damage to the lower legs of caribou when they break through to the softer snow underneath, leading not only to pain and discomfort but also to rapid transmission of diseases such as hoof-rot (Valkenburg et al. 2003). These snow conditions are more likely during warmer weather and when snow is melting, providing a probable mechanism for the observed increase in migration time in years with earlier snow melt. Along with our findings, these examples support the importance of snow and ice conditions during spring caribou migrations and the adaptive value of that barren-ground caribou using local snow conditions on the winter and early migratory ranges as a cue for migration.

We found that peak calving occurred earlier in years with less snow on the calving area and along the migratory route. Although the timing of parturition in caribou is primarily related to the timing of the rut and the length of gestation, some plasticity in the length of gestation could be selectively advantageous and allow otherwise underweight foetuses longer developmental periods to increase the likelihood of survival (Bergerud et al. 2008). Plasticity in the length of gestation might then allow for some modification of the timing of parturition depending on annual conditions on the calving area. We would not expect this effect to dramatically override nutritional effects throughout gestation or female condition coming out of the previous summer (Cameron et al. 1993; Gerhart et al. 1997; Pachkowski et al. 2013), and the lesser influence of calving area conditions on peak calving can be seen in the smaller effect sizes of environmental predictors on peak calving that the other behaviours modeled (Table 4.2). Chen *et al.* (2018) found that peak calving dates of the Bathurst barren-ground caribou herd were altered by both the previous year's conditions and the start of the growing season in the current year, and Paoli *et al.* (2018) documented earlier reindeer calving dates in response to reduced April snow cover. Both of these examples support our findings that spring conditions can alter the timing of calving in the same year.

Whereas there have been some reports of advancing breeding phenology in response to changing environmental conditions in avian and ungulate species (e.g., Moyes et al. 2011; Dunn & Møller 2014), very few studies have reported climate-mediated advancement in the breeding phenology of an Arctic ungulate (Paoli et al. 2018, 2019). Le Corre *et al.* (2017) recently investigated the effects of climate conditions on migration phenology of caribou in northern Quebec and Labrador, Canada. Although they observed an advancement of spring migration departure dates, they found no trend in dates of arrival on the calving area, which suggested deteriorating conditions for movement during migration in the spring. Chen *et al.* (2018) reported that peak calving dates in the Bathurst barren-ground caribou herd likely resulted from cumulative climate-driven habitat changes across multiple years, but did not find a temporal trend in the timing of parturition. Paoli *et al.* (2018) found that the calving of a population of reindeer in Finland had advanced by around 7 days between 1970 and 2016 in response to reduced April snow cover and warmer spring temperatures.

Our findings suggest the existence of two phenomena. First, it appears that changes to spring phenology, at least in terms of snowmelt and vegetation green-up, have occurred across the Qamanirjuaq herd's range. Second, it appears that over the study period, phenological changes on the herd's winter and migratory range have allowed caribou to keep pace with changes occurring on the calving range. Because of this, we observe no trend in the temporal separation between green-up and calving over the study period, and therefore no support for the development of a trophic mismatch (Figure 4.8). This lack of trend results from the similar magnitude in advancement of snowmelt, green-up, and calving. Although we are confident that in general a relatively small number of collared cows reflect the spatial distribution of female caribou during the calving period, but as sample size decreases the chance of not capturing behaviour reflective of the entire herd increases. In some years our sample size is quite low (i.e., 5 tracked animals in 2004, 9 tracked animals in 2010), and so some degree of caution is necessary in our interpretation.

The vulnerability of a species to the effects of trophic mismatch depends partly on their life history strategies. For example, animals that undertake long-distance migrations might be more susceptible to trophic mismatches than non-migratory species (Both et al. 2009). Species with more proximate seasonal ranges, such as the caribou in this study, may be better positioned to adjust to phenological changes that arise at comparable rates across their total annual range. Both Veiberg *et al.* (2016) and Gustine *et al.* (2017) suggested that because caribou and reindeer are primarily capital breeders (Taillon et al. 2013), the influence of spring phenology should be less important than that of maternal winter body condition on reproductive success, and this strategy for financing reproduction could mitigate the effects of changing or variable spring phenology (Williams et al. 2017). Substantial evidence, including from this study, indicates that many barren-ground caribou populations often calve well in advance of green-up (Fleck & Gunn 1982; Reimers et al. 1983; Crête & Huot 1993; Bergerud et al. 2008; Gustine et al. 2017; Veiberg et al. 2017; see review by Mallory & Boyce 2018), reducing the potential importance of concurrent timing of these events. Although barren-ground caribou are well-adapted to highly variable and often difficult conditions during parturition, cows and calves certainly benefit from earlier access to high-quality forage and improved nutritional income at this time of year. In fact, the early onset of spring can benefit caribou cows and calves by providing earlier access to high-quality forage and supplement the nutritional costs of lactation (Pettorelli et al. 2005; Cebrian et al. 2008; Helle and Kojola 2008; Couturier et al. 2009b; Tveraa et al. 2013), and Paoli et al. (2019) reported that reindeer calves in northern Finland were born heavier and had higher over-summer survival in years with an earlier onset of vegetation growth. Accessible and nutritious forage near parturition and during lactation remains important, and it stands to reason that caribou who can maintain calving behaviour that keeps pace with changes to forage phenology might have better reproductive success than those who do not. Although the evidence for the possible development of a true "trophic mismatch" for most *Rangifer* populations examined is scant, the timing of the onset of vegetation growth can have consequences for calf and cow nutrition, and phenological changes that reduce either the availability or quality of forage at this time of year will still have some implications for these northern ungulates (Couturier et al. 2009b; Tveraa et al. 2013; Paoli et al. 2019).

Though we have insufficient data to investigate links between advancing reproductive and migratory phenology with demographic parameters, studies of other species provide basis for speculation. Analysis by Møller *et al.* (2008) revealed that European bird species with migratory behaviour that had not advanced in response to changing climate conditions experienced stronger population declines than species that had advanced the timing of their migrations. Similarly, the inability of roe deer (an income breeder) in France to adjust their breeding phenology to cope with earlier spring onset resulted in negative demographic effects in the population (Plard et al. 2014). In contrast, the reproductive phenology of some northern mammals such as red deer (*Cervus elaphus*; Moyes et al. 2011) have responded strongly to changing climate conditions, with advancing parturition dates and other phenological traits. These examples suggest that the apparent ability of barren-ground caribou to adjust their migratory and reproductive phenology in response to the earlier onset of spring could provide resilience to climate change. However, other factors also can disrupt caribou migratory and calving behaviour, such as anthropogenic disturbance. Caribou have been widely reported to avoid anthropogenic disturbance and negatively respond to human activity (Cameron et al. 2005; Johnson et al. 2005; Vistnes and Nellemann 2008; Festa-Bianchet et al. 2011; Boulanger et al. 2012; Johnson and Russell 2014), and in some cases these disturbances have disrupted the migratory behaviour of individuals (Mahoney and Schaefer 2002; Vistnes et al. 2004; Wilson et al. 2016). The potential for caribou to adjust migratory behaviour in response to changing environmental cues could be hampered by novel disturbances along their migratory routes, and it is therefore imperative that decision makers give adequate weight to these effects when considering human activities on caribou ranges.

Our analysis indicates that in years with more variable snow conditions and earlier snowmelt, caribou spend longer periods migrating (Fig. 4.7). If the observed trends in phenology continue it is possible that the time taken to migrate could increase further. Barren-ground caribou expend tremendous resources during migration at a time when forage resources are poor. We think it reasonable to contemplate the possible negative effects to caribou should the length of migration increase. Longer durations spent in poor forage conditions during spring migration would be expected to negatively affect the condition of cows and calves, potentially reducing calf survival (Crête and Huot 1993; Gerhart et al. 1996; Sharma et al. 2009).

Our study reports climate-mediated advancement in the reproductive phenology of an Arctic ungulate. This advancement results from changing spring snow conditions on the caribou herd's winter and migratory range that provide earlier cues for migration and calving. Earlier calving and migratory behaviour have allowed caribou to keep pace with earlier green-up, and we found no evidence to suggest the development of a detrimental trophic mismatch. In fact, as evidenced by their life history characteristics and empirical evidence (Taillon et al. 2013; Gustine et al. 2017), *Rangifer* populations appear unlikely to be broadly susceptible to trophic mismatches at the timing of parturition.

Caribou and reindeer have huge socioeconomic importance across the circumpolar world and the ways in which a changing climate might affect the conservation of these populations has become an important area of research (e.g., Sharma et al. 2009; Turunen et al. 2009; Uboni et al. 2016). Although the potential consequences of climate change for *Rangifer* populations are many (Mallory and Boyce 2018), we suggest that the ability of caribou to adjust calving and migratory behaviour in response to shifting environmental cues could be a critical behaviour for climate change adaptation.

5 Identifying migratory corridors for barren-ground caribou adjusting to climate change

5.1 Introduction

Declines in migratory populations have been documented globally across numerous taxa (Sanderson et al. 2006; Bolger et al. 2008; Wilcove and Wikelski 2008; Flockhart et al. 2015). The significance of the loss of migratory species extends beyond individual species due to the importance of migration in ecosystem function (Bauer and Hoye 2014). As with changes to many other ecological phenomena, the predominant drivers behind declining movement and migratory behaviours are anthropogenic (Bolger et al. 2008; Tucker et al. 2018). Habitat degradation along movement corridors caused by the urbanization and industrialization of vast swathes of habitats is the primary culprit for terrestrial species, but climate-mediated environmental change also plays a role (Robinson et al. 2009). In the Arctic, where climate change is happening at more than twice the rate of temperate regions (Serreze et al. 2009; Richter-Menge et al. 2017), species such as caribou (*Rangifer tarandus*) are likely to be challenged to adapt their migratory behaviours to changing environmental conditions (Sharma et al. 2009; Leblond et al. 2016; Le Corre et al. 2017; Mallory and Boyce 2018).

Impediments to movement, from slowing or diverting migrations to the complete loss of migratory behaviour, can have dramatic consequences for wildlife populations (Bolger et al. 2008). Migration by ungulates can reduce predation risk and provide access to improved forage quality and habitats suitable for birthing and raising young (Fryxell and Sinclair 1988; Alerstam et al. 2003). The fitness advantages conferred by migratory life history strategies are undermined by the disruption or complete loss of migratory behaviour (although some species and populations exhibit substantial flexibility in their migratory behaviour, e.g., Boyce 1991;

Eggeman et al. 2016; Hebblewhite et al. 2018). For many species, the energetic and nutritional resources expended during long-distance migrations can be considerable and vary in response to animal decisions regarding the timing, duration, and route of migration (Fancy and White 1987b; Brown et al. 1996; Altizer et al. 2011; Leonard and McCormick 2011; Flack et al. 2016). Partial disruption of traditional migratory routes, say by animals travelling extra distance to avoid human activities or difficult terrain (including large bodies of open water or fast-flowing rivers), can increase the costs of what is already a costly behaviour (Miller et al. 1972; Leblond et al. 2016; Plante et al. 2018). Caribou have documented sensitivity to anthropogenic disturbance (Reimers and Colman 2006; Vistnes and Nellemann 2008; Boulanger et al. 2012; Johnson and Russell 2014; Plante et al. 2018), and along with a host of other migratory mammals such as pronghorn (*Antilocapra americana,* Seidler et al. 2015), Mongolian gazelle (*Procapra gutturosa*, Ito et al. 2005), and wildebeest (*Connochaetes taurinus,* Bolger et al. 2008), can have their migratory behaviour disrupted by humans. For example, some individuals in the Western Arctic Herd in Alaska were reported to delay migration by an average of 33 days when encountering a road (Wilson et al. 2016). Migration by reindeer (*R. t. tarandus*) in Norway was delayed 5 days while they appeared to search for an undisturbed area to cross a road (Panzacchi et al. 2013).

Caribou migrations also might be disrupted or altered by the effects of climate change as it relates to local and regional weather. Warmer spring temperatures can lead to changes in snow and ice phenology along the migratory route, including earlier or more rapid melting and increased ice crust formation. These phenological changes could disrupt caribou movements and behaviour through lengthened routes to avoid unseasonal open water, dangerous ice conditions, ice crusts (Leblond et al. 2016), or by increased energy expenditure resulting from walking through thick soft or slushy snow (Le Corre et al. 2017). Disruptions to migratory behaviour are in many cases analogous to losses of landscape connectivity, which is “the degree to which a landscape facilitates or impedes movement of organisms among resource patches” (Taylor et al. 1993), and connectivity between seasonal ranges is necessary for migration (Sawyer et al. 2005; McClure et al. 2016).

Concerns surrounding the loss of migratory populations have led to development and application of methods for identifying migratory corridors (Benz et al. 2016). Technological advancements that allow animals to be tracked at a fine scale provide for empirical parameterization of movement models, reducing the need for subjectivity in delineating movement corridors. Integrated step selection analysis (iSSA) is an extension of step-selection functions (Fortin et al. 2005; Thurfjell et al. 2014) that simultaneously integrates movement parameters (e.g., turn angles and step lengths) and resource selection within the same model (Avgar et al. 2016), reducing possible biases when interpreting resource selection parameters (Forester et al. 2009). Resource selection analyses, including iSSA, provide insight into how animals use their environment, which can be applied to predict habitat quality or suitability across the landscape (e.g., Johnson et al., 2004; Chetkiewicz and Boyce, 2009). These measures can indicate the relative probability with which an animal will choose to use or move through a given area and improve our understanding of how animals use the landscape during behaviours such as migration (Bastille-Rousseau et al. 2015).

Similar advances in methods have been made in connectivity analysis. For example, using circuit theory to analyse landscape connectivity allows for the consideration of multiple pathways across a continuous surface rather than defining a single least-cost path between two patches (McRae et al. 2008; Moilanen 2011). The continuous surface over which connectivity is analysed can be derived from measures of habitat suitability, such as those produced by iSSA. Indeed, a recent review by Abrahms et al. (2017) indicates that resource selection best estimates connectivity when the behavioural state of the animal (e.g., migration) is taken into account and that effective identification of movement corridors requires consideration of movement behaviour.

Barren-ground caribou (*R. t. groenlandicus*) is a subspecies of caribou that spends all or part of the year above the treeline on the tundra. Many barren-ground caribou populations are migratory and travel hundreds of kilometres in spring and fall between winter and summer ranges. In spring, migratory herds move from winter ranges to calving areas for which they display strong fidelity (Gunn and Miller 1986). The Qamanirjuaq herd is presently one of the largest caribou herds in North America at approximately 288 000 individuals. Like many barren-ground caribou herds, the Qamanirjuaq has declined in abundance since the 1990s, although not at the precipitous rate experienced by some other populations (Boulanger et al. 2018; Mallory et al. 2018a). Our previous work indicates that the Qamanirjuaq herd is adjusting the timing of its spring migration in response to advancing spring phenology (Chapter 4). Although these adjustments could provide some resilience to negative effects of climate change (Mallory and Boyce 2018), we found that earlier migration and warmer springs are associated with a longer time taken to migrate. We hypothesize that this results from the influence of snow conditions on movement. Here, we used generalized linear models to investigate the effects of snow conditions on caribou movement characteristics during spring migration. We further used iSSA to determine how landscape attributes influence spring migratory movement behaviour for the Qamanirjuaq barren-ground caribou herd. We transformed the results of our iSSA to predict landscape resistance between winter and calving ranges and applied circuit theory to delineate the most important regions of the migratory corridor. The Qamanirjuaq spring and summer ranges remain relatively undisturbed at present, with only a handful of remote communities and little in the way of active year round industrial development, however increasing development pressure from extractive industries are anticipated in Canada's north and within the Qamanirjuaq herd's tundra range (BQCMB 2014; COSEWIC 2016). By identifying the herd's critical habitat before significant habitat alteration occurs, we provide opportunity for proactive conservation measures and responsible development in hopes that we might pre-emptively avoid the land use conflicts that are common across much of the caribou range in North America (Festa-Bianchet et al. 2011; Hebblewhite 2017). By minimizing other potential disturbances during migration, caribou might be better able to adjust to changing environmental conditions resulting from global climate change.

5.2 Materials and Methods

5.2.1 Study area

Qamanirjuaq caribou winter at or below the treeline in northern Manitoba, northern Saskatchewan, and the eastern to southeastern Northwest Territories (Fig. 5.1), although some individuals will remain on the tundra in Nunavut in some years (Fleck and Gunn 1982). Over the course of their spring migration, Qamanirjuaq caribou travel from areas of boreal forest to tundra habitats characterized by continuous permafrost, bedrock outcrops, sandy granitic tills, eskers, and large tracts of wetland (Campbell et al. 2010). Extensive snow cover normally remains during spring migration. We defined the extent of our study area (Fig. 5.1), approximately 58°N to 64° and 108°W to 92°W, using the locations of caribou between the years of 2004 and 2017 during spring migration.

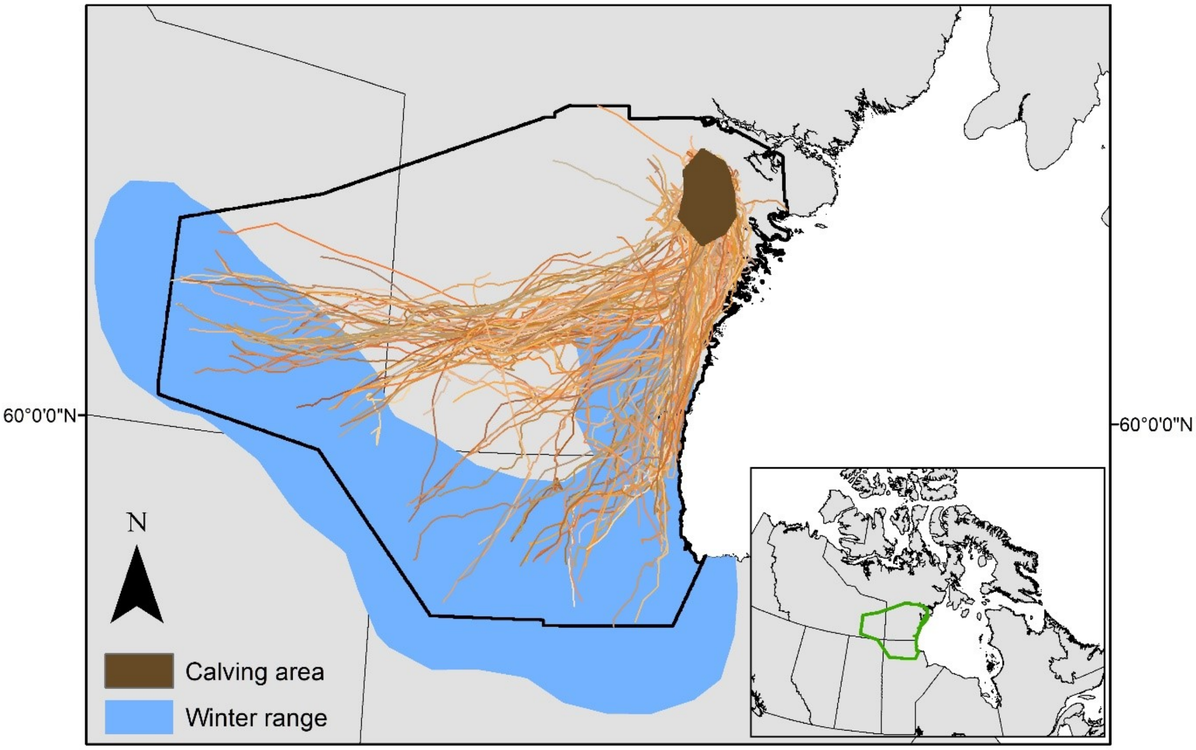

Fig 5.1 Qamanirjuaq barren-ground caribou (*Rangifer tarandus groenlandicus*) spring migratory range. The orange lines are 194 individual migration paths from the years 2004 and 2006-2017. The extent of our integrated step selection analysis and circuit theory analysis is represented by the black polygon.

5.2.2 Delineation of migratory and calving periods

We mapped individual migratory paths (Fig. 5.1) for a total of 127 female caribou from 2004 to 2017 (excluding 2005 due to insufficient telemetry data). Some animals were tracked for multiple years, resulting in a total of 194 spring migrations analyzed. Satellite collar fix rates changed over the study period and included frequencies of 1-day (57 individuals), 12-hour (7 individuals), 6-hour (13 individuals), and 4-hour (50 individuals).

Following the observed low daily movements of the sedentary winter period, caribou movement rates increase at the start of migration. For each individual we estimated the start of migration as the first of three consecutive days of movement rates above 10 km per day (the average start date of migration was May 3rd). At the end of migration movement rates decline as caribou reach their calving area, and we estimated the end of migration as the first of three consecutive days with movement rates below 10 km per day (the average end date of migration was June 6th). We then created a path from all relocations between those dates. We also used changes in movement rates to estimate the calving period, which is characterized by low movement rates when the maternal care of newborn calves limits breeding cow movement (Griffith et al. 2002; Chen et al. 2018). The end of migration was considered the start of the calving period, and the end of calving was determined using the increase in daily movement associated with post-calving dispersal. Again, we used the first of three consecutive days of movement rates above 10 km/day to identify this change in behaviour (the average end date of calving was June 25th).

We selected a three-day window to detect changes in movement behaviour such that short periods of high or low movement rates would not be identified as the beginning or end of migration. Previous work on Qamanirjuaq movement indicated that a threshold of 10 km per day would be adequate for identifying changes in behaviour. Nagy (2011) found that average late winter movement rates of Qamanirjuaq caribou were 4.17 km/day, average spring migration movement rates were 11.98 km/day, average calving movement rates were 8.67 km/day, and average post-calving movement rates were 14.65 km/day. After estimating the dates of changes in movement behaviour, each migratory path was visually inspected to assess whether the algorithm had selected unrealistic or erroneous dates locations. If our method could not clearly identify the changes in movement behaviour for an individual in a given year, the individual was excluded from that year's analysis (n = 19).

The total study area for the iSSA was defined by the minimum bounding geometry of all migration locations (100% minimum convex polygon). The boundary was extended by approximately 20 km where it was immediately adjacent to caribou locations to accommodate potential random steps during the iSSA analysis (i.e. 100% minimum convex polygon + 20km). Qamanirjuaq caribou display strong fidelity to traditional calving grounds (Fleck and Gunn 1982), and we calculated the 50% utilization distribution (kernel method, *href* smoothing parameter) from points of all individuals during the calving period to represent a high-density proportion of the area used by the herd for calving. All utilization distributions were calculated using the *adehabitatHR* package in R (Calenge 2006).

5.2.3 Caribou movement metrics

To investigate the effects of snow cover on caribou migratory movements, we analyzed trends in snow cover on the Qamanirjuaq winter range and migratory corridor from 2004-2016. Snow cover trends were interpreted through Moderate Resolution Imaging Spectroradiometer (MODIS) fractional snow cover originating from daily MODIS Terra MOD10A1 version 6 at 500-m grid cells. Fractional snow cover across the study area was determined daily and produced as the average of grid cells, each of which has a snow cover value of 0-100%. We used variability in mean snow cover to provide an index of snow conditions for a given area and time series (winter range in late April [last two weeks] and migratory corridor in early May [first two weeks]), where higher variability (standard deviation) reflected patchy or melting snow conditions (Chapter 4). Winter and migratory range polygons for snow cover analysis were derived from the 90% contour of the utilization distribution of Qamanirjuaq caribou locations for the respective periods.

Telemetry relocations for each individual during migration were converted into steps (i.e., the straight line connecting consecutive relocations). We calculated the lengths and turn angles for all steps and compared these caribou movement metrics from 2004 to 2016 to investigate the effects of snow cover during migration. We restricted the data for this analysis to 1-day fix rates to allow comparison of migratory movements from 2004 to present. We modelled step length using generalized linear models with a gamma distribution and log link function, and tested models with and without individual migration as a random effect. Model covariates included snow conditions on the winter and migratory ranges, along with the number of days since the start of migration and migration distance. We tested interaction terms between snow conditions and the number of days since the start of migration because we expected that caribou rates of travel along the migratory route would be influenced by snow conditions and likely change through the migration period.

5.2.4 Integrated step selection analysis

We estimated the relative probabilities of caribou space use during spring migration using an iSSA. Observed migratory steps were each matched to 25 available steps. To generate each available step, the turn angle and step length were drawn randomly from von Mises and gamma distributions that were fitted to the observed turn angle and step length distributions respectively (Avgar et al. 2016). The habitat and movement attributes of each observed step were then compared to those of the available steps using conditional logistic regression. Models were fit individually to avoid pseudoreplication and to examine variation in behaviour among animals in our analysis.

Our iSSA tested the influence of habitat covariates, including landcover, slope, elevation, ruggedness, and snow cover on caribou movement during migration. Landcover classes were derived from the 2010 Land Cover of North America at 30 meters (Latifovic et al. 2017; NALCMS 2017). We incorporated the sub-polar or polar shrubland-lichen-moss (hereafter "shrub"), sub-polar or polar grassland-lichen-moss (hereafter "grass"), and sub-polar or polar barren-lichen-moss from the NALCMS 30-m landcover into our analysis. Terrain characteristics, slope, elevation, and terrain ruggedness index, were retrieved and derived from the Canadian Digital Elevation Model (NRCan 2016) at 30-m resolution using ArcGIS 10.4.1 (Esri 2015). For each step, habitat covariates values were extracted along the path as the mean value (for terrain characteristics) or proportion (for landcover classes).

Previous work has shown that caribou select frozen waterways during spring migration for ease of travel and visibility (Pruitt 1959; Sharma et al. 2009; Leblond et al. 2016), and so we expected caribou to select areas closer to fresh water for movement (if frozen). If not frozen, caribou might still select areas near streams, rivers, and lakes for access to drinking water and potentially more productive vegetated areas. A turn angle of 0° indicates continued movement in the same direction, with increasing values reflecting a greater change in direction until the maximum value of 180° which occurs when an animal turns completely and moves back along the same path. During migration caribou move with strong directional persistence from their winter range to the calving area. This behaviour should result in small turn angles being favoured in our iSSA.

Covariate selection for our final iSSA model ended up being rather straightforward. Most of the covariates described above were uninformative at the population level (i.e. had confidence intervals that overlapped zero) across almost all model formulations. In contrast, several covariates were consistently informative (had confidence intervals that did not overlap zero) across different models. To determine whether covariates were informative, we used a 1000-iteration nonparametric bootstrap to estimate population-level bias-corrected and accelerated confidence intervals for beta coefficients from individual-level iSSAs. Our final model included the covariates that were informative at the population level. Covariates with confidence intervals that overlapped zero were not included in the final model. All statistical analysis was performed in R (R Core Team 2018) and iSSAs were estimated using the amt package (Signer et al. 2019).

5.2.5 Landscape resistance

We predicted habitat suitability across the landscape using parameter estimates for landscape variables from our iSSA. Doing so implicitly assumes that selection of habitats by animals is proportional to habitat suitability, or in this case, that during migration caribou are selecting habitats suitable for migration. Habitat suitability was then transformed to estimate landscape resistance to movement. We note that although movement is a priority during migration caribou do continue to forage while migrating, and the resistance values derived from our iSSA also reflect caribou selection of habitat types suitable for feeding.

Landscape resistance is often derived as a negative linear function of habitat suitability, however, Keeley et al. (2016) showed that a negative exponential function best described the relationship between resistance and habitat suitability. We derived landscape resistance (scaled from 1 to 10) as:

$$Landscape\ resistance = 10 - 9 * \left(\frac{1 - \exp(-c * iSSA)}{1 - \exp(-c)}\right)\ (Eq. 1)$$

where $iSSA$ represents habitat suitability scaled between 0 and 1, and c is a factor that adjusts the shape of the curve (Keeley et al. 2016). Increasing the value of c increases the nonlinearity of the response. We selected a moderate value of 1 for c to allow a larger fraction of habitat suitability values to have lower resistance while avoiding the loss of variation in resistance values across habitat suitability that occurs with high values of c.

Using methods similar to Cushman et al. (2010, 2011) we evaluated the performance of our iSSA and landscape resistance surface by generating 14 “random” paths for each observed migratory path. Generated paths had identical spatial topology to their paired observed path but were rotated randomly between 0° and 360° and shifted randomly between -30 and 30 km in both latitude and longitude. We generated paths such that their extent remained inside our study area. Using values from our landscape resistance layer, the cost distance for each path was calculated by summing the all resistance values along the path. A rank was then assigned for all 15 paths within each set of paired observed and generated paths, with a rank of 1 identifying the path with the lowest cost, and a rank of 15 signifying the highest cost. We then calculated the mean cost rank (MCR) for all observed paths, which provides an indication of performance of the resistance model in predicting long-distance paths (Keeley et al. 2016). If our resistance layer is poor, then we would expect the observed paths to perform no better than a random path. If the resistance layer predicts caribou resistance to movement during migration well, then observed paths should have a lower cost rank. If the MCR for the observed caribou paths is below the median rank (8 for $n = 15$) then the resistance model (and by extension the iSSA used to create it) performs well.

5.2.6 Identifying important migratory areas with circuit theory

To delineate the most important areas within the spring migratory corridor for Qamanirjuaq caribou, we employed methods from circuit theory. We used the software Circuitscape (McRae et al. 2013) to model connectivity between the herd's winter range and calving area and to map current density across the study area. The resistance layer derived from our iSSA was used as a conductive surface into which current was simultaneously injected at the starting location of each migratory path (source nodes) and flowed to the calving area as defined by the 50% contour of the utilization distribution of calving locations (ground node). The resulting current density represents the probability of random walkers (i.e., caribou) moving through a given grid cell (McRae et al. 2008). To delineate the most important regions during migration we classified areas on the landscape by equal-area current density percentiles. For example, the area above the 90th percentile would contain the top 10% of all grid cells with the highest current density. We calculated the number of observed caribou telemetry locations contained within each area defined by the top 20 percentiles. By examining the rate of change in proportion of locations within each percentile as area decreases, we identified empirical thresholds that signify the most important areas during migration.

5.3 Results

5.3.1 Caribou movement metrics

Caribou step lengths were larger in years with better snow conditions (lower variability in snow cover), particularly early in migration. Our step length model with the smallest AICc value (model 1) included migration distance, number of days since the start of migration (hereafter "day of migration"), late April snow conditions on the winter range, early May snow conditions on the migratory corridor, and interactions between these snow conditions and the number of days since the start of migration (Table 5.1, Fig 5.2). Mixed effects models that included individual migration as a random effect did not appreciably improve model fit, and so here we report only the fixed effects models. We found that caribou tended to take longer steps when migrating longer distances ($\beta = 0.011$, 95% CI [0.0099, 0.013]) and that steps shortened as migrations progressed regardless of snow conditions ($\beta = -0.023$, 95% CI [-0.028, -0.019]). Poorer snow conditions, indicated by increasing variability in snow cover, tended to reduce step lengths in late April and in early May, however the interaction terms reveal an interesting pattern. When snow conditions were good, caribou moved longer distances at the beginning of their migration and slowed down over its duration (Days since start of migration:late April snow cover $\beta = 0.00064$, 95% CI [0.00022, 0.0011]; Days since start of migration:early May snow cover $\beta = 0.00068$, 95% CI [0.00035, 0.0010]). However, when snow conditions were poor, caribou movement rates were lower early in migration and declined much less over its course (Fig. 5.3). Although our pseudo-R^2 values (Table 5.1) suggest that our models do not explain a large proportion of the variability in step length during migration, an expectation that they should is misplaced. Our models only seek to identify the influence of certain environmental covariates, which they do, and not to capture the complete breadth of factors that influence the distance between two consecutive relocations of an individual caribou.

Table 5.1 Comparison of models for step length during spring migration of Qamanirjuaq barren-ground caribou (*Rangifer tarandus groenlandicus*) from 2004 to 2016 (excluding 2005) using Akaike's Information Criterion corrected for small sample size (AIC_c). SC: snow cover, MSC: migration snow cover, WSC: winter snow cover, SD: standard deviation. R^2_{LR} is a pseudo-R^2 for nonlinear regression models based on the likelihood ratio test.

Model	**Covariates**	**ΔAICc**	**ωi**	**R^2_{LR}**
1	Early May MSC SD*day of migration+ Late April WSC SD* day of migration + Migration distance	0.00	1.00	0.093
4	Late April WSC SD* day of migration + Migration distance	11.09	0.00	0.088
3	Early May MSC SD* day of migration + Migration distance	21.82	0.00	0.085
5	Early May MSC SD + Late April WSC SD + day of migration + Migration distance	23.12	0.00	0.085
6	Early May MSC SD + Late April WSC SD + Migration distance	108.59	0.00	0.058
2	Migration distance	148.27	0.00	0.044
7	1	282.70	0.00	0

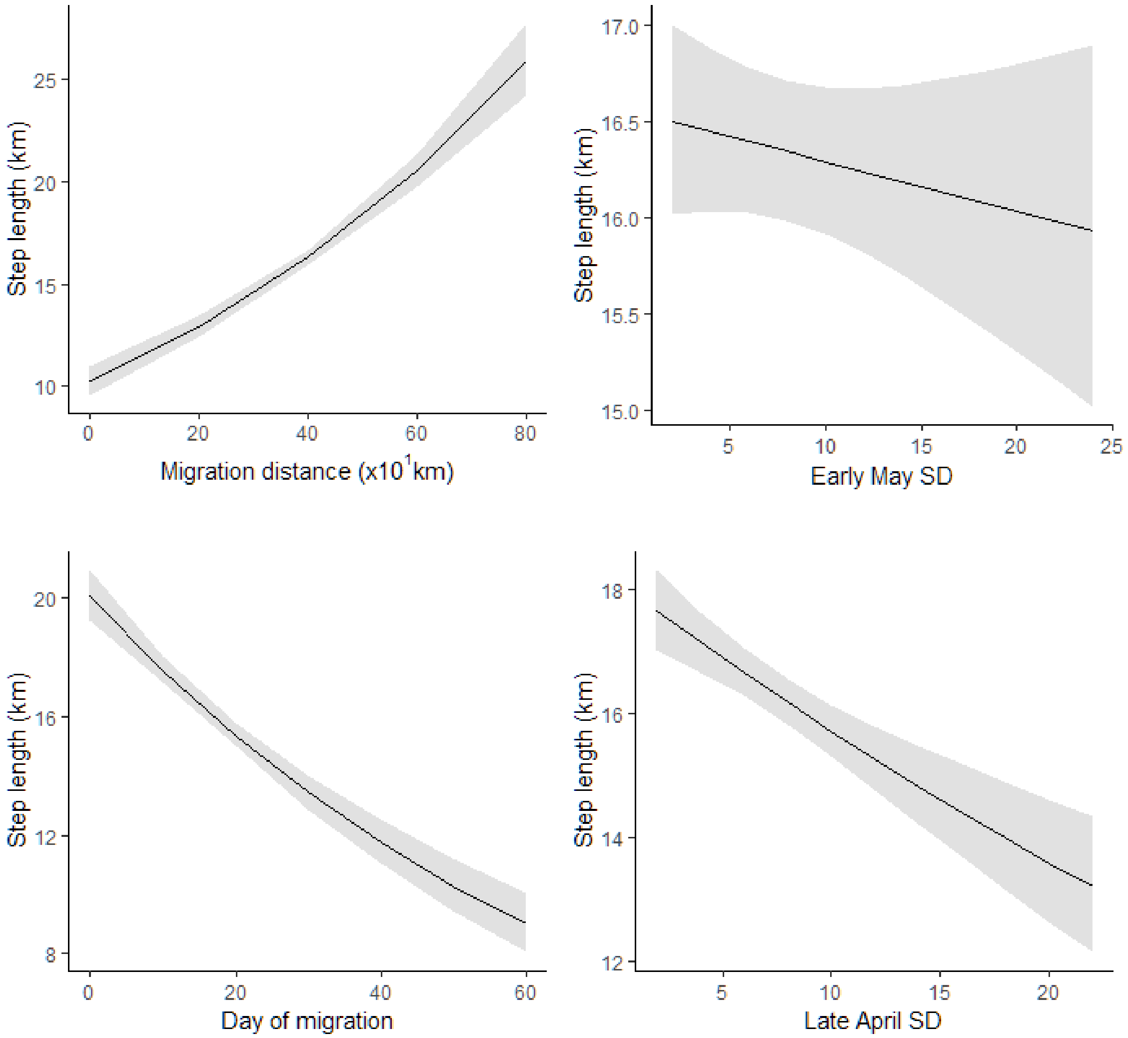

Fig 5.2 Predicted relationships for covariates in our most supported model (model 1) for step length during migration. Shaded areas represent 95% confidence intervals. SD: standard deviation in snow cover.

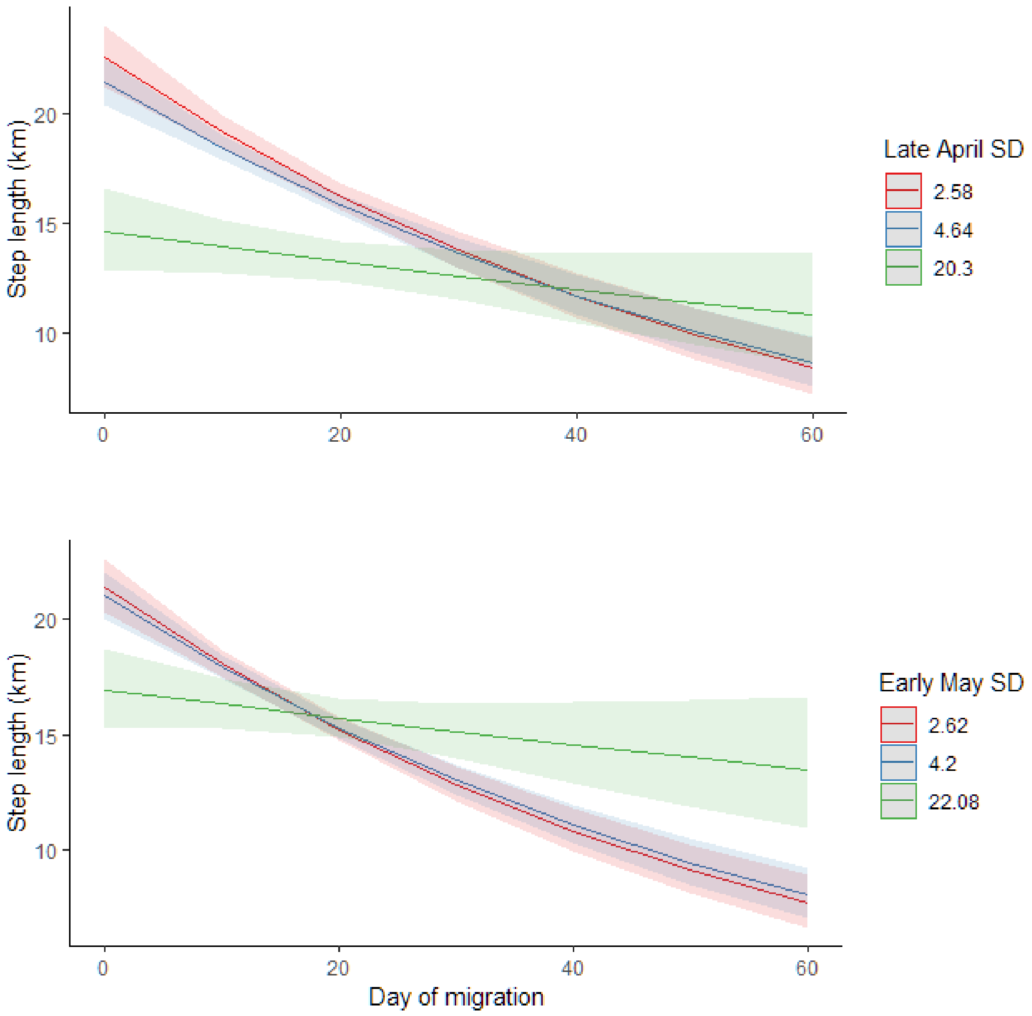

Fig 5.3 Predicted interactions between snow cover covariates and day of migration from our most supported model (model 1) for step length during migration. The top panel displays the effect on step length of the interaction between variation in late April snow cover on the winter range and the day of migration, and the bottom panel shows the effect of the interaction between variation in early May snow cover on the migratory range and the day of migration Shaded areas represent 95% confidence intervals. Interactions are plotted for the minimum (red), median (blue), and maximum (green) values of snow cover SD. SD: standard deviation in snow cover.

5.3.2 Integrated step selection analysis

Our final iSSA model included covariates for proportion of shrub and grass landcover types, distance to freshwater, ln-transformed step length (hereafter “step length”), and absolute turn angle (Fig. 5.4). We tested models with other landcover covariates, including barren, forest, and wetland, however their coefficients were indistinguishable from zero at the population level. Further, because we evaluated landcover by proportion along a step, selection for high proportions of shrub and grass implicitly suggests avoidance of other types, such as barren and forest. None of the terrain characteristics (slope, elevation, ruggedness) were informative at the population level, likely due to the low-lying nature of the study area. Caribou displayed a negative response to increasing turn angle, suggesting strong directional persistence in movement. The coefficient for step length was positive, reflecting selection for longer steps during migration. Caribou selected steps closer to fresh water, and with higher proportions of shrub and grass landcover types.

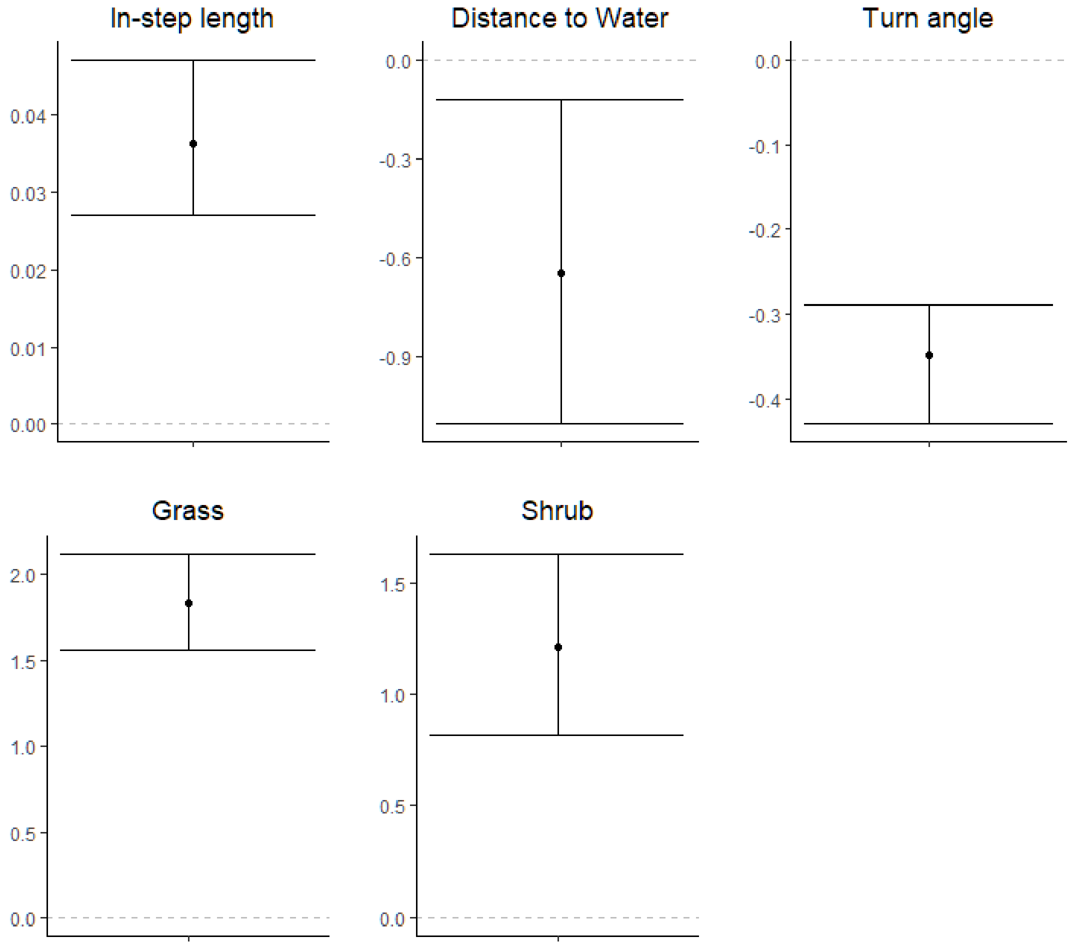

Fig 5.4 Population-level means and bootstrapped 95% bias-corrected and accelerated confidence intervals for beta coefficients of our top integrated step-selection analysis model for Qamanirjuaq caribou during spring migration. Population-level coefficients were estimated from models for each individual migration.

5.3.3 Landscape resistance

We tested the performance of our landscape resistance layer by generating paired "random" paths for each observed migration and comparing the cost distances between observed and generated paths. Because we generated paths with identical topology and that were bounded by the study area, they typically followed a realistic route from the winter to calving range. Thus, the paired paths we compared to the used paths were viable alternatives rather than implausible random paths across the landscape. The MCR for observed paths was 6.2, less than the median rank of 8 that would be expected for random paths. The most frequent rank for observed paths was 3. Because the observed caribou migration paths had a lower MCR than random paths of identical topology, we can infer that the resistances derived from the iSSA performed adequately in predicting migration paths.

5.3.4 Identifying migratory corridors using circuit theory

The highest current densities, which represent the probability of caribou moving through a grid cell, were found along the coast of Hudson Bay, and along the southwestern edge of the 50% high density calving utilization distribution contour (Fig. 5.5). High current densities in these areas are consistent with observed migration paths, of which the majority travel north along the coast of Hudson Bay or in a west to northwest direction from winter ranges in the southeastern NWT or northern Saskatchewan (Fig. 5.1). Increasing current density is expected in proximity to the calving area, as the paths of animals that traveled different routes from the winter range begin to converge as they approach their destination. We extracted the top 20 equal-area percentiles of grid cells based on current density from the surface produced by Circuitscape (Fig. 5.5). The areas of these regions ranged from approximately 4000 km^2 (top 1% of grid cells) to 75 000 km^2 (top 20% of grid cells) and contained from approximately 7.5% of caribou locations (top 1% of grid cells) to 50% of caribou locations (top 20% of grid cells) (Fig. 5.6). The mean rate of change in the number of caribou locations by area increases above the top 5% of grid cells, from 1.8% (95% CI [1.5%:2.0%]) to 4.0% (95% CI [2.8%:5.1%]) of caribou locations lost per percent area (Fig. 5.7). The loss of caribou locations for every one-percent decrease in area above the 95th percentile more than doubles and suggests a threshold and that the area containing the top 5% of grid cells is a priority area for caribou migration.

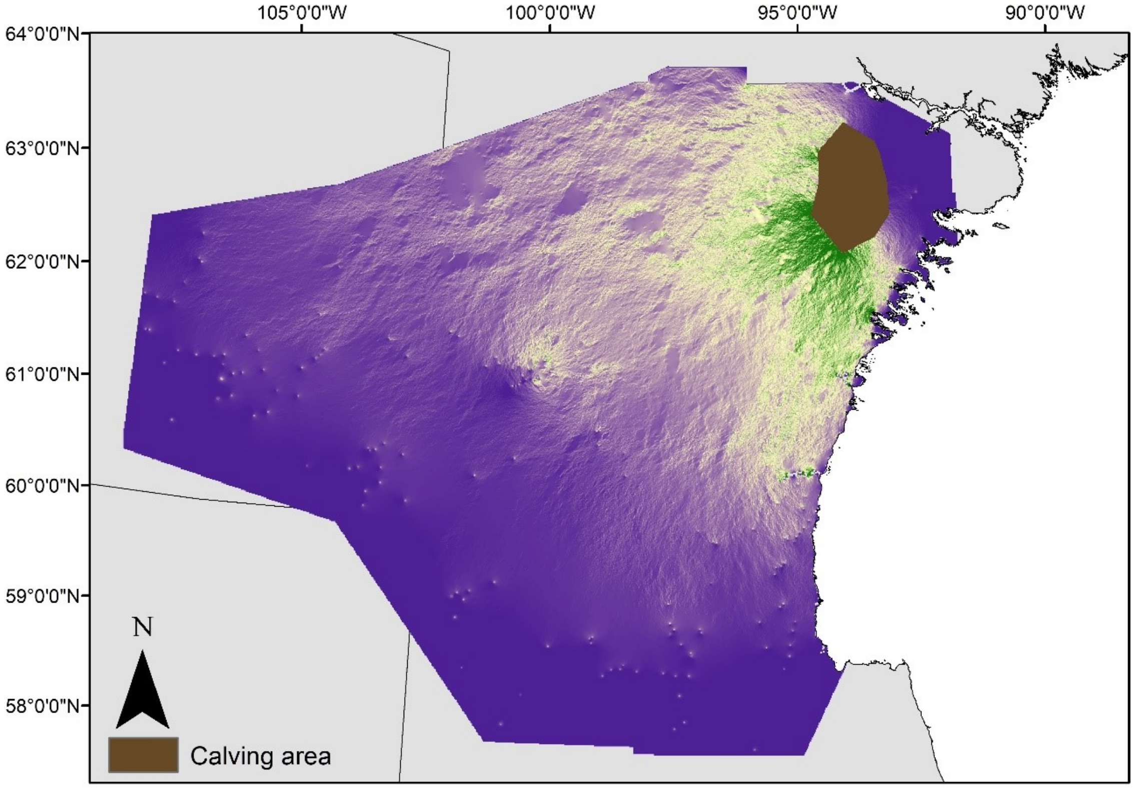

Fig 5.5 Predicted current density between Qamanirjuaq barren-ground caribou (*Rangifer tarandus groenlandicus*) winter and calving ranges during spring migration. Current density was modelled using a resistance surface derived using our integrated step-selection analysis.

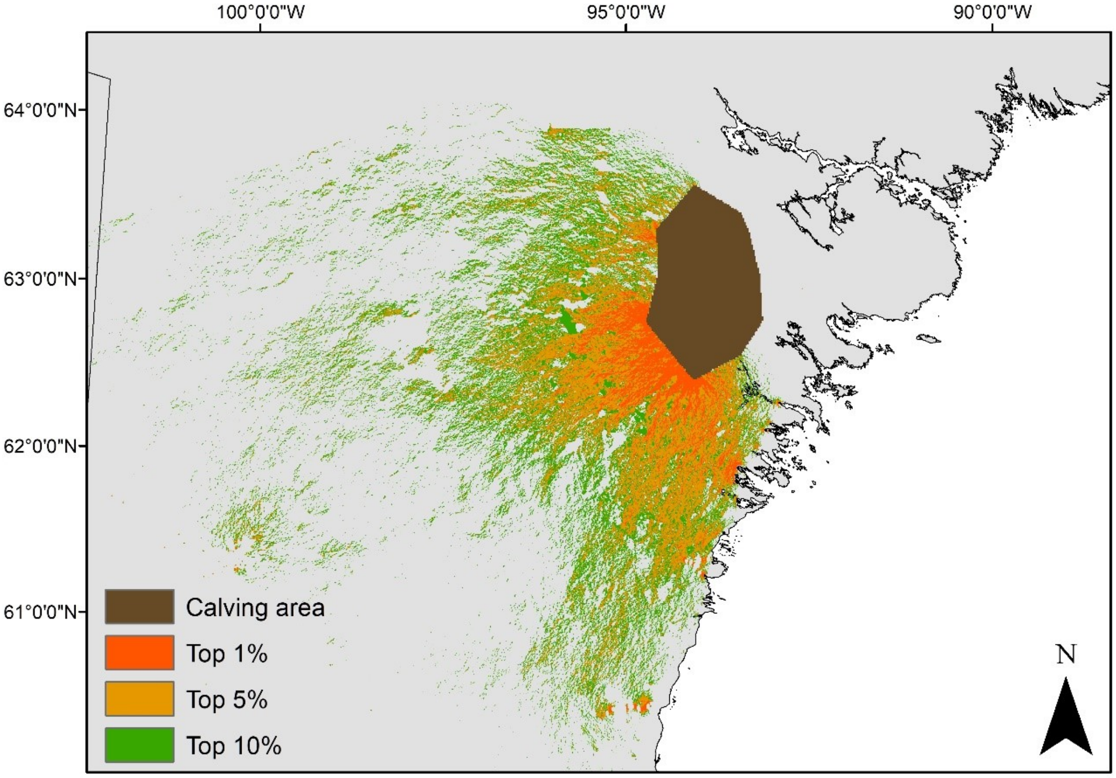

Fig 5.6 Key areas within the Qamanirjuaq spring migratory corridor derived from the highest current density grid cells of the current density surface. Colours represent the area of the total surface that provides the indicated percent of highest current density grid cells.

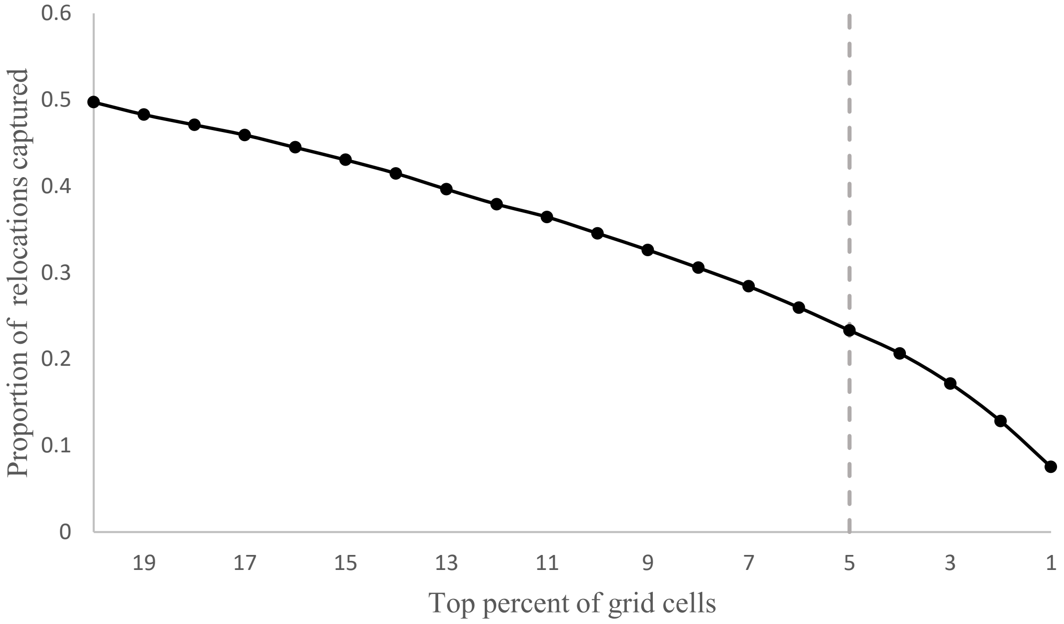

Fig 5.7 Proportion of caribou relocations captured by the top 1% to 20% of grid cells by current density. Grey hashed line indicates threshold after which the rate of loss of caribou locations for every one-percent decrease in area more than doubles. The mean rate of change in the number of caribou locations by area increases above the top 5% of grid cells, from 1.8% (95% CI [1.5%:2.0%]) to 4.0% (95% CI [2.8%:5.1%]) of caribou locations lost per percent area.

5.4 Discussion

Climate change is altering ecosystems and ecological interactions around the globe (Post et al. 2009; Pecl et al. 2017). Much attention has been paid to the potential for phenological or trophic mismatches, and the ability for species at higher trophic levels to maintain temporal synchrony with the phenology of lower trophic levels (Donnelly et al. 2011). Our work (Chapter 4) has indicated that Qamanirjuaq barren-ground caribou were able to adjust the timing of spring migration such that they kept pace with advancing phenology on their calving range, however we also found that caribou took a longer time to migrate in years with earlier onset of spring. Our analysis here suggests that when possible caribou might take advantage of hard, packed snow early in the migratory period to travel quickly (Fig. 5.3). Over the course of migration spring progresses and snow conditions deteriorate and become soft and slushy during the day. In general, deep and soft snow makes movement more difficult, increases energy expenditure exponentially (Fancy and White 1987b), and likely results in a decline in daily movement rates. In years when snow conditions are poor, caribou have decreased movement rates early in spring migration, and movement rates throughout the migratory period decline at a slower rate (Fig. 5.3). The net effect of these differences in movement rates appears to be an increase in length of the migratory period in years with poor snow conditions. Our findings suggest that caribou may use phenological cues to adjust the timing of their migration but might be physically constrained by accelerating snow melt that hinders movement. As climate change continues, warmer springs and earlier snow and ice melt are expected, which could challenge the plasticity in caribou migratory behaviour. Leblond et al. (2016) predicted that changing climate conditions leading to earlier spring melt could lead to a 28% increase in the distance of caribou migrations in Northern Québec, Canada, due to the extra distance required to travel around open water rather than cross ice. Considering these findings along with our results, it appears likely that climate change will increase both the distance, time, and energy expenditure of spring migrations for some caribou populations in Northern Canada. Although caribou might be able to partially adjust their migratory behaviour to earlier springs, further research is required to understand the effectiveness of this plasticity.

Considering these potential challenges to migratory movements from climate change, wildlife and land-use decision makers should avoid actions that could further disrupt or negatively affect caribou migrations. To provide insight into caribou movement during spring migration, we estimated barren-ground caribou migratory habitat selection using a mechanistic movement model. The results were then used to evaluate connectivity between the Qamanirjuaq herd's winter and calving ranges and identify areas most important for migration. The parameters estimated by our iSSA movement model were generally as expected for caribou during spring migration. Caribou showed strong directional persistence and selected longer steps, consistent with migratory behaviour from the winter to calving ranges.

During the late winter and early spring, the ground remains snow covered and green-up has not yet begun. Caribou diets during this period are typically dominated by lichens and at times evergreen shrubs, rather than low-quality senescent shrubs, forbs, and graminoids (Thomas and Hervieux 1986; Klein 1990). Throughout the course of migration caribou are focused on movement and are expected to select areas conducive to efficient walking, such as on frozen water bodies (Sharma et al. 2009; Leblond et al. 2016), and at times selection for foraging opportunities may be a secondary consideration. However, caribou must still forage effectively to attempt to maintain body condition during migration. At this time of year, pregnant caribou cows are subject to competing instincts to both move toward the calving ground and to maximize forage intake to meet the nutritional requirements of pregnancy (Duquette and Klein 1987). The results of our iSSA were consistent with this pattern, with selection for longer steps and directional persistence indicative of migratory movements, and the selection of shrub and grass habitat types providing feeding opportunities. Caribou also selected areas closer to fresh water, potentially reflecting their use of frozen water bodies for travel during spring migration.

Connectivity analyses that incorporate behavioural preferences estimated by some type of resource selection analysis (in our case iSSA) have been shown to predict habitat use during movement, and usually better than other methods like species distribution modelling or expert opinion (Fattebert et al. 2015; Abrahms et al. 2017; Zeller et al. 2018). The connectivity surface we produced identifies the distribution of current density across the study landscape, which represents the probability of caribou moving through an area (Fig. 5.5). By dividing our connectivity surface into equal-area percentiles and comparing these regions to relocation data from caribou, we were able to empirically evaluate the performance of our model. Zeller et al. (2018) found that when applying circuit theory to their dispersal data, the top 10% of their connectivity surface captured 75% - 87% of the dispersal process. However, the top 10% of our connectivity surface captured a smaller 35% of migratory locations. In our analysis we set individual migration start locations as source nodes, and the calving area as the ground node. We did not use a pairwise model thus current flowed only from the source to the ground. Current was injected at locations that were often distant from each other and all flowed toward one location, which mimics the migratory behaviour of caribou that often begin migration in groups spanning across the winter range (Fig. 5.1) and come together to form larger aggregations along the migratory corridor, eventually reaching the highest densities at the calving area (Duquette and Klein 1987). Current densities closer to the destination will be much higher than near the source locations, and the earlier segments of migration will not be captured in the top 10% of the connectivity surface.

Many methods for identifying migration, dispersal, and movement corridors have been employed across numerous species and study systems including Brownian bridge movement models (Sawyer et al. 2009; Nicholson et al. 2016), species distribution modeling (Guisan and Thuiller 2005; Vasudev et al. 2015), resource selection analysis (Chetkiewicz and Boyce 2009), least-cost path analysis (Adriaensen et al. 2003), and circuit theory (McRae et al. 2008). However, in some conservation contexts, identification of the entire migratory corridor might not be the most pragmatic objective. For some wide-ranging species, such as barren-ground caribou, migratory corridors could span tens of thousands of square kilometres. Our application of iSSA and circuit theory provides an intuitive means by which to identify key areas of movement and migration corridors for wildlife populations that move between seasonal ranges. We consider this a valuable conservation approach for species that use very large migratory corridors where large scale conservation efforts might be challenging practically or politically.

We were able to empirically evaluate the performance of different thresholds to identify critical areas within the spring migratory corridor using minimal subjectivity or value judgements. By comparing the proportions of caribou locations contained from within the top 20% to top 1% of the connectivity surface, we determined a change in slope of the relationship between the area of the corridor and the proportion of caribou locations it captures (Fig. 5.7 shows the top 10%, 5%, and 1% of grid cells). This threshold delineates an area of greater importance for migration and could warrant special consideration or protection in land use and management decisions. Conservation and management decisions typically, but not always, involve some perceived trade-off between habitat protection and economic potential, and thus the size of the area under consideration is central to any discussion. The results from this method are easily adjusted to produce the most valuable grid cells for any given area and so provide opportunity for flexible conservation and management initiatives.

Maintaining sufficient connectivity between seasonal ranges of migratory species is paramount to their persistence or at least their persistence as migrants. Migratory species can be more vulnerable to habitat loss due to the dependencies among distant and distinct ranges (Runge et al. 2014). For example, calving areas of migratory caribou often are considered the most important habitats for the population and most deserving of protection (Taillon et al. 2012). While we do not dispute the critical importance of these areas for caribou persistence, their value is dependent on their accessibility by caribou. If migratory routes are disrupted and caribou cannot reach traditional calving areas by the time of calving, having those areas protected is futile. Cessation of migratory behaviour has been linked to large declines in populations (Bolger et al. 2008), and although a remnant population might remain, it will not fulfil the ecological functions associated with migrations (Bauer and Hoye 2014). Further, losses of migrant populations can have socioeconomic consequences for communities who rely on the seasonal availability of animals such as caribou (Vors and Boyce 2009; Festa-Bianchet et al. 2011) for food and other economic opportunities. The Beverly and Qamanirjuaq herds, for example, provide an estimated $20 million in food replacement value alone to northern communities that harvest from them (InterGroup Consultants Ltd. 2008).

Recently, focus in caribou research has expanded to include the effects of climate change (e.g., Sharma et al. 2009; Witter et al. 2012; Gustine et al. 2014; Leblond et al. 2016; Chen et al. 2018; see review in Mallory and Boyce 2018). Due to the diffuse and global nature of its causes, conservation actions at local levels to mitigate the effects of climate change on ecosystems are difficult, but some options exist. For example, establishing protected areas and conservation corridors in key areas could help to mitigate the effects of climate change by providing species refuge from other anthropogenic disturbances and the opportunity to shift ranges and adapt to new conditions (Killeen and Solórzano 2008). For this type of strategy to be effective for barren-ground caribou, conservation actions should be taken sooner rather than later. Our research suggests that caribou migrations will be, and to some extent already are, challenged by climate change and provides information that is immediately applicable to the conservation of one of the largest caribou populations in North America (Mallory et al. 2018). The predominant threats to migratory populations are anthropogenic and as such can be mitigated or even removed completely given the right information and the willingness of decision makers to undertake conservation actions (Berger et al. 2008). The timely establishment of conservation corridors and protected areas for migratory barren-ground caribou could help prevent outcomes like those for boreal caribou, where conservation strategies such as habitat protection, habitat restoration, and controversial predator control measures have been given serious consideration at policy levels long after the need arose, compromising their potential efficacy (Hervieux et al. 2015; Hebblewhite 2017; Hebblewhite and Fortin 2017; Serrouya et al. 2017).

6 Prioritization of landscape connectivity for the conservation of Peary caribou

6.1 Introduction

Maintaining and restoring connectivity between isolated patches of suitable habitat on heterogeneous landscapes has been a topic of considerable research in ecology for well over three decades (Fahrig and Merriam 1985, 1994; Saunders et al. 1991; Opdam and Wascher 2004; Kindlmann and Burel 2008). Indeed, sufficient connectivity among habitat patches enables a variety of behaviours integral to long-term population persistence, from finer-scale movements between patches by individuals for foraging (FitzGibbon et al. 2007; Henry et al. 2007; Frey-Ehrenbold et al. 2013), to larger-scale movements related to dispersal, reproduction, and migration (Rabasa et al. 2007; Rabinowitz and Zeller 2010; McClure et al. 2016). Furthermore, at broader temporal scales, connectivity facilitates colonization and recolonization of ranges (Hanski 1998; Franken and Hik 2004) and gene flow between populations (Holderegger and Wagner 2008), which in turn determines potential for genetic differentiation, inbreeding depression, local adaptation, and the geographic spread of novel adaptations (Keyghobadi et al. 2005).

Recent interests in connectivity in conservation biology are largely driven by increased habitat fragmentation and habitat loss associated with anthropogenic activities such as forestry, agriculture, and urban development (Haila 2002; Cushman 2006; Fischer and Lindenmayer 2007; Haddad et al. 2015). However, anthropogenic activities also can have important indirect effects on connectivity through intermediate mechanisms such as climate change (Heller and Zavaleta 2009). In particular, changing sea ice conditions are predicted to have large implications for some Arctic species (Post et al. 2013), including caribou (*Rangifer tarandus*), Arctic fox (*Vulpes lagopus*), and Arctic wolf (*Canis lupus*), that use sea ice to move between island habitats across the High Arctic (Miller et al. 1977, 2005; Carmichael et al. 2008; Poole et al. 2010; Norén et al. 2011; Jenkins et al. 2016; Mallory and Boyce 2018). Sea ice cover has declined at a faster rate than anticipated by many studies (Comiso et al. 2008; Stroeve et al. 2012), and projections of future Arctic ice loss warrant continued attention within conservation biology (Overland and Wang 2013). Understanding how declining sea-ice coverage will affect connectivity is necessary to anticipate, and potentially mitigate, some negative consequences of climate change for these species.

Peary caribou (*R. t. pearyi*) is a subspecies of caribou that resides in the Canadian High Arctic near the northern limit of vegetation growth (Miller and Gunn 2003b). Characterized by their small stature (approximately 90 centimetres at the shoulder), Peary caribou live at low densities and move seasonally between Arctic islands to forage across areas of higher productivity, a behaviour that also could reduce pressure on limited forage resources (Miller et al. 1977). Between-island movements also might involve attempts to avoid predators (Miller 2002) and to move away from areas that have been subject to extreme weather or icing events (NWT Species at Risk Committee 2012; Jenkins et al. 2016). Although caribou typically dig through snow to access vegetation in a behaviour called cratering (Fancy and White 1985), they are unable to dig through basal layers of ice, which can lead to starvation (Tyler 2010). Mass starvation of Peary caribou (Miller and Gunn 2003b; Miller and Barry 2009) and Svalbard reindeer (*R. t. platyrhynchus*) (Tyler 2010; Hansen et al. 2011) following severe snow and icing events are well documented, and sea-ice that allows animals to move away from areas where forage has been rendered inaccessible might help caribou avoid starvation (Loe et al. 2016).

The delineation of Peary caribou populations used by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2015) and Environment and Climate Change Canada (ECCC) (Johnson et al. 2016) comprises four local populations named for their geographic areas: Banks/Victoria Islands (BV), Prince of Wales/Somerset/Boothia (PSB), Western Queen Elizabeth Islands (WQEI) and Eastern Queen Elizabeth Islands (EQEI) (Fig 6.1). A large decline in Peary caribou numbers across their range, in part due to catastrophic die-offs related to extreme snow and icing events, led to their listing as endangered under the Canadian *Species at Risk Act* in 2011. More recently in 2015, COSEWIC assessed Peary caribou as threatened in light of increasing or stable population trends in three of four local populations (COSEWIC 2015). The most recent surveys addressing the PSB population occurred in 2004, 2006, and 2016 (Gunn et al. 2006; Jenkins et al. 2011; Anderson 2016) and recorded only a single caribou among all three surveys. While observations of small numbers of caribou have been reported by local people (Anderson 2016), this population appears to be near extirpation (Johnson et al. 2016).

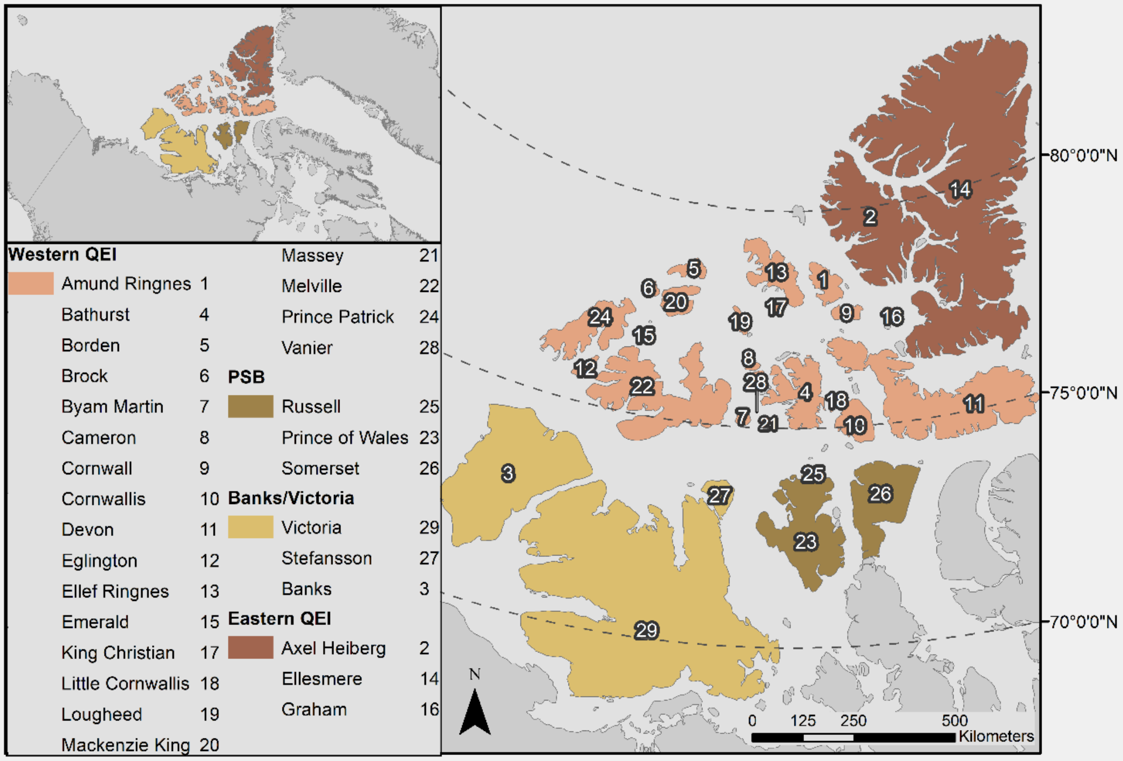

Fig 6.1 Study area and Peary caribou (*Rangifer tarandus pearyi*) local populations within the Canadian Arctic Archipelago. Islands with gray fill were not considered in our analysis. Inset map shows study area location within Canada.

Genetic evidence suggests that sea-ice has historically facilitated reliable and effective connectivity between Peary caribou populations (Jenkins et al. 2016, 2018). However, work by Jenkins et al. (2016) identified that projected longer ice-free seasons across the Arctic are likely to reduce connectivity between caribou populations restricted to islands, leading to increased genetic and demographic isolation. Building on these findings, our objective is to identify areas of Peary caribou habitat that contribute most to maintaining connectivity during annual periods important for movement, and project how this might change in the future. Specifically, we used future climate projections, circuit theory, and least-cost models to: a) map connectivity across the Canadian Arctic Archipelago, b) determine how specific connections might be altered under climate change scenarios, and c) identify those areas which contribute most to maintaining connectivity across Peary caribou populations.

6.2 Materials and Methods

To investigate landscape connectivity across Peary caribou range, we employed methods from circuit theory and least-cost path (LCP) analysis. Both methods represent the landscape as a surface on which different habitat types are assigned different *a priori* resistance values reflecting ecological constraints to movement (McRae et al. 2008). LCP analysis identifies the optimal path between two locations in terms of lowest "cost" or "resistance" (Adriaensen et al. 2003), whereas circuit theoretic approaches consider the flow of current through multiple alternative pathways across a continuous surface. Aspects of electrical circuits can be directly related to random walks, providing a straightforward link to movement ecology, with current flow interpreted as the "expected net movement probabilities of random walkers moving through a node…" or cell (McRae et al. 2008). Measures of network centrality, which evaluate the contribution of habitat nodes in facilitating ecological flows across the landscape, also can be derived from landscape connectivity models. By considering paths between all nodes, centrality metrics rank the importance of individual habitat nodes to maintaining connectivity throughout the network. For example, a node through which many paths in the network pass would have a higher centrality score than a node through which only a few paths pass (Carroll et al. 2012). Centrality provides an analytical method by which conservation priorities for maintaining connectivity can be identified (e.g., Theobald *et al.*, 2012; Dutta *et al.*, 2016; Osipova *et al.*, 2018).

6.2.1 Study area

We analyzed connectivity among 29 islands in the Canadian Arctic Archipelago (Fig 6.1). Our study area stretches approximately from 126°W to 61°W and 68°N to 82°N, from the Beaufort Sea in the west to Greenland and Baffin Bay in the east, and from the Canadian mainland in the south to the Arctic Ocean in the north. We excluded sections of the archipelago that are not Peary caribou range (e.g., Baffin and Bylot Islands). Characteristics of islands and habitats considered in our connectivity analysis vary considerably. Island area ranges from approximately 450 km^2 to 220 000 km^2 (Massey and Victoria Islands, respectively). Habitats vary from areas of graminoid tundra at the southern extent of the study area to regions of sparse vegetation and barren polar desert as latitude increases (Gould et al. 2003; Olthof et al. 2008a). There is also substantial variability in productivity within some islands and latitudes, such as in Polar Bear Pass (Nanuit Itillinga) National Wildlife Area on Bathurst Island, and on the Fosheim Peninsula and Lake Hazen regions of Ellesmere Island. These "High Arctic oases" have much higher productivity and species diversity than typically found across the archipelago (Sheard and Geale 1983; France 1993; Michelutti et al. 2013).

6.2.2 Data sources

We defined two seasons to investigate changes in habitat connectivity, an early-winter season (November – December) and a spring season (April – June). These seasons were chosen due to their importance for movement between island habitats. Although movement data are limited, spring migration has been recorded in April–June, while early-winter movements often begin in late October or November (Gunn and Dragon 2002; Johnson et al. 2016). Sea ice concentration (SIC) projections were taken from the output of the Canadian Regional Climate Model (CanRCM4) produced by the Canadian Centre for Climate Modelling and Analysis (Scinocca et al. 2016). SIC estimates the percent coverage of sea ice within each 25-km grid cell. Our analysis considered three scenarios: a recent historical climate scenario (1991 – 2005), the Representative Concentration Pathway (RCP) 4.5 scenario, and the RCP 8.5 scenario. The RCP scenarios represent projected atmospheric composition under different greenhouse gas (GHG) emission regimes (Meinshausen et al. 2011; van Vuuren et al. 2011). The RCP 8.5 scenario projects increasing GHG emissions beyond 2100, while the RCP 4.5 scenario reflects a more moderate trajectory with emissions reaching a maximum around 2040 and declining thereafter (Meinshausen et al. 2011).

Monthly values for SIC were retrieved for the historical climate scenario from 1991 to 2005, and for the RCP 4.5 and RCP 8.5 scenarios from the year 2021 to 2100. For the winter season, we considered SIC in the months of November and December, and for the spring season, SIC in April, May, and June. For each grid cell in the study area, we calculated the mean SIC value across these months for both seasons for each year. Annual seasonal means were then collected into decadal groups (e.g., 2021 – 2030, 2031 – 2040, 2091 – 2100, etc.) and the mean SIC for each grid cell was calculated for both seasons in each decade.

We used Peary caribou habitat models developed by ECCC to inform the terrestrial portions of our connectivity analysis. A complete description of the modeling approach and results can be found in Johnson et al. (2016), and here we only provide a brief discussion to highlight the information necessary for our study. Peary caribou seasonal habitat use models were developed using Maxent (Phillips et al. 2006). Habitat use was modeled for three seasons, April to June, July to October, and November to March. Known caribou locations were derived from surveys, radio-collared animals, and information from communities on Peary caribou distribution (Johnson et al. 2016). The models relate these known locations to environmental predictor variables, including snow depth, land cover, and wind speed. From these models, ECCC produced relative probability of use by Peary caribou for the Canadian Arctic Archipelago at 1-km resolution. We resampled the relative probability of use data from the April to June and November to March models to the same resolution (25 km) as the SIC data for use in our spring and winter connectivity analysis.

6.2.3 Landscape resistance

Estimates of landscape resistance were derived from two sources. We reclassified the spring and winter probability of use rasters into 10 bins as shown in Table 6.1. Rather than transform probability of use values into resistance by some function, we chose to bin ranges of probability values to reflect the variation that was lost by resampling probabilities from 1-km to 25-km grid cells. The classification bin with the highest probability of use was given a resistance value of 1, and the value of each successive bin was increased by 1. The two bins with the lowest probability of use (approximately 0 – 15%) were given resistance values of 20 and 30. We greatly increased the value of these lowest two bins so that in habitats or on islands where probability of use was very small, caribou would be more likely to move onto or across the sea ice than through those habitats.

Table 6.1 Terrestrial landscape resistance values derived from the reclassification of Peary caribou (*Rangifer tarandus pearyi*) probability of use across the Canadian Arctic Archipelago.

	Probability of use	
Resistance	**Spring**	**Winter**
1	0.73 - 0.83	0.76 - 0.88
2	0.65 - 0.73	0.64 - 0.76
3	0.58 - 0.65	0.55 - 0.64
4	0.50 - 0.58	0.48 - 0.55
5	0.41 - 0.50	0.39 - 0.48
6	0.33 - 0.41	0.30 - 0.39
7	0.24 - 0.33	0.23 - 0.30
8	0.16 - 0.24	0.15 - 0.23
20	0.09 - 0.16	0.07 - 0.15
30	0.00 - 0.09	0.00 - 0.07

Resistance values for sea ice were derived from the SIC for each 25×25km cell. SIC was transformed to a resistance value by multiplying SIC by -1 and then adding 100, such that high SIC values were given low resistance scores. SIC values less than 70 were set to null (infinite resistance) to render them impassable for our connectivity analysis, and 10 was added to all remaining values (i.e., a grid cell with SIC 99 would be assigned resistance 11, and a SIC grid cell with SIC 70 would have resistance 40). Values were shifted by 10 so that in our analysis, unless a terrestrial grid cell has very low probability of use (i.e., the 20 or 30 resistance bins) moving onto or across sea ice presents higher resistance to caribou than travelling on land. Previous work has suggested that caribou require at least 90% ice coverage to make crossings (Poole et al. 2010), and in their connectivity analysis Jenkins et al. (2016) differentiated resistance only between sea ice and ice-free waters. Although our use of 70% ice coverage for caribou to make crossings is likely unrealistic at a finer scale, the coarse resolution of our analysis and potential variability of ice conditions within a 25×25km cell necessitated a lower cut-off, particularly in near-shore areas where a grid cell contains both ocean and land.

Assigning values to a resistance surface often involves some subjectivity (Spear et al. 2010; Zeller et al. 2012), and our study is no exception. However, because we focus on the changes to connectivity resulting from complete loss of permeability of a grid cell (i.e., SIC < 70%) our analysis is relatively robust to the specific resistance values of individual grid cells. So long as the rank order of grid cells derived from the probability of use analysis remains constant, changing resistance scores will affect the absolute values returned by our analysis, but should have little effect on the overall patterns we report.

6.2.4 Connectivity analysis

We used Linkage Mapper (McRae and Kavanagh 2011), Circuitscape (McRae et al. 2013), Centrality Mapper (McRae 2012), and ArcMap 10.4.1 (Esri 2015) to investigate changes in connectivity across Peary caribou habitat. These programs provide methods which combine circuit theory with LCP analysis. To analyze connectivity across the study area, we used Circuitscape to iteratively calculate current flow across all possible pairs of islands (McRae et al. 2013). For each pair, one amp of current was injected into one of the islands while the other was connected to ground. For each calculation, the islands of the focal pair were treated as homogenous regions of zero resistance, but all other regions maintained their assigned resistance values. The current densities from each calculation were then summed to produce maps of cumulative current density across the study area for each decade and climate scenario.

We then used Linkage Mapper to identify and construct a network across adjacent core areas (in our case islands of the archipelago). Linkage Mapper then calculated cost-weighted distances and LCPs between islands (core areas) and produced a map of the resulting least-cost corridors. After corridors were mapped we ran Centrality Mapper, which uses circuit theory (through Circuitscape) to calculate current flow centrality across the nodes and linkages of the least-cost path network. Centrality Mapper treats each island as a node and links between nodes are given a resistance value derived from the cost-weighted distance of each particular least-cost corridor. Core areas are paired, and the program injects current into one core area while setting the other to ground. Centrality Mapper iterates over all pairs and sums the resulting current for all nodes and links in the network. We standardized the resulting centrality values for each island by dividing the centrality value by the island's area.

To estimate projected changes in landscape connectivity across Peary caribou range, we compared current density and the number of linkages between islands for each decade from 2020 to 2100. To identify which islands contribute most to maintaining landscape connectivity, we evaluated current flow centrality for all islands for each climate scenario and decade. We ran these analyses for all decades from 2020 to 2100, but to be concise we report a representative subset here to illustrate our findings.

6.3 Results

Our analysis indicates that a longer ice-free season in the Canadian High Arctic will dramatically decrease connectivity between Peary caribou island habitats during important movement periods in both winter and spring. In Figure 6.2 we display changes in cumulative current density under the RCP 4.5 and 8.5 scenarios. In spring, modelled cumulative current density under the RCP 4.5 scenario increased as the loss of sea-ice and higher resistance of remaining ice reduced the number of paths current could take across the study area, leading to increased current flow across some islands. Under the spring RCP 8.5 scenario a more rapid loss of sea-ice resulted in more variable changes in modelled cumulative current. Current density increased for some islands until 2080 as occurred under the more moderate scenario (e.g., Bathurst, Mackenzie King), but declined by 2100 as SIC continued to decrease and connectivity was lost. In other cases, the complete loss of connectivity between islands lead to reduced cumulative current density by 2080 (e.g., Victoria and Somerset Islands). Under the RCP 4.5 scenario, mean cumulative current density on land increased by approximately 27% by 2080, and 51% by 2100. Under the RCP 8.5 scenario, mean cumulative current density increased 35% by 2080 but declined 29% from its historical value by 2100. For the winter period, the faster rate of sea ice loss resulted in large reductions in cumulative current density across the study area. Under the RCP 4.5 scenario, mean cumulative current density declined by approximately 78% by 2080, and 99% by 2100. Under the RCP 8.5 scenario, declines are sharper, with a 68% loss in cumulative current density by 2040 and 99% by 2050. Changes in cumulative current flow are represented spatially in Figures 6.3, 6.4, and 6.5.

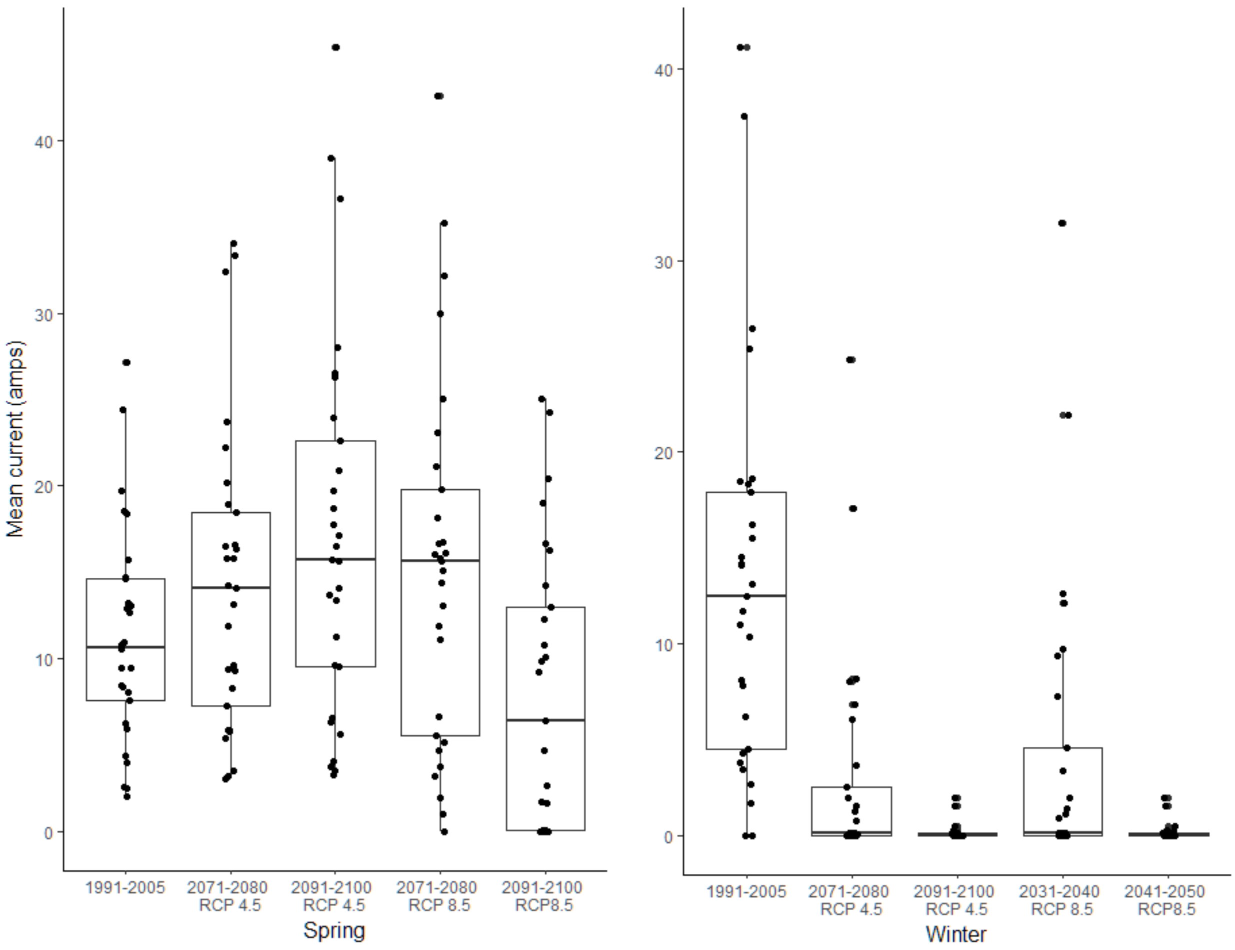

Fig 6.2 Mean cumulative current density for study islands in the Canadian Arctic Archipelago grouped by decade and climate scenario. Each point represents the mean cumulative current passing through the cells of a given island.

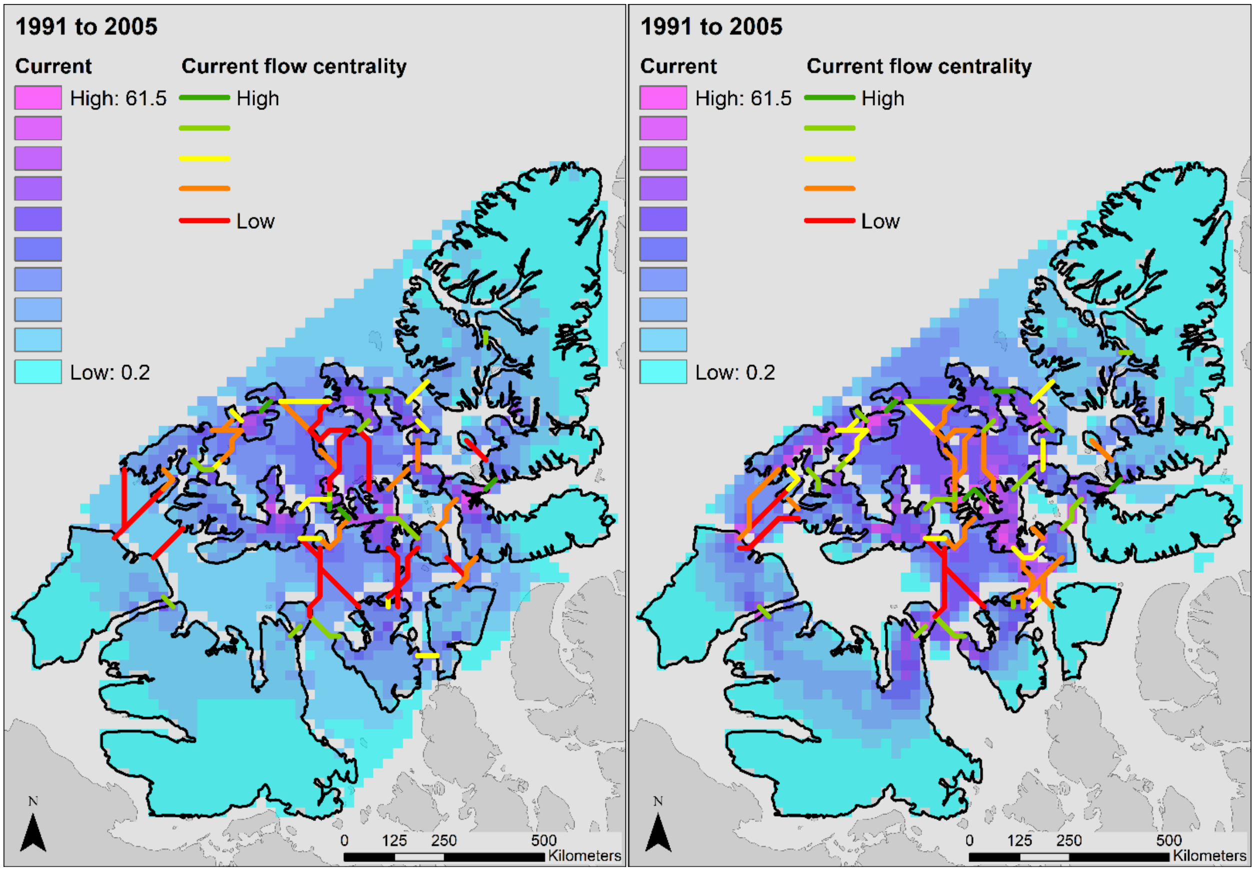

Fig 6.3 Cumulative current density (amps) across the study area in the Canadian Arctic Archipelago in spring (left) and winter (right) under the historical (1991-2005) Canadian Regional Climate Model (CanRCM4) scenario. Cumulative current density can be interpreted to reflect movement probabilities of Peary caribou (*Rangifer tarandus pearyi*).

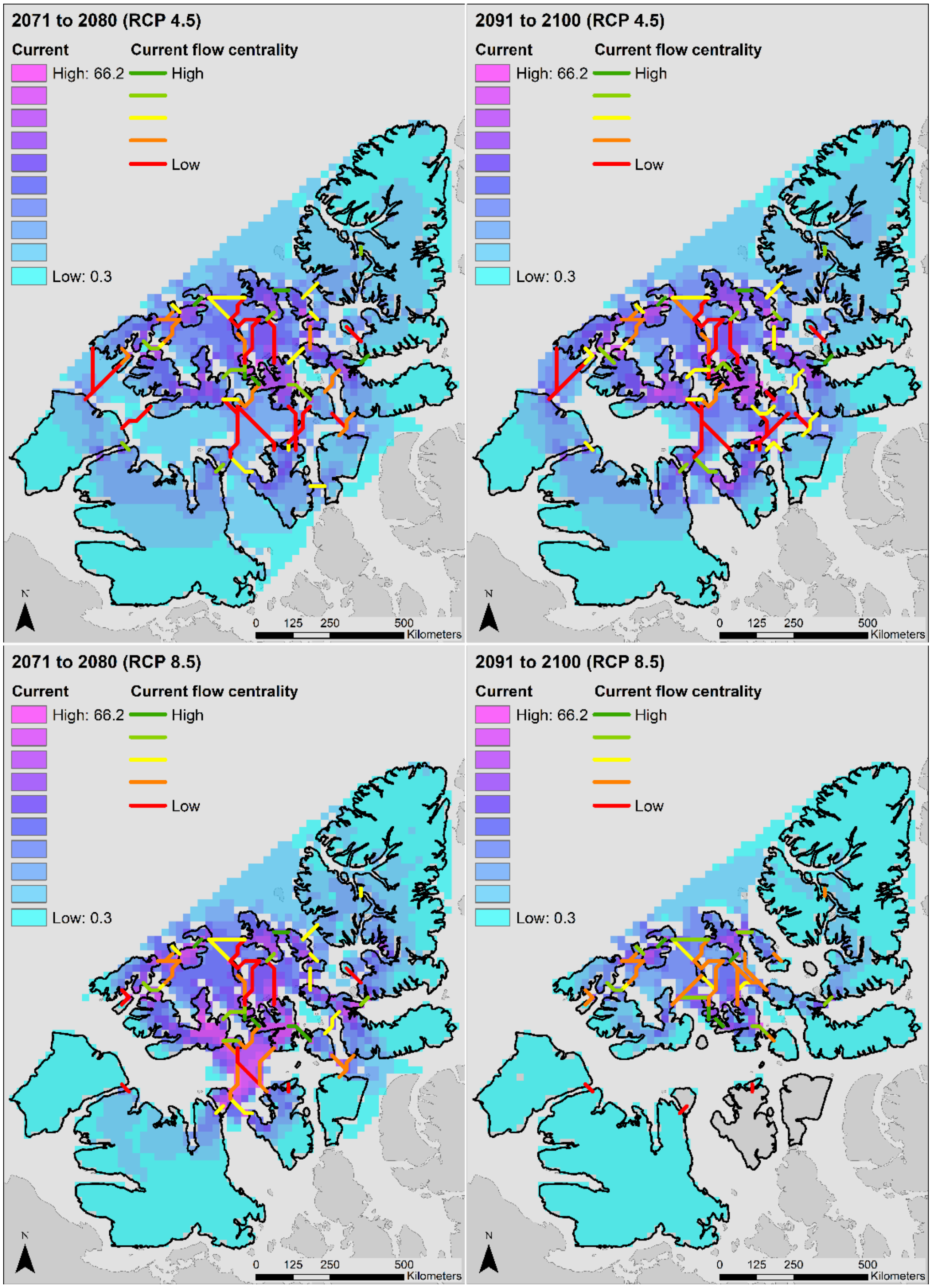

Fig 6.4 Cumulative current density (amps) across the study area in the Canadian Arctic Archipelago in spring under RCP 4.5 (top) and RCP 8.5 (bottom) projections from the Canadian Regional Climate Model (CanRCM4). Cumulative current density can be interpreted to reflect movement probabilities of Peary caribou (*Rangifer tarandus pearyi*).

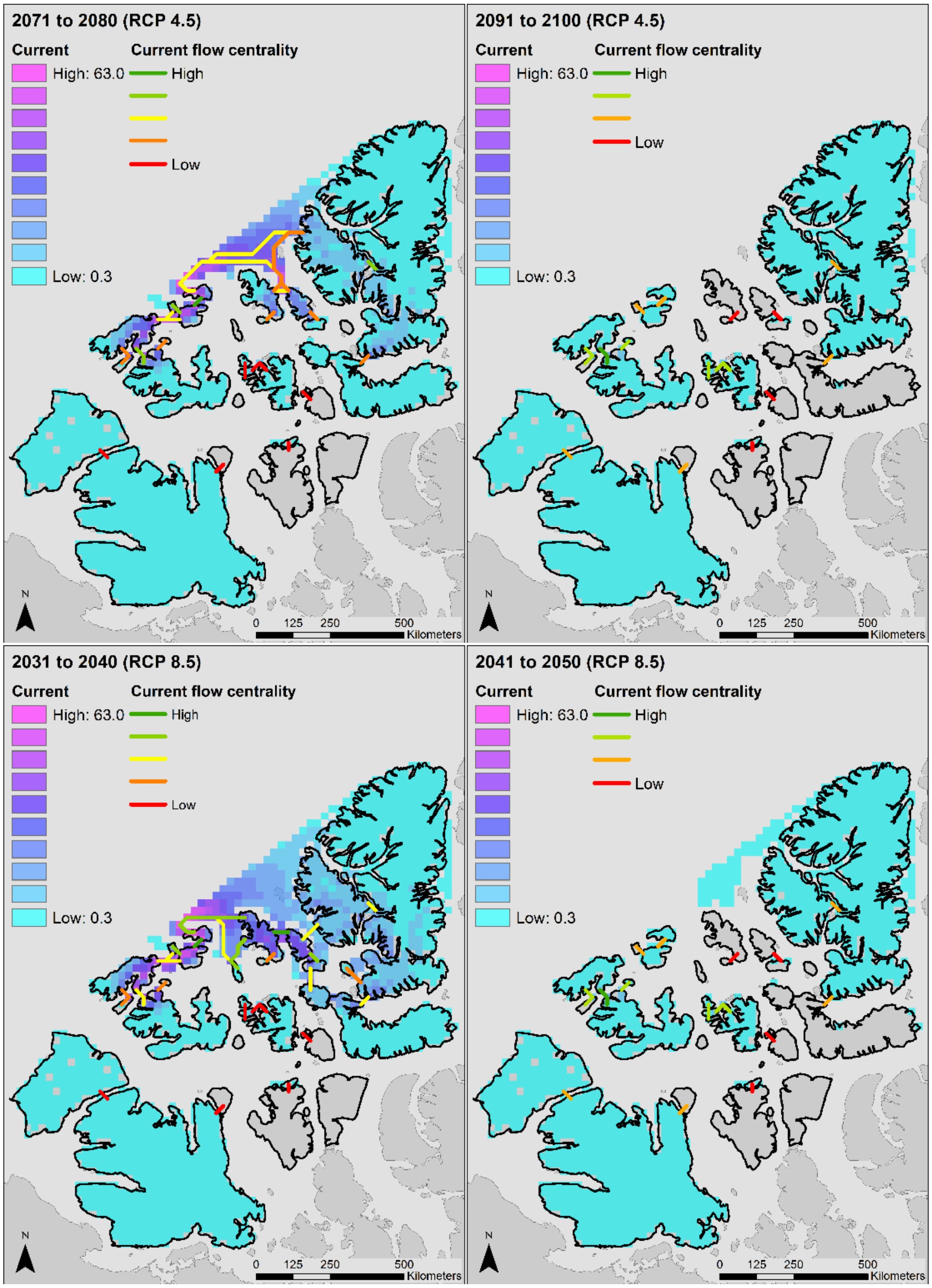

Fig 6.5 Cumulative current density (amps) across the study area in the Canadian Arctic Archipelago in early winter under RCP 4.5 (top) and RCP 8.5 (bottom) projections from the Canadian Regional Climate Model (CanRCM4). Cumulative current density can be interpreted to reflect movement probabilities of Peary caribou (*Rangifer tarandus pearyi*). Note that the time periods shown here are not the same as in Fig 6.4.

6.3.1 Least cost paths

Loss of connectivity was projected to be severe during the early-winter period, when all connectivity between islands further apart than the minimum resolution of our analysis (25 km) was lost under the RCP 8.5 scenario by 2050. Under the RCP 4.5 scenario, other than between some western Queen Elizabeth islands, all early-winter connectivity was lost by 2100. In spring, all between-population connections (e.g., BV-WQEI, WQEI-PSB) were lost by 2100 under the RCP 8.5 scenario. The number of modelled connections between islands dropped from 49 to 33 (33%) by 2100 and all remaining connections were between western Queen Elizabeth islands. Loss of spring connectivity under the RCP 4.5 scenario was less severe, with connections between populations maintained. Under the spring RCP 4.5 scenario, only two connections were lost, from 49 to 47. In winter, connections decreased from 49 to 25 (49 %) by 2040 under the RCP 8.5 scenario, and by 2050 all connections of greater distance than the minimum resolution were lost. Under the winter RCP 4.5 scenario, connections declined from 49 to 16 (67%) by 2100. The 16 remaining connections were between western Queen Elizabeth Islands (Fig 6.4).

6.3.2 Current flow centrality

We used two measures of current flow centrality to determine the importance of islands in the Canadian Arctic to maintaining Peary caribou connectivity: raw current flow centrality, and area-corrected current flow centrality. The rankings of islands by current flow centrality are reported in tables in Appendix I, and current flow centrality across the study area is shown in Figure 6.6.

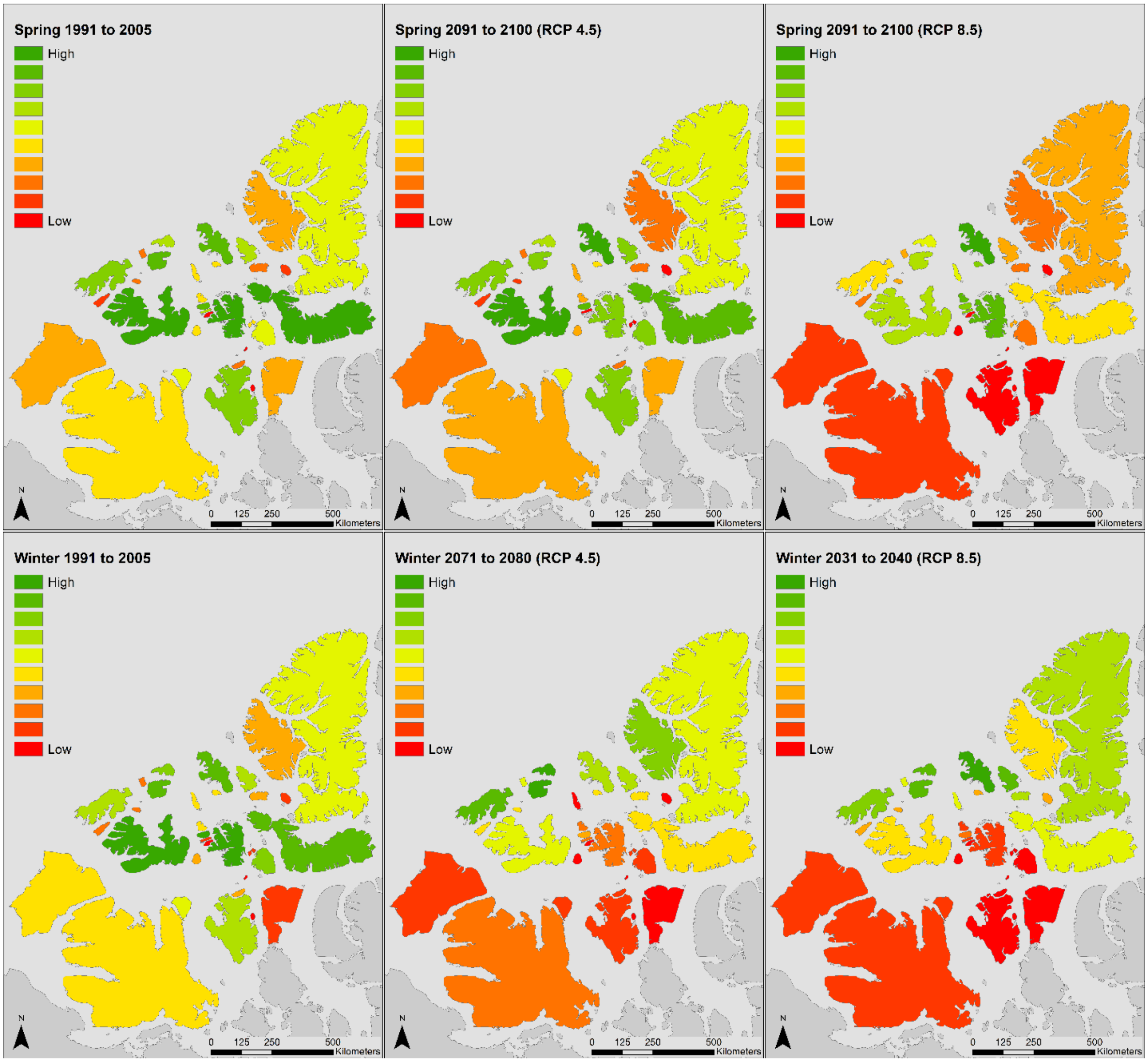

Fig 6.6 Current flow centrality across the study area in the Canadian Arctic Archipelago under the historical climate model (1991-2005), and selected decades from our RCP 4.5 and RCP 8.5 analyses. Current flow centrality represents the contribution made by an island to maintaining landscape connectivity across Peary caribou (*Rangifer tarandus pearyi*) range.

Under the historical spring climate scenario, Bathurst Island had the highest centrality value followed by Melville, Devon, Mackenzie King, and Vanier Islands. When current flow centrality was corrected for island area, the importance of smaller islands in the archipelago (i.e., Massey, Little Cornwallis, King Christian, Vanier, and Emerald) became clear. Our projections indicated that by 2100 under the RCP 8.5 scenario, the most important islands for maintaining spring connectivity were Ellef Ringnes, Bathurst, Cameron, Vanier, King Christian, and Massey. When corrected for area, Massey, King Christian, Little Cornwallis, Cameron, and Vanier Islands had the highest centrality. Centrality rankings remained largely consistent over time in the RCP 4.5 scenario because of the smaller changes to landscape resistance (a notable exception is that by 2100 Ellef Ringnes Island holds the highest centrality and Bathurst Island ranks number 8).

In early-winter, our model for the historical period from 1991 to 2005 indicated that Bathurst, Melville, Vanier, Devon, and Ellef Ringnes Islands had the highest centrality values. When corrected for area, Vanier, King Christian, Emerald, Brock, and Cameron Islands were most important for maintaining connectivity. By 2080 under the RCP 4.5 scenario, Borden, Mackenzie King, Prince Patrick, Axel Heiberg, and Amund Ringnes islands had the highest centrality. By 2040 under the RCP 8.5 scenario, Ellef Ringnes, Borden, Amund Ringnes, Mackenzie King, and Prince Patrick contributed most to maintaining connectivity. Although Table 3 (Appendix I) provides rankings based on centrality for the RCP 4.5 2091-2100 and the RCP 8.5 2041-2050 periods, they should be interpreted cautiously because absolute current flow centrality values are very low due to the limited remaining connectivity and current flow across the landscape.

6.4 Discussion

Other than the practical and financial difficulties associated with research in a vast and remote landscape (Mallory et al. 2018b), Peary caribou provide a compelling example with which to study the effects of connectivity and fragmentation on a metapopulation that experiences regular random extirpations (or near-extirpations) within local populations (Miller and Barry 2009). Peary caribou exist in a naturally fragmented landscape, with strong seasonal variation in the level of connectivity. Decades of research on metapopulation dynamics have shown that connectivity between unstable local populations is necessary for long-term metapopulation persistence (Fahrig and Merriam 1985, 1994; Leimar and Norberg 1997; Hanski 1998; Kindlmann and Burel 2008). Recent work on Peary caribou indicates that connectivity between local populations has declined over the past several decades, and is expected to further decrease with reduced Arctic sea ice cover (Jenkins et al. 2016). Here, we explored further the projected loss of connectivity for Peary caribou to identify those areas most important to maintaining linkages between populations.

In terms of connectivity loss, our results were broadly similar to those of Jenkins et al. (2016). Declines in sea ice coverage during our early-winter period (November – December) exceeded those during our spring period (April – June), such that almost all connectivity was lost under both moderate (RCP 4.5) and high (RCP 8.5) GHG concentration scenarios for the winter period, while some connectivity remained in both spring scenarios (Figs 6.2, 6.4, 6.5). Only the RCP 4.5 spring scenario retained connectivity between all Peary caribou local populations. All connections between populations were lost in winter by 2050 and 2100 in both the RCP 8.5 and 4.5 scenarios, respectively. Some early-winter connections remained between WQEI and EQEI by 2040 (RCP 8.5) and 2080 (RCP 4.5), but may be unrealistic ecologically. For example, the connection between Borden Island and Axel Heiberg Island is approximately 315 km (Fig 6.5).

Although Miller et al. (2005), reviewed a number of very long-distance sea ice crossings by caribou and reindeer (including 340 km and 380 km crossings), these types of movements are rarely documented and are unlikely to offset projected reductions in connectivity. Remaining connections between Ellesmere Island and Devon Island (approximately 14 km) and Axel Heiberg Island and Amund Ringnes Island (approximately 50 km) are more likely to be used. Across scenarios, islands inhabited by the WEQI local population remained the most connected, with islands in the Bathurst Island Complex (i.e., Bathurst, Cameron, Massey, and Vanier) and Melville and Prince Patrick Islands maintaining some measure of internal connectivity.

Islands in the Western Queen Elizabeth group are most important to maintaining connectivity across Peary caribou range (Appendix I, Tables 1 and 2). The Bathurst Island complex, Melville and Prince Patrick Islands, and the Sverdrup Islands (specifically Amund Ringnes and Ellef Ringnes) appear critical to maintaining connectivity across the study area (Fig 6.6). Patches that lie toward the centre of a study landscape generally have higher centrality scores than those at the periphery (Carroll et al. 2012; Dutta et al. 2016). Centrality scores in our study landscape typically follow this pattern, with islands in the centre of the archipelago having high centrality (e.g., the Bathurst Island Complex), and those at the boundary having low centrality (e.g., Ellesmere and Victoria Islands). This is because to connect islands (or patches) near the edges, the shortest paths for current usually flow through the central islands. In many cases it would thus be prudent to analyze connectivity some buffered distance beyond a study's area of interest to avoid introduction of these biases. However, for our study, the likelihood of any movement of Peary caribou not captured within the boundary of our analysis is very low. There have been some historical reports of Peary caribou crossing from Ellesmere Island to Greenland, but this would constitute a very small flow of individuals (COSEWIC 2015). To the south, it is possible for Peary caribou to reach the mainland through Boothia Peninsula or by crossing south of Victoria Island, and indeed there are some reports of local people observing Peary caribou in these areas. Again however, this behaviour by Peary caribou does not seem to be common. Lastly, Peary caribou are not found on Baffin Island. We are thus confident the boundaries of our analysis are appropriate.

The importance of the western Queen Elizabeth Islands for connectivity that we report here appears to be reflected in patterns of Peary caribou gene flow across the archipelago. McFarlane et al. (2014) showed that genes flowed in a southern direction in the archipelago, from the WQEI population to the BV and PSB populations. No northward movement of genes was detected, thus highlighting the importance of WQEI as a source population for gene flow to more southern regions. Our models project that by 2100, unless atmospheric GHG concentrations are maintained at RCP 4.5 levels or below, all connectivity between WQEI and the BV and PSB populations will be lost during our spring and early-winter periods (Figs 6.4 and 6.5). Although sea ice facilitated connectivity will remain during the late-winter period (January to March), we consider the probability of long-distance dispersals during this period to be lower. During the cold late-winter period, caribou typically display more sedentary behaviour. Movement rates are usually very low at this time of year (but not always, see Stuart-Smith et al. (1997)) and movements to winter ranges often occur in the fall or early winter (Brown et al. 1986; Fancy et al. 1989; Bergman et al. 2000; Ferguson and Elkie 2004; Nagy 2011). Movement data are sparse for Peary caribou, but analysis indicates seasonal ranges are smallest in winter (Miller and Barry 2009) and most reports of long distance dispersals are in spring (Miller et al. 1977, 2005). In some areas of the archipelago the majority of precipitation occurs in early winter, and loss of connectivity during this period could delay or increase the difficulty of escape from severe icing or snow conditions (Gunn and Dragon 2002; Miller and Gunn 2003a).

Sea ice coverage that reduces the dispersal and inter-island movement ability of Peary caribou could have very serious consequences for long-term metapopulation persistence. Given their small populations and the already limited connectivity, Peary caribou have reduced genetic diversity and heterozygosity compared to barren-ground caribou (*R. t. groenlandicus*) on the Canadian mainland (Jenkins et al. 2018). Further loss of genetic variation could prove harmful, as the negative consequences of low genetic variability, such as reduced fitness and ability to adapt to environmental change, can be severe (Lande 1988; Lacy 1997; Petersen et al. 2010). Reduced genetic variability warrants increased attention in the current context of climate change, where an improved ability to adapt to a changing environment associated with strong genetic variation across a population could greatly influence resilience and population persistence (Hoffmann and Sgró 2011; Moritz and Agudo 2013). However, it should be noted that to maintain genetic diversity, rates of immigration into populations need not be high. Low rates of immigration can contribute significantly to genetic diversity (Mills and Allendorf 1996; Tallmon et al. 2004). For Peary caribou, migration rates from the WQEI to PSB population have been estimated at 16-22% and from WQEI to the BV populations at 17% (McFarlane et al. 2014). Under moderate to low GHG concentration scenarios, it might be possible that enough rare dispersal events still occur during the shortened period of sea ice coverage to temper the loss of genetic variation.

A more immediate consequence of a longer ice-free season is that recolonization of ranges from which caribou have been extirpated becomes more challenging. A specific example is that continued loss of seasonal connectivity means that the reestablishment of the PSB population will become increasingly improbable. As with the other populations across the archipelago, the abundance of PSB caribou has fluctuated over time. PSB caribou were reported to be at low numbers from the 1940s to early 1970s, with the population recovering to approximately 6000 animals by 1980 (Gunn et al. 2006) before declining sharply and remaining at present levels of near extirpation (Anderson 2016; Johnson et al. 2016). In order for the PSB area to be recolonized from WQEI (McFarlane et al. 2014) individuals are required to cross approximately 50 to 100 km of Barrow Strait. As the ice-free season lengthens, opportunities for this crossing to occur will diminish.

Our results provide priority areas for future conservation and management efforts that target connectivity between Peary caribou populations. We reiterate the importance of islands with high centrality, such as the Bathurst Island complex and Melville Island, for maintaining connectivity across the entire archipelago. Connections across the Parry Channel, which separates the WQEI from the BV and PSB populations, have high conservation value despite their low centrality scores (Figs 6.3 and 6.4), and these links are vulnerable to being completely lost during important movement periods. The importance of the links between Bathurst, Melville, and Prince Patrick Islands (WQEI) and Banks, Victoria, Prince of Wales, and Somerset Islands (BV and PSB) comes from their critical role in facilitating the flow of genes between these three populations. While still important, higher-latitude linkages between the WQEI and EQEI should have less conservation priority because they are more likely to persist over intermediate timescales. By considering area-corrected centrality scores, our analysis highlights the importance of relatively small islands, including Little Cornwallis, King Christian, Borden, and Brock for landscape connectivity (Miller 2002).

Typical conservation measures for enhancing connectivity are likely to involve undertakings such as protecting movement corridors, construction of wildlife crossing structures, and matrix restoration (Beier and Noss 1998; Ng et al. 2004; Donald and Evans 2006). However, the loss of connectivity across sea ice resulting from a warming climate presents a much different conservation problem for which these types of endeavors have limited applicability. What types of measures might then be effective? Of primary importance is the reduction of GHG emissions to limit further climate change. Across many studies, the projected negative effects of climate change on species and ecosystems are reduced under lower emissions scenarios (e.g., Urban, 2015; Garciá Molinos *et al.*, 2016). From our findings, we observe that lower atmospheric GHG concentrations significantly improve the outlook for Peary caribou habitat connectivity. In a sense this is good news for Peary caribou conservation, as GHG emission control and reduction is an important international subject with implications extending far beyond the ability of northern ungulates to move between islands. This means that global climate change mitigation efforts should have benefits for landscape connectivity in the Canadian Arctic Archipelago as a by-product.

Habitat protection is another means by which conservation measures might be implemented. Although human and industrial activity in the Canadian High Arctic is currently low, extractive industries have existed in the region before (e.g., Polaris mine on Little Cornwallis Island, Bent Horn oil field on Cameron Island). Warmer temperatures and a longer shipping season are predicted to increase future levels of industrial development (Prowse et al. 2009). Regulators must carefully consider the potential effects to Peary caribou habitat connectivity that the loss of seemingly small areas of habitat could cause (i.e., pinch points, areas where landscape current flow is bottlenecked (Dutta et al. 2016)). For habitat protection, steps in this direction have already been taken with the establishment of Qausuittuq National Park on September 1, 2015. The park encompasses part of the Bathurst Island complex, including the northwestern portion of Bathurst Island and Vanier, Massey, Alexander, Helena, and several smaller islands in the complex. However, in their analysis of Peary caribou distribution in relation to the boundaries of Qausuittuq National Park, Poole et al. (2015) suggested mixed effectiveness of the park area in protecting Peary caribou habitat. Notably, the northeastern areas of Bathurst Island and the entirety of Cameron Island are excluded from the park due to their mineral and petroleum potential (Poole et al. 2015).

Finally, disruption to Peary caribou movement can occur through ice breaking. Ice breaking activities have been observed to disrupt caribou migrations across sea ice (Dumond et al. 2013), and while marine traffic in the High Arctic is currently limited, much like industrial activity it is expected to increase as sea ice coverage declines and the shipping season lengthens (Prowse et al. 2009). Beyond the climate-driven lengthening of shipping windows, increasing development could bring with it pressure to artificially extend shipping seasons with ice breaking, or even year-round shipping. These types of activities must be evaluated carefully and should not occur through connections between Peary caribou habitat during important movement periods in the spring and early winter.

6.4.1 Limitations of our analysis

Due to the nature of predictive climate modeling at a coarse scale, we must be cautious in interpreting our results. For example, although various climate models project Arctic sea ice decline, the specific spatial and temporal patterns of sea ice loss and formation can be variable across studies (e.g., Stroeve et al. 2007). However, we suggest that the patterns we report should be generalizable across varying sea ice scenarios. In general, sea ice declines will occur more rapidly in southern regions of the study area and lead to loss of connectivity sooner at lower latitudes. Also, the Bathurst Island complex will have high centrality stemming from its central location within the distribution of Peary caribou. We reason that the many of the findings of our study should be robust and applicable beyond the particularities of our climate data and uncertainties therein.

6.4.2 Conclusions

Peary caribou are distributed at low densities over a vast area and a major threat to their persistence, loss of connectivity due to climate change, cannot be addressed directly by local land and resource managers. The extinction risk that climate change presents is difficult to curtail other than through coordinated international efforts to slow and limit GHG emissions (Thomas et al. 2004; Maclean and Wilson 2011; Bellard et al. 2012; Urban 2015). However, we are hopeful that our research can help to highlight priority areas and actions that, when coupled with global reductions in GHG emissions, could help to mitigate the most negative consequences of connectivity loss.

7 Conclusions

The overall objective of my research was to improve our understanding of potential current and future impacts of climate change on Arctic caribou, with specific focus on several populations in Nunavut, Canada. Through this work I sought to 1) review and synthesize the existing literature on caribou and climate, 2) test whether broad climate patterns could help to explain synchrony of three adjacent barren-ground caribou herds, 3) identify whether evidence of trends consistent with climate change signals exist for environmental covariates on Qamanirjuaq barren-ground caribou range, 4) examine behavioural responses by Qamanirjuaq caribou to any trends that might exist, and 5) explore how projected sea-ice loss will affect connectivity between Peary caribou groups in the High Arctic. My findings suggest that climate change impacts to caribou are likely to vary regionally. Some aspects of climate change, such as increased primary productivity, could benefit caribou (Tews et al. 2007a; Sharma et al. 2009; Tveraa et al. 2013), but many others, such as increases in wildfire frequency, insect harassment, and extreme winter weather, are likely to be detrimental (Vors and Boyce 2009; Joly et al. 2012; Witter et al. 2012b; Hansen et al. 2014; Albon et al. 2017). Depending on environmental conditions across the habitat of a given group of caribou, these various factors could result in a different net effect. Research that seeks to evaluate multiple factors concurrently will be important to clarify and disentangle the interconnected aspects of environmental change.

Large-scale climate oscillations have been reported to influence caribou populations dynamics and could contribute to regional synchrony in *Rangifer* abundance (Klein 1991; Gunn et al. 2011; Joly et al. 2011). In chapter two, I tested the hypothesis that the Arctic Oscillation (AO) influences the abundance and population synchrony of the Bathurst, Beverly, and Qamanirjuaq barren-ground caribou herds. I found relationships between the AO and temperature, growing conditions, and caribou body condition. I also identified that population trajectories of these three caribou herds broadly followed the trends in the intensity of the AO. My findings suggest that the AO influences barren-ground caribou population dynamics through effects on summer-range quality, caribou physical condition, and herd productivity. The effects of regional climate oscillations, such as the AO, on local climate trends and patterns can add further complexity to identifying potential positive and negative effects of climate change for caribou and reindeer (Joly et al. 2011).

Changing phenology is a widely reported consequence of climate change (Post et al. 2018), and the capacity of species to adapt to altered phenologies will be critical to their success under climate change scenarios. In chapter four, I investigated the response of Qamanirjuaq barren-ground caribou to changing spring phenology using data from GPS telemetry and satellite imagery. From 2004 to 2016, I found that green-up on the herd's calving area advanced by 7.25 days, while the start of migration advanced by 13.64 days, the end of migration advanced by 6.02 days, and the date of peak calving advanced by 9.42 days. Over the study period, caribou migratory and reproductive behaviours appeared to keep pace with advancing phenology at lower trophic levels, with changing snow cover on the late winter and migratory ranges found to be the most-supported driver of advancing migratory behaviour. The ability of caribou to adjust the timing of migratory and reproductive behaviour in response to changing environmental conditions demonstrates the potential resilience of the species to some aspects of climate change.

In chapter five, I used integrated step selection analysis (iSSA) to estimate barren-ground caribou habitat selection across 194 individual spring migrations and investigate the effect of snow conditions on barren-ground caribou movement during spring migration. I found that warmer mean spring temperatures leading to the earlier onset of spring snow melt negatively influenced caribou movement, and caribou travelled slower in years with highly-variable melting and patchy spring snow conditions which led to longer time spent in migration. Using a data-driven approach based on these iSSA movement models, I delineated the most important areas for caribou in our study during migration. We can help to maintain caribou migrations by targeting these specific areas for protection and ensuring minimal disturbance during movement periods to provide caribou opportunity to adjust to rapid environmental change.

In chapter six I used least-cost path analysis and circuit theory (Adriaensen et al. 2003; McRae et al. 2008) to model connectivity across Peary caribou range, and future climate projections to investigate how this connectivity might be affected by a warming climate. Further, I used measures of current flow centrality to estimate the role of High Arctic islands in maintaining connectivity between Peary caribou populations and to identify and prioritize those islands and linkages most important for conservation. My results suggested that the Bathurst Island complex plays a critical role in facilitating connectivity between Peary caribou populations. Large islands, including Banks, Victoria, and Ellesmere have limited roles in connecting Peary caribou. Continued connectivity across the Canadian Arctic Archipelago, and possibly Peary caribou persistence, ultimately hinges on global commitments to limit climate change. The results of chapter six highlight priority areas where, in addition to emission reductions, conservation efforts to maintain connectivity would be most effective. Climate change impacts to species might be mitigated through conservation areas that allow species to adapt or adjust to changing conditions (Lawler 2009).

I will briefly elaborate here on some of the limitations of my thesis, particularly in terms of data and analysis. This section should not be interpreted as undermining the results of my work, but rather as insight into sources of uncertainty and how this or similar studies could be improved. Climate data tend to exhibit high interannual variability, which can present difficulty in determining patterns over short and intermediate timescales (Santer et al. 2011). Further, although satellite imagery provides many powerful tools, particularly in facilitating analysis in remote areas, the spatial and temporal scales, while adequate, were not ideal. In chapters 4 and 5, I used the behaviour of tracked Qamanirjuaq cows to make inferences at the population level. Some uncertainty in the phenological and behavioural trends reported here is introduced with sample size. Although I am confident that in general a relatively small number of collared Qamanirjuaq cows reflect the spatial distribution of female caribou during the calving period, in some years the sample size was quite low (i.e., 5 tracked animals in 2004, 9 tracked animals in 2010), and so some degree of caution is necessary in our interpretation. Model diagnostics did not indicate any points from these (or any) years that were overly influential on the trends I report, but as sample size decreases the chance of not capturing the behaviour reflective of the majority of the herd increases.

Although my research suggests that caribou and reindeer could have some resilience to climate change, current global trends in abundance undermine all but the most precautionary outlooks. Ultimately, the conservation of *Rangifer* populations will require careful management that considers the local and regional manifestations of climate change.

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Appendix I Current flow centrality rankings of islands in the Canadian Arctic Archipelago

Table 1. Spring current flow centrality rankings for all study islands in the Canadian Arctic Archipelago grouped by spring climate scenario. Dashed lines indicate zero connectivity. Islands are listed in order of highest centrality from 1991-2005. Local populations: Western Queen Elizabeth Islands (WQEI), Eastern Queen Elizabeth Islands (EQEI), Prince of Wales/Somerset/Boothia (PSB), Banks/Victoria (BV).

		Centrality					**Area-corrected centrality**				
		Historical	**RCP 4.5**		**RCP 8.5**		**Historical**	**RCP 4.5**		**RCP 8.5**	
Island	**Local population**	1991 -2005	2071 -2080	2091 -2100	2071 -2080	2091 -2100	1991 -2005	2071 -2080	2091 -2100	2071 -2080	2091 -2100
Bathurst	WQEI	1	1	8	1	2	20	20	21	20	15
Melville	WQEI	2	2	2	2	8	23	22	23	22	18
Devon	WQEI	3	3	3	6	11	25	25	25	24	19
Mackenzie King	WQEI	4	5	5	5	7	14	14	14	13	10
Vanier	WQEI	5	4	4	4	4	4	4	2	4	5
Ellef Ringnes	WQEI	6	6	1	3	1	19	19	19	19	13
Prince of Wales	PSB	7	10	9	17	25	22	23	22	23	24
Prince Patrick	WQEI	8	7	7	12	12	21	21	20	21	16
Massey	WQEI	9	8	27	10	6	1	1	7	2	1
Borden	WQEI	10	9	11	9	9	11	11	11	10	9
Amund Ringnes	WQEI	11	11	6	8	13	17	16	15	15	14
Ellesmere	EQEI	12	12	12	15	14	28	28	28	27	23
Stefansson	BV	13	13	13	14	23	15	17	16	14	22
Cornwallis	WQEI	14	14	10	11	18	18	18	18	18	17
Byam Martin	WQEI	15	19	17	13	-	8	8	6	6	-
King Christian	WQEI	16	15	14	16	5	3	3	1	3	2
Cameron	WQEI	17	17	16	19	3	7	7	4	7	4
Little Cornwallis	WQEI	18	16	28	7	15	2	2	9	1	3
Lougheed	WQEI	19	18	15	18	10	10	9	8	9	7
Victoria	BV	20	20	19	24	22	29	29	29	29	26
Banks	BV	21	21	22	26	24	27	27	27	28	25
Somerset	PSB	22	22	18	25	-	24	24	24	25	-

Axel Heiberg	EQEI	23	23	21	21	19	26	26	26	26	21
Russell	PSB	24	26	23	27	26	9	10	10	12	20
Cornwall	WQEI	25	24	20	20	20	13	13	13	11	12
Brock	WQEI	26	25	24	22	16	6	6	5	8	8
Emerald	WQEI	27	27	25	23	17	5	5	3	5	6
Eglington	WQEI	28	28	26	28	21	12	12	12	17	11
Graham	EQEI	29	29	29	29	-	16	15	17	16	-

Table 2. Winter current flow centrality rankings for all study islands in the Canadian Arctic Archipelago grouped by winter climate scenario. Dashed lines indicate zero connectivity. Islands are listed in order of highest centrality from 1991-2005. Years with an asterisk indicate that some islands during this period have equivalent centrality rank. Local populations: Western Queen Elizabeth Islands (WQEI), Eastern Queen Elizabeth Islands (EQEI), Prince of Wales/Somerset/Boothia (PSB), Banks/Victoria (BV).

		Centrality					**Area-corrected centrality**				
		Historical	**RCP 4.5**		**RCP 8.5**		**Historical**	**RCP 4.5**		**RCP 8.5**	
Island	**Local population**	1991 -2005	*2071 -2080	*2091 -2100	*2031 -2040	*2041 -2050	1991 -2005	2071 -2080	2091 -2100	2031 -2040	2041 -2050
Bathurst	WQEI	1	11	3	15	3	20	20	16	23	16
Melville	WQEI	2	8	2	12	2	22	17	18	19	18
Vanier	WQEI	3	10	1	14	1	1	10	3	13	3
Devon	WQEI	4	9	4	10	4	24	19	21	20	21
Ellef Ringnes	WQEI	5	6	5	1	5	19	11	19	11	19
Mackenzie King	WQEI	6	2	3	4	3	14	5	11	7	11
Cornwallis	WQEI	7	13	5	17	5	18	21	17	24	17
Borden	WQEI	8	1	4	2	4	11	3	10	4	10
Amund Ringnes	WQEI	9	5	5	3	5	15	7	15	8	15
Prince Patrick	WQEI	10	3	2	5	2	21	12	14	14	14
Prince of Wales	PSB	11	13	5	17	5	23	23	22	25	22
Ellesmere	EQEI	12	8	3	6	3	28	22	24	22	24
Stefansson	BV	13	12	4	16	4	17	18	12	21	12
King Christian	WQEI	14	9	5	13	5	2	4	8	5	8
Victoria	BV	15	11	3	15	3	29	25	25	27	25
Banks	BV	16	12	4	16	4	27	24	23	26	23
Lougheed	WQEI	17	-	-	9	-	10	-	-	2	-
Cameron	WQEI	18	11	3	15	3	5	13	4	15	4
Byam Martin	WQEI	19	-	-	-	-	9	-	-	-	-
Cornwall	WQEI	20	9	5	7	5	13	9	13	6	13
Russell	PSB	21	13	5	17	5	6	16	9	17	9
Axel Heiberg	EQEI	22	4	4	11	4	26	15	20	18	20
Brock	WQEI	23	7	4	8	4	4	1	5	1	5

Emerald	WQEI	24	9	3	13	3	3	2	2	3	2
Eglington	WQEI	25	9	3	13	3	12	6	7	10	7
Somerset	PSB	26	-	-	-	-	25	-	-	-	-
Massey	WQEI	27	11	3	13	3	7	-	1	9	1
Little Cornwallis	WQEI	28	13	5	15	5	8	14	6	12	6
Graham	EQEI	29	-	-	17	-	16	8	-	16	-