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

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1 **Observed and predicted effects of climate change on Arctic caribou and reindeer**

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Abstract

The ability of many 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. We examine the literature to provide a thorough and full consideration of the many environmental factors that limit caribou and reindeer populations, and how these might be affected by a warming climate. Our review suggests that the response of *Rangifer* populations to climate change is, and will continue to be, varied in large part to their broad circumpolar distribution. While 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.

Key words: climate change, caribou, reindeer, *Rangifer*, Arctic.

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; Fall 2016). 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 et al. 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. 2012a; Loe et al. 2016; Albon et al. 2017; Le Corre et al. 2017). The extensive distribution of *Rangifer* globally (Fig. 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*; Fig. 2), Peary caribou (*R.t.*

93 *pearyi*), Svalbard reindeer (*R.t. platyrhynchus*), reindeer (*R.t. tarandus*, *R. tarandus*) in
94 Scandinavia and northern Eurasia, and caribou (*R.t. caribou*) in northern Quebec and
95 Labrador, Canada. We divide our review into five categories: i) summer range
96 conditions, ii) parasites and disease, iii) movement, migration, and distribution, iv)
97 extreme weather and icing events, and v) winter range quality. Finally, we provide
98 discussion of how these effects may interact.

99
100 **Summer range conditions**

101 Summer is a critical foraging period for *Rangifer* populations. During the brief
102 period of high-quality green vegetation in the Arctic summer, caribou and reindeer must
103 forage effectively to recover from the nutritional stress of the previous winter (Gerhart et
104 al. 1996; Parker et al. 2009; but there are some examples of caribou gaining fat over
105 winter, e.g., Couturier et al. 2009a) and to build fat reserves and body condition in
106 anticipation of upcoming food constraints over the next winter (Mörschel and Klein
107 1997). During the summer, lactation by females places additional energetic demands on
108 cows (Parker et al. 1990; Barboza and Parker 2008; Parker et al. 2009) that must be met
109 through adequate nutrition (Gerhart et al. 1996). Males must also be able to forage
110 sufficiently to build the necessary body reserves for the fall rut (Barboza et al. 2004;
111 Skoog 1968). Availability of quality summer forage has been linked, through improved
112 body condition, to positive effects on fecundity for *Rangifer* (Reimers 1983; Cameron et
113 al. 1993; Gerhart et al. 1997; Pachkowski et al. 2013). Conversely, poor summer forage
114 conditions are associated with reductions in life-history traits and increased overwinter
115 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. (2016), 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. 2016).

Both Veiberg et al. (2016) 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; Veiberg et al. 2016; Gustine 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. 2007a; 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; Pettoirelli et al. 2005; Courturier 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).

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. 2012b). 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. 2012a), 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; Kutz et al. 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 2010; Tompkins et al. 2011).

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; Skogland 1984; Klein 1992; 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 avoided 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 1987; 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 2003). 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 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).

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 2003; 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. 2013).

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. 2016) 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 (Bonan and Shugart 1989; Rowe and Scotter 1973) 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 et al. 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; Cameron et al. 1993; Crête and Huot 1993; Cameron 1994; Mahoney and Shaefer 2002; Couturier et al. 2009b).

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 2003; 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. 2008) 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.

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,

641 providing earlier access to forage (and thus offsetting the costs of parturition and
642 lactation), and generally increasing the quantity and period of available forage (Tews et
643 al. 2007a; Cebrian et al. 2008; Helle and Kojola 2008; Tveraa et al. 2013; Veiberg et al.
644 2016). However, this same increase in temperature will also likely increase insect
645 harassment, provide opportunity for predators, potential competitor species, parasites,
646 and diseases that have historically been restricted to more southerly ranges to expand
647 northward, and alter plant community composition to be dominated by potentially less
648 nutritious species (Sharma et al. 2009; Witter et al. 2012a; Kutz et al. 2013; Thompson
649 and Barboza 2014; Simard et al. 2016). Additionally, all *Rangifer* populations may not
650 respond positively to the advancement of spring (Post and Forchhammer 2008; Kerby
651 and Post 2013).

652 The interplay of potential effects in the winter is similarly convoluted. Although
653 increased temperatures and shorter winters may benefit *Rangifer* by improving access to
654 forage, warm weather also produces more frequent icing events, which can lead to mass
655 starvation, or at least displacement from preferred habitat, in populations (Hansen et al.
656 2014; Loe et al. 2016; Langlois et al. 2017). Increases in wildfire activity on winter
657 ranges of caribou populations can degrade habitat quantity and quality, while improving
658 it for other ungulate species whose ranges could then expand (Joly et al. 2012; Anderson
659 and Johnson 2014).

660 Confounding the understanding of the interaction between the various impacts of
661 climate change is the potential for distributional shifts of *Rangifer* populations, and
662 changes in migratory behaviour. Though we may predict the effects of climate change on
663 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. (2007a) 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). Nicolson 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. 2013, 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).

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1404 **Figure Captions**

1405 **Fig. 1.** Approximate global distribution of caribou and reindeer (*Rangifer tarandus*).

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1407 **Fig. 2.** Barren-ground caribou (*Rangifer tarandus*) in autumn south of Kugluktuk,

1408 Nunavut, Canada. © Mathieu Dumond/ Umingmak Productions Inc.

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Draft

Fig. 1. Approximate global distribution of caribou and reindeer (*Rangifer tarandus*).

279x215mm (300 x 300 DPI)

Fig. 2. Barren-ground caribou (*Rangifer tarandus*) in autumn south of Kugluktuk, Nunavut, Canada. © Mathieu Dumond/ Umingmak Productions Inc.

73x48mm (300 x 300 DPI)