FACTORS INFLUENCING THE DISTRIBUTION OF BATHURST BARREN-GROUND CARIBOU (*RANGIFER TARANDUS GROENLANDICUS*) DURING WINTER

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ABSTRACT

Across the circumpolar north, many herds of *Rangifer* have decreased in abundance. In the Canadian central Arctic, the Bathurst herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) declined from 472,000 ± 72,900 (± 95% confidence interval) caribou in 1986 to 31,900 ± 10,900 caribou in 2009 (Gunn *et al.* 2008, Adamczewski *et al.* 2009). A reduction in winter forage due to forest fires has been suggested as a factor contributing to the decline. I employed a multi-scale study design to identify the influence of vegetation, fire history, snow cover, and predation risk on the occupancy of winter habitats by Bathurst caribou. Between 2008 and 2009, I collected forest stand and understory data at habitats used by caribou, as well as paired control sites. At a larger spatial scale, I used animal location data recorded from 1996 - 2009 to characterise the spatial and temporal distribution of Bathurst caribou on the winter range.

At the scale of the feeding patch, caribou foraged in habitats with a high-percentage ground cover, high biomass of lichen, and few or small trees. Similarly, the consensus among the models of habitat selection was that collared caribou avoided areas of the winter range with a high density of burns and favoured older patches of forest characterised by a high percentage of ground cover of lichen and herbaceous forage and a close proximity to lakes and rivers. However, there was considerable use of habitats adjacent to the burn boundary, and some caribou occupied early-seral habitats significantly more than expected. Although the abundance of fruticose (having branched, shrubby thalli) lichens was relatively high (2464 kg/ha) in areas burned within the last 43 - 264 years, my results suggest that an increased incidence and severity of forest fires due to climatic warming could cause a temporary decrease in the habitat available to the Bathurst caribou herd during winter. In the event that reduced lichen availability becomes a limiting or regulating factor for caribou, fire suppression may be necessary to mitigate other climate- and anthropogenic-related pressures affecting the population and distribution dynamics of Bathurst caribou.

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CHAPTER 1 - THESIS INTRODUCTION

CONTEXT

Barren-ground caribou (*Rangifer tarandus groenlandicus*) are arguably the most physiologically adapted Cervidae inhabiting the northern taiga (Telfer and Kelsall 1984, Klein 2000). Fossils dating to 1.8 million years ago reveal a long evolutionary history, and an ability to endure great environmental change. An important adaptation of caribou for survival during prehistoric climatic extremes was their wide-ranging food habits, which included lichens, bryophytes and the deciduous spermatophytes (Klein 1982, Russell *et al.* 1993, Bergerud *et al.* 2008). Furthermore, caribou developed physiological and morphological adaptations that have allowed them to withstand temperature extremes of -60° to +33 °C (Russell *et al.* 1993, Bergerud *et al.* 2008).

Today, wild caribou and reindeer herds encompass much of the circumpolar north, varying from boreal and montane ecotypes, to the mainland-migratory subspecies (CARMA 2010). Across the Canadian central Arctic, seven distinct populations of migratory barren-ground caribou span both tundra and taiga ecozones (Appendix A). These caribou are known for their long-distance migrations, where herds may travel up to several hundred km to reach distinct seasonal ranges. During the summer, barren-ground caribou dwell primarily on the tundra. Here, they rely on a quick-growing, nutrient-dense diet of graminoids, sedges, and shrubs to acquire adequate protein and fat stores for the winter (Russell *et al.* 1993). In contrast, winter ranges for most migratory herds are below treeline, and are characterised by mature coniferous forest yielding abundant fruticose (having branched, shrubby thalli) lichens (Klein 1982, Thomas *et al.* 1996, Bergerud *et al.* 2008).

Winter is a critical period for caribou. Continuous snow cover and ice-bound vegetation can significantly limit access to forage resources. Taiga woodlands provide shelter from the wind and expansive mats of ground-dwelling lichens. Caribou often consume a diet of 60 - 80% terrestrial lichens during winter (Parker 1981, Thomas and Hervieux 1986, Gauthier *et al.* 1989, Klein 1991, Jandt *et al.* 2003). Moreover, nutritional analyses reveal that lichens contain high levels of available energy, making them ideal winter forage for caribou (Wales *et al.* 1975) when supplemented with high-protein vascular vegetation (Jacobsen and Skjenneberg 1975). Although lichens often comprise a large proportion of available phytomass in northern ecosystems (Helle and Aspi 1983), they grow slowly (4 to 6 mm yr^{-1}, Pegau 1968) and they are vulnerable to disturbance, including foraging and trampling by caribou (Pegau 1969, Moser *et al.* 1979, Joly *et al.* 2007b, 2010). Following a major disturbance such as fire or heavy grazing pressure, the recovery of lichen mats may take a lengthy period of time (~45 kg ha^{-1} yr^{-1}, Auclair 1985) preventing their use by caribou for up to 50 years (Scotter 1964, Kelsall 1968, Klein 1982, Joly *et al.* 2003, 2007a, Jandt *et al.* 2008).

Fire is a dominant disturbance agent in boreal forests (Johnson 1992) that may have a negative influence on caribou habitat due to the slow recovery of mat-forming lichens. Lichen species favoured by caribou (e.g., *Cladina rangiferina*, *C. mitis*) are associated with late-successional seral stages in boreal forests (Maikawa and Kershaw 1976), and in the short term are lost following fire. Many authors have argued that fire plays an important regenerative role in boreal forests (Bergerud 1974, Miller 1976), and may be necessary for the long-term productivity of lichen stands (Klein 1982, Schaefer and Pruitt 1991, Sulyma and Coxson 2001). By consuming organic materials bound in the forest floor, fires immediately increase nutrient availability (Viereck and Schandelmeier 1980), and provide the periodic mineralisation necessary to sustain fruticose lichens, as well as renew growth of alternative caribou forage such as sedges and shrubs (Kershaw *et al.* 1975). Fires also enable mature forests to retain an open canopy, which allows sunlight to penetrate the tree cover and sustain terrestrial lichens (Bonan and Shugart 1989). Extensive lichen mats, in turn, reduce soil temperatures and sunlight infiltration to the forest floor. This retards both tree growth and seedling development, essentially maintaining a microclimate that supports lichen establishment (Kershaw *et al.* 1975, Maikawa and Kershaw 1976).

Although fire produces more heterogeneous northern forests (Miller 1976, 1980), there is a long-standing concern about the amount and the connectivity of mature forested habitat available to caribou on winter range (Klein 1982). In addition to lower lichen biomass, recently burned habitats yield deeper and denser snowpacks and greater amounts of accumulated deadfall (Schaefer and Pruitt 1991). Especially in interiors of burns, increased sun and wind exposure usually result in greater snow depths and a thicker layer of surface crust (Thomas *et al.* 1998). Alternatively, older forests provide greater thermal cover and more favourable snow conditions compared to younger stands (Thomas *et al.* 1998). Mature or near-mature spruce forests (*Picea glauca* and *P. mariana*) >80 - 100 years of age generally contain lower snow depths, and, where thick tree branches are present, can prevent ice layers from forming on lichen mats (Thomas 1998b). This may be especially important to caribou in late winter, when snow depth and hardness attain maximum levels (Thomas 1998a).

Snow cover can limit the availability of terrestrial lichen for caribou (Bergerud 1974, Thomas *et al.* 1998). Greater snow depths increase the energetic requirements of locomotion and foraging (Fancy and White 1985), and higher snow densities impede the ability of caribou to detect lichens even where snow accumulation is relatively shallow (Fancy and White 1985). Maximum snow-depth thresholds for effective cratering (foraging for ground vegetation by pawing through snow) by caribou are 50 - 80 cm (Pruitt 1959), and particularly deep or wind-hardened snow can decrease the availability of forage by up to 90% (Collins and Smith 1990). Numerous studies have shown that caribou select foraging sites with relatively lower snow depth, snow hardness, or both (LaPerriere and Lent 1977, Cichowski 1993, Johnson *et al.* 2001). At a larger spatial scale, some barren-ground herds have likely adapted to the long-term variation in snow depth across their winter ranges. The Beverly and Porcupine herds (*R. t. groenlandicus* and *R. t. granti*, respectively), for example, generally occupy areas that will later support greater snow accumulation early in the winter, before heavy snowfall impedes movement and foraging (Russell *et al.* 1993, Thomas 1998b).

The reduction in the availability of forage resulting from snow and ice can lead to malnutrition or even death of caribou (Cameron *et al.* 1993). This is particularly true for herds that are confined to small, insular ranges and cannot migrate to areas where food is more accessible (Tucker *et al.* 1991). Numerous die-offs have occurred in such spatially-restricted populations, especially where harsh snow conditions coincided with high population densities (Klein 1968, Skogland 1985, Gates *et al.* 1986, Adamczewski *et al.* 1988). Although mainland populations of caribou rarely starve due to their flexible range use (Skoog 1968), severe winter-weather events have been linked to both reductions in annual recruitment and fitness of calves, likely due to the inability of females to meet the heightened nutritional requirements of pregnancy (Bergerud 1971, Couturier *et al.* 1990, Cameron *et al.* 1993, Adams and Dale 1998).

The importance of winter versus summer forage in the density-dependent regulation of caribou remains controversial (Heggberget *et al.* 2002, Bergerud *et al.* 2008). While a shortage of winter lichens may not lead to starvation for caribou in good physical condition, inadequate forage intake during summer can amplify the effects of winter-forage restriction, leading to increased mortality (Bergerud *et al.* 2008). More importantly, a rapid reduction in forage resources due to any combination of seasonal factors can markedly disrupt population dynamics. Insufficient forage intake during winter can reduce the body condition of females, causing low birth weights of calves (Chan-McLeod *et al.* 1999, Adams 2005, Tveraa *et al.* 2007), and may ultimately affect future reproductive potential if body condition does not recover to allow conception the following autumn (Cameron *et al.* 1993). Likewise, climate-related increases in harassment by biting and parasitic insects can restrict time spent foraging and the use of preferred summer habitats (Russell *et al.* 1993). Such losses are especially detrimental for newborn calves, as adequate forage for cows is crucial for supporting a calf's growth and development and preventing premature weaning (Russell *et al.* 1993, Brotton and Wall 1997).

Northern landscapes are changing at an unprecedented rate (Johnson *et al.* 2005, Joly *et al.* 2009a, Vors and Boyce 2009). A warming climate will likely affect the distribution and the availability of terrestrial lichens, via higher frequencies of fire, extreme winter-weather events, and changes in the composition of plant communities (Cornelissen *et al.* 2001, Olthof *et al.* 2008, Joly *et al.* 2009a, Vors and Boyce 2009). Such conditions both increase the energy required to search for food resources (Fancy and White 1985, Brotton and Wall 1997) and decrease the nutrient gains obtained from foraging for lichens. Moreover, these losses could be additive with poorer summer-range condition and increasing human disturbance across seasonal ranges (Harrington and Veitch 1991, Dyer *et al.* 2001, Mahoney and Schaefer 2002, Frid 2003, Nellemann *et al.* 2003, Johnson *et al.* 2005). Changing plant and insect phenologies will likely influence caribou movements and energy budgets (Vors and Boyce 2009), and the expansion of anthropogenic activities may disrupt long-term patterns of caribou distribution and the availability of preferred habitats across seasonal ranges (Bergerud *et al.* 1984, Johnson *et al.* 2005). Ultimately, a reduction in the availability or quality of forage resources could cause herds to adopt an alternative geographic distribution (Joly *et al.* 2009a, 2010), distant from dependent human communities.

Vors and Boyce (2009) reported that at least 34 of 58 major caribou and reindeer herds throughout Russia, Alaska, and Canada are currently declining. Especially in the Canadian central Arctic, numbers of barren-ground caribou have markedly decreased since the late twentieth century. For example, the Bathurst barren-ground herd was estimated at 472,000 ± 72,900 (± 95% confidence interval) caribou in 1986, slowly declined through the 1990s, and then more rapidly during the late 2000s (Figure 1; Gunn *et al.* 2008, Adamczewski *et al.* 2009). The June 2009 census of the Bathurst herd revealed 31,900 ± 10,900 animals, representing a decline of 70% in three years (Adamczewski *et al.* 2009). Although conditions for individual herds of caribou and reindeer are undoubtedly unique, a changing climate may be driving these declines at a large spatial scale (Gunn 2003, Vors and Boyce 2009).

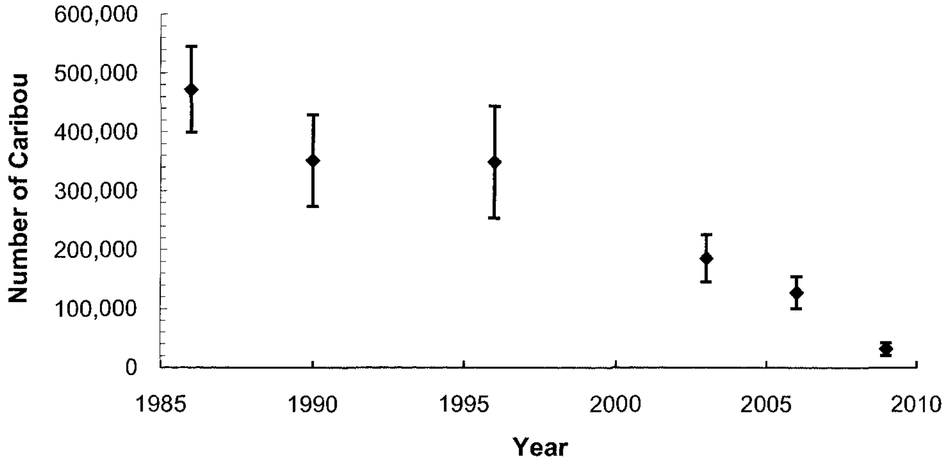

Figure 1. Population estimates and 95% confidence intervals for the Bathurst caribou herd. Values are based on calving ground photo surveys.

The recent precipitous decline of Bathurst caribou is consistent with that of the neighbouring Cape Bathurst and Bluenose-West barren-ground caribou herds. As with the Bathurst herd, these populations initially decreased at a steady rate of about 5% per year. At lower herd sizes, rates declined dramatically by up to 23% per year in the Bathurst herd. Late calving and low calf-cow ratios revealed that the caribou from these three herds were likely nutritionally limited from 2000 to 2006, and would have experienced a downward trend from natural factors alone (J. Nagy, Government of the Northwest Territories - Department of Environment and Natural Resources, unpublished data). Recent improvements in body condition and calf-cow ratios suggest that environmental conditions for Bathurst caribou improved in 2007 to 2009; however, a more variable climate, and the overall trend towards warmer and wetter conditions could result in future declines (Adamczewski *et al.* 2009).

Although increases in temperature and precipitation have increased plant biomass on the Bathurst range, forage quality has generally declined. On the summer range, an increase in mean foliage biomass over the last half of the 20th century is contrasted with a general decline in leaf nitrogen, an index of forage protein content (1985 - 1996, Adamczewski *et al.* 2009). Furthermore, lichen-rich habitats, vital to caribou during winter, have decreased largely due to increases in forest fires, which are shown to correlate with an increase in mean summer (June 1 - September 30) temperature over the Bathurst winter range (1959 - 2006, Chen *et al.*, Natural Resources Canada - Canada Centre for Remote Sensing, unpublished manuscript). Also, warmer winter temperatures have caused denser and harder snowpacks. Such unfavourable snow and ice conditions decrease the accessibility of lichen mats for caribou (Bergerud 1974, Thomas *et al.* 1998). Of greater concern, warmer winters can result in an increase in the frequency of freezing-rain events that lock lichen pastures under impenetrable layers of ice. The mobility of Bathurst caribou to relocate to other areas of the winter range may dampen the effects of localised forage restriction via extreme winter-weather events. However, Chen *et al.* (Natural Resources Canada - Canada Centre for Remote Sensing, unpublished manuscript) revealed increasing ice layers in snow in association with a warming climate across the range of the Bathurst herd, 1960 - 2006.

Considering the recent declines in the numbers of Bathurst caribou, an examination of the combined effects of seasonal limiting factors is necessary for developing effective range or caribou management practices. If the rate of climate warming continues, as predicted, the frequency and severity of fire in northern forests will increase (Stocks *et al.* 1998). Although increased precipitation during summer could compensate for the effects of hotter temperatures on the fire regime (Thomas 1998b), current models suggest that high rates of burning will likely continue to consume even greater areas of forested habitat that serves as winter range (McCoy and Burn 2005). Furthermore, a changing climate may result in heavier snowfall and more frequent ground-icing (Brotton and Wall 1997), thereby compounding the effects of fire-induced limitations on forage availability. Given the current consensus on global climate change (IPCC 2007) and simultaneous declines of *Rangifer* herds across the circumpolar north (Vors and Boyce 2009), increased understanding and awareness of the processes that affect Bathurst caribou on the winter range are both vital and timely.

STUDY OBJECTIVES

To assess ecological factors affecting the distribution of Bathurst caribou during winter, I examined the use of winter range at multiple spatial and temporal scales. I used both field-based and remote-modelling techniques to evaluate the influence of ecological features such as lichen abundance and snow conditions on the occupancy of winter habitats. The global objective of the thesis was to identify areas on the winter range that were important to the persistence of the Bathurst caribou herd, and to provide insights into the significance of fire and snow on the forested ranges of barren-ground caribou in the Northwest Territories, Canada. Specifically, I addressed the following two research objectives:

1) assess the influence of forest stand attributes on foraging-site selection by Bathurst caribou during late winter; and
2) model resource selection by Bathurst caribou in the early- and late-winter seasons, focusing on differences in selection among individuals within the population.

THESIS ORGANISATION

This thesis is organised into two separate results chapters following this introduction. They are based on a hierarchical study design for understanding the foraging and distribution dynamics of Bathurst caribou on the winter range. The field-based study (Chapter 2) involved a survey of ecological conditions at experimental (i.e., observed caribou foraging) and control plots. Using these data, I identified habitat attributes that influenced selection of areas of winter range by caribou for foraging. At a broader spatial and temporal scale, I used 13 years of location data for Bathurst caribou to develop resource selection functions. Using these statistical models, I identified the combination of habitat attributes that best predicted the occurrence of a caribou across the early- and late-winter range (Chapter 3). The thesis concludes with a comparison of the results from both the fine- and landscape-level investigations, as well as a discussion of the management implications of my findings.

CHAPTER 2 - SELECTION OF FORAGING PATCHES BY BATHURST BARREN-GROUND CARIBOU DURING LATE WINTER

SUMMARY

I used an Information Theoretic Model Comparison (ITMC) approach to investigate the influence of forest stand attributes on the occupancy of winter habitats by Bathurst caribou (*Rangifer tarandus groenlandicus*) in the Northwest Territories, Canada. I used field data describing forest stand and understory attributes to develop multinomial regression models that predicted feeding-site selection of Bathurst caribou on the winter range. Eight models were compared using Akaike's Information Criterion (AIC). These analyses identified a combination of ground cover type and tree volume (i.e., stand basal area) as best able to describe the observed selection of feeding sites. An observed increase in the percent ground cover of lichen had a positive influence on site selection, while an increase in the percent rock cover and basal area of conifer trees had a negative influence on selection of feeding sites by caribou. The most parsimonious regression model predicted with an accuracy of 87% whether or not Bathurst caribou foraged at a patch of winter range habitat. Lastly, I used equations developed by Moen *et al.* (2007) to determine the biomass of fruticose lichens on experimental and control sites classified as unburned. My data indicate that fruticose lichen biomass on the winter range of Bathurst caribou is high compared to winter habitats of caribou in Alaska and the Yukon Territory, and falls in the general range of lichen values reported for the more easterly Beverly herd, as well as portions of Saskatchewan, Manitoba, and Ungava. Overall, the analyses of feeding-site selection suggest that Bathurst caribou forage in areas with a high-percentage ground cover and a high biomass of lichen, and that future increased incidence and severity of forest fires could cause a temporary decrease in the winter habitat available to the herd.

INTRODUCTION

Scenarios depicting future climates for northern latitudes predict that warmer annual temperatures and drier summer weather may lead to an increased frequency and severity of forest fires (Rupp *et al.* 2006), as well as deeper and denser snowpacks, with an increase in severe winter-weather events (Vors and Boyce 2009). In addition, climate-induced increases in the abundance of vascular plants will likely result in declining macrolichen biomass in subarctic ecosystems (Cornelissen *et al.* 2001). Such conditions could substantially alter both the distribution and the accessibility of winter habitat for barren-ground caribou. From a management perspective, it is crucial to have an understanding of what effect, if any, a change in the amount or connectivity of lichen-rich habitat may have on the current distribution and foraging ecology of caribou.

At least 34 of 58 major *Rangifer* herds throughout Russia, Alaska, and Canada are currently declining in numbers (Vors and Boyce 2009). In particular, populations of barren-ground caribou in the Canadian central Arctic have markedly decreased since the late 20th century. For example, the Bathurst barren-ground herd was estimated at 472,000 ± 72,900 (± 95% confidence interval) caribou in 1986, slowly declined through the 1990s, and then more rapidly during the late 2000s (Figure 1; Gunn *et al.* 2008, Adamczewski *et al.* 2009). The June 2009 photo survey of the Bathurst herd provided an estimate of 31,900 ± 10,900 caribou, representing a decline of 70% in three years (Adamczewski *et al.* 2009). In addition to the rapid decline in numbers of caribou, potential shifts in their geographical distribution threaten northern communities with strong cultural and subsistence ties to the land. A further reduction in the availability or quality of forage could cause herds to adopt an alternative winter range (Joly *et al.* 2009a, 2010), distant from dependent human communities.

The influence of forage type and snow conditions on the selection of winter feeding sites by barren-ground caribou has been relatively well studied. Most literature suggests that caribou prefer mature, forested habitat with abundant mat-forming lichens (Scotter 1964, Kelsall 1968, Klein 1982). These authors believe that fire has a negative effect on caribou habitat, due to the slow recovery time of terricolous (ground-dwelling) lichens that form the majority of a caribou's diet during winter (60 - 80%; Scotter 1964, Kelsall 1968, Klein 1982, Fleischman 1990, Joly *et al.* 2003). Although researchers have noted that caribou sometimes forage in recently burned habitats (Johnson and Rowe 1975, Joly *et al.* 2003), they are mostly observed to avoid these areas in favour of older, lichen-rich communities (>55 years of age; Klein 1982, Thomas *et al.* 1996, Joly *et al.* 2003, 2009a). Lichen species preferred by caribou (e.g., *Cladina rangiferina*, *C. mitis*) are associated with late-successional seral stages in boreal forests (Maikawa and Kershaw 1976), and in the short term are lost following fire (Klein 1982, Thomas *et al.* 1996; Joly 2003, 2007a, 2009a).

In addition to a high biomass of terricolous lichens, mature stands of winter range generally yield more favourable snow conditions compared to younger stands (Thomas *et al.* 1998), allowing caribou to access lichen mats while expending less energy (Pruitt 1959, Skogland 1978, Fancy and White 1985). When snow is particularly deep or hard, the amount of energy required to excavate a feeding crater increases substantially, decreasing the nutritional gain from ingesting lichens (Fancy and White 1985, Russell *et al.* 1993, Brotton and Wall 1997). Snow cover can also affect caribou at larger spatial and temporal scales (Turney and Heard 1991, Russell *et al.* 1993, Thomas *et al.* 1998), even where snow is not particularly deep. The Beverly and Porcupine herds (*R. t. groenlandicus* and *R. t. granti*, respectively), for example, generally occupy areas that will later support greater snow accumulation early in the winter, before heavy snowfall impedes movement and foraging (Turney and Heard 1991, Russell *et al.* 1993, Thomas 1998b, Thomas *et al.* 1998), and Bluenose caribou use areas of the winter range at lower elevations that are characterised by lower snow depth and hardness (Carruthers *et al.* 1986).

I assessed the influence of forest stand attributes on the occupancy of winter habitats by a population of barren-ground caribou. I focused sampling and analysis on components of caribou habitat that were related to vegetation dynamics following wildfire. Between 2008 and 2009, I collected forest stand and understory data at habitats used by caribou, as well as paired control sites on the winter range of the Bathurst herd, located in the Northwest Territories, Canada. I used multinomial logistic regression and an Information Theoretic Model Comparison (ITMC) approach to identify factors associated with the use of forest patches by caribou as foraging habitat. I present these findings in the context of other populations of migratory caribou experiencing changing fire dynamics and range quality.

STUDY AREA

I investigated winter range habitat for the Bathurst caribou herd across a broad area north and northwest of Yellowknife, Northwest Territories, Canada. Sample sites were dictated by locations of collared caribou monitored during February and March of 2008 and 2009. Historical boundaries of the winter range were approximately delineated by Territorial borders to the north and east, and by Great Slave Lake and Great Bear Lake to the south and northwest, respectively; however, the distribution of Bathurst caribou has extended as far south as northern Saskatchewan (Figure 2; Gunn *et al.* 2002).

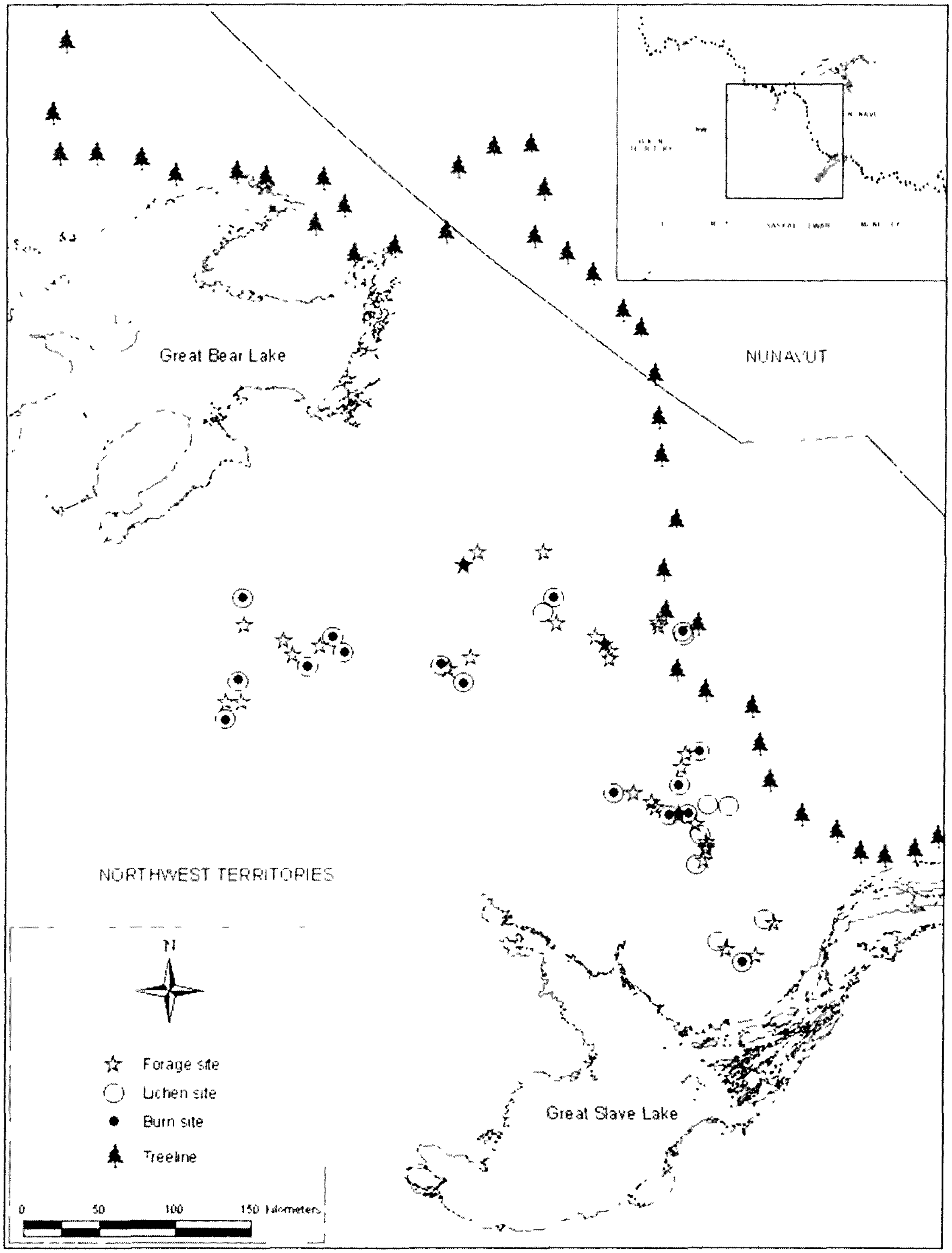

Figure 2. Locations of field sites investigated during late winter and summer (2008 - 2009) on the winter range of the Bathurst caribou herd in the Northwest Territories. Treeline represents the northern extent of forested habitat.

The winter range of the Bathurst herd spans both Taiga Shield and Southern Arctic ecozones, which are divided by the northern treeline (Ecological Stratification Working Group 1996). Above treeline, lichen barrens and graminoid-tundra and dwarf-shrub communities characterise most of the caribou summer range, as well as portions of the winter range. Below treeline, vegetation on the winter range is characterised by northern boreal forest ecosystems where dominant tree and shrub species include black spruce (*Picea mariana*), white spruce (*P. glauca*), jack pine (*Pinus banksiana*), willow (*Salix*) and blueberry/cranberry (*Vaccinium*) species. Gently rolling hills, punctuated by numerous small lakes and eskers, are visible across the landscape, and are overlain by discontinuous permafrost (Walton 2000). The climate reflects that of the semi-arid Canadian continental interior. Temperatures often fall below -30°C in winter, while average summer highs are 10°C (Walton 2000). Annual snowfall is approximately 150 cm with accumulations reaching maximum depths in late winter and on southeastern portions of the winter range (Gunn *et al.* 2002).

METHODS

Sample Design and Field Methods

I premised sample design and resulting field methods on the comparison of three treatment types: forest sites used by caribou (n = 33), paired control sites of similar vegetation classification (i.e., random lichen-bearing habitats, n = 22), and burned (≥20 and ≤40 years post-fire, GNWT - RWED 2002, n = 20) habitats where caribou were absent during late winter. I defined a foraging site as a collection of feeding craters occupying a plot of forest (also referred to as patches henceforth). Likewise, control sites consisted of forest stands where caribou did not feed. Caribou occupied less than 1% of burned sites that

I investigated, allowing me to justify the use of burned sites with no documented feeding activity as controls. The age class for burned habitat reflected the post-fire interval at which lichen-bearing vegetation communities were assumed to be unproductive caribou habitat (Klein 1982, Joly *et al.* 2003). Foraging sites were chosen based on recent locations of collared caribou. Control sites consisted of random plots of adjacent lichen-bearing and burned habitat near lakes that were within 17.5 km of the paired foraging site (Figure 3). The acceptable radius for sampling random lichen-bearing and burned control sites was defined by the average distance collared caribou move in a week (Gunn *et al.* 2002) during late winter (February - March). By using this radius to guide my selection of control plots, I assumed that these sites were within a distance that was accessible to caribou, but that caribou chose to occupy the paired foraging site instead. Based on my observations of the Bathurst winter range, there is a high heterogeneity of vegetation types within the 17.5-km buffer. This phenomenon should increase the odds of a caribou travelling farther to reach optimal foraging habitat, as well as the likelihood of a caribou using both the lichen-bearing and burned control sites.

During February and March of 2008 and 2009, I used a small fixed-wing aircraft to locate areas on the Bathurst winter range where caribou were observed foraging and not (i.e., controls). The primary purpose of these investigations was to confirm caribou activity at experimental sites and the absence of caribou at control sites (n = 75 total sites). Upon landing at 27 sites, I measured snow depth, density, and hardness using a ruler, cylinder of known volume, and a homemade ramsonde penetrometer (Skogland 1978) at three randomly selected undisturbed and open locations.

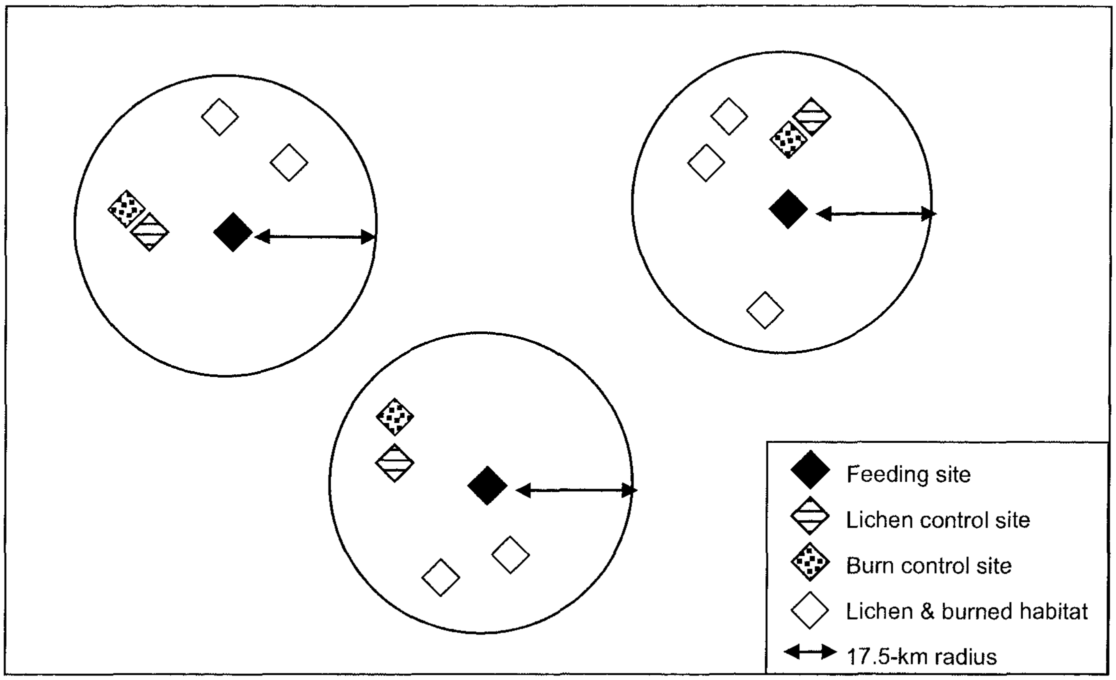

Figure 3. Sampling design used to investigate feeding and control sites on the Bathurst winter range. Feeding sites showed evidence of foraging by caribou. I randomly selected control sites from nearby lichen-bearing and burned habitats where caribou did not feed. Control sites consisted of adjacent 0.09-ha plots of lichen-bearing and burned habitat that fell within a 17.5-km radius from the paired feeding site.

During July and August of 2008 and 2009, I revisited all sites and documented lichen diversity and abundance, as well as forest stand attributes that may have influenced the distribution of caribou relative to forage availability. Specifically, I measured the following: percent ground cover of lichen; volume of terrestrial lichen; occurrence of bryophytes, shrubs, and graminoids; tree and shrub cover; canopy closure; and stand age. Each foraging and control site that I investigated was approximately 0.09 hectares (30 m x 30 m), representing the minimum size of a foraging area noted during initial field investigations of the Bathurst winter range (February - March 2008). At each foraging and control site, I flagged seven, 30-m transects occurring at 5-m intervals perpendicular to the baseline transect (Figure 4).

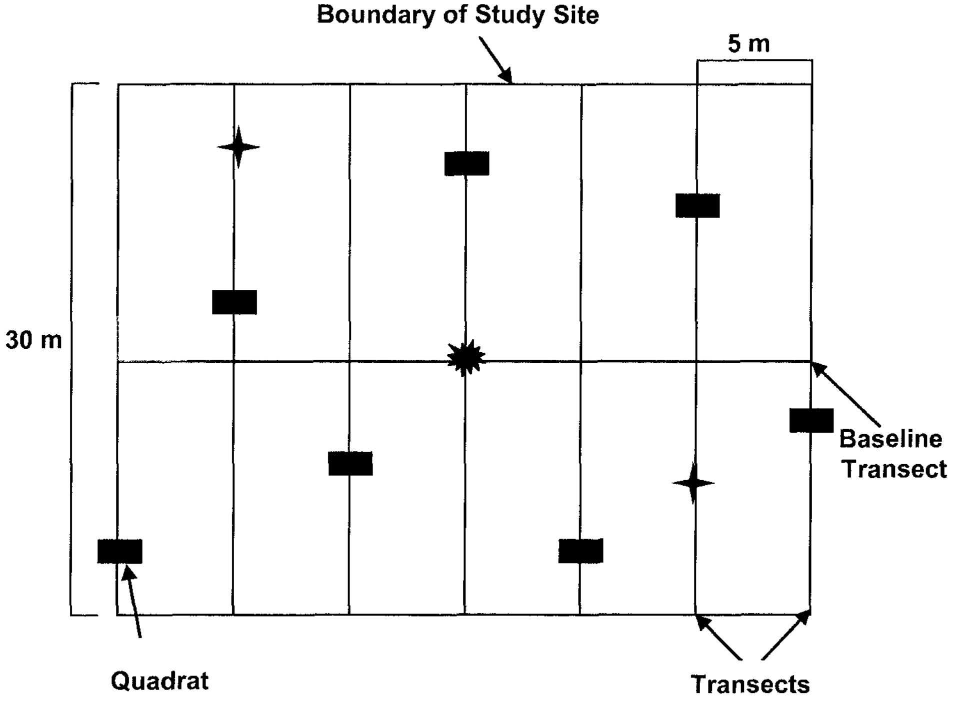

Figure 4. Sampling scheme for summer vegetation inventories. I randomly sampled seven quadrats with a 50 x 50-cm, 16-point frame to determine the abundance and cover of terrestrial lichen (■). I measured canopy closure and tree cover from two random locations occurring on transects two and six (✦), and I measured shrub cover from a 5.64-m radius plot at the centre of the site (✸).

I used a 50 x 50-cm point frame with 16 pins to determine the volume of terrestrial lichen taxa at seven randomly selected quadrats at each study site. Quadrat sampling for volume required that observations were independent, the area sampled was known, and the organisms were relatively immobile (Higgins *et al.* 2005). In order to meet the assumption of independence, eliminate bias, and ensure a representative measurement, I used a systematic random sampling design to mark one location per transect for quadrat sampling. At each pin on the point frame, I recorded the species (or at least genus) and height of lichen or other ground cover. I later used equations developed by Moen *et al.* (2007) to estimate the biomass of fruticose lichens at experimental and control study sites classified as unburned. I categorised percent ground cover of vegetation into species and groups based on relevance to caribou foraging ecology and reliability of identification in the field (Holleman and Luick 1977, Thomas *et al.* 1984, 1996, Russell *et al.* 1993). Specifically, I identified five taxa of lichen found in abundance on the winter range of barren-ground caribou including *Cladina*, *Cladonia*, *Cetraria*, *Peltigera*, and *Stereocaulon* species. I classified *Cladina stellaris*, *C. rangiferina* / *stygia*, *C. mitis* / *arbuscula*, *Cladonia uncialis*, *Cl. gracilis*, *Cetraria nivalis*, *Cet. cucullata*, and *Cet. islandica* / *ericetorum* as caribou forage lichens and all other taxa as non-forage lichens. I also considered graminoids, forbs, bryophytes, dwarf shrubs (<30 cm tall), litter, soil, and rock as independent groups of ground cover.

I used a systematic random design to select two locations within a site on transects two and six, and I measured crown closure and tree cover at each location. I obtained crown closure with a spherical densiometer. I then used a metric clear-glass prism with a basal area factor of four to separately estimate the basal area of surrounding coniferous and deciduous trees. Next, I used a fixed-area plot (5.64-m radius, 0.01 hectares) placed at the centre of the site to visually estimate percent cover of short and tall shrubs (≤2 and >2 m, respectively). In order to estimate stand age, I extracted wood core samples from several of the largest trees of each species within a site. Core samples were later analysed using dendrochronological techniques to determine the approximate stand age of each site.

Model Development and Assessment

I used multinomial logistic regression to contrast forest stand and understory attributes measured at sites used by caribou and paired control sites of similar vegetation classification, as well as burned habitats where caribou were absent. Choosing from the predictor variables identified at study sites, I developed a set of eight candidate models to assess the influence of percent cover of vegetation and associated forest stand attributes on feeding-site selection by caribou (Table 1). These models represented ecologically-plausible hypotheses that explained the distribution of barren-ground caribou across forest patches relative to their foraging ecology. Weather and time constraints prevented me from completing assessment of snow conditions at all study sites during the winter field seasons ($n = 27$ of 75 total sites). Also, we could not reliably age all stands. Thus, snow and stand age data were not considered within the model comparison procedure. Here, I assumed that lichen volume and cover served as an appropriate proxy for stand age (Russell *et al.* 1993, Thomas *et al.* 1996). I used tolerance scores to assess excessive collinearity (threshold of ≤ 0.2) among the variables in each model (Menard 2001).

Adopting an ITMC approach for model selection, I used Akaike's Information Criterion (AIC_c) for small sample sizes (Anderson *et al.* 2000) to select the most parsimonious model of the candidate set. The 'best' model had the lowest AIC_c score. Also, I reported the ΔAIC and Akaike weights (w), which represented the difference in AIC_c values between each model and the lowest ranked model, and the approximate probability that a particular model was the best in the candidate set, respectively. One of the main criticisms of the ITMC method is that it allows for too many models to be tested (Guthery *et al.* 2005). I avoided this problem by limiting the number of competing hypotheses to eight.

Table 1. Candidate models for predicting feeding sites used by Bathurst caribou during late winter (2008 - 2009).

Model Theme	Model Parameters
Lichen volume + Forest understory	Volume of *Cladina*, *Cladonia*, *Cetraria*, and *Stereocaulon* species; % cover of moss and litter
Percent lichen cover + Forest understory + Tree cover	% cover of lichen, moss, litter, and rock; basal area of conifers
Lichen volume + Forest understory + Tree cover	Total lichen volume; % cover of shrubs, moss, litter, and rock; basal area of conifers
Lichen volume + Forest understory (short shrubs only) + Tree cover	Volume of *Cladina mitis*, *C. rangiferina*, *Cetraria nivalis,* and *Stereocaulon* species; % cover of short shrubs, moss, litter, and basal area of conifers
Percent lichen cover + Forest understory + Forest canopy	% cover of lichen, shrubs, moss, litter, and rock; % canopy closure
Lichen volume + Forest understory + Forest canopy	Total lichen volume; % cover of shrubs, moss, litter, and rock; % canopy closure
Percent lichen cover + Forest understory + Tree cover + Forest canopy	% cover of lichen, moss, litter, and rock; basal area of conifers; % canopy closure
Full model	Total lichen volume; % cover of lichen, shrubs, moss, litter, and rock; basal area of conifers; % canopy closure

I used the receiver operating characteristics (ROC) score to assess the ability of the model to differentiate between sites classified as used and random. The area under the ROC curve (AUC) is useful for determining predictive accuracy when true presence and absence data are available (Fielding and Bell 1997). The AUC is the proportion of correctly and incorrectly classified cases when presence is predicted across the entire range of probability thresholds (0 to 1, Fielding and Bell 1997). AUC values of 0.5 indicate that a model has no predictive ability to discriminate beyond random assignment of cases, and a value of 1.0 indicates that a model is a perfect predictor. Values ranging between 0.7 and 0.9 suggest that the model possesses good discriminatory ability (Fielding and Bell 1997). I used 95% confidence intervals to assess the relative strength of selection or avoidance for each covariate in the models. Covariates with confidence intervals that did not overlap zero were considered significant predictors of the distribution of barren-ground caribou across forest patches relative to their foraging ecology. I used odds ratios to interpret the effect of each covariate on the differentiation of site types. In order to provide a relative measure of habitat features not included in the models, I used 95% confidence intervals to test for differences in mean stand age and snow conditions between used and control sites. All statistical analyses were completed using Stata (ver. 9.2, StataCorp LP, 2006).

RESULTS

Stand Attributes

I sampled 75 sites over two winter and summer field seasons. Of these sites, 33 showed evidence of caribou foraging, 22 were random lichen-bearing habitats, and 20 were random burned habitats (Appendix B). During 2009, snow depth at used and random lichen-bearing habitats averaged 56.6 ± 4.6 (± 95% confidence interval) and 59.3 ± 3.6 cm, respectively. Contrary to my hypothesis, snow hardness and snow density were slightly greater at used (0.158 ± 0.016 g/cm^2 and 0.222 ± 0.034 g/cm^3) than at random (0.141 ± 0.016 g/cm^2 and 0.218 ± 0.016 g/cm^3) sites (Figure 5). Snow conditions at sites used by caribou differed significantly between years. Average snow depth was 24.7% higher in 2009 than 2008 (56.6 ± 4.6 cm versus 45.4 ± 2.2 cm, respectively); however, both snow hardness and snow density were significantly lower in 2009 than in 2008 (Figure 5).

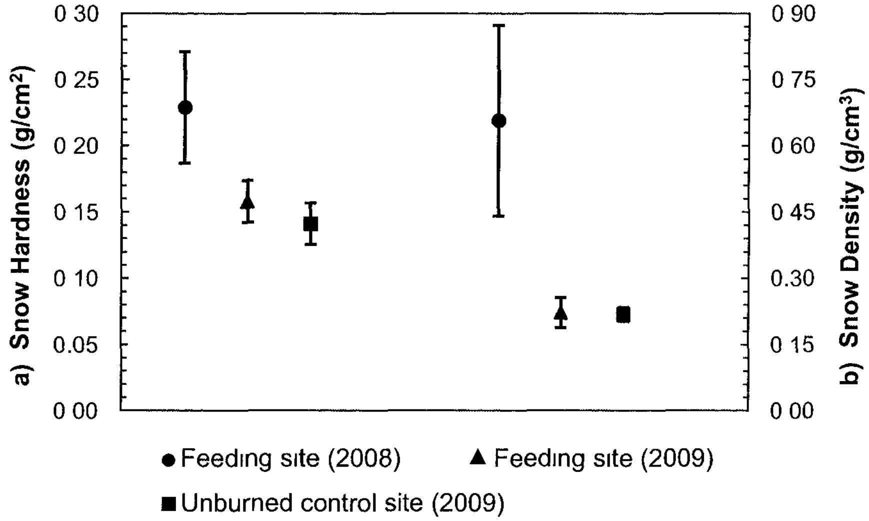

Figure 5. Mean (± 95% confidence intervals) a) snow hardness and b) snow density at caribou feeding sites (n = 5 in 2008, n = 11 in 2009) and random sites classified as unburned (n = 11 in 2009) on the Bathurst winter range.

Eleven distinct species of ground-dwelling fruticose lichens and eight types of ground cover were regularly observed at both feeding and control sites. Arboreal lichens (*Bryoria* species) were also present in some areas, but they were not prevalent enough to be included in the analysis. Percent cover and volume of lichens were greater at feeding sites than at random lichen-bearing and burned sites (Figure 6). *Cladina* species such as *C. mitis* and *C.*

rangiferina were the most prevalent at used sites, averaging 27% and 18% of total lichen volume, respectively (Figures 7, 8). *Stereocaulon* species and *Cetraria nivalis* were also common. In contrast, control sites classified as unburned had a greater percent cover of moss, grass, and forbs than feeding sites (Figure 9). Burned sites were characterised by a low biomass and cover of ground lichens (Figure 6), as well as a comparatively high percentage of ground cover of litter and rock (Figure 9).

Biomass of fruticose lichens did not differ significantly between used and random sites classified as unburned, perhaps due to the past foraging as observed at most feeding sites. The average biomass of fruticose lichens at feeding sites was 241 ± 34 g/m^2 (2412 ± 338 kg/ha), compared to 252 ± 37 g/m^2 (2516 ± 370 kg/ha) at unburned controls.

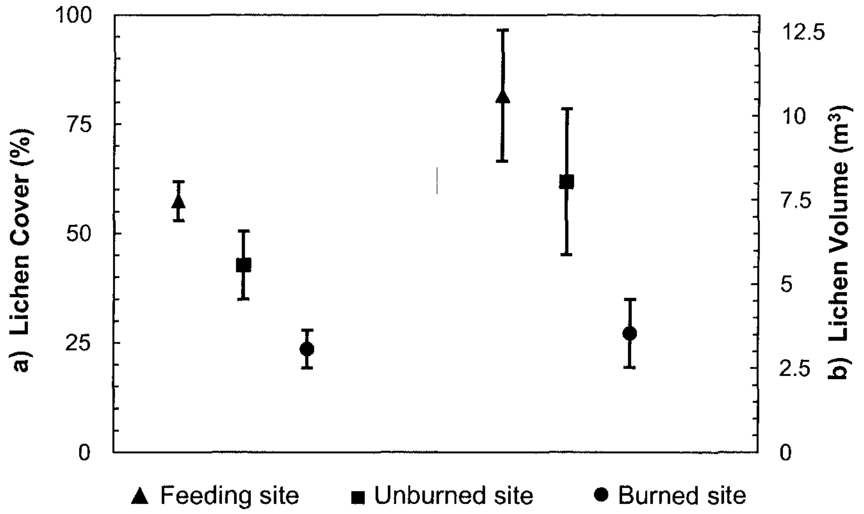

Figure 6. Mean (± 95% confidence intervals) a) lichen cover and b) lichen volume at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008 - 2009).

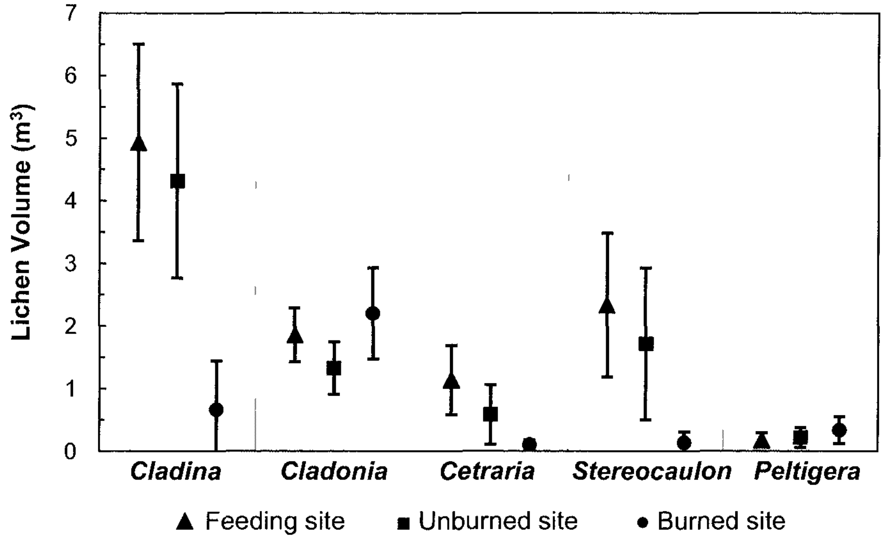

Figure 7. Mean (± 95% confidence intervals) volume of lichen taxa at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008 - 2009).

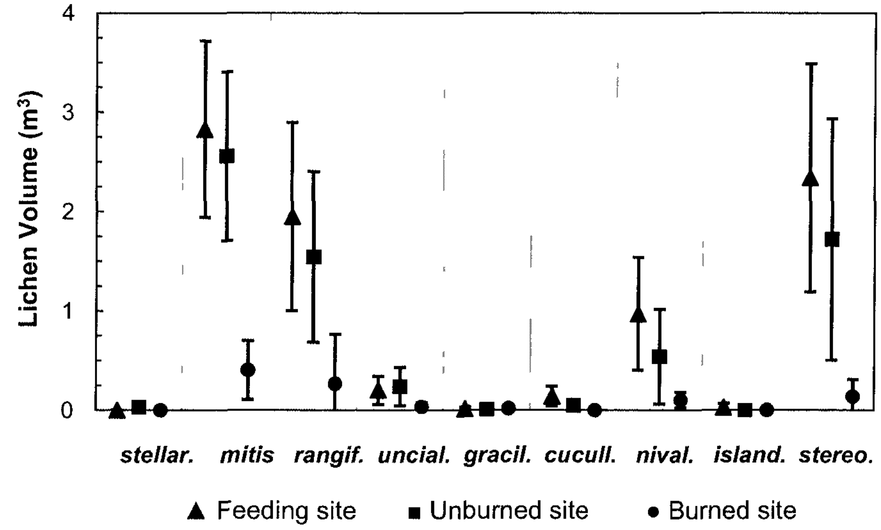

Figure 8. Mean (± 95% confidence intervals) volume of lichen species at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008 - 2009). Lichen species, as listed from left to right: *Cladina stellaris*, *C. mitis*, *C. rangiferina*, *Cladonia uncialis*, *Cl. gracilis*, *Cetraria cucullata*, *Cet. nivalis*, *Cet.islandica*, and *Stereocaulon* species.

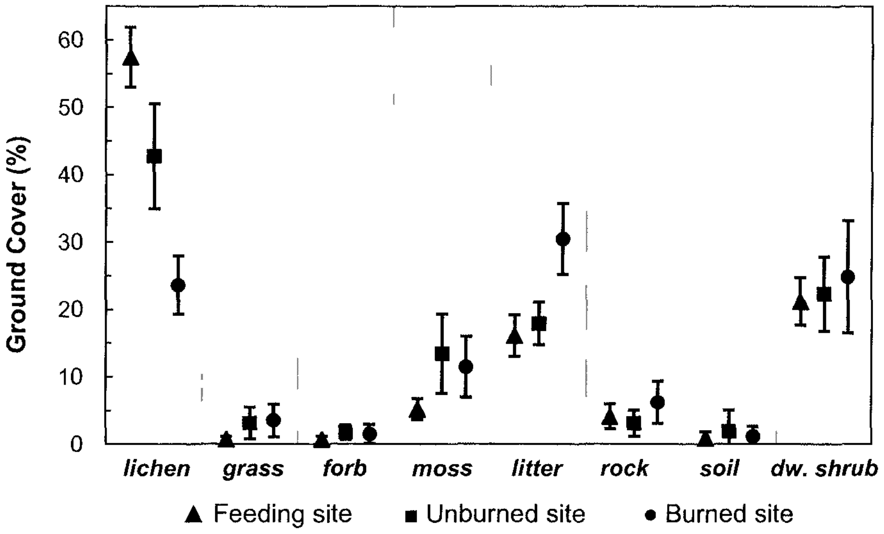

Figure 9. Mean (± 95% confidence intervals) percent ground cover of vegetation at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range (2008 - 2009). 'Dw. shrub' indicates dwarf shrub, which is classified as woody vegetation <30 cm tall.

Lichen biomass was not calculated for burned sites because these types of sites did not fit the assumption of a lichen-dominant habitat, which is required to compute reliable assessments of biomass (Moen *et al.* 2007). Instead, I relied on lichen volume as an indicator of lichen quantity in burned habitats. A comparison of all three site types showed that burned sites had the lowest amount of terrestrial lichen, most of which were *Cladonia* species, a genus not highly sought after by caribou (exceptions include *Cladonia uncialis* and *Cl. gracilis*, Russell *et al.* 1993) (Appendix B).

Total shrub cover was less on feeding sites than on paired unburned and burned controls (1.6 ± 1.8%, 5.7 ± 3.4%, and 6.5 ± 5.9%, respectively), predominantly due to a low cover of short shrubs in areas used by caribou. Basal area of conifer trees was also less on used sites than on lichen-bearing control sites (6.4 ± 2.0% and 11.7 ± 3.9%, respectively), but higher than values for burned sites (4.7 ± 2.1%). Similarly, canopy closure was lower at feeding sites than at unburned control sites, ranging from an average of 17.5 ± 5.6% at used sites to 27.4 ± 8.8% at random lichen sites. The trees at feeding sites (n = 13) were older than those at lichen-bearing control sites (n = 8). The average stand age of a feeding site was 143 ± 35 years compared to 96 ± 19 years for random sites in comparable habitat types. However, these differences were not statistically significant, perhaps because of the relatively small sample size (n = 75 sites for all attributes except snow and stand age) (Appendix B).

Model Fit

The most parsimonious multinomial logistic regression model used to describe selection of feeding sites by caribou contained predictors for basal area of conifers, percent ground cover of lichen, moss, litter, and rock (Table 2). The second ranked model differed by nearly three AIC points and included an additional variable for percent canopy closure. The best model had good discriminatory ability (AUC = 0.873). Variables that had a positive influence on feeding-site selection included percent ground cover of lichen, litter, and rock; basal area of conifers and percent ground cover of moss had a negative influence on feeding-site selection (Table 3). Burned sites were more likely to have a lower basal area of conifers and percent ground cover of lichens, with a higher percent ground cover of moss, litter, and rock. However, only lichen cover made a statistically significant ($\beta = 0.057 \pm 0.055$) contribution to the differentiation between feeding sites and unburned control sites; both lichen and rock cover had a significant ($\beta = 0.152 \pm 0.090$ and $\beta = -0.225 \pm 0.218$, respectively) effect in distinguishing feeding sites from burned sites (Table 3). The odds ratio implied that for every 1% increase in lichen cover, caribou were 15.2% more likely to use a known feeding site versus a burned site. Similarly, a 1% increase in lichen cover would raise the likelihood of a caribou choosing a known feeding site over a random unburned site by 5.7%.

Holding values for all other covariates in the best model at their mean (i.e., basal area of conifers and percent ground cover of moss, litter, and rock), I calculated the probability of a caribou choosing a known feeding site over both lichen-bearing and burned control sites as the percent ground cover of lichen increased (Figure 10). Relative to unburned areas, caribou were more likely to feed in a patch of forest when cover of lichen exceeded 43%. Similarly, these data suggest that caribou will occupy previously burned patches of forest when lichen cover is greater than 33%. Considering only the percent cover of lichen, caribou have a lower threshold for using burned sites compared to unburned sites where no signs of foraging were detected.

Table 2. Model-selection statistics for candidate models used to predict feeding-site selection by Bathurst caribou during late winter (2008 - 2009).

Model	Rank	Δ_{AICc}	w
Percent lichen cover + Forest understory + Tree cover	1	0.00	0.7720
Percent lichen cover + Forest understory + Tree cover + Forest canopy	2	2.97	0.1750
Percent lichen cover + Forest understory + Forest canopy	3	5.41	0.0516
Lichen volume + Forest understory	4	13.38	0.0010
Lichen volume + Forest understory + Tree cover	5	15.99	0.0003
Lichen volume + Forest understory + Forest canopy	6	17.49	0.0001
Lichen volume + Forest understory (short shrubs only) + Tree cover	7	19.60	<0.0001
Full model	8	53.25	<0.0001

Table 3. Selection coefficients for parameters in the best (Table 2) multinomial logistic regression model used to predict feeding-site selection by Bathurst caribou during late winter (2008 - 2009).

Feeding Sites vs. Unburned Control Sites (n = 75)

Model Parameters	β	SE	95% CI	Odds Ratio
Basal area of conifers	-0.071	0.054	-0.177 - 0.035	-7.1%
Lichen cover	0.057	0.028	0.002 - 0.112	+5.7%
Moss cover	-0.061	0.057	-0.173 - 0.051	-6.1%
Litter cover	0.180	0.043	0.096 - 0.264	+18.0%
Rock cover	0.003	0.067	-0.128 - 0.134	+0.3%
Constant	-1.710	2.076		

Feeding Sites vs. Burned Control Sites (n = 75)

Model Parameters	β	SE	95% CI	Odds Ratio
Basal area of conifers	0.022	0.088	-0.151 - 0.195	+2.2%
Lichen cover	0.152	0.046	0.062 - 0.242	+15.2%
Moss cover	-0.031	0.064	-0.156 - 0.094	-3.1%
Litter cover	-0.091	0.053	-0.200 - 0.013	-9.1%
Rock cover	-0.225	0.111	-0.443 - -0.007	-22.5%
Constant	-2.054	2.434		

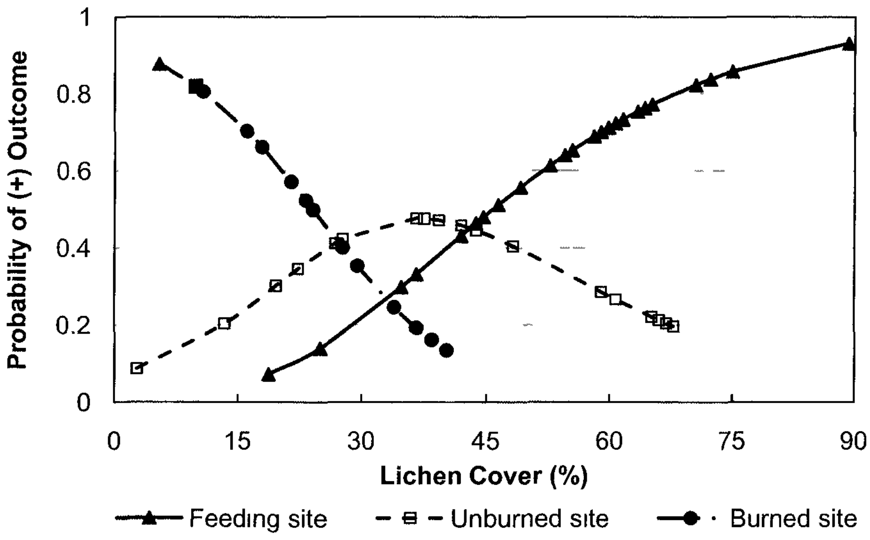

Figure 10. Predicted probability of a positive identification of forest stands, relative to the percent cover of lichens measured at three site types on the winter range of Bathurst caribou. Values for all other covariates in the model (i.e., basal area of conifers and percent ground cover of moss, litter, and rock) were held at their mean.

DISCUSSION

Most continental populations of caribou forage primarily on terricolous lichens throughout winter, focusing on fruticose species such as *Cladina rangiferina* and *C. mitis* (Pegau 1968, Russell *et al.* 1993, Thomas *et al.* 1996, Joly *et al.* 2007b), and choosing mature forested habitats over recently burned areas of winter range (Klein 1982, Thomas *et al.* 1996, Joly *et al.* 2003, 2007a). My results agree with those findings. With few exceptions (Joly *et al.* 2007a), however, most studies have failed to investigate habitat selection at a geographic scale that is representative of the movement patterns of caribou during the winter. Rather, studies of the foraging ecology of barren-ground caribou have focused on quantifying general winter range conditions (Russell *et al.* 1993, Jandt *et al.* 2008) and feeding habits (Thomas and Hervieux 1986, Russell *et al.* 1993), examining patterns of habitat use (Carruthers *et al.* 1986), assessing feeding-site selection within a foraging patch (Saperstein 1996), and comparing site conditions and caribou use at burned and unburned habitats across the seasonal range (Thomas *et al.* 1996, Joly *et al.* 2010). Here, I have expanded upon those works by quantifying the influence of lichen cover and associated stand characteristics on the selection of feeding sites by Bathurst caribou with respect to paired random unburned and burned sites at a geographic scale that is equivalent to the weekly movement patterns of the herd.

Selection of Feeding Sites by Caribou

Using data collected over two successive winter and summer field seasons, I developed a model to predict feeding-site selection by Bathurst caribou on late-winter range. This model contained covariates for basal area of conifers and percent ground cover of lichen, moss, litter, and rock. Predictive accuracy of the model was relatively high (87.3%), but may have improved with the inclusion of other ecologically-plausible variables. For example, snow conditions, particularly snow depth and snow hardness, are important to caribou when selecting an area to forage during winter (Pruitt 1959, Carruthers *et al.* 1986, Tucker *et al.* 1991, Saperstein 1996). Although average snow depths across the Bathurst winter range were considered low in 2008 and 2009 (45.4 ± 2.2 and 56.6 ± 4.6 cm, respectively) compared to previous years (Adamczewski *et al.* 2009), these values still approach thresholds of maximum snow depth for effective cratering by caribou (50 - 80 cm, Pruitt 1959). In fact, numerous studies have shown that caribou choose to forage at sites yielding lower snow depth, snow hardness, or both, within a habitat (LaPerriere and Lent 1977, Cichowski 1993, Saperstein 1996, Johnson *et al.* 2001). Research on the adjacent Bluenose caribou herd (*R. t. groenlandicus*) revealed that caribou disproportionately occupied areas with lower snow depth and snow hardness, compared to unoccupied habitats across their winter range (Carruthers *et al.* 1986). Likewise, the Beverly and Porcupine herds generally inhabit areas that will later support greater snow accumulation early in the winter, before heavy snowfall impedes movement and foraging (Turney and Heard 1991, Russell *et al.* 1993, Thomas 1998b, Thomas *et al.* 1998).

Considering the importance of lichens on feeding-site selection by caribou, the lack of difference in biomass of fruticose lichens at used and random sites classified as unburned suggests that my data for lichen abundance underestimated the pre-foraged ground cover and height of lichen at feeding sites. Although I rarely observed evidence of caribou trampling or cropping the entire lichen thallus, caribou may have reduced the lichen mat through ancillary digging and pawing actions while cratering (Pegau 1969). If present, this bias would force me to test a more conservative model that reduced the likelihood of differentiating foraging sites from random controls and surveyed burns. Alternatively, one could use exclosures to quantify the long-term effects of grazing on lichen abundance.

Influence of Ecological Factors on Site Selection

Past research on the winter ecology of barren-ground caribou suggests that herds prefer areas with a high abundance of fruticose lichen, low snow depths, and access to small lakes (Klein 1982, Carruthers *et al.* 1986, Thomas *et al.* 1996, Joly *et al.* 2010). Although the role of fire is widely debated, most researchers agree that a lack of available forage caused by frequent fire activity can influence the distribution dynamics of caribou on forested winter range (Klein 1982, Thomas *et al.* 1996, Joly *et al.* 2003, 2007a). The most notable research on caribou winter range in northern Canada consisted of a seven-year comprehensive study of the more easterly Beverly herd. Thomas *et al.* (1996) reported that lichens preferred by caribou required 80 - 150 years to reach maturity, and that an abundance of these lichens may be a primary reason that caribou favour stands that are 151 - 250 years of age. Within the context of these works, my results add to the understanding of feeding-site selection on a small spatial scale by illuminating differences between used and comparable random and burned habitats. Furthermore, I show that percent ground cover of lichen may be a primary factor driving the selection of feeding sites by Bathurst caribou. However, the discrepancy in lichen thresholds when comparing foraged to burned and unburned sites (Figure 10) suggests that other factors influence the foraging decisions of caribou. For example, a lower volume of trees on burned sites relative to feeding sites (Appendix B) may provide some ecological gain for caribou related to travel or predator detection.

My model of feeding-site selection indicates that Bathurst caribou chose to forage in areas that are characteristic of mature stands of spruce. Used sites displayed a high percentage of ground cover of lichen and a low volume of conifer trees compared to control sites. Feeding sites were also older than random sites in comparable habitats (143 ± 35 years versus 96 ± 19 years, respectively). These findings are in accordance with studies of winter foraging ecology of caribou across North America. For example, Thomas *et al.* (1996) reported that caribou favoured stands with a high abundance of terricolous lichens, particularly *Cladina mitis* and *Cetraria nivalis*, and generally occupied forests older than 150 years. Likewise, Saperstein (1996) found that Alaskan caribou (*R. t. granti*) disproportionately cratered at sites yielding high lichen to moss ratios, and Joly *et al.* (2003) determined that caribou in the Nelchina Alaskan herd avoided burned areas <50 years old.

Although feeding-site selection does not appear to be linked to specific species of terrestrial lichen, caribou in this study selected habitats with a greater percent ground cover and volume of certain fruticose lichens, suggesting their importance to the Bathurst herd during late winter. The majority of lichens at used sites were *Cladinas*, with *C. mitis* and *C. rangiferina* exceeding all other species in cover and volume except *Stereocaulon* species (Appendix B). *Cetraria nivalis* was another biologically significant species. This coincides with Thomas *et al.* (1996) findings that Beverly caribou responded most to the forage lichens *Cladina mitis* and *Cetraria nivalis*, and to a lesser extent, *Cladina rangiferina.*

Below-average snow depths during 2008 and 2009 (Adamczewski *et al.* 2009) may have masked the effect of snow on the selection of feeding sites by caribou. Frid (1998) identified a similar phenomenon regarding crater-site selection by woodland caribou in the Yukon Territory, likely due to the shallow snowpack of the study area (31.5 cm ± 5.8 SD).

Alternatively, it is possible that caribou displayed a selection response to snow at a finer spatial scale than observed in this study. For example, Saperstein (1996) reported that snow depth and hardness were significant factors influencing the selection of feeding craters by Alaskan caribou. Although there were no significant differences in snow conditions between burned and unburned areas of Alaskan winter range, snow near feeding craters was often shallower and softer than in adjacent undisturbed areas. A second possibility is that caribou responded to snow conditions at a much larger spatial scale, as observed in studies of the winter ecology of the Beverly and Porcupine caribou herds (Russell *et al.* 1993, Thomas *et al.* 1996).

Importance of Lichen Biomass

There is increasing evidence that abundant lichen forage is an important determinant of caribou distribution on winter range (Klein 1982, Thomas *et al.* 1996; Joly *et al.* 2003, 2007a, b, 2010). In the absence of sufficient lichen forage, caribou herds may experience altered distribution patterns (Joly *et al.* 2003; 2007a, b; 2010) and in some cases declining recruitment (Skogland 1986). However, moderate lichen depletion has not been shown to affect caribou population dynamics in North America, except during unusually severe winters (Fleischman 1990). Until recently, the Beverly caribou herd maintained a high reproductive rate and fair body condition (Thomas and Kiliaan 1998) despite a high frequency of forest fires on their winter range (Scotter 1964, Miller 1976, Thomas 1991, Thomas and Kiliaan 1998). According to Fleischman (1990), depletion of lichens is mostly a concern on early-winter ranges, as lichen availability in late winter is typically low. In order to determine the amount of lichens sufficient to prevent significant fitness effects, one must take into account the availability of alternative forage, distribution of lichen habitats (i.e., foraging efficiency), abundance of lichens on non-traditional ranges, severity of snow conditions, and body condition at the onset of winter.

Although my data on lichen abundance fall short of a range-wide analysis, I was able to capture site conditions in traditional areas of the winter range used by Bathurst caribou. I employed equations developed by Moen *et al.* (2007) to determine the biomass of fruticose lichens (excluding *Stereocaulon* species) at experimental and control sites classified as unburned. My data indicate that the biomass of fruticose lichens on the winter range of Bathurst caribou is high (2464 ± 248 kg/ha) compared to winter habitats of caribou in Alaska and the Yukon Territory (Fleischman 1990, Russell *et al.* 1993), and falls in the general range of lichen values reported for winter habitats of the more easterly Beverly herd, as well as portions of Saskatchewan, Manitoba, Ungava, and Scandinavia (Table 4; Scotter 1970, Miller 1976, Gaare and Skogland 1980, Helle 1981, Crête *et al.* 1990, Thomas *et al.* 1996, Arsenault *et al.* 1997, Bergerud *et al.* 2008).

Differences in study design and sampling technique are inherent limitations when comparing data from multiple studies. My data are based on values of lichens from mature lichen-dominant communities (43 - 264 years old), while some studies report the mean value of lichen biomass from all community types. In addition, I separated the live portions of the lichen thallus from the base when measuring height values used to calculate biomass. I believe that this provides a more accurate depiction of the amount of lichen available to caribou for food and generates a more conservative measure of biomass. Furthermore, many researchers have included lichen biomass of *Stereocaulon* species in their assessments, while I did not.

Table 4. Lichen biomass measurements for select winter ranges of caribou and reindeer (*Rangifer tarandus*). Range types reported in the various studies included habitats used by caribou versus those not used by caribou, distinct age classes of habitat, lichen-dominated communities, heath forests, and all community types present. Thallus indicates whether or not the dead bases of lichen thalli were included in the biomass estimates.

Location	Herd	Range Type	Thallus	Biomass (kg/ha)	Reference
Northwest Territories	Bathurst	Used unburned forest	No	2412	This study
Northwest Territories	Bathurst	Random unburned forest	No	2516	This study
Northwest Territories	Beverly (west block)	All present	No	2594	Thomas *et al.* 1996
Northwest Territories	Beverly (east block)	All present	No	6250	Thomas *et al.* 1996
N. Saskatchewan	Beverly/Kaminuriak	Lichen-dominant	No	810	Scotter 1970
N. Saskatchewan	Kaminuriak	Lichen-dominant	Yes	5850	Miller 1976
N. Manitoba	Kaminuriak	Lichen-dominant	Yes	4270	Miller 1976
Ungava	Leaf River	Lichen-dominant	Unknown	1223	Crête *et al.* 1990
Ungava	George River	All present	Unknown	3170	Bergerud *et al.* 2008
N. Québec	George/Leaf River	Forests <30 years	No	530	Arseneault *et al.* 1997
N. Québec	George/Leaf River	All present	No	2800	Arseneault *et al.* 1997
N. Québec	George/Leaf River	Forests >90 years	No	8010	Arseneault *et al.* 1997
N. Québec	George/Leaf River	Lichen-dominant	No	5440	Arseneault *et al.* 1997
Central Yukon	Porcupine	All present	Yes	508	Russell *et al.* 1993
Central Alaska	Delta (traditional areas)	All present	Unknown	100 - 850	Fleischman 1990
Central Alaska	Delta (peripheral areas)	All present	Unknown	>2000	Fleischman 1990
Northwest Alaska	Western Arctic Herd	Used unburned forest	Unknown	3007	Joly *et al.* 2010
Northwest Alaska	Western Arctic Herd	Random unburned forest	Unknown	1260	Joly *et al.* 2010
Northwest Alaska	Western Arctic Herd	Random burned forest	Unknown	818	Joly *et al.* 2010
N. Finland	Reindeer	Heath forest	No	520	Helle 1981
Norway	Reindeer	Climax forest stands	Unknown	11000	Gaare and Skogland 1980

Based on estimates provided by Bergerud *et al.* (2008:166,495,497,500,501), my data for lichen abundance suggest that conditions on the late-winter range of Bathurst caribou may support a herd density of approximately 1 - 2 animals per km^2 in unburned areas. Considering that the area of mature winter range (i.e., not classified as post-fire) below treeline totals approximately 240,186 km^2, current lichen stores could support between 240,186 and 480,372 caribou. Given the number of ecological factors that are known to affect barren-ground caribou populations (e.g., weather, insects, plant phenology; Post and Stenseth 1999), this is a very simplistic index of population carrying capacity. Also, I did not perform a systematic sampling of lichen abundance across the entire winter range. Nonetheless, these estimates offer some insight on possible mechanisms for the recent decline of Bathurst caribou. A shortage of winter forage has not likely contributed to the decline of the herd, which peaked at a density of 1.83 ± 0.28 caribou per km^2 (472,000 ± 72,900 caribou) across the winter range in 1986. However, a more conclusive analysis of winter range conditions would account for the size and distribution of mature lichen communities, since spatial variation contributes largely to foraging efficiency (Fleischman 1990). Possible causes of the decline in numbers of Bathurst caribou include a deterioration in the quality of summer forage as well as a reduced time spent foraging due to insect harassment on the summer range, both likely driven by large-scale climatic factors (Gunn 2003). Population dynamics aside, a change in the spatial availability of caribou can have large implications for access by harvesters. My data suggest that wildfire can influence the distribution of caribou as they seek out individual stands or areas of the winter range with longer fire-return intervals and more abundant terrestrial lichen.

CONCLUSIONS

Specific habitat features such as lichen cover and stand age are important variables to consider when evaluating winter range for barren-ground caribou in the Northwest Territories. Bathurst caribou selected for mature habitats with a high percentage of ground cover of fruticose lichen and few or small conifer trees. Estimates of lichen biomass show that sufficient winter forage is present for the current population of Bathurst caribou; however, more frequent and severe wildfires resulting from climate warming (Stocks *et al.* 1998, Rupp *et al.* 2000, McCoy and Burn 2005) may temporarily reduce the quantity and quality (e.g., changes in the composition of lichen communities) of lichen resources available to caribou (Joly *et al.* 2007b, 2010). As demonstrated in other herds, such reductions could lead to declines in recruitment and body size of adult females (Skogland 1986), as well as altered distribution patterns (Joly *et al.* 2003; 2007a, b; 2010).

Although forage was the most important variable to explain feeding-site selection during winter in this study, the observed pattern of caribou distribution may actually be a product of numerous environmental and cognitive factors that vary from early to late winter, and at broader spatial scales. Confounding factors related to foraging conditions, but not quantified in this study, include: distribution of predators, snow conditions, and ease of mobility (e.g., steepness of terrain). A hierarchical analysis that examines foraging ecology at multiple spatial and temporal scales should be pursued in order to more fully understand the effects of lichen abundance and associated stand attributes on caribou distribution during winter (Johnson 1980, Johnson *et al.* 2001). Future research on the winter range ecology of the Bathurst herd should also take into account the distribution of mature lichen communities and the abundance of lichens on non-traditional and early-winter ranges.

CHAPTER 3 - SPATIAL AND TEMPORAL DISTRIBUTION DYNAMICS OF BATHURST BARREN-GROUND CARIBOU ON WINTER RANGE

SUMMARY

Scientists have not fully quantified the range-wide and long-term use of winter habitats by barren-ground caribou. Given the current consensus on climate change and likely increases in wildfire across northern forests, models quantifying patterns of habitat use by caribou can help direct management strategies by revealing important resources that may affect the persistence of a population. I used an Information Theoretic Model Comparison (ITMC) approach to investigate the influence of ecological variables on the distribution of Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) in the Northwest Territories, Canada, during winter. Specifically, I used logistic regression-based resource selection functions (RSFs) to model habitat selection by caribou on early- and late-winter range according to environmental variables related to snow cover, vegetation, fire history, and predation risk. I evaluated multiple sets of models constructed across years for all caribou (pooled models) and for individual caribou by season (early and late winter). Winter range habitats important to caribou were characterised by a high percentage of ground cover of lichen and herbaceous forage and a close proximity to lakes and rivers. The consensus among the pooled and individual models was that caribou avoided areas densely populated with burns; however, there was considerable use of habitats adjacent to the burn boundary. Also, the data documenting the distribution of caribou and burns suggested that some individuals used early-seral habitats. Disparate selection strategies among caribou highlight the importance of investigating both individual and global resource selection models. These results suggest

that at some spatial and temporal scales, barren-ground caribou of the Bathurst herd may be less averse to fire than previously thought.

INTRODUCTION

There is a long-standing and entrenched concern about the frequency of fire and the area of burned habitats on the winter range of barren-ground caribou (Clarke 1940). Early literature suggests that fire has a negative influence on caribou habitat, due to the slow recovery of mat-forming lichens (Scotter 1964) which constitute the majority of a caribou's diet during winter (60 - 80%; Scotter 1964, Kelsall 1968, Parker 1981, Klein 1982, Thomas and Hervieux 1986, Gauthier *et al.* 1989, Klein 1991, Jandt *et al.* 2003). Some researchers have argued that fire plays an important restorative role in boreal forests (Bergerud 1974, Miller 1976). These authors believe that fire destroys a minor amount of caribou habitat, but improves forests by maintaining heterogeneity within stands and across landscapes (Miller 1976, 1980).

Although fire may be necessary for the long-term productivity of lichen stands by eliminating competing vegetation (Klein 1982, Schaefer and Pruitt 1991, Sulyma and Coxson 2001), the short-term effects of fire can be negative for caribou (Scotter 1964, Kelsall 1968, Klein 1982, Thomas *et al.* 1996, Thomas and Kiliaan 1998, Thomas *et al.* 1998; Joly *et al.* 2003, 2007a, b, 2010). The post-fire period required for most forage lichens to attain a significant biomass exceeds 50 years, and the types of lichens preferred by caribou generally do not occur in the initial stages of succession (Maikawa and Kershaw 1976). The greatest abundance of forage lichens occurs 60 - 80 years following fire, when the *Cladina* species prevail in robust growth forms (Thomas 1998a).

Some researchers have posited that a graminoid-dominated diet, as opposed to a diet consisting predominantly of lichens, may be more optimal for overwintering *Rangifer* populations (Bergerud 1974, Heggberget *et al.* 2002); however, such claims are generally based on insular or non-migratory herds that are limited to confined winter grazing areas. Studies of winter habitat use by migratory herds of caribou have primarily shown an overwhelming avoidance of portions of the range consisting of early-seral forests (Thomas *et al.* 1996, Joly *et al.* 2003, 2007a). Use of burned habitats typically occurs on a limited temporal basis and as a means of accessing upland areas of unburned forest or during movements through large post-fire areas (Thomas *et al.* 1998).

Alternatively, an abundance of vascular forage available in burned habitats may attract caribou for brief periods such as during the early winter or spring when snow accumulations are low (Joly *et al.* 2003). Shallow and soft snowpacks during early winter enable efficient foraging and easy access to vegetation growing in depressions and lowland areas (Fleischman 1990). In addition, many wintergreen foods are higher in protein and minerals during early winter (Luick 1977, Fleischman 1990) especially when compared to the traditional winter diet of lichen. Recent studies of migratory caribou herds in Alaska revealed that use of burned habitats was greatest in early winter (November - December), likely due to the presence of early-successional graminoids and other vascular forage typically found in burns. When available, certain herbaceous and woody species (e.g., fireweed [*Epilobium augustifolium*], mountain cranberry [*Vaccinium vitis-idaea*], and labrador tea [*Ledum groenlandicum*]) are avidly sought by caribou (Scotter 1964, Kelsall 1968); however, their abundance and palatability decline in as little as two decades post-fire (Viereck and Schandelmeier 1980, Thomas and Kiliaan 1998).

Unfavourable snow conditions and a high density of dead, fallen trees have been suggested as deterrents to caribou movement and use of recent burns (Schaefer and Pruitt 1991). Immature stands typically yield deeper and denser snowpacks, as well as a greater accumulation of debris and a lower biomass of fruticose lichens compared to mature stands. Especially in interiors of burns, increased sun and wind usually result in higher snow density and a thicker layer of surface crust (Thomas *et al.* 1998). Although increased visibility and ease of movement in sparsely treed or open areas may prompt caribou to use burn perimeters as a movement corridor or for predator avoidance, interiors of burns are largely avoided by caribou on the winter range. For example, Joly *et al.* (2003) described the selection strategies of Nelchina caribou in Alaska as strongly averse to burned habitats, with core areas of burns being the most underutilized.

The effects of wildfire on the winter range ecology of caribou are complex and potentially wide-ranging (Klein 1982). Barren-ground caribou display variable responses to post-fire habitats across seasonal ranges, and a lack of understanding of these relationships limits predictions of the consequence of future climate-related events for populations of caribou. An increase in the frequency and severity of fire is predicted to impact northern landscapes across the winter ranges of barren-ground caribou herds (Rupp *et al.* 2006), potentially reducing the quantity and altering the distribution of lichen resources available to caribou (Cornelissen *et al.* 2001, Olthof *et al.* 2008). From a management perspective, it is crucial to have an understanding of what effect, if any, a change in the amount or connectivity of lichen-rich habitat may have on the current distribution and foraging ecology of the Bathurst herd.

I assessed the influence of ecological features on the occupancy of winter habitats by a population of barren-ground caribou. Considering the hypothesised influence of wildfire and snow on caribou distribution (Klein 1982, Schaefer and Pruitt 1991, Thomas 1991, Thomas *et al.* 1998; Joly *et al.* 2003, 2007a, 2010), I focused my analysis on forest stand attributes that are a result of fire history, as well as ecological parameters related to foraging efficiency during winter, such as snow cover and risk of predation. I hypothesised that Bathurst caribou would spend more time in herbaceous- and shrub-dominant habitats early in the winter, and that selection for lichen-rich areas would predominate in late winter, when vascular plants are less accessible and less nutritious. Alternatively, forage type may predominantly influence habitat selection early in the winter, whereas snow conditions become more important in late winter as forage availability declines (Russell *et al.* 1993, Thomas 1998b) and the risk of predation by wolves (*Canis lupus*) increases (Adams 2005).

The study was based on locations of individual caribou recorded between 1996 and 2009 using global positioning system (GPS) and satellite collars. These data were used to develop logistic regression-based resource selection functions that represented habitat selection by Bathurst caribou on early- and late-winter range. I used an ITMC approach to compare multiple sets of models across years for all caribou (pooled models) and for individual caribou by season. I discuss the implications of these findings for the distribution of barren-ground caribou in the context of forage availability, snow conditions, and the risk of predation as influenced by wildfire.

STUDY AREA

The winter range of the Bathurst caribou herd is located in the eastern-interior region of the Northwest Territories, Canada, and encompasses an area of approximately 260,000 km^2. Locations of satellite- and GPS-collared caribou monitored during the winters of 1996 through 2009 suggest a winter range boundary delineated by Territorial borders to the north and east, and by the Great Slave Lake and Great Bear Lake to the south and northwest, respectively; however, the distribution of Bathurst caribou has extended as far south as northern Saskatchewan (Figure 11; Gunn *et al.* 2002). A more detailed description of the study area can be found in Chapter 2.

METHODS

Animal Locations and Designation of Seasons

I used animal location data collected during previous studies of caribou and grey wolves to generate the models of habitat selection by Bathurst caribou (Walton *et al.* 2001, Gunn *et al.* 2002). Eighty-four female caribou of the Bathurst herd were fitted with ST-10 and ST-14 satellite radio-collars (Telonics, Mesa, AZ, USA; Ballard *et al.* 1995) using standard helicopter darting techniques and monitored between 1996 and 2009 (Gunn *et al.* 2002). In the fall of 2008, 20 additional female caribou were captured and equipped with GPS collars. Satellite collars were programmed to transmit locations every 5 (ST-10 collars) to 7 (ST-14 collars) days during the winter seasons. GPS collars collected locations at 4-hour intervals and were monitored during the winter of 2008 and 2009.

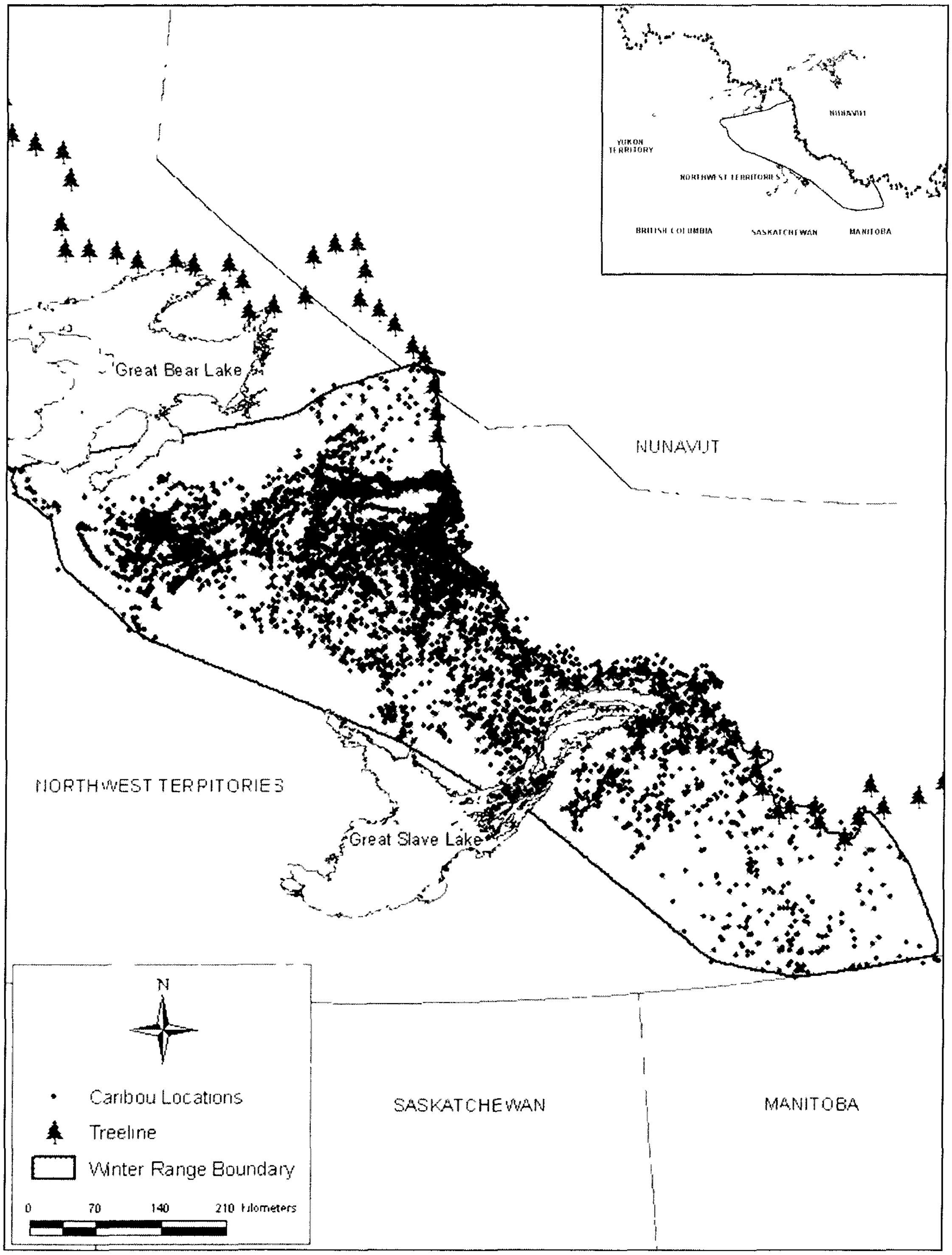

Figure 11. Winter range boundary delineated by locations of Bathurst caribou collected from 1996 - 2009. Treeline represents the northern extent of forested habitat.

A total of 23 wolves from 19 different packs were fitted with ST-10 and ST-14 satellite collars using a net fired from a helicopter and monitored every 5 (ST-10) to 14 (ST-14) days during the winters of 1997 (n = 151), 1998 (n = 785), and 1999 (n = 958). The number of satellite- and GPS-collar locations obtained per caribou varied from 2 - 169 and 303 - 879 with a mean of 53 and 825 locations, respectively. The accuracy of animal locations collected with satellite collars ranged from 150 - 1000 m (Argos 2011). The potential error radius for GPS-collar locations was less, at 10 - 30 m for all locations. Details of capture efforts and deployment histories are documented elsewhere for satellite-collared caribou and wolves (Cluff *et al.* 2002, Gunn *et al.* 2002).

I defined the winter season as occurring from November 1 - March 31. Bathurst caribou migrate annually from summer habitats in the tundra to forested areas south of treeline during winter (Gunn *et al.* 1997). The southern migration of caribou usually occurs between September 1 and October 31, and coincides with the rut. By the middle of April, caribou begin their northern spring migration back towards the calving grounds, marking the end of winter. Because of suspected within-season differences in forage availability, I divided winter into two periods, November - December and January - March, which were designated as early and late winter, respectively.

Environmental Variables for Resource Selection Models

I identified environmental variables that may explain the observed distribution of Bathurst caribou on winter range. These variables represented three broad explanatory mechanisms for resource selection: vegetation, disturbance history as a function of wildfire, and predation risk. I derived vegetation types from Landsat Thematic Mapper satellite imagery compiled and air-truthed by the Northwest Territories Forest

Management Division (GNWT - RWED 2002). Classification accuracy of the study area ranged from 75 - 80% for all vegetation types, excluding non-forested wetland types (GNWT - RWED 2002). To increase accuracy and improve confidence in statistical analyses, I reclassified the 22 original vegetation types into seven super types relating to the winter foraging ecology of barren-ground caribou (Table 5).

I obtained geographic information system (GIS) coverage of burn perimeters dating to 1965 from the Government of the Northwest Territories, Forest Management Division. Fire history maps for the study area were not available prior to 1965. At the scale of the patch, I classified burned area into five different age classes: ≤10, 11 - 20, 21 - 30, 31 - 40, and 41 - 44 years since fire. These categories were based on patterns of vegetation succession in taiga regions (Viereck 1973, Collins and Schwartz 1998) and their applicability to barren-ground caribou foraging ecology (Thomas *et al.* 1996, Joly *et al.* 2003). Also, I tested the influence of the ecotone separating burned from unburned areas on the distribution of GPS-collared caribou. I generated 500-m wide buffers inside and outside the perimeter of the burn and compared use by caribou in these areas with interior burned areas and unburned areas >500 m outside the burn perimeter.

I investigated the effect of burned area on caribou distribution at a scale larger than the single patch. I classified burns into three classes based on the area affected by fire: <10,000 ha, ≥10,000 - <50,000 ha, and ≥50,000 ha. I based these class breaks on the work of Thomas *et al.* (1998) who reported that Beverly caribou generally avoided small burns <10,000 ha in size and that larger burns, ≥50,000 ha in size caused caribou to deflect their movement pattern upon encountering the burn perimeter.

Table 5. Independent variables used to model resource selection by Bathurst caribou on winter range in the Northwest Territories (1996 - 2009).

Variable	Description
Vegetation Types	
Non-vegetated	<1% vegetative cover
Sparsely-vegetated	1-10% vegetative cover
Shrub-dominant	≥75% deciduous shrubland cover
Deciduous-dominant	>75% deciduous crown cover
Conifer-dominant	>75% evergreen crown cover
Herb-dominant	≥75% herbaceous cover
Lichen-dominant	≥50% lichen cover
Fire-Related Variables	
Burned Area	
0 - 10 years	Post-fire areas ≤10 years old
11 - 20 years	Post-fire areas >10 and ≤20 years old
21 - 30 years	Post-fire areas >20 and ≤30 years old
31 - 40 years	Post-fire areas >30 and ≤40 years old
41 - 44 years	Post-fire areas >40 and ≤44 years old
Burn density	Regional density of post-fire areas
Burn Perimeter Use	
Core	Burned area >500 m inside the burn boundary
Inner buffer	Burned area ≤500 m inside the burn boundary
Outer buffer	Unburned area ≤500 m outside the burn boundary
Unburned area	Unburned area outside the outer burn buffer
Distance to Burned Area	
Distance to small burns	Distance (km) to the nearest burn <10,000 hectares
Distance to medium burns	Distance (km) to the nearest burn ≥10,000 and <50,000 hectares
Distance to large burns	Distance (km) to the nearest burn ≥50,000 hectares
Predation-Risk Variables	
Wolf occurrence	Predicted likelihood of encountering a wolf relative to vegetation type and snow conditions
Snow water equivalent (SWE)	Interpolated map of snow water equivalent values
Distance to watercourse	Distance (km) to the nearest lake or river

For each caribou location, I calculated the distance to the nearest burn perimeter and recorded both the distance to the perimeter of the burn and the size class of the burn. I used a Gaussian (i.e., distance squared) term to consider nonlinear responses by caribou to the proximity of burned habitat. Lastly, I calculated the relative density of patches of burned area (1965 - 2008) on the winter range. Density was the number of patches (i.e., pixels 60 m x 60 m) classified as burned found within an area approximating the average home range of individual Bathurst female caribou during winter (13,230 km^2; 1996 - 2009; T. Barrier, unpublished data). I hypothesised that caribou would avoid areas of the winter range that contained a high density of burned habitat.

I generated an interpolated map of snow water equivalent (SWE) (Derksen 2008) to gauge the effect of snow conditions on the large-scale distribution of Bathurst caribou during late winter. Snow water equivalent is an indicator of both snow depth and snow density, and is determined by the relative quantity of moisture in the snowpack. Specifically, I used the inverse distance weighted (IDW) technique to create a continuous surface of SWE from values plotted in a grid at 25-km intervals. Interpolated values were more strongly influenced by SWE data that were geographically closer. This method allowed me to estimate snow conditions for each pixel (i.e., 60 m x 60 m) across the study area. I predicted that caribou would associate with lower SWE values in order to reduce the energetic demands of foraging and movement (e.g., travel or predator escape) in high-SWE habitats.

I used maps predicting the distribution of wolves during early and late winter to investigate the influence of predation risk on the distribution of caribou. The maps were generated using a similar method to that reported for the caribou resource selection functions. In the case of wolves, however, covariates predicting distribution were restricted to vegetative cover and snow water equivalent (SWE data available for late winter only). These maps represented the relative probability of wolf occurrence across the winter range, assuming that habitat-use patterns of tundra wolves have remained relatively stable over the past decade. Although the distribution of both caribou and wolves has fluctuated to some extent, I assumed that large-scale patterns of habitat use exhibited by these species remained consistent over time. I hypothesised that caribou would avoid high-risk areas throughout winter, and that the greatest avoidance of habitats frequented by wolves would occur during February and March when snow accumulation peaks. Wolf kill rates of ungulates typically increase during late winter when snow depth and snow density reach maximum annual values (Chan-McLeod *et al.* 1999, Adams 2005). Thus, I also considered SWE values as a proxy for predation risk.

As a third measure of risk-averse behaviours by caribou, I measured the distance from each caribou location to the nearest lake or river. Here, I also included a Gaussian term to account for nonlinear responses by caribou as distance to the nearest watercourse increased. Traditional and scientific ecological knowledge suggests that caribou spend a significant amount of time on frozen lakes and watercourses to reduce the risk of predation (Ferguson and Elkie 2005). Thus, caribou may forage in habitats closer to watercourses as an escape strategy to minimize the risk of being ambushed by wolves.

Model Development and Assessment

I used RSFs to quantify the relationship between the observed occurrence of caribou and vegetation type, fire history, snow cover, and risk of predation. An RSF is a mathematical equation consisting of weighting coefficients (β values) that indicate the relative probability of occurrence of an organism relative to some set of resource features (Manly *et al.* 2002). For these analyses, I used logistic regression to generate coefficients representing the strength of selection or avoidance of a resource feature relative to the availability of that feature.

I used locations collected from adult female caribou to identify habitat use. For each caribou location, I generated five, paired random locations that represented the availability of each resource. These random locations were selected from within an area based on the potential distance that a caribou could have traveled between known locations. Availability radii were equal to the 95% movement distance for a particular collar relocation interval (Manly *et al.* 2002, Johnson *et al.* 2005).

For caribou locations collected with satellite collars and matched random locations, I generated spatial buffers with radii equal to the quality of the location (10 - 1,000 m). I used a GIS to extract the mean value of each resource feature within that buffer in order to obtain the most accurate representation of habitat conditions for a particular location, despite the variability inherent within large spatial buffers. For location data collected with GPS collars I extracted the exact resource value.

I constructed four different candidate sets of logistic regression models to explain the distribution of satellite- and GPS-collared caribou on early- and late-winter range. Location data for the satellite-collared caribou were pooled to maintain sufficient sample sizes for analysis. In contrast, I constructed RSF models for individual caribou monitored with GPS collars. I used a matched fixed-effects logistic regression to contrast caribou and paired random locations (Manly *et al.* 2002). This method allowed me to apply a more precise definition of availability recognising that selection may change throughout the winter and across the seasonal range.

I used an ITMC approach to rank models within each of the four model sets. This technique is more robust than standard null-hypothesis tests (Anderson *et al.* 2000), as it allows for an analysis of multiple, competing hypotheses, each representing a biologically-plausible explanation for the observed data. The ITMC approach is particularly advantageous in complex ecological systems where multiple variables may be involved.

I used Akaike's Information Criterion (AIC) (Anderson *et al.* 2000) to select the most parsimonious model of the candidate set. The 'best' model had the lowest AIC score. I also reported the ΔAIC and Akaike weights (*w*) which represented the difference in AIC values between each model and the lowest ranked model and the approximate probability that a particular model is the best, respectively. AIC provides a relative measure of model performance, but does not assess the predictive performance of the models (Pearce and Ferrier 2000). Thus, I used *k*-fold cross-validation (Boyce *et al.* 2002) to assess the ability of the top models to predict the distribution of caribou. I performed the *k*-fold procedure five times for each top model. In addition, tolerance scores were used to test for excessive collinearity (threshold of ≤ 0.2) among the variables in each model (Menard 2001).

I calculated averaged resource selection coefficients and their variance for covariates from individual resource selection models. Because individual caribou of the Bathurst herd occupied unique home ranges, I assumed that each caribou was independent of other sampled caribou. I averaged the individual resource coefficients and calculated a conservative estimate of variance (Equation 1), which accounted for inter-animal variation as well as the variance due to calculating the individual coefficients (Marzluff *et al.* 2004):

$$[1] \quad Var\left(\hat{\hat{\beta}}_j\right) = \frac{1}{(n-1)} \sum_{i=1}^{n} (\hat{\beta}_{ij} - \hat{\hat{\beta}}_j)^2$$

These 'average' coefficients allowed me to test for population-wide consistency in selection and to rank the relative importance of each resource to the population. For all models, I used 95% confidence intervals to assess the strength of selection or avoidance by caribou to each predictor covariate. Responses of caribou to resource features were considered significant where coefficients and their confidence intervals did not overlap with zero.

I used the RSF value [$w(x)$] as a relative measure of habitat quality across the winter range of Bathurst caribou (Manly *et al.* 2002):

$$[2] \quad w(x) = exp(\beta 1x1 + \beta 2x2 + \ldots + \beta ixi)$$

Specifically, I applied the RSF coefficients generated for satellite-collared female caribou to the respective GIS data (Equation 2). This map represented the relative probability of occurrence of caribou, and thus the relative value of those habitats for Bathurst caribou across the study area. I used quartiles to categorise the continuous surface of RSF values into four classes defined as poor-, low-, good-, and high-quality habitat. The resolution of the map was equal to the size of the pixel used to calculate habitat selection in the RSFs (60 m x 60 m). All statistical and GIS analyses were completed using Stata (ver. 9.2, StataCorp LP, 2006) and ArcMap (ver. 9.3, ESRI, 2008), respectively.

RESULTS

A total of 55 and 15 satellite- and GPS-collared female caribou provided location data from 1996 - 2009 and from 2008 - 2009, respectively. Satellite-collared animals were evenly distributed across the winter range of Bathurst caribou, an area encompassing approximately 260,000 km^2. However, GPS-collared caribou were aggregated mostly in the northern region of the winter range near the towns of Gameti and Wekweti, Northwest Territories, Canada (Figure 2).

Resource Selection: Individual versus Pooled Models

Due to seasonal differences in forage availability, I hypothesised that caribou would use early-seral vegetation types during low-snow conditions and that selection for lichen-rich stands would intensify as winter progressed. In contrast to my hypothesis, the RSF models for pooled animal locations from satellite-collared caribou showed that caribou avoided post-fire vegetation types throughout winter, while selecting stands comprised largely of herbaceous forage and terricolous lichens. Models for GPS-collared caribou reflected similar patterns of selection, but also showed an affinity for sparsely-vegetated habitats. Especially during late winter, GPS-collared caribou preferred habitats characterised by sparse and low-growing herbs and shrubs in addition to lichen-rich areas.

There was a relatively high conformity between the covariates present in the top models of pooled and individual caribou (Tables 6, 7). The 'best' logistic regression models used to describe selection of feeding patches by satellite-collared caribou contained covariates for vegetation type, post-fire age of a habitat patch, distance to the nearest watercourse, distance to the nearest burn and size of burn, regional density of burned area, and wolf occurrence (covariate present in late-winter model only) (Table 6). The most parsimonious logistic regression models used to describe the distribution of GPS-collared caribou contained the covariates for vegetation, fire parameters, proximity to watercourses, snow water equivalent, and wolf occurrence with substantial differences in selection occurring among individuals (Table 7). Models of satellite-collared caribou offered good predictive success ($\bar{r}_s = 0.758$ and 0.860 for early- and late-winter models, respectively) compared to models for individual animals ($\bar{r}_s = 0.118$ - 0.731). Likewise, the maps used to investigate the influence of predation risk on caribou distribution proved to be reliable predictors of wolf occurrence across the winter range ($\bar{r}_s = 0.826$ and 0.761 for early- and late-winter models, respectively).

Table 6. Differences in Akaike's Information Criterion (AIC) scores (Δ) and AIC weights (w) for candidate resource selection models for satellite-collared caribou monitored from 1996 - 2009 across the Northwest Territories. Data representing snow conditions were not available for early-winter models. Variables are defined in Table 5.

Model	AIC Δ_i	AIC w_i
Early Winter		
Veg. + burned area + distance to water + distance to burns + burn density	0	0.694
Veg. + burned area + distance to water + distance to burns + burn density + wolf	1.77	0.286
Veg. + burned area + distance to water + distance to burns + wolf	7.67	0.015
Veg. + burned area + distance to burns + burn density	9.85	0.005
Veg. + burned area	17.27	<0.001
Veg. + burned area + distance to water + burn density + wolf	46.12	<0.001
Late Winter		
Veg. + burned area + distance to water + distance to burns + burn density + wolf	0	0.667
Veg. + burned area + distance to water + distance to burns + burn density + wolf + snow	1.79	0.273
Veg. + burned area + distance to water + distance to burns +burn density	6.39	0.027
Veg. + burned area + distance to water + distance to burns + burn density + snow	6.69	0.024
Veg. + burned area + distance to water + distance to burns + wolf + snow	8.63	0.009
Veg. + burned area + distance to burns + wolf	122.89	<0.001
Veg. + burned area + distance to water + burn density + wolf	159.14	<0.001

Table 7 Number of top-ranked RSF models and mean (SD) and range of AIC weights for GPS-collared caribou (n = 15 in early winter, n = 14 in late winter) for each hypothesised model Individual GPS-collared caribou were monitored from 2008 - 2009 across the Northwest Territories Data for snow conditions were not available for early-winter models Variables are defined in Table 5

Top Model	No of Caribou	$\bar{X}$ AIC w_i	SD	Range
Early Winter				
Veg + burned area + distance to water + distance to burns + buffer use	6	0 715	0 214	0 472 - 0 986
Veg + burned area + distance to burns + buffer use	4	0 527	0 225	0 340 - 0 813
Veg + burned area + distance to water + buffer use	3	0 452	0 136	0 299 - 0 559
Veg + burned area + distance to water	1	0 632		
Veg + burned area + distance to water + burn density + buffer use	1	0 993		
Late Winter				
Veg + burned area + distance to water + distance to burns + burn density + buffer use + wolf	5	0 529	0 161	0 304 - 0 724
Veg + burned area + distance to water + distance to burns + burn density + buffer use + snow	4	0 406	0 052	0 336 - 0 462
Veg + burned area + distance to water + buffer use + wolf	2	0 562	0 252	0 383 - 0 740
Veg + burned area + distance to burns + buffer use	1	0 654		
Veg + burned area + distance to burns + burn density + buffer use + wolf	1	0 422		
Veg + burned area + distance to water + distance to burns + burn density + buffer use + wolf + snow	1	0 316		

Although there were some seasonal differences in the selection or avoidance of resource variables represented in the top models for pooled caribou, the majority of covariates produced consistent coefficients across the two winter seasons. This was not true, however, for habitat selection modelled for individual caribou. These analyses revealed disparate and inconsistent selection strategies within the herd, particularly with regards to the use of burned areas (Tables 7, 8). While the top seasonal models for satellite-collared caribou differed only by the inclusion of wolf occurrence in the late-winter season, a mere 40% and 36% of GPS-collared caribou displayed identical selection strategies during early and late winter, respectively, as indicated by the choice of the best model (Table 7). In addition, none of the models for individual caribou corresponded completely with the types and magnitude of coefficients included in the pooled models. For example, caribou avoided sparsely-vegetated and recently burned areas (11 - 20 years) during early winter according to the selection coefficients for satellite-collared caribou, but at least half of the individual models demonstrated an affinity for habitats within the core or perimeter (≤500 m inside the burn boundary) areas of burns throughout winter (Table 8).

Vegetation Type

Satellite-collared caribou consistently avoided non- or sparsely-vegetated and shrub-dominant areas and selected for herbaceous and lichen-dominant areas throughout the winter, with little differences occurring as the season progressed (Figure 12, Appendix C). Although GPS-collared caribou avoided non-vegetated areas and selected for herbaceous and lichen-dominant areas, they also selected for sparsely-vegetated stands (Figure 13).

Table 8. Significant selection coefficients for covariates from pooled and individual resource selection models of Bathurst caribou on early- and late-winter range. Numbers listed under + and − represent the number of individuals (n = 15 in early winter, n = 14 in late winter) that displayed a significant response to a particular attribute. 'GPS' indicates average values for significant β coefficients from the individual models (Marzluff *et al.* 2004). 'Satellite' indicates values for significant β coefficients in the pooled satellite models.

Covariate	Early Winter				Late Winter			
	(+)	(−)	GPS	Satellite	(+)	(−)	GPS	Satellite
Vegetation Types								
Non-vegetated	0	7	-0.33		0	4	-0.26	-0.22
Sparsely-vegetated	1	0	0.20	-0.32	0	0	0.19	
Shrub-dominant	0	0	-0.25	-0.34	0	0	0.18	-0.40
Deciduous-dominant	2	1			0	7	-0.34	-0.30
Conifer-dominant	0	2			1	0		
Herb-dominant	2	0	0.23	0.52	3	0	0.18	0.49
Lichen-dominant	7	0	0.18	0.27	5	0	0.22	0.30
Fire-Related Variables								
Burned Area								
0 - 10 years	0	2	-0.79		0	1		
11 - 20 years	0	2	-0.61	-1.93	0	0		
21 - 30 years	1	2			0	1		
31 - 40 years	0	2			0	3	-1.07	
41 - 44 years	8	1			5	0	0.42	
Burn density	0	1	-0.05	-0.002	2	2		-0.002
Burn Perimeter								
Core	4	0		NA	0	0		NA
Inner buffer	7	0	0.40	NA	6	0	0.68	NA
Outer buffer	0	8	-0.52	NA	1	7		NA
Unburned area	1	6		NA	0	3		NA
Distance to Burned Area								
Distance to small burns (km)	2	3		-0.01	4	2		-0.06
Distance to small burns (km^2)	5	3		-0.001	1	4		0.002
Distance to medium burns (km)	1	0	0.15		5	2		0.04
Distance to medium burns (km^2)	0	1	0.003		0	4		-0.001
Distance to large burns (km)	1	0	0.06		2	0	0.22	0
Distance to large burns (km^2)	0	1	-0.001		0	2	-0.01	0
Predation-Risk Variables								
Wolf occurrence					1	2		2.43
Snow water equivalent			NA	NA	4	1		
Distance to watercourse (km)	1	0	0.15	-0.02	1	2		-0.24
Distance to watercourse (km^2)	2	1	-0.08	0.01	1	0		0.06

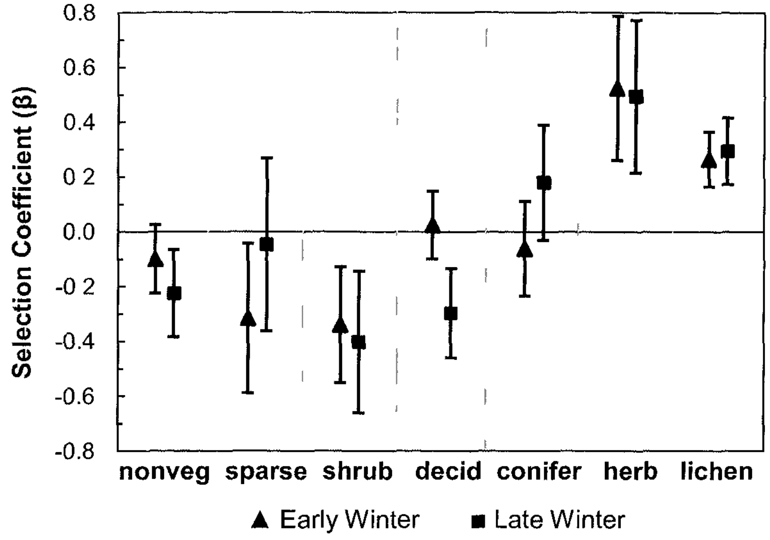

Figure 12. Selection coefficients and 95% confidence intervals for vegetation types used by satellite-collared caribou on early- and late-winter range in the Northwest Territories (1996 - 2009). 'Nonveg' represents non-vegetated habitat, 'sparse' represents sparsely-vegetated habitat, 'shrub' represents shrub-dominant habitat, 'decid' represents deciduous-dominant habitat, 'conifer' represents conifer-dominant habitat, 'herb' represents herb-dominant habitat, and 'lichen' represents lichen-dominant habitat.

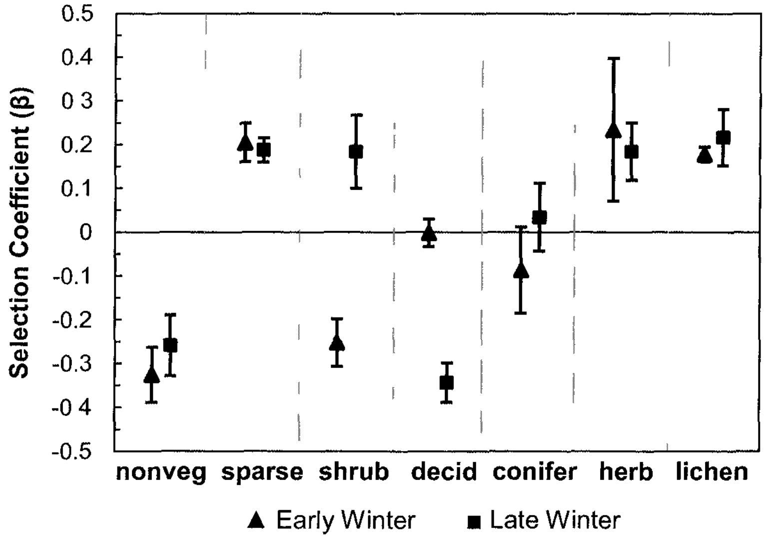

Figure 13. Averaged selection coefficients and their variance (Marzluff *et al.* 2004) for vegetation types used by GPS-collared caribou on early- and late-winter range in the Northwest Territories (1996 - 2009). See Figure 12 for a description of abbreviations for vegetation covariates.

Especially during late winter, GPS-collared caribou collectively sought habitats with a large component of shrubs and post-fire vegetation types and avoided deciduous stands.

Predation Risk

The pooled model of habitat selection showed that caribou favoured areas with a higher risk of predation during late winter (Table 8). However, two out of three individuals with a response to wolf occurrence selected areas that were less likely to be occupied by wolves, and the 'average' response of GPS-collared caribou was not statistically significant. The analysis of snow water equivalent also revealed conflicting results. In contrast to my hypothesis, four out of five caribou preferred habitats with high SWE values during late winter, indicating that caribou sought out habitats with a deeper, denser snowpack compared to surrounding areas. As a third measure of risk-averse behaviours, I tested for patterns of resource use based on proximity to watercourses. In contrast to the RSF- and SWE-based measures of predator avoidance, late-winter habitats occupied by satellite-collared as well as the majority of GPS-collared animals were significantly closer to lakes and rivers than random locations.

Fire History

Range-wide use of areas categorised as 11 - 20 years post-fire was much lower than younger and older age classes (1 - 10, 31 - 40, and 41 - 44 years). Individual caribou showed the greatest aversion to recently burned areas; individuals avoided all burns <40 years old and only selected stands 41 - 44 years post-fire (Table 8). GPS-collared caribou also showed an aversion to areas of the winter range landscape with a high density of burned area. Models for pooled caribou revealed selection for areas closer to small burns (<10,000 ha) and farther from medium burns (10,000 - 50,000 ha) during late winter

(Figure 14). Although overall use of burned areas was significantly lower than expected based on their availability, models of resource use by individual caribou confirmed an affinity for habitats adjacent to the burn boundary. According to the 'averaged' selection coefficients, GPS-collared caribou selected burned areas within 500 m of the burn perimeter throughout the two winter seasons, and they were also located within core areas of burns significantly more than expected during early winter (Table 8).

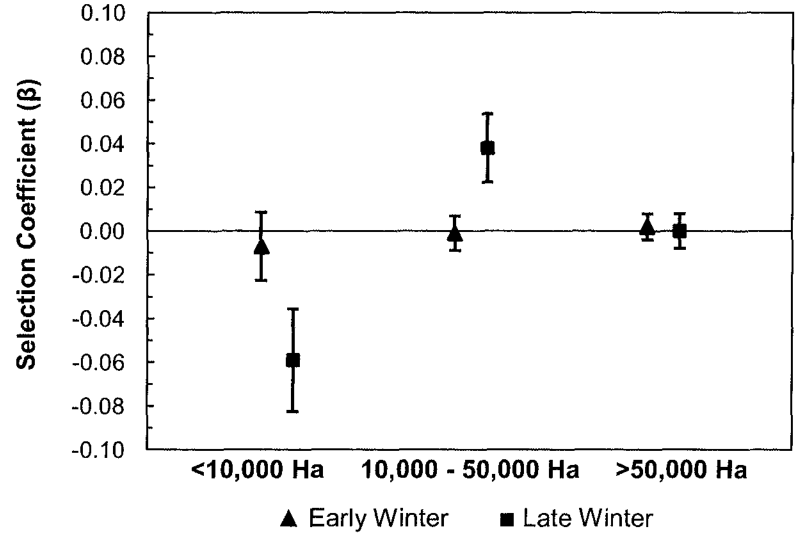

Figure 14. Selection coefficients and 95% confidence intervals for proximity to burns of various sizes from habitats used by satellite-collared caribou on early- and late-winter range in the Northwest Territories (1996 - 2009).

Spatial Representation of Resource Selection

Although there were some discrepancies in habitat selection between the pooled and individual models, an emphasis on mature lichen-bearing areas close to water was prevalent throughout the analyses. Models of satellite-collared caribou offered better predictive success ($\bar{r}_s = 0.832$) and were representative of a much longer period of time than the GPS models (13 years versus 1 year). Hence, I relied on the specific values of resource variables associated with the pooled model of satellite-collared caribou (Appendix D) to generate a map of the predicted value of habitats for caribou on winter range in the Northwest Territories (Figure 15). The greatest concentrations of high-quality habitat occurred in the northwestern and southern regions of the winter range. In particular, areas with fewer and smaller young burns appeared to be most favoured by caribou.

DISCUSSION

My findings on the spatial-temporal dynamics of barren-ground caribou in the Northwest Territories complement previous studies of habitat use by other herds during winter (Skoog 1968, Bergerud 1972, Miller 1976, 1980, Schaeffer and Pruitt 1991, Thomas 1991, Russell *et al.* 1993, Thomas *et al.* 1996; Joly *et al.* 2003, 2007a, 2010). Most studies of migratory caribou populations, however, have employed a herd-wide analysis of habitat use and have failed to recognise the individual-level variation in resource selection. I have expanded upon these works by quantifying patterns of habitat selection demonstrated by both the individual caribou and a subset of the population. In addition, I used location data from collared caribou monitored over a relatively long period of time (13 years) to investigate habitat selection during two winter seasons.

Selection Patterns of Post-fire Habitats

My findings corroborate research from migratory populations of caribou in Alaska (Joly *et al.* 2003, 2009a) and elsewhere in northern Canada (Thomas *et al.* 1996).

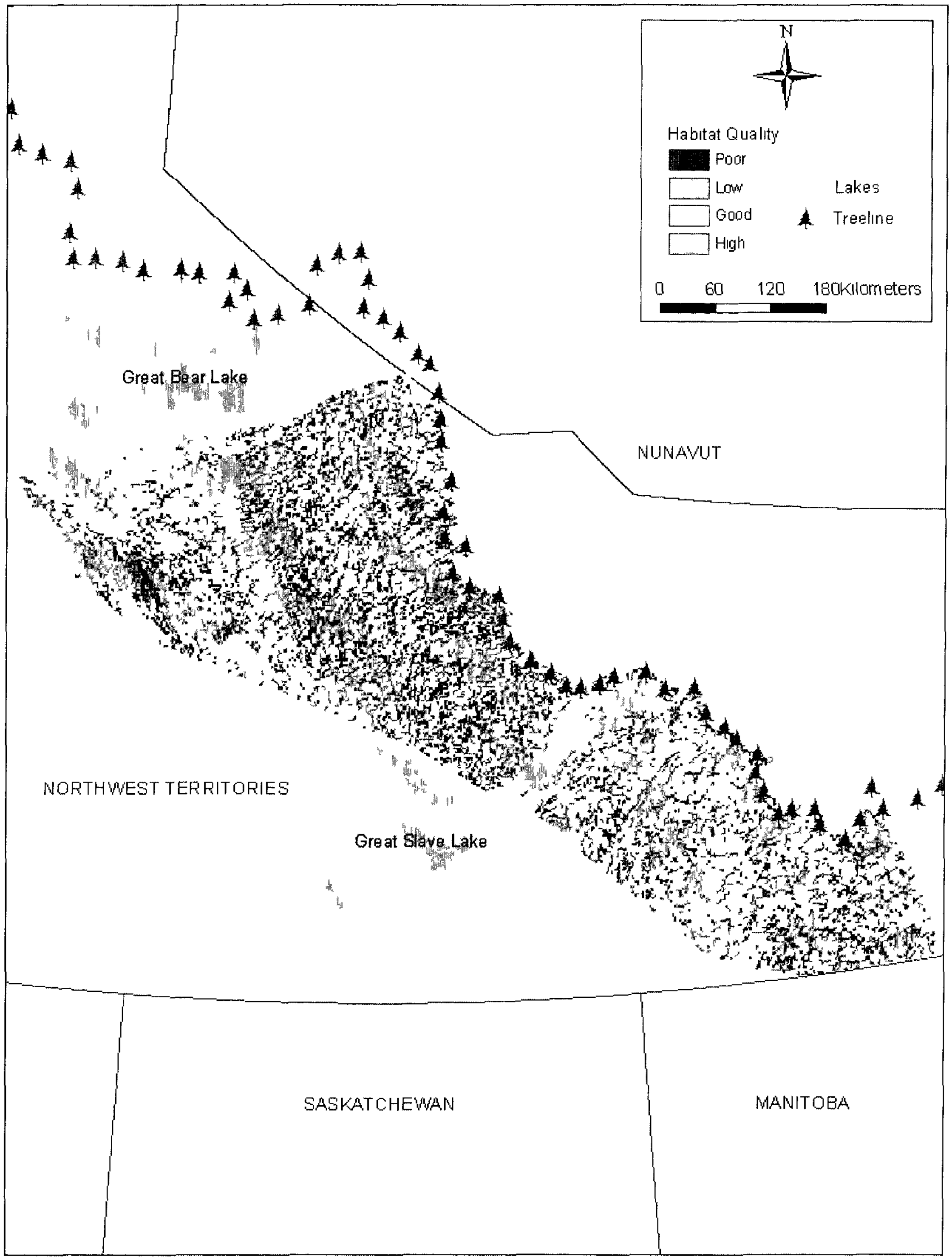

Figure 15. Ranked selection of habitats by barren-ground caribou on the winter range in the Northwest Territories. Habitat quality was predicted using a resource selection function for satellite-collared caribou monitored from 1996 - 2009.

Caribou selected mature stands for winter range habitat (>40 years old) and avoided younger stands, with few observed differences in selection between collar type and season. Although caribou mostly avoided recently burned patches of winter range and large tracts of burned taiga, there was significant selection of early-seral habitats and stands adjacent to the burn boundary. In particular, some individual caribou displayed an affinity for post-fire vegetation (i.e., sparse and low-growing herbs and shrubs), areas with a high density of burned habitat, and burned areas within 500 m of the burn boundary.

Researchers have posited that an increased abundance of vascular plants present in burned areas may benefit caribou by providing ample quantities of nutrients and protein (Joly *et al.* 2003). My research shows that while caribou generally avoided burned habitats on winter range, they disproportionately occupied burned stands adjacent to the burn boundary, as well as those characterised by sparse, low-growing herbs and shrubs. Joly *et al.* (2003) reported similar findings for Nelchina caribou in Alaska, attributing the use of 11- to 20-year-old stands to an abundance of vascular forage found in immature habitats. Use and selection of post-fire areas adjacent to the burn boundary suggests that these habitats provide some ecological gain for caribou related to travel, foraging, or predator avoidance. By providing access to diverse forage types and enhanced visibility for predator detection, the juxtaposition between burned and mature habitat may serve an important function for wintering caribou.

Selection Patterns in Relation to Predators and Snow

My findings failed to support the hypothesis that caribou favour habitats estimated to have a lower risk of predation. Satellite-collared caribou on late-winter range actually selected for habitats more likely to be inhabited by wolves. Similarly, four out of five individual caribou used habitats with comparatively high values of SWE during late winter, indicating that these caribou sought out or incidentally used areas with denser or deeper snowpacks, potentially causing them to be more vulnerable to predation (Adams 2005). Mattson *et al.* (2009) reported a slight positive trend between wolves and areas with a greater amount of caribou habitat. Hence, my findings of selection for high-risk habitats by caribou may have occurred as a consequence of wolves seeking habitats where caribou are more likely to be found.

Caribou may have few options to avoid wolves at the scale of the winter landscape. However, at a finer spatial and temporal scale, caribou likely display behavioural responses to predation risk such as changes in vigilance and aggregation (Creel and Christianson 2007). Due to the lack of alternate prey such as moose (*Alces alces*), tundra wolves in the Northwest Territories may track the distribution of wintering caribou versus occupying traditional pack ranges (Walton *et al.* 2001). Wolves in this study displayed patterns of habitat selection similar to caribou, indicating that wolves sought areas with a greater amount of high-value caribou habitat. Specifically, both wolves and caribou avoided non-vegetated areas and targeted high-SWE habitats yielding a high percentage of ground cover of herbaceous and lichen forage, especially during late winter. Maintaining large group sizes and remaining close to lakes and open habitats (i.e., young burns, mature spruce-lichen stands) with adequate escape routes may be the most effective strategy for avoiding predation by wolves. Analyses of the Bathurst herd reinforced these anti-predator behavioural responses in that caribou frequently congregated in groups of 25 - 50 individuals (Mattson *et al.* 2009, T. Barrier, unpublished data), and chose to occupy habitats close to lakes and rivers, especially during late winter. Alternatively, caribou may use waterways to navigate the winter range to locate predictable forage patches and to maximize movement efficiency due to the improved traction afforded by shallower and harder snow on frozen lake surfaces (Bergerud *et al.* 2008).

Individual Variation in Resource Selection

Resource selection functions are a common approach for examining the distribution and habitat selection of wildlife species. Typically, individual animals are monitored and pooled in order to gauge population-level responses to resources (Gillingham and Parker 2008). However, these types of analyses risk losing important information on individual variability. In order to quantify variation in resource selection by Bathurst caribou, I used location data from both pooled and individual animals. My analyses show that despite the general agreement in selection coefficients between collar types, patterns of habitat selection varied greatly among individuals. In addition, inferences drawn from the 'average' response of GPS-collared animals were often based on only a few caribou, and sometimes led to misleading conclusions. For example, data from averaged individuals suggested that caribou avoided areas of early-winter range with dense aggregations of burned habitats; however, this inference was based largely on the selection coefficient for one individual. The late-winter data showed that this particular caribou displayed conflicting selection strategies when compared to other individuals. These results suggest that where pooled data are used for resource selection functions, one should attempt to minimize bias by maintaining a balanced sample size of locations among individuals or determine individual differences using a random effect (Gillies *et al.* 2006, Hebblewhite and Merrill 2008).

The RSF models generated using locations from satellite-collared caribou offered good predictive success ($\bar{r}_s$ = 0.758 and 0.860 for early- and late-winter models, respectively) compared to models for individual animals ($\bar{r}_s$ = 0.118 - 0.731) suggesting that most individual models were unable to differentiate habitats used frequently by caribou. Possible errors may have included an inability of the model to detect differences between used and random sites (i.e., Nielsen *et al.* 2002, Boyce *et al.* 2003) due to a relatively constrained definition of habitat availability (i.e., shorter availability radii resulting from a relatively short time lapse between each known location). In addition, caribou may have perceived their environment according to various unidentified habitat features prevalent at finer spatial scales (Johnson *et al.* 2001). Although the predictive accuracy of these models was low, it is worth noting that many of the covariates had significant coefficients. Individual caribou were selecting for attributes of the environment.

Although global models of resource selection are often the most practical approach for guiding the management of wildlife populations (Saher and Schmiegelow 2005), my study indicates that variation among individual animals is an important consideration. Caribou employed diverse and variable selection strategies, which would have been masked by a global model. Animals will likely display many departures from the average selection responses predicted by global models, and differences among these individuals should be investigated, as they may illuminate important variation in the use and availability of resources across the landscape (Gillingham and Parker 2008).

Individuals that deviated in the use of post-fire areas, for example, may have occupied distinct home ranges with a higher proportion of burned to mature habitats.

IMPLICATIONS FOR MANAGEMENT

My data suggest that specific habitat features such as stand age, vegetation composition, and proximity to burns and watercourses are important considerations when evaluating the availability of winter habitat for barren-ground caribou in the Northwest Territories. Bathurst caribou displayed an affinity for mature stands of forest with a high percentage of ground cover of lichen and herbaceous forage as well as post-fire areas adjacent to the burn boundary. Although my data do not reveal directly the mechanisms of selection or reasons for particular habitat use, other studies suggest that these habitats provided ecological benefits related to foraging, travel, or predator avoidance (e.g., Chapter 2). Assuming that current climatic trends continue (IPCC 2007), an increase in fire activity across northern landscapes will substantially reduce the availability of forested taiga (Rupp *et al.* 2006) for caribou. In addition, warmer annual temperatures may have consequences for lichen abundance via changes in the composition of plant communities (Cornelissen *et al.* 2001, Olthof *et al.* 2008). My analyses suggest that at some spatial and temporal scales, barren-ground caribou of the Bathurst herd may be less averse to burned areas than previously thought. However, models of resource selection indicate that caribou in this study maintained access to mature patches of lichen and alternate forage species (i.e., herbaceous vegetation) throughout winter, despite use of early-seral habitats. According to the RSF map of the predicted value of habitats for caribou (Figure 15), larger and more abundant burns, in addition to fewer older and lichen-rich stands, could significantly reduce the area or connectivity of high-quality habitat on the winter range of Bathurst caribou. Ultimately, a reduction in the availability or quality of winter range could lead to density-dependent effects of winter forage restriction including reductions in recruitment and body size of adult females (Skogland 1986), as well as altered distribution patterns (Joly *et al.* 2003; 2007a, b; 2010) that would influence access to caribou by harvesters.

RSF models and maps from this study can help fire managers by providing a baseline data set for the development of modelling scenarios illustrating the consequences of various rates and intensities of fire activity for the distribution and area of habitat on the caribou winter range. In addition, maps can be used to delineate the magnitude of effects of proposed resource activities on winter range and to visualize the consequences of development on caribou habitat over a large geographic area (Johnson *et al.* 2005). However, these insights on large-scale patterns provide only partial understanding of the dynamics of barren-ground caribou during winter. Future research on the winter range ecology of the Bathurst herd should investigate the relationship between habitat quality (i.e., area of high-quality habitat and amount of lichen forage) and caribou population demographics in order to define mechanistic links between fire activity, winter severity, and caribou distribution (Boyce and McDonald 1999, Johnson *et al.* 2005). Such works might include long-term monitoring of body condition and population trends, models linking animal nutrition, habitat supply, and reproduction, and finer-scale studies that reveal individual mechanisms driving the larger-scale processes that I observed. Ultimately, these studies would be linked to investigations on other seasonal ranges to provide a more complete understanding of the factors that drive caribou population cycles.

CHAPTER 4 - GENERAL CONCLUSIONS AND RECOMMENDATIONS

SUMMARY

Many *Rangifer* herds across the circumpolar north are currently experiencing severe declines in numbers and distribution (Vors and Boyce 2009). In the Canadian central Arctic, the Bathurst barren-ground herd declined from 472,000 ± 72,900 (± 95% confidence interval) caribou in 1986 to 31,900 ± 10,900 caribou in 2009 (Gunn *et al.* 2008, Adamczewski *et al.* 2009). A reduction in winter forage due to forest fires has been suggested as a factor contributing to the decline. I employed a multi-scale approach to identify the influence of ecological variables related to vegetation, fire history, snow cover, and predation risk on the occupancy of winter habitats by caribou. Between 2008 and 2009, I collected forest stand and understory data in areas used by caribou, as well as at paired control sites. At a larger spatial scale, I used animal location data recorded from 1996 - 2009 to characterise the spatial and temporal distribution of Bathurst caribou. Considering the recent decline of caribou in the central Arctic, these models are useful for exploring factors that may limit or influence the distribution of caribou herds on winter range. Habitat relationships derived for the Bathurst caribou herd may have application to other herds of barren-ground caribou experiencing similar dynamics and possible increases in fire frequency resulting from climate warming.

Caribou-Habitat Relationships

At the scale of the feeding patch, caribou foraged in habitats with a high-percentage ground cover, high biomass of lichen, and few or small trees. Similarly, the consensus among the models of habitat selection by collared caribou was that they avoided areas of the winter range densely populated with burns and favoured older patches of forest characterised by a high percentage of ground cover of lichen and herbaceous forage and a close proximity to lakes and rivers. However, there also was considerable selection for habitats adjacent to the burn boundary, and some individual caribou occupied early-seral habitats significantly more than expected, indicating that these sites provided ecological benefits related to foraging, travel, or predator avoidance.

The flush of herbaceous and woody forage species associated with immature patches of winter range may be a prominent attractant to caribou. Quick-growing vascular species found in young stands have been described as highly desirable to caribou (Scotter 1964, Kelsall 1968) on a winter diet otherwise lacking in protein-rich forage (Fleischman 1990). Alternatively, caribou may occupy burns to minimize predation risk or to maximize movement efficiency when traveling between patches of foraging habitat (Miller 1976, Thomas *et al.* 1998). Caribou generally travel along waterways and lowland areas; thus, continuing along these routes when they bisect burns would require less energy than detouring around a burn (Thomas *et al.* 1998).

The strong association between the distribution of caribou and lichen cover, which covaries with stand age across two different spatial scales (i.e., the forest patch and the winter range landscape), indicates that barren-ground caribou in the Northwest Territories rely on mature patches of the winter range to obtain forage resources. Even where caribou selected for post-fire habitats near the burn boundary, they also chose to occupy mature stands of forest yielding abundant lichen. Contrary to my hypothesis, caribou did not appear to avoid habitats likely to be inhabited by wolves, and selection models revealed that caribou used habitats with comparatively high values of SWE. Both results suggest that at the scale of the landscape, caribou did not or could not avoid areas of relatively high predation risk. Although I was unable to identify or test behavioural factors that allowed caribou to reduce the hunting success of wolves, these may have occurred at a finer scale than I measured (e.g., Creel and Christianson 2007).

Pooled and Individual Resource Selection Models

Although global models of resource selection are often the most practical approach for guiding the management of wildlife populations (Saher and Schmiegelow 2005), my study indicates that individual variation is an important consideration. Caribou employed diverse and variable selection strategies that would have been masked by a global model. In addition, inferences drawn from the ‘average’ response of individual animals were often based on only a few caribou, and sometimes led to misleading conclusions. Despite the general agreement in selection coefficients between collar types, none of the models for individual caribou corresponded completely with the types and magnitude of coefficients included in the pooled models. These results suggest that differences among individual animals should be investigated, as they may illuminate important variation in the use and availability of resources across the landscape (Gillingham and Parker 2008). Caribou that deviated in the use of post-fire habitats, for example, may have occupied distinct home ranges with a higher proportion of burned to mature habitats. Alternatively, where pooled data are used for resource selection functions, one should attempt to minimize bias by maintaining a balanced sample size of locations among individuals or determine individual differences using a random effect (Gillies *et al.* 2006, Hebblewhite and Merrill 2008).

Forage Supply

Accepting the guidance of Bergerud *et al.* (2008:166,495,497,500,501), my data on lichen abundance suggest that conditions on the late-winter range of Bathurst caribou could support a herd density of approximately 1 - 2 animals per km^2 in unburned areas (240,186 - 480,372 total caribou). Given the number of ecological factors that are known to affect barren-ground caribou populations (e.g., weather, insects, plant phenology; Post and Stenseth 1999), this is a very simplistic index of population carrying capacity. Nonetheless, these estimates offer some insight on possible mechanisms for the recent decline of Bathurst caribou. A shortage of winter forage has not likely contributed to the decline of the herd, which peaked at a density of 1.83 ± 0.28 caribou per km^2 (472,000 ± 72,900 caribou) across the winter range in 1986. Assuming that current climatic trends continue (IPCC 2007), an increase in fire activity across northern landscapes would substantially reduce the availability of forested taiga (Rupp *et al.* 2006) for caribou. In addition, warmer annual temperatures may have consequences for lichen abundance via changes in the composition of plant communities (Cornelissen *et al.* 2001, Olthof *et al.* 2008). My analyses suggest that at some spatial and temporal scales, barren-ground caribou of the Bathurst herd may be less averse to fire than previously thought. However, models of resource selection indicate that caribou in this study maintained access to mature patches of lichen and alternate forage species (i.e., herbaceous vegetation) throughout winter, despite use of early-seral habitats. According to the RSF map of the predicted value of habitats for caribou (Figure 15), larger and more abundant burns, in addition to fewer older and lichen-rich stands, could significantly reduce the area or connectivity of high-quality habitat on the winter range of Bathurst caribou.

Ultimately, a reduction in the availability or quality of winter range could lead to density-dependent effects of winter forage restriction including reductions in recruitment and body size of adult females (Skogland 1986), as well as altered distribution patterns (Joly *et al.* 2003; 2007a, b; 2010) that would influence access to caribou by harvesters.

RECOMMENDATIONS

Considering current climate uncertainty and a lack of research on winter range ecology, we require an increased understanding of caribou-winter range relationships to ensure effective management and conservation of caribou (Joly *et al.* 2007a, 2009a, b; Jandt *et al.* 2008). Findings of this study suggest that fires affect the distribution of caribou at two spatial scales. However, my sampling of lichen abundance across a portion of the winter range, while limited, suggests that the aggregate amount of lichen forage is likely adequate given historical numbers of Bathurst caribou. Furthermore, availability of lichen for Bathurst caribou is comparable or greater than many other herds of caribou with similar population dynamics and foraging ecology (Table 4).

In the event that reduced lichen availability becomes a limiting or regulating factor for caribou, fire suppression may be necessary to mitigate other climate- and anthropogenic-related pressures affecting the population and distribution dynamics of barren-ground caribou. For example, a warming climate will likely affect the distribution and the availability of terrestrial lichens via higher frequencies of fire, extreme winter-weather events, and changes in the composition of plant communities (Cornelissen *et al.* 2001, Olthof *et al.* 2008, Joly *et al.* 2009a, Vors and Boyce 2009). These losses could be additive with poorer summer-range condition and increasing human disturbance across other seasonal ranges (Harrington and Veitch 1991, Dyer *et al.* 2001, Mahoney and Schaefer 2002, Frid 2003, Nellemann *et al.* 2003, Johnson *et al.* 2005). Changing plant and insect phenologies will likely restrict time spent foraging and influence caribou movements and energy budgets (Russell *et al.* 1993, Vors and Boyce 2009), and the expansion of anthropogenic activities may disrupt long-term patterns of caribou distribution and the availability of preferred habitats (Bergerud *et al.* 1984, Johnson *et al.* 2005).

The remoteness of caribou winter range from human settlements is a major limitation to effective fire management. If predicted increases in fire activity occur (Stocks *et al.* 1998), fire suppression may be necessary to maintain the area or connectivity of mature winter habitat available to caribou. Identifying priority areas for fire suppression based on the current distribution of Bathurst caribou in relation to fire-fighting centres may be a realistic goal for strategic fire management where resources and access are limited. Caribou typically inhabited regions of the winter range within close proximity to Gameti and Wekweti, Northwest Territories, as well as areas to the south and southeast of these towns following treeline towards the East Arm of the Great Slave Lake. Managing these areas for long fire-return intervals would allow lichen stands to reach maximum levels of production, thereby increasing their value to caribou. Specifically, fire managers should focus on retaining select tracts of mature forested habitat (>90 years) within a mosaic of stand types, while allowing numerous small (<10,000 ha) fires to burn. In addition to contributing to the natural cycles of renewal and succession in taiga ecosystems (Bergerud 1974, Kershaw *et al.* 1975, Miller 1976), numerous small fires would serve as a firebreak for future large fires (Beverly and Qamanirjuaq Caribou Management Board 1994).

Future research should focus on:

1) *More intensive inventory and monitoring of lichen abundance across the winter range of Bathurst caribou.* A reduction in the prevalence of lichen communities is expected to occur as a consequence of increased dominance of vascular plants across the ranges of caribou (Cornelissen *et al.* 2001, Olthof *et al.* 2008). In addition, a changing climate may result in heavier snowfall and more frequent ground-icing (Brotton and Wall 1997), thereby decreasing the accessibility of lichen mats for caribou (Bergerud 1974, Thomas *et al.* 1998).

2) *Monitoring wolf numbers on the winter range of Bathurst caribou.* Few studies have quantified the influence of wolf predation during winter on the population dynamics of barren-ground herds. However, Bergerud *et al.* (2008) suggested that a density of seven wolves per 1000 km^2 could cause caribou populations to decline. Wolf numbers will likely increase as an indirect result of climate warming across caribou ranges (Bergerud *et al.* 2008). Coupled with a deeper snowpack and possibly a shorter duration and extent of the frozen lake period, caribou will be especially vulnerable to predation. However, this may be less of a concern if wolf productivity is regulated by caribou abundance.

3) *Modelling the expected effects of future fire regimes (i.e., fire frequency, severity, and size), climate (i.e., snow indices), and succession of lichen woodlands on winter range habitats to forecast the long-term availability of lichen-bearing range for Bathurst caribou.* Scenarios depicting future climates for northern latitudes predict that

warmer annual temperatures and drier summer weather may lead to an increased frequency and severity of forest fires (Stocks *et al.* 1998, Rupp *et al.* 2000, McCoy and Burn 2005), which could reduce the quantity and alter the distribution of lichen resources available to caribou (Cornelissen *et al.* 2001, Olthof *et al.* 2008). Large-scale predictive modelling is a useful approach for developing strategic insight and objectives for managing winter range.

4) *Identifying linkages between habitat quality and caribou population demographics in order to define mechanistic links between fire activity, winter severity, and caribou distribution.* An understanding of such relationships will allow wildlife managers to evaluate winter range conditions and proposed developments in terms of risks to population numbers and the distribution of caribou relative to harvesters (Boyce and McDonald 1999, Franklin *et al.* 2000, Johnson *et al.* 2005). Also, such approaches, either modelling or monitoring, will allow for a better understanding of the connections between winter range dynamics and population change as influenced by other seasonal constraints on caribou distribution and productivity.

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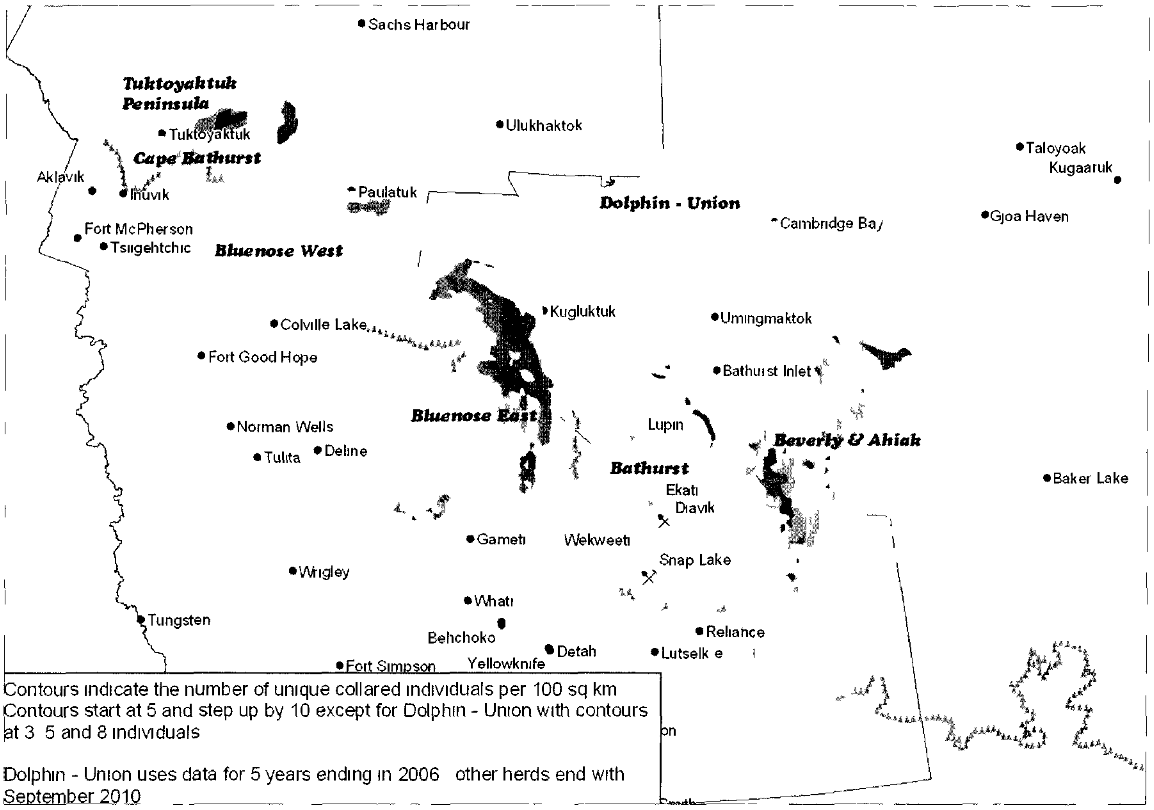
APPENDIX A - MAP OF ANNUAL RANGE USE BY BARREN-GROUND CARIBOU HERDS ACROSS THE NORTHWEST TERRITORIES

Figure A. Annual range use by collared female caribou from barren-ground herds across the Northwest Territories (Dolphin - Union herd, 2001 - 2006; all other herds, 2005 - 2010).



APPENDIX B - STATISTICAL SUMMARY OF FOREST STAND AND UNDERSTORY ATTRIBUTES ON THE BATHURST WINTER RANGE IN THE NORTHWEST TERRITORIES

Table B Statistical summary of forest stand and understory attributes at caribou feeding sites (n = 33) and random lichen-bearing (n = 22) and burned sites (n = 20) on the Bathurst winter range in the Northwest Territories (2008 - 2009) All units represent site attributes per 0 09-ha plot

Stand Attribute	Feeding Site			Unburned Site			Burned Site		
	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE
2008 Snow Cover									
Snow depth (cm)	5	45 360	1 105	0	-	-	0	-	-
Snow density (g/cm^3)	5	0 657	0 110	0	-	-	0	-	-
Snow hardness (g/cm^2)	5	0 229	0 022	0	-	-	0	-	-
2009 Snow Cover									
Snow depth (cm)	11	56 561	2 358	11	59 288	1 851	0	-	-
Snow density (g/cm^3)	11	0 222	0 017	11	0 218	0 008	0	-	-
Snow hardness (g/cm^2)	11	0 158	0 008	11	0 141	0 008	0		-
Lichen Height (cm)	33	1 98	0 14	22	2 07	0 18	20	1 79	0 25
Lichen Volume (cm^3)									
Total lichens	33	10583365	992335	22	8029972	1106393	20	3531496	516728
Fruticose lichens	33	10280844	981543	22	7982752	1204163	20	3123884	482716
Cladina species	33	4935633	803343	22	4321753	790891	20	670179	394680
Cladina stellaris	33	0	0	22	29221	22769	20	0	0
C mitis	33	2828571	452979	22	2555357	434659	20	402991	150381
C rangiferina	33	1947078	482939	22	1541761	437753	20	267188	252674
Cladonia species	33	1860633	219669	22	1326258	214612	20	2205402	372691
Cladonia uncialis	33	201136	72133	22	237419	98414	29	34152	21671
Cl gracilis	33	14610	8711	22	7305	7305	20	16875	16875
Stereocaulon species	33	2339367	585468	22	1718547	620222	20	138616	87226
Foliose lichens	33	302435	65252	22	357589	89150	20	407411	107492
Cetraria species	33	1140097	282313	22	585146	241899	20	103661	40267
Cetraria cucullata	33	140260	50084	22	47484	24031	20	0	0
Cet nivalis	33	969399	289382	22	537662	242840	20	101652	40483
Cet islandica	33	30438	19316	22	0	0	20	2009	2009
Peltigera species	33	179221	57628	22	219521	81987	20	339911	109755
Crustose lichens	33	85 2	32 2	22	105 9	57 3	20	200 9	84 6
Ground Cover (%)									
Lichen	33	57 44	2 27	22	42 74	3 97	20	23 62	2 20
Graminoid	33	0 75	0 20	22	3 14	1 20	20	3 56	1 24
Forb	33	0 73	0 26	22	1 76	0 55	20	1 50	0 73
Bryoid	33	5 20	0 79	22	13 47	3 00	20	11 46	2 30
Litter	33	16 13	1 58	22	17 95	1 62	20	30 48	2 68
Rock	33	4 11	0 94	22	3 10	0 99	20	6 24	1 61

Soil	33	0.92	0.49	22	1.87	1.62	20	1.16	0.75
Dwarf shrub (<30 cm)	33	21.23	1.81	22	22.32	2.82	20	24.84	4.25
Shrub Cover (%)									
Total shrubs	33	1.628	0.932	22	5.700	1.746	20	6.518	3.031
Short shrubs (≤2 m)	33	1.589	0.923	22	5.301	1.598	20	5.363	2.868
Tall shrubs (>2 m)	33	0.038	0.038	22	0.400	0.369	20	1.155	0.613
Basal Area of Trees (%)									
Total trees	33	7.15	1.13	22	12.91	2.32	20	6.00	1.18
Deciduous trees	33	0.73	0.39	22	1.18	0.50	20	1.30	0.70
Coniferous trees	33	6.42	1.02	22	11.73	2.01	20	4.70	1.07
Crown Closure (%)	33	17.51	2.84	22	27.36	4.51	20	19.47	5.13
Stand Age (years)	13	142.6	17.8	8	95.9	9.4	20	29.0	2.1
Elevation (m)	33	338.9	8.0	22	340.4	12.5	20	346.2	11.2

APPENDIX C - SUMMARY OF VEGETATION USE BY BATHURST CARIBOU ON WINTER RANGE IN THE NORTHWEST TERRITORIES

Table C Summary of vegetation use by satellite- and GPS-collared female caribou of the Bathurst herd monitored from 1996 - 2009 (November - March) across the Northwest Territories. ‘Total Locs’ represents the total number of used and available locations acquired for each caribou and collar type. Data under numbers 1 - 7 represent the percentage of caribou and random locations in each vegetation type during early and late winter. Data for satellite-collared caribou represent the average area of each vegetation type within the buffered caribou locations ‘One’ represents non-vegetated cover, ‘2’ represents sparsely-vegetated cover, ‘3’ represents shrub-dominant cover, ‘4’ represents deciduous-dominant cover, ‘5’ represents conifer-dominant cover, ‘6’ represents herb-dominant cover, and ‘7’ represents lichen-dominant cover

Caribou	Early Winter								Late Winter							
	Locs	1	2	3	4	5	6	7	Locs	1	2	3	4	5	6	7
Satellite (Used)	**2217**	**20.7**	**2.5**	**4.5**	**16.8**	**7.2**	**2.4**	**43.6**	**1452**	**20.7**	**2.8**	**4.4**	**14.0**	**6.9**	**3.4**	**45.8**
Satellite (Avail.)	**9865**	**24.1**	**3.7**	**6.1**	**17.4**	**7.9**	**2.0**	**36.3**	**6862**	**23.2**	**3.3**	**6.8**	**18.0**	**6.9**	**2.4**	**36.9**
GPS (Used)	**5479**	**17.2**	**3.7**	**1.0**	**17.2**	**5.6**	**3.1**	**52.3**	**4897**	**16.1**	**3.1**	**0.6**	**10.9**	**3.3**	**7.2**	**58.6**
GPS (Avail.)	**27359**	**24.5**	**3.3**	**1.3**	**17.5**	**5.9**	**2.5**	**45.1**	**24290**	**20.8**	**2.8**	**0.5**	**15.0**	**3.4**	**6.1**	**51.4**
Caribou 1 (Used)	370	18.7	3.0	0.3	20.3	4.3	5.7	47.8	354	24.9	4.5	0	9.3	5.7	6.5	49.2
Caribou 1 (Avail.)	1849	26.9	2.4	0.5	20.1	5.0	3.6	41.3	1770	30.6	3.0	0	14.5	5.3	4.6	42.0
Caribou 2 (Used)	399	16.0	0	2.5	18.3	10.0	0	53.1	353	16.2	0	4.0	16.2	9.4	0	54.4
Caribou 2 (Avail.)	1991	25.8	0	3.2	18.3	8.6	0.2	43.9	1764	25.1	0	4.1	18.7	8.3	0	43.7
Caribou 3 (Used)	347	13.6	8.7	0	27.1	5.5	5.5	39.8	334	16.8	6.6	0	21.0	5.4	7.2	43.1
Caribou 3 (Avail.)	1725	24.8	8.8	0.4	22.3	5.9	6.4	31.5	1670	21.6	8.0	0	27.6	7.0	5.8	30.0
Caribou 4 (Used)	362	11.1	2.2	0.6	9.4	3.9	2.8	70.2	353	11.9	0	0	1.1	0	3.7	83.3
Caribou 4 (Avail.)	1807	17.3	2.9	0.2	11.8	3.4	2.5	61.8	1747	17.5	0	0	3.2	0	5.0	74.3
Caribou 5 (Used)	350	16.3	1.7	0.6	11.4	6.0	1.1	62.9	354	20.3	2.0	0	9.6	5.9	4.5	57.6
Caribou 5 (Avail.)	1749	25.3	2.7	0.5	15.0	4.8	1.3	50.4	1770	28.7	1.7	0	13.3	5.9	2.2	48.2
Caribou 6 (Used)	360	21.9	3.6	0.3	11.1	3.1	2.5	57.5	351	21.7	0	0	7.1	0	4.8	66.4
Caribou 6 (Avail.)	1795	27.0	2.9	0.3	15.3	3.5	2.9	48.1	1749	23.3	0	0	13.7	0	3.1	60.0
Caribou 7 (Used)	363	16.5	3.9	0.3	14.9	5.0	2.5	57.0	354	7.4	0	1.1	13.3	0	16.1	62.2

Caribou 7 (Avail.)	1813	22.5	4.0	0.4	15.4	4.6	2.1	51.0	1764	9.4	0	1.1	20.1	0	11.7	57.8
Caribou 8 (Used)	361	16.9	3.6	0.6	13.3	1.4	8.0	56.2	351	16.2	0	0	0	0	5.4	78.4
Caribou 8 (Avail.)	1805	23.2	2.8	0.8	13.7	3.4	3.7	52.5	1647	22.4	0	0	0	0	5.2	72.4
Caribou 9 (Used)	414	13.5	3.4	3.4	22.5	4.4	6.5	46.4	352	15.9	10.2	0	18.5	2.3	8.8	44.3
Caribou 9 (Avail.)	2070	23.9	2.0	2.5	20.5	5.7	3.6	41.9	1741	14.8	8.6	0	26.1	4.0	9.8	36.8
Caribou 10 (Used)	365	11.8	6.3	0	17.0	9.0	0	55.9	355	8.5	3.1	0	9.3	6.5	1.1	71.6
Caribou 10 (Avail.)	1825	18.7	7.5	0.4	16.6	11.3	0	45.5	1775	14.4	3.8	0	13.4	7.4	1.6	59.4
Caribou 11 (Used)	385	19.0	7.5	0	24.2	4.7	7.8	36.9	350	12.6	6.9	0	21.7	0	26.9	32.0
Caribou 11 (Avail.)	1923	24.3	6.0	1.1	28.8	5.7	5.7	28.3	1747	17.3	6.2	0	21.8	0	22.5	32.2
Caribou 12 (Used)	328	18.9	6.1	1.2	25.3	7.6	2.1	38.7	351	20.8	3.4	0	12.3	9.7	6.6	47.3
Caribou 12 (Avail.)	1636	22.3	4.0	1.7	24.6	7.6	1.3	38.5	1756	26.3	2.5	0	18.4	6.2	5.1	41.7
Caribou 13 (Used)	371	16.4	4.9	1.1	14.8	4.6	1.9	56.3	333	16.2	0	0	0	0	6.0	77.8
Caribou 13 (Avail.)	1853	24.9	3.6	1.0	14.7	5.1	3.4	47.3	1630	19.7	0	0	0	0	5.3	75.0
Caribou 14 (Used)	301	30.6	0	1.7	8.6	6.3	0	52.8	0	-	-	-	-	-	-	-
Caribou 14 (Avail.)	1505	34.4	0	2.7	8.4	5.9	0	48.6	0	-	-	-	-	-	-	-
Caribou 15 (Used)	403	17.4	0	2.7	19.6	7.7	0	52.6	352	15.3	6.8	2.6	13.1	6.0	3.4	52.8
Caribou 15 (Avail.)	2013	26.8	0	3.7	16.2	8.3	0	45.1	1760	19.9	6.0	1.8	19.7	3.5	3.2	45.9

APPENDIX D - RESOURCE SELECTION FUNCTION VALUES USED TO MAP HABITAT QUALITY FOR BARREN-GROUND CARIBOU ON WINTER RANGE IN THE NORTHWEST TERRITORIES

Table D. Parameters of the 'best' global resource selection model for satellite-collared female caribou of the Bathurst herd monitored from 1996 - 2009 (November - March) across the Northwest Territories. Coefficient values (β) were used to map habitat quality for barren-ground caribou on the winter range in the Northwest Territories (Figure 15).

Model Parameters	β	SE	95% CI
Vegetation Types			
Non-vegetated	-0.121	0.050	-0.219 - -0.024
Sparsely-vegetated	-0.225	0.104	-0.428 - -0.021
Shrub-dominant	-0.401	0.083	-0.564 - -0.239
Deciduous-dominant	-0.093	0.050	-0.191 - 0.004
Conifer-dominant	0.022	0.067	-0.110 - 0.154
Herb-dominant	0.524	0.097	0.334 - 0.714
Lichen-dominant	0.295	0.038	0.219 - 0.370
Fire-Related Variables			
Burned Area			
0 - 10 years	-0.009	0.435	-0.862 - 0.843
11 - 20 years	-0.992	0.537	-2.045 - 0.061
21 - 30 years	0.013	0.531	-1.028 - 1.054
31 - 44 years	0.988	0.583	-0.154 - 2.130
Burn density	-0.002	0	-0.002 - -0.001
Burn Perimeter			
Core	NA	NA	NA
Inner buffer	NA	NA	NA
Outer buffer	NA	NA	NA
Unburned area	NA	NA	NA
Distance to Burned Area			
Distance to small burns (km)	-0.019	0.006	-0.032 - -0.007
Distance to small burns (km^2)	0	0	0
Distance to medium burns (km)	-0.001	0.003	-0.007 - 0.005
Distance to medium burns (km^2)	0	0	0
Distance to large burns (km)	-0.002	0.002	-0.006 - 0.002
Distance to large burns (km^2)	0	0	0
Predation-Risk Variables			
Wolf occurrence	NA	NA	NA
Snow water equivalent	NA	NA	NA
Distance to watercourse (km)	-0.055	0.027	-0.108 - -0.001
Distance to watercourse (km^2)	0.011	0.002	0.006 - 0.015