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North American Caribou Workshop
Girdwood, Alaska, USA
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Preface

Approximately 180 people attended the 10th North American Caribou Workshop which was held immediately following the annual meeting of the Northwest Section of The Wildlife Society. Participants came from Canada, Greenland, Finland, Norway, Russia, Sweden, and the United States (primarily Alaska). Over 80 papers and posters were presented and about 25% of those are published here in this special edition of Rangifer. Many of the papers, including the keynote address by Dr. Gunter Weller, concerned climate change and global warming. The large body of evidence on climate change and the strong link to increased CO_2 strongly suggests that caribou in most areas will be dealing with warmer temperatures and changed patterns of precipitation (with the possible exception of Northern Quebec and Labrador). How caribou will be affected is still largely unknown and the subject of a great deal of interesting speculation. There were many interesting formal and informal discussions on these subjects at the caribou workshop, and some of these will undoubtedly lead to some new ideas for future research.

In addition to the poster and oral papers, there were two panel discussions involving experienced hunters and field biologists from Alaska and northern Canada and these addressed the issues of "Coping with change: caribou management and indigenous peoples of North America" and "Effects of severe storms on caribou in North America." Caribou are still an important part of northern cultures and economies, despite an increasing reliance by northern people on government spending, the cash economy, and importation of nonlocal products. People are rightly concerned about how escalating global consumption of energy will affect life in the north. At this juncture, biologists have little information to contribute, but hopefully, research over the next decade or two will begin to shed some light on the positive and negative effects of climate change on caribou across the circumpolar north.

A primary function of workshops such as this is to provide a forum for discussion among biologists who usually have little contact with others because of geographic separation. Over the last 20 years an increasingly important function of the North American Caribou Workshop is to provide a forum for interaction between biologists and resource users who often have little contact because of both geographic and cultural separation. In both these regards the workshop appeared to be a great success.

Patrick Valkenburg, Conference Chairman

The Tenth North American Caribou Workshop,
Girdwood, Alaska, USA,
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Recent changes in seasonal variations of climate within the range of northern caribou populations

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Abstract: The Arctic is one region where it is expected that the impacts of a globally changing climate will be readily observed. We present results that indicate that climate derivatives of potential significance to caribou changed during the past 50 years. Many temperature derivatives reflect the increasing overall temperature in the Arctic such as decreases in the number of days with low temperatures, increases in the number of days with thaw, and days with extremely warm temperatures. Other derivatives reflect changes in the precipitation regime such as days with heavy precipitation and number of days when rain fell on snow. Our results indicate that specific caribou herds from across the Arctic were subjected to different variations of these derivatives in different seasons in the recent past. Examination of temperature and precipitation at finer time-steps than annual or monthly means, shows that climatic variations in the region are neither consistent through the seasons nor across space. Decadal changes in seasonal patterns of temperature and precipitation are shown for selected herds. A process for assessing caribou-focused climate derivatives is proposed.

Key words: climate, derivatives, *Rangifer tarandus*.

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Introduction

Many studies have reported increases in Arctic temperatures during the later portion of the 20th century (McBean *et al.*, 2004). Such changes have potential impacts on both the ecosystems and the people who inhabit these regions. Many of the studies have focused on changes in mean annual temperature of the Arctic regions (Polyakov *et al.*, 2002a, b). Recently, studies have begun to examine the general warming of the Arctic by examining changes in finer detail. Some studies focus on seasonal changes (Polyakov *et al.*, 2002b), some on spatial changes (Polyakov *et al.*, 2003), and others on decadal changes in fine seasonal features (Whitfield *et al.*, 2004). While such climatological studies increase our confidence in the magnitude and distribution of the changes in temperature and precipitation taking place, they are not always directly transferable into ecological impacts.

Animals and plants adapted to the Arctic have evolved to accommodate seasonal and spatial variations in climate. For thousands of years, caribou (*Rangifer tarandus*) herds have moved across individual ranges in the Arctic, congregating for calving in spring, rutting in fall, and distributing themselves across the range during the winter. The movements, while not necessarily driven by climate, are clearly linked in a manner that allows caribou to be successful as a species. However, changes in climate have the potential to present energetic challenges at key stages in the annual cycles of these nomadic animals. Such changes will also impact those people dependent on caribou for their lifestyle (Eamer *et al.*, 1997).

Climatologists and modelers have demonstrated considerable success in resolving climatic variations when averaged across time and space. We know with a high degree of certainty that the temperature of the earth has increased by 1.5 °C in the past 100 years (IPCC, 2001). This has been confirmed by analysis of observational data (Mann *et al.*, 1999) and the outcomes of global climate models (e.g., IPCC, 2001). At the other extreme, individual organisms live on finite portions of the earth and are subjected to day-to-day changes in weather at a scale where climatologists and global climate models do not excel.

It appears almost paradoxical that warmer temperatures would be detrimental to an Arctic species such as caribou. Two important climate-related habitat features that influence caribou are the occurrence of snow and the prevalence of insects (Gunn & Skogland, 1997). Any changes that make foraging more difficult on a consistent basis would impact caribou energetics (Russell *et al.,* 1993). Almost all climate models project more precipitation in a greenhouse future, particularly in the Arctic. The Arctic is dry, receiving an average of 4 cm of precipitation annually, mostly in the form of snow. Models suggest that doubling the levels of greenhouse gases in the atmosphere could cause a 30–50% increase in Arctic snowfall (Russell, 1993). During periods of heavy snow, caribou must expend considerable energy foraging for the lichen (Russell & Martell, 1984). Decreased forage availability under deep snow cover has been associated with high calf mortality (Adamczewski *et al.*, 1988). A deeper winter snow pack may also increase vulnerability to predation because wolves may travel on snow crusts that caribou would sink through (Brotton & Wall, 1997) or concentrate caribou in regions where wolves are abundant. The carry-over effects of poor winter conditions include low calf birth weight and subsequent calf survival (Skogland, 1984).

Increased summer temperatures are correlated with increased insect harassment on caribou resulting in decreased feeding times during the critical post-calving period (Russell *et al.*, 1993). Bad insect years can have impacts on fall body condition which in turn impacts weaning strategies, decreased probability of pregnancy (Cameron & Ver Hoef, 1994), early intra-uterine loss in lactating females (Russell *et al.*, 1998) and overwinter calf survival (Clutton-Brock & Albon, 1990).

Ecologists and climatologists may benefit from convergence of their independent but obviously related perspectives. If the ecological impacts of climate variations take place at fine time and space scales important to ecologists, then climatologists need to converge towards this reality. In the present study, we explore the potential for convergence by linking zonal trends and fine scale decadal variations in temperature and precipitation to selected herds of caribou in the Arctic.

Methods

For this analysis we selected 4 herds that are representative of different regions in the north: the Porcupine caribou herd (PCH) in western North America, the George River Herd east of Hudson Bay, the Queen Elizabeth island "group," representative of high arctic conditions and the Taimyr Herd in Russia.

The climatological information presented here was derived from 2 global Arctic databases described by Groisman *et al.* (2003) and Whitfield *et al.* (2004) from climate observation sites in all countries in the Arctic. Climate derivatives are simple forms based on the temperature and precipitation data obtained from individual climate sites. Groisman *et al.* (2003, 2004) assessed trends in daily climate derivatives: rain on snow; days of thaw, extremely warm days and cold nights, and days with "heavy" precipitation. They report trends in all these for derivatives that are consistent with warming of the Arctic climate in winter and spring. Whitfield *et al.* (2004) assessed recent patterns of decadal shifts in temperature and precipitation from observations from the circumpolar arctic. They describe spatial areas where climate variations between decades were consistent. These clusters of stations are described in detail in that paper. Here we examine the shift-pattern of those clusters that overlap the range of the 4 caribou herds being considered. In this first stage we chose to compare only a limited set of the interactions between herds and the shifts in climate, limiting our consideration to only 2 temperature shift-patterns and 3 for precipitation shift. Finally, we consider evidence that climate is affecting the distribution of the Porcupine caribou herd.

Zonal climate derivatives are estimates of the series of annual or seasonal occurrence of climatic derivatives. The results are a weighted measure of the frequency of events that can be directly calculated from daily climate observations, and provide a robust measure of changes in these types of events. While differences between these series exist with respect to magnitude and directions of shifts, Groisman *et al.* (2003, 2004) show that significant trends for a variety of measures exist that are consistent with those expected from models of climate that include increasing CO_2.. The number of days with rain on snow is used as an example of those zonal trends. Rain on snow is simply the count of the number of days with precipitation when temperatures were above zero and snow was present on the ground. These simple algorithms are based on the climatic record alone, and not confirmed by comparison with local weather conditions.

Seasonal variations were assessed using the method described by Whitfield *et al.* (2004) where temperatures for 11-day intervals (33 periods per year) and precipitation for 5-day intervals (73 periods per year) were compared between the 2 decades 1976–85 and 1986–95. Results for individual stations were clustered based on the probability of a shift in the variables with the annual time span. Whitfield *et al.* (2004) showed that these shifts in seasonal pattern are spatially homogenous in different areas within the Arctic; and different regions in the Arctic have changed in different ways.

Determining the distribution of the Porcupine caribou herd in winter during years of deep or shallow snow conditions and in spring during years of early and late snowmelt was based on satellite locations of collared cows. The locations were analyzed using kernel analysis to produce utilization density grids for the 4 classes (deep/shallow snow and early/late spring). The proportional use by caribou in polygons representing community hunting was calculated within ArcView by dividing the total use in a polygon compared to the total use of all polygons. The variance of use among years was determined using jackknife analysis. We conservatively concluded that polygons were significantly different with respect to caribou use if the 95% confidence intervals did not overlap. See McNeil *et al.,* this volume for a more detailed description of the methodology

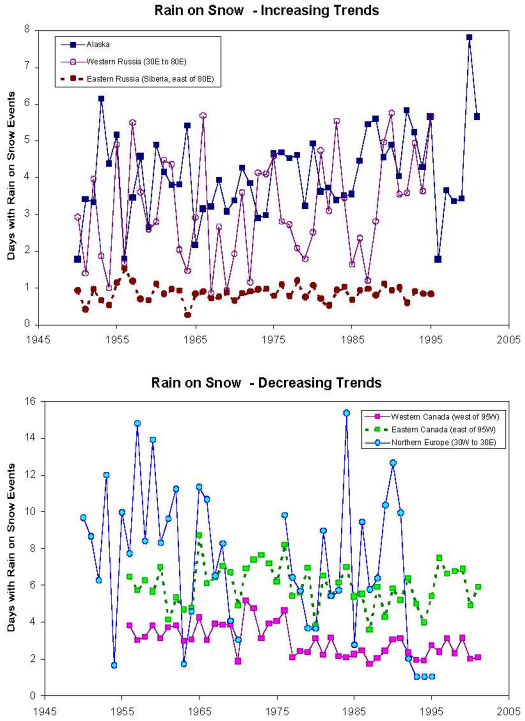

Fig. 1. Number of days with rain on snow events from 1950 to 2000. Zonal averages were calculated using the method described by Groisman *et al.* (2003, 2004). Upper panel shows zones where rain on snow events are increasing, lower panel zones with decreases.

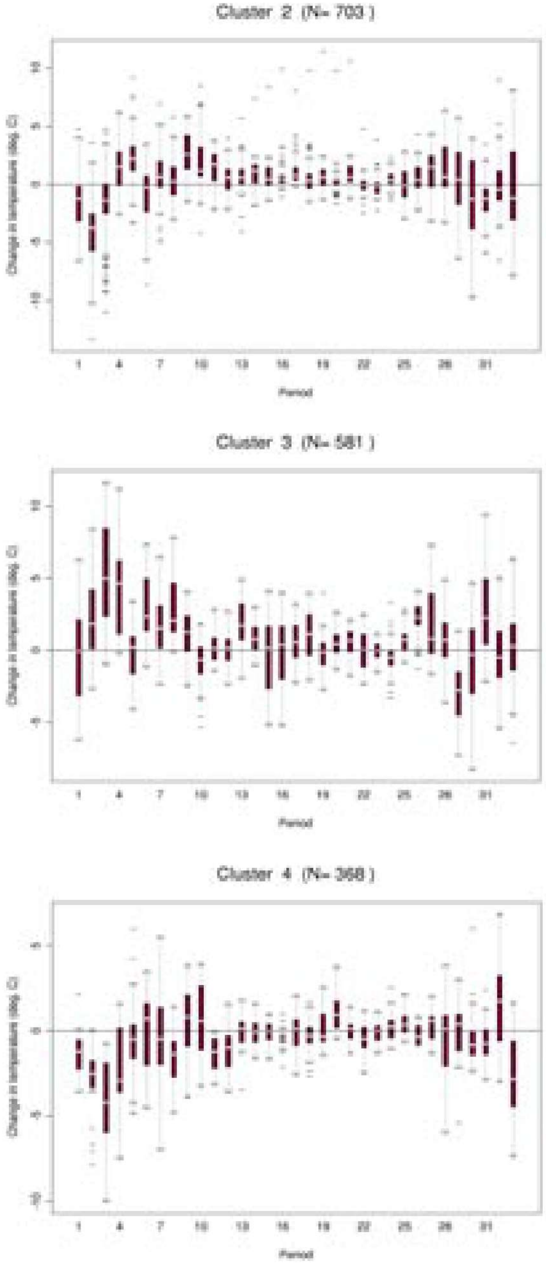

Fig. 2. Patterns of 11-day period decadal temperature shifts for clusters that correspond to the caribou herds described in the text. Numbering of temperature clusters is based on those described by Whitfield *et al.* (2004), and N indicates the number of observational stations within that cluster.

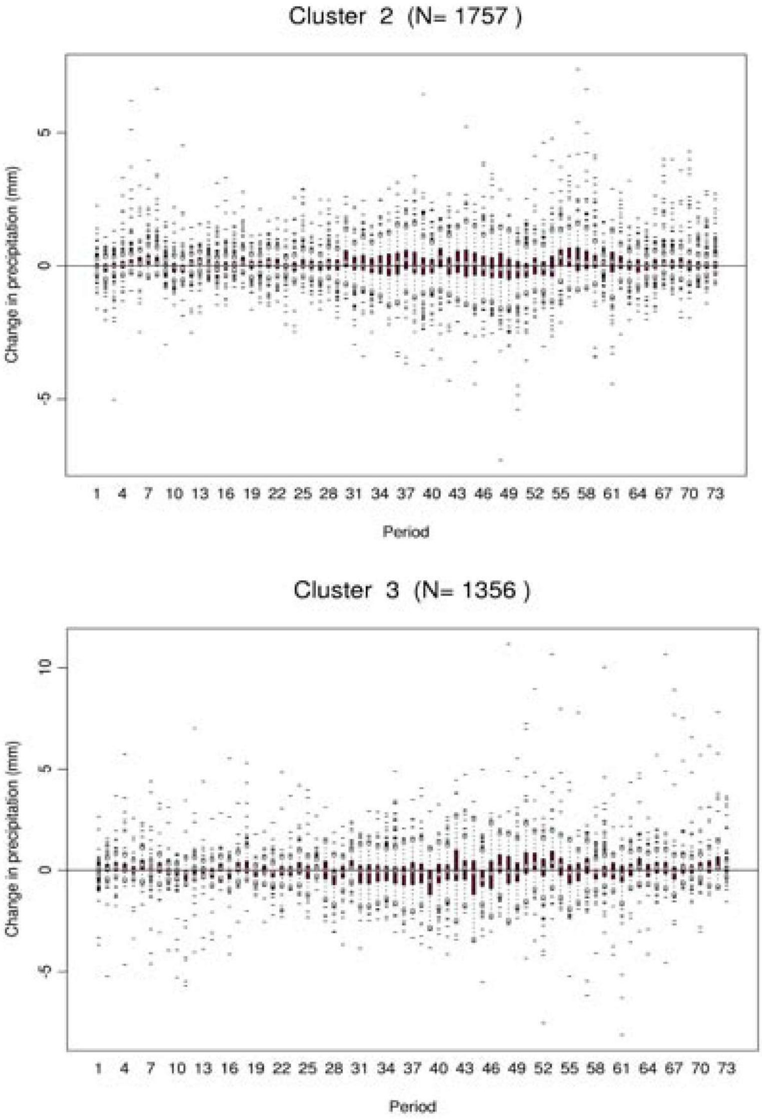

Fig. 3. Patterns of 5-day period decadal precipitation shifts for clusters that correspond to the caribou herds considered. Numbering of precipitation clusters is based on those described by Whitfield *et al.* (2004), and the N indicates the number of observational stations within that cluster.

Results

The frequency of rain on snow events in 6 zones of the circumpolar Arctic are shown in Fig. 1. Increases in the frequency of rain on snow events were observed in Alaska, Eastern and Western Russia, while decreasing trends were observed in Northern Europe, and Eastern and Western Canada over the period 1950–2000 (Fig. 1). While Groisman *et al.* (2004) report that this shift was more pronounced in the south than the north, the large differences between these broad regions shows strong regional differences, in frequency, in variability and in the direction of change. For example, in Eastern Russia, rain on snow events are infrequent with a zonal average of approximately one event per year and generally low variability, while the highest frequency of occurrence is in Northern Europe where the range (6–15) and variability is much larger.

The decadal shifts in temperature and precipitation in clusters that contain observation stations within or adjacent to the range of the 4 caribou herds are shown in Figs. 2 and 3. Fig. 2 shows the 3 temperature shift-patterns. For example, temperatures in cluster "T2," which represents the ranges of the Porcupine caribou herd and the Queen Elizabeth Island caribou herds, were warmer during much of the winter in recent decades except for late December and early January when significant cooling was observed. Significant mid winter warming was observed in cluster "T3" (representing the Taimyr Herd range), while in "T4" the George River Herd faced significant winter cooling during December and January.

Changes in precipitation may differ both in the shift-pattern and the seasonal pattern (Fig. 3). In "P2," precipitation occurred throughout the year and there has been a significant decrease during the late summer period and an increase during fall and winter. This pattern is common to the Taimyr, Eastern Queen Elizabeth Islands and eastern range of the George River herds. In "P3," precipitation was more focused in the summer months, the largest changes occurred between the decades during this period. There have been significant, albeit small, increases in

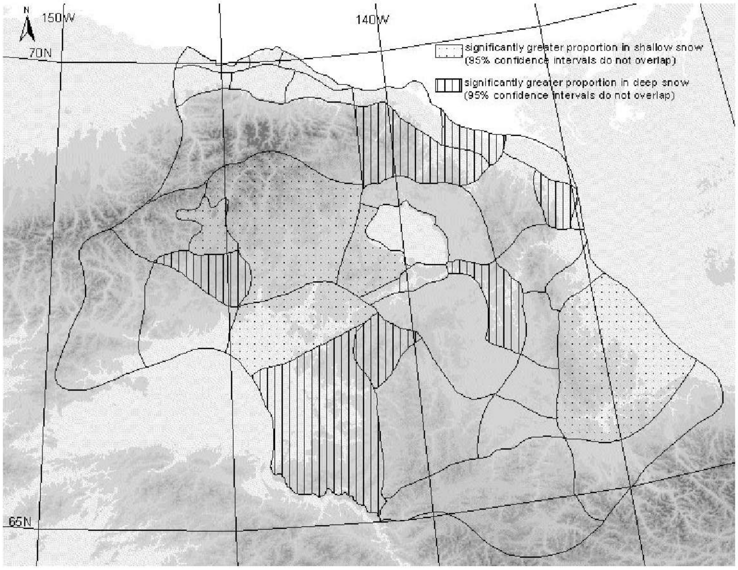

Fig. 4. Distribution of satellite tracked-female caribou in the Porcupine caribou herd during winters with heavy snowfall (stripes) and light snowfall (dots). Polygons represent hunting zones for nearby communities.

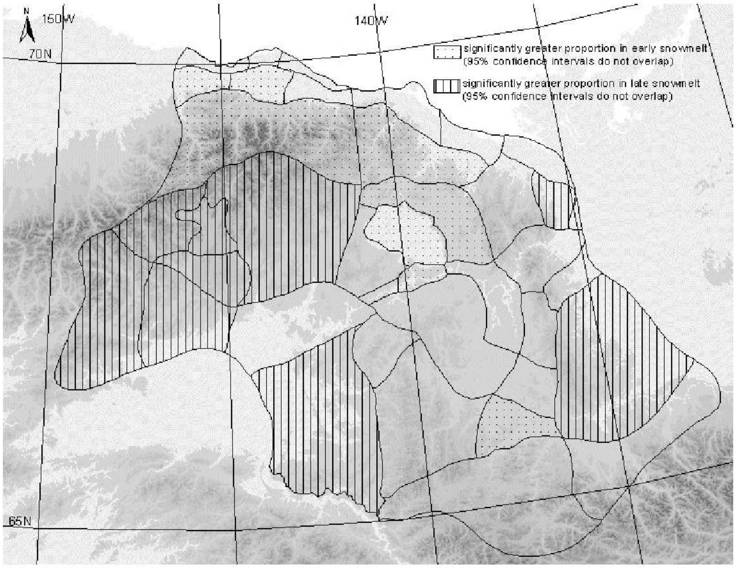

Fig. 5. Timing of spring migration for female caribou in the Porcupine Herd between winters with early snowmelt (dots) and late snowmelt (stripes). Polygons represent hunting zones for nearby communities.

precipitation during winter within the ranges of the Porcupine and western George River herds, although there is generally little winter precipitation within the range of the Porcupine caribou herd.

Distribution of caribou of the Porcupine Herd appears to be sensitive to variations in climatic conditions (Figs. 4 and 5). Female caribou distribute themselves differently between heavy snowfall years and light snowfall years (Fig. 4). During heavy snowfall years the herd tended to be more scattered occupying regions with low snow accumulation such as the Richardson Mountains (a windy region with many snow free ridges) and the Ogilvie basin (lies in a snow shadow of the Ogilvie Mountains; Russell *et al.*, 1993). When snowmelt was early, the females moved north towards the calving ground sooner than when snowmelt was late (Fig. 5).

Discussion

Climate derivatives indicate that most areas in the Arctic have many fewer extremely cold days, and more extremely warm days, and that these are occurring throughout the year. Such changes are indicative of the general warming predicted for the Arctic (Polyakov *et al.*, 2002a, b, 2003). Groisman *et al.* (2003, 2004) report on zonal analysis that assesses annual series derived from observed records. They assessed the frequency of extremely warm and cold days within an annual series by counting the number of days within a year that are 2 standard deviations greater than the mean for that day [for warmer] or less that 2 standard deviations below the mean [for colder]. The "heavy" precipitation derivative is a count of the days per year when the amount of precipitation is greater than 2 standard deviations of the annual precipitation. The number of days of thaw is the total number of days when the mean temperature is above zero. All these derivatives show trends consistent with this warming pattern, such as the number of thaw days, decreases in extremely cold days and increases in extremely warm days (Groisman *et al.*, 2003). Figure 1 illustrates one climate derivative, rain on snow events, and the zonal differences in frequency, variability, and trend. Although these results and those of Groisman *et al.* (2003, 2004) are statistically robust, they are spatially very coarse and the

Table 1. *Rangifer tarandus* seasonal activity, climate and snow derivatives important during each season and the implications for *R. tarandus* based on dates for the Porcupine caribou herd.

Rangifer "stage"	Time period	Climate derivatives[a]	Snow derivatives[b]	Implications to *Rangifer*
Calving	1 Jun–30 Jun	Late spring temperatures; winter snow depth	Thawing degree days	Stall migration; delayed calving; poor post-calving forage quality; higher initial calf mortality.
Autumn	15 Sep–1 Oct	Rain on frozen ground	Basal icing	Forage unavailable; major distribution shifts.
Early winter	1 Dec–30 Jan	Heavy snow		Trade-off between energy intake *vs.* energy output; feeding times decrease; cratering times increase.
			Internal icing	Energy cost of cratering increases.
Late winter	10 Feb–30 Mar	Heavy snow		Shift to more open terrain; delay initiation of spring migration.
			Internal icing	Energy cost of cratering increases.
Spring migration	1 Apr–30 May	Rain on snow icings	Surface icing	Impacts timing of spring migration; increase energy cost of foraging; shift to wind-blown ridges; more susceptible to predation.

[a] Climate derivates are typically counts of numbers of events and have no memory.

[b] Snow derivatives are measures of persistence that contain memory.

zones extend over large areas, and for broad seasonal periods. Climatologists use "annual" or "seasonal" to represent period longer than the response time of individual animals, and do not reflect critical life stages. For example, the effect of a rain on snow event during calving may have a direct effect, while an early winter event might impact winter feeding success. In addition these derivatives are "transplanted" from southern areas where they provide insight into social, economic, and ecological impacts of a general nature. They can be used as an indicator of tendency, but not relative to direct impacts on a single species such as caribou. To assess the direct and indirect effects of such events requires analysis to be done on climate derivatives at time and space scales appropriate to the animal.

Our results show that daily climate derivatives are changing in the Arctic and that these changes have potential for impacting caribou. Different areas of the Arctic are exhibiting different recent variations in temperature and precipitation, some areas with warmer winters, some with cooler, and some with a combination. Similarly, different areas of the Arctic have different precipitation regimes and different patterns of recent change. At the scale of our 4 caribou herds, shifts in seasonal patterns in temperature and precipitation are unique to each herd. The Porcupine and Eastern Queen Elizabeth Island herds were exposed in recent periods to warmer temperatures in early winter, with cooler temperatures in January, and warmer temperatures in the April, May, June and July (Fig. 2, T2). The Taimyr Herd was subjected to cooler temperatures in November and warmer temperatures in December through June (Fig. 2, T3). The George River Herd was cooler throughout the entire period from December through May (Fig. 2, T4). These temperature shifts have varying magnitudes with some changes in some individual periods being greater than 5 °C (e.g., late January for the Taimyr Herd, Fig. 2, T3).

Precipitation shift-patterns are much more complicated, and less easily described. The landscapes used by the Taimyr Herd, the Eastern Queen Elizabeth Island Herd, and the eastern portion of the George River Herd have increased precipitation during much of the year although predominantly during winter, with increased variability (Fig. 3). The Porcupine and western portion of the George River herds have greater amounts of precipitation in July through September. The differences between these 2 alone could have impacts on caribou because higher precipitation in autumn has potential for icings that persist through the winter, while increased precipitation through the winter may reflect deeper accumulations of snow. These results are persistent across a decade, so although they cannot be used to infer the direct impact on an annual basis they suggest that the members of these herds could be subject to persistent changes.

Caribou appear sensitive to climatic features, as reflected in their distribution and timing of movement. The results presented here illustrate that the Porcupine Herd responds to deep snow by distributing itself differently under conditions of deep snow versus shallow snow and also by distributing differently if the spring snow melt begins early or late. Because the range of the Porcupine caribou herd generally has low winter precipitation, it might be more sensitive to variations in snow accumulation than herds where larger winter snow accumulations are common.

Although there appear to be links between the behavior of caribou and climatic conditions, we should reconsider how to assess climatic variations from the perspective of caribou herds. Climate derivatives suggest that conditions potentially unfavorable to caribou are becoming more common, such as rain on snow events, extreme warm temperatures during winter and the amount of winter snowfall. Griffith *et al.* (2002) indicated that the recent decline in the Porcupine caribou herd might be related to the documented increase in freeze-thaw events during spring migration. We expect that the linkages would be clearer if we could develop climate derivatives associated with a "caribou domain," keying in on life stages that have sensitivity to specific weather/climate events while maintaining the robust statistical attributes of zonal derivatives. We are pursuing such derivatives linking specific time periods, defined by caribou life stages, and coupled with specific new derivatives that relate to features impacting on caribou during those periods. We are exploring 2 types of climate derivatives. One type is similar to existing climate derivatives in that they are simply counts of events or occurrences. The second type is a "snow derivative" that accounts for short-term persistence. This allows us to deal with a variety of conditions that are critical for the formation of ice within the snowpack, such as diurnal temperature fluctuations, a series of warm days, and rainfall on cold snow. Internal icings are formed when either rain on snow takes place or warm temperatures and water move from the surface into the snowpack before freezing at a layer. Basal icings are formed when rain freezes on frozen ground, snow on frozen ground melts and refreezes, or rain on thin snow forms a high water content frozen later at the ground surface. Surface icings are formed by surface melting without percolation into the snow pack, by snow metamorphosis that may be wind-driven or as the product of solar radiation. Table 1 contains a summary of the seasonal activity of caribou using time periods for the Porcupine caribou herd (Russell *et al.*, 1993), and the climate and snow derivatives that will be assessed based on key implications for *Rangifer* during each period.

Conclusions

The preliminary results presented here indicate that there have been recent changes in climate derivatives that are of general significance in the Arctic, and that different herds of caribou have been subjected to different seasonal changes in precipitation and temperature. The Porcupine Herd shows sensitivity to snow accumulations and melting and this sensitivity may have implications to caribou availability for harvest by communities within the range of the herd. New climate and snow derivatives that may be more relevant to stages of the caribou seasonal cycle are proposed. Finally, a process to shift the study of climate and snow derivatives to a scale relevant to individual herds is needed.

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Extraordinary movements of the Denali caribou herd following the perfect storm

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Abstract: Although historic literature is replete with anecdotes about atypical and far-reaching movements of caribou (*Rangifer tarandus granti*) herds in Alaska, very few such events have been described since the late 1970s proliferation of radiotelemetry studies in the region. In September 1992, several herds in Alaska made unusual movements away from their typical year-round ranges as a result of highly unusual weather conditions that affected a broad swath of the state. We describe the movements of 113 radiocollared caribou from the Denali caribou herd during this phenomenon and the subsequent year. The majority of caribou in the Denali Herd left their typical range during 26–28 September 1992, traveling distances up to 221 km and remained out of the area through much of the winter. While the outmigration was highly consolidated and easily noticed, the return was protracted with caribou drifting back to their typical range from October 1992 to early September 1993. All radiocollared caribou that survived the 1992–93 winter ultimately returned to their typical year-round range.

Key words: Alaska, Denali National Park, migration, Mount Pinatubo eruption, range expansion, weather.

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Introduction

Caribou are well-known for their long-distance migrations and understanding of seasonal distribution and movements of populations is commonly sought by caribou managers and researchers (Kelsall, 1968; Skoog, 1968; Valkenburg, 2001). While most caribou populations exhibit relatively predictable seasonal movement patterns, occasionally movements do not fit within those norms and are a fascinating aspect of caribou behavior. Prior to the advent of radiotelemetry, there was conjecture about the regular seasonal movements of caribou populations and substantial focus on their sporadic, atypical movements, primarily because such unusual and unexpected movements were reported widely and well-remembered (Valkenburg, 2001). In his seminal treatise, Skoog (1968) provided an exhaustive summary of the historical record of caribou movements and distribution in Alaska over the preceding century, and concluded that emigration appears to be the principal means for limiting numbers within any one subpopulation. At the time, unusual mass movements of caribou were viewed as evidence of that emigration.

With the broad use of radiotelemetry over the last 30 years, and the application of molecular genetics more recently, we now recognize that caribou herds are relatively distinct populations and interchange of individuals among herds is uncommon (Valkenburg *et al.*, 2002). However, herd ranges do change over time and overlap among adjacent herds can occur (Valkenburg *et al.*, 2002). While we have abundant information on the normal seasonal movements of many caribou populations, opportunities to document the extraordinary movements have been rare. In September 1992, a highly unusual snowstorm and unseasonal cold temperatures in much of Alaska set in motion a mass exodus of caribou from the Denali Herd out of their normal year-round range.

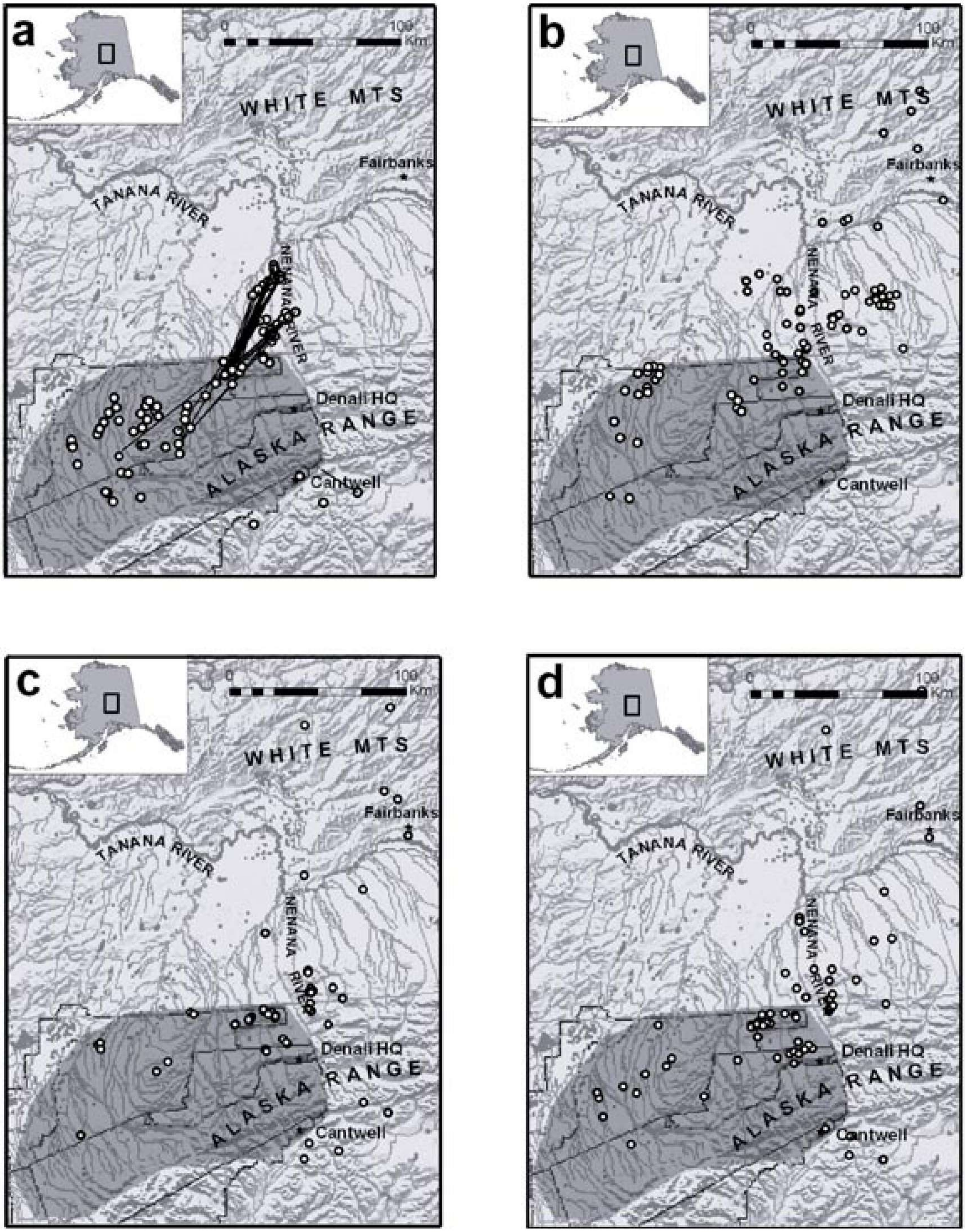

Fig. 1. Distributions of radiocollared caribou from the Denali Herd, Alaska, USA during: a) 22–28 September 1992 (lines indicate movements of caribou from 22–24 September to 26–28 September); b) 2–5 November 1992; c) 8–12 February 1993; and d) 12–22 March 1993. Shading indicates typical herd range.

For this paper, we describe the movements of 113 radiocollared caribou from the Denali Herd during this weather event, the subsequent winter, and their return to the typical year-round range of the herd.

Material and methods

Study area

In September 1992, the Denali caribou herd numbered approximately 2300 animals and normally utilized about 10 000 km^2 in and adjacent to Denali National Park (Fig. 1; 63°N, 150°W). The area is composed of mountain peaks > 3000 m flanked by lower mountains and broad lowland flats. Areas used by caribou during the year include alpine habitats at higher elevations (800–2200 m elevation) and boreal forest or tussock (*Eriophorum* spp.) tundra habitats below. Approximately 2000 moose (*Alces alces*), and 1700 Dall sheep (*Ovis dalli*) also inhabit the caribou herd's range. Caribou are preyed upon by gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*) (Murie, 1944; Adams *et al.*, 1995a,b).

The region has a subarctic, montane climate with annual precipitation averaging 38 cm of water deposited primarily as snow during late September to mid-May. Since 1924, winter snowfall has averaged 207 cm, ranging from 86 cm to 441 cm. Snow normally accumulates early in the winter with 50% of the total annual snowfall occurring from late September to mid-December. Snow accumulation on the ground approaches maximum depths by mid-January and remains relatively constant throughout the remainder of the winter until the onset of snowmelt after 15 April.

Weather

We evaluated weather records from Denali National Park to characterize the events of September 1992 compared to average weather conditions for that period. Snowfall and temperature records are complete back to September 1933, except for the 1949–50 winter.

Caribou movements

As of 24 September 1992, 113 caribou ≥1 year old carried radio collars in the Denali Herd, including 78 females and 35 males. Details on capturing and instrumenting caribou can be found elsewhere (Adams *et al.*, 1995a; Adams & Dale, 1998). We located all the instrumented caribou during 22–24 September 1992 in preparation for an aerial composition survey to be conducted by helicopter on 25 September 1992. After detecting the exodus of caribou from their normal range during the helicopter survey, we conducted additional radiolocation flights during 26–28 September and 5 October 1992 to locate caribou involved in the movements north. We continued to radiolocate caribou throughout the winter, in cooperation with Alaska Department of Fish and Game staff. We completed nearly comprehensive radiolocation efforts 4 times during the winter: 2–5 November 1992, 9–18 December 1992, 8–12 February 1993, and 12–22 March 1993. On 6 May 1993, we initiated efforts to locate all the instrumented females daily as part of an ongoing calf mortality study and most were detected by 10 May 1993. We continued to listen for signals from the remaining females, as well as instrumented bulls, as the calf mortality study progressed through May and early June. By early June, only 1 radiocollared caribou had not returned to the herd's normal range and we monitored her location approximately every month until she was relocated within the herd's range.

Results

Weather

September 1992 began with temperatures that were 2–3 °C lower than average in Interior Alaska (Fig. 2). These cold temperatures were at least in part a result of global cooling from the 15 June 1991 eruption of Mount Pinatubo in the Philippines. The Mount Pinatubo eruption was the largest volcanic eruption on record since the 1912 Mount Katmai eruption in southwestern Alaska (Newhall & Punongbayan, 1996). Mount Pinatubo created a dense aerosol cloud that was slow to penetrate the higher latitudes taking about a year to cover the entire globe (Self *et al.*, 1996). Direct solar shading by the Mount Pinatubo emissions resulted in global cooling of at least 0.5–0.7 °C by September 1992 (Dutton & Christy, 1992; Robock & Mao, 1995).

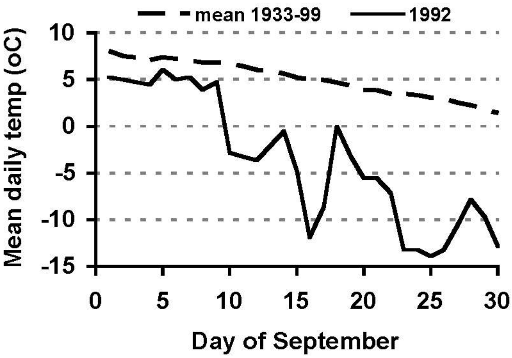

Fig. 2. Mean daily temperatures ([max+min]/2) by date for September 1992 versus September 1933–1999 (no data for 1949), Denali National Park headquarters, Alaska, USA.

With the unusually cool temperatures in place, a powerful winter storm tracking in from the northwest hit Interior Alaska on 12 September 1992. Meteorological events leading to this storm were described by Cole *et al.* (1999) as follows: … a high-pressure system north of Wrangel Island in Russia set up a northwesterly flow aloft across Interior Alaska. By Saturday, 12 September, at the surface, a warm front stretched in a generally northwest–southeast line across the Fairbanks hills with a strong moisture-laden southwest flow off of the Bering Sea at ground levels. During 12–15 September 1992, 97 cm of wet, heavy snow fell at Denali National Park headquarters (Fig. 3), or nearly half of the snowfall for an average winter. This storm resulted in the third greatest snowfall event (total for consecutive days with measurable snowfall) on record and the only measurable snowpack for mid-September. Snow showers lingered through 22 September and as the skies cleared, temperatures dropped with lows averaging -12 °C through the end of the month (Fig. 2). For the month of September 1992 at Denali National Park, precipitation was 330% of normal and monthly average temperatures were 8.4 °C below normal, the coldest September in 100 years (Cole *et al.*, 1999).

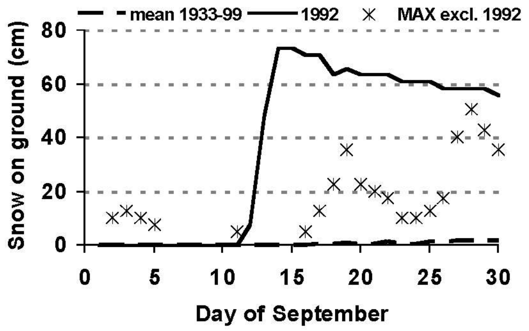

Fig. 3. Snowpack depth by date for September 1992 versus September 1933–1999 average (no data for 1949), Denali National Park headquarters, Alaska, USA. MAX excl. 1992 = maximum snow depth on that date in years other than 1992.

Caribou Movements

During 22–24 September 1992, immediately following the snowstorm, radiocollared caribou were scattered throughout the typical winter range of the herd (Fig. 1a). However, on 25 September during a helicopter composition survey, we encountered >1000 caribou on the northeastern edge of the herd's range headed north en masse down the foothills west of the Nenana River and very few caribou remained on the eastern half of the herd's winter range. Radiotracking during 26–28 September confirmed the movements north along the Nenana River away from the park (Fig. 1a) and mixing with the adjacent Delta caribou herd, which also exhibited unusual movements away from the Alaska Range (Valkenburg *et al.*, 2002). While nearly all caribou on eastern winter ranges left the area, most of the caribou in the western region (west of the Kantishna Hills) remained on typical winter ranges. A few caribou south of the Alaska Range prior to the storm moved east to join caribou within the range of the Nelchina Herd (Fig. 1a).

Table 1. Status of radiocollared caribou monitored from mid-September 1992 through winter 1992–93, Denali caribou herd, Alaska.

	Cows	Bulls
Total	78	35
Remained in typical range	25	5
- Survived to May 1993	23	3
- Died	2	2
Left typical range	53	30
- Returned to typical range	47	17
- Survived to May 1993	43	15
- Died	4	1
- Dropped collar		1
- Died out of typical range	6	11
- Dropped collar out of typical range		2

Of the 113 radiocollared caribou, 83 left the herd's normal range during late September to early December (Table 1). While the proportion of radioed bulls that left was significantly greater than that for females (86% vs. 68%, respectively; $\chi^2 = 3.91$, 1 d.f., $P = 0.048$), that difference was probably not representative of the population. Most of the bulls (29 of 35) had been captured during 15–24 September 1992 in areas that were subsequently vacated by caribou, and therefore the proportion of bulls in our sample that left the normal range was probably higher than that of the population.

During early October–November, Denali caribou scattered throughout the Tanana Flats and the hills north and east of Fairbanks, where they remained through much of the winter (Figs. 1b, 1c, 1d). Radio-collared caribou were located at distances of 6–221 km from their normal range (median = 50 km; Fig. 4) and mixed with caribou from 3 other herds (Delta, White Mountains, and Nelchina). Denali caribou were scattered throughout nearly 50 000 km^2, compared to a typical winter distribution of about 6000 km^2. By mid-March, caribou within 50 km of the Alaska Range generally moved back into the foothills with some returning to the herd's typical

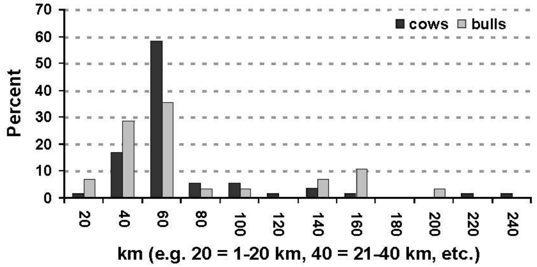

Fig. 4. Maximum distances that radiocollared caribou (*n*=53 cows and 30 bulls) were located from the typical herd range during late September 1992–March 1993, Denali caribou herd, Alaska, USA.

range and the remainder concentrating in areas to the east (Fig. 1d) in the Delta Herd's range. Those near Fairbanks or further north remained at these distant locations.

Movements away from the typical range occurred almost entirely during a 4-day period in late September (Fig. 5). We suspect that many of the individuals that were detected outside of the typical range in early November did in fact leave during or shortly after the main September movement even though we did not confirm their departure until later.

While the movements from the park were consolidated and occurred primarily over just a few days, caribou began returning shortly after the outmigration was detected and continued to drift back in throughout the winter (Fig. 5). In particular, over half of the surviving bulls returned prior to the mid-March radiotracking. Most cows returned between mid-March and early May, the typical period for their movements towards calving areas. Of the 7 cows that returned during mid-May, 4 were still north of the Tanana River in mid-March and the remaining 3 were southeast of Denali National Park. Two of these 7 cows had 1992 calves that survived and both returned with their mothers to the herd's typical range. The final caribou to return was a female that spent its yearling winter southeast of Cantwell in the northern Talkeetna Mountains with resident caribou there, and returned as a 2-year old in late August or early September 1993, almost a year after her departure. With her return, all surviving caribou that had left the herd's typical range had made their way back.

Discussion

The movements we witnessed in early winter 1992 were highly atypical for the Denali caribou herd. The Denali Herd has been the subject of radiotelemetry

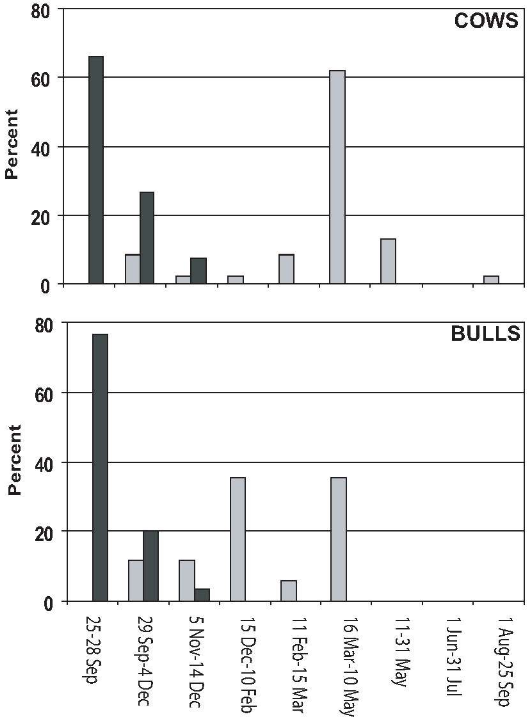

Fig. 5. Timing of departures from (black bars) and returns to (gray bars) the normal range of the Denali caribou herd, Alaska, USA, by radiocollared caribou during late September 1992–September 1993.

studies during 1976–78 (Troyer, 1981) and continuously since 1986 (Adams *et al.*, 1995a,b; Adams & Dale, 1998). In those 21 years of telemetry studies, while some seasonal ranges have shifted, the Denali Herd has stayed within the confines of its typical range except for the events of 1992 described here.

The weather patterns that preceded the September 1992 movements were equally unique. Although the climatic trigger for the unusual movements by caribou was not clear, they did remain within their typical range during the entire period of snowfall and left with the declining temperatures that followed. Their movements, along with similar movements by the adjacent Delta caribou herd, were north out of the mountains and towards lower elevations near Fairbanks, where only about half as much snow fell (Cole *et al.*, 1999). Surprisingly, some caribou continued on into the mountains north of Fairbanks and spent the winter there.

The movements of the Denali and Delta herds out of the Alaska Range occurred over just a few days and were well synchronized and highly noticeable. Nearly all of the Denali caribou on the 2500 km^2 of their eastern winter ranges converged and exited en masse down the Nenana River Valley, joining the

Delta caribou herd along the way. These caribou traveled near or through rural communities and down the George Parks Highway and Alaska Railroad corridor along the Nenana River. They were subject to great interest in Fairbanks as some continued north through the town's western edge, the first time in nearly 50 years that caribou had been observed there (Valkenburg *et al.*, 2002). Some caribou remained throughout the winter in populated areas along the Tanana River from Fairbanks to Eielson Air Force Base.

While the September movements away from the park were dramatic, returns to their typical range were much more subtle with caribou drifting back immediately following the September exodus and continuing to return for nearly a year. However, a group of about 200 returning caribou did make their way through Fairbanks in mid-April, with the help of a police escort, en route to the Tanana Flats (P. Valkenburg, Alaska Department of Fish and Game, pers. comm.). It is noteworthy that many historical accounts of atypical caribou movements are of mass movements away from typical ranges with no mention of subsequent returns, and these observations served as the basis for claims that mass emigrations were important mechanisms of population change for Alaskan caribou (Skoog, 1968). These purported mass emigrations could have been only the first half of accounts similar to ours where all surviving caribou ultimately returned to their original range, but the return movements were relatively undetected.

Although there was no exchange of individuals between the Denali and Delta herds (this study; Valkenburg *et al.*, 2002) resulting from these atypical movements, it is likely that there was genetic interchange given that the 2 herds mixed together throughout the annual breeding season. A few Denali individuals were also with the Nelchina Herd in the vicinity of Cantwell during the rut.

The propensity to make long-distance seasonal migrations is a defining life history characteristic of many caribou populations in North America (Miller, 2003) and is employed to seasonally exploit high-quality forage resources (Kuropat & Bryant, 1979; Skogland, 1980; Russell & Martell, 1984) and reduce predation risk (Skogland, 1991; Adams *et al.,* 1995a; Hayes & Russell, 2000). However, the sporadic and atypical movement events, such as described here, are more difficult to explain. To the best of our knowledge, in September 1992 Denali caribou traveled into areas where they had never been before, at least for several generations. They faced additional risks by traveling through unfamiliar country and either returned to their typical range during winter or spent the winter in areas that were ostensibly little improvement over their typical winter range. Further, this was a singular event, and the caribou subsequently returned to the same seasonal cycle of movements they employed prior to September 1992. Such atypical movement events are fascinating in that they largely defy explanation.

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Calving distribution of the Teshekpuk caribou herd, 1994–2003

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Abstract: Parturient female caribou from the Teshekpuk caribou (*Rangifer tarandus granti*) herd (TCH) have been observed across the western North Slope, but most cows that were seen with calves during the calving period were in the area surrounding Teshekpuk Lake. During surveys conducted between 1994 and 2003, 155 (91%) of 171 collared cows seen with calves were within an area given protected status in the 1998 Bureau of Land Management Final Integrated Activity Plan/Environmental Impact Statement (IAP/EIS). The percentage of adult collared cows seen with a calf between 1994 and 2003 has ranged from 44% to 86%, with a mean of 66%. The years with the lowest percentage of collared cows seen with calves were 1997 (50%) and 2001 (44%). In 1997 most of the herd migrated much farther south than usual, and in 2001 unusually deep, persistent snow restricted spring migration, resulting in fewer cows returning to the traditional calving area during the calving period. When snowmelt dates were earlier, calving locations were farther north. Average standardized travel rates for parturient cows were significantly greater before they had calves (7.25 km/day) than after 3.89 (km/day). Geographically, protections granted by the 1998 BLM IAP/EIS appear to adequately cover the concentrated calving grounds, allowing for variance in the annual distribution of calving cows.

Key words: barren-ground caribou, caribou calving, coastal plain, petroleum development, *Rangifer tarandus*.

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Introduction

Justification for the protection of barren ground caribou (*Rangifer tarandus granti*) calving grounds is based on the premise that access to those habitats has direct population level fitness consequences. A multitude of techniques have been used to assess the importance of the calving grounds to the ecology of barren-ground caribou. While the fitness benefits gained through use of the calving grounds, or some definable region within the calving grounds, are only occasionally quantified (Griffith *et al.*, 2002), descriptions of how habitat varies between calving and peripheral areas are more common (e.g., Eastland *et al.*, 1989; Fancy & Whitten, 1991; Nelleman & Cameron, 1996; Young & McCabe, 1998; Wolfe, 2000; Kelleyhouse, 2001; Barten *et al.*, 2001). The latter studies relied on the assumption, central to habitat selection studies, that differences between selected and avoided habitats represented variation in habitat quality, with subsequent fitness implications. Observations of fidelity to historical calving grounds are also highlighted when discussing the importance of calving grounds to annual cycles (e.g., Gunn & Miller, 1986; Fancy & Whitten, 1991; Schaefer *et al.*, 2000; Mahoney & Schaefer, 2002; Russell *et al.*, 2002; Ferguson & Elkie, 2004).

The primary mechanisms for increased calf survival on the calving grounds are thought to include reduced risk of predation and access to newly emergent, high quality forage with the relative magnitude and scale of importance of these factors in calving ground selection varying among herds (e.g., Kelsall, 1968; Klein, 1970; Bergerud & Page, 1987; Whitten & Cameron, 1980; Fancy & Whitten, 1991; Russell *et al.*, 1993; Barten *et al.*, 2001; Griffith *et al.*, 2002;

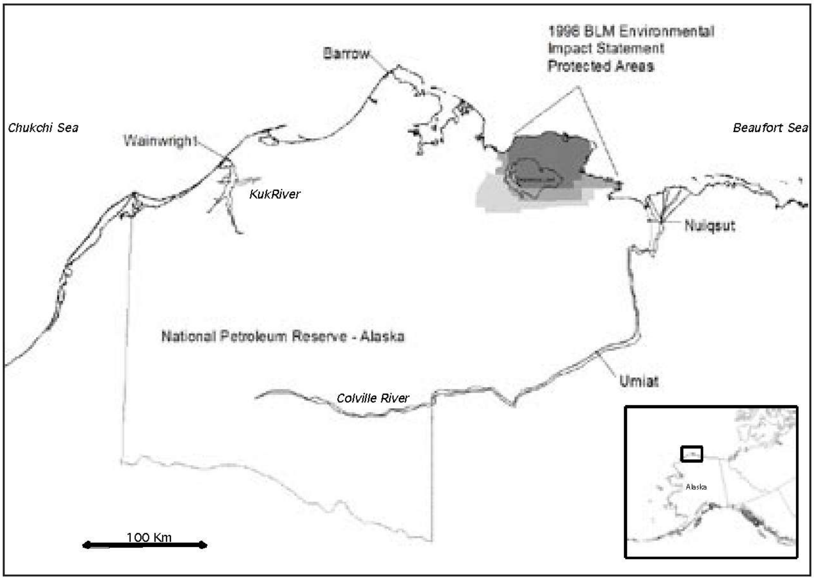

Fig. 1. The western portion of the North Slope Alaskan coastal plain, with National Petroleum Reserve – Alaska boundary in dashed line. Three stipulation areas from the 1998 Bureau of Land Management Final Integrated Activity Plan/ Environmental Impact Statement (EIS) are shaded. From north to south, they are termed "no leasing," "no surface activity," and "special caribou stipulations." Collectively, we have termed this area the "protective boundary," which was used for further analyses.

Russell *et al.*, 2002). Despite the variation in analytical tools used to assess the importance of the calving grounds to the productivity of caribou, the preponderance of information suggests that calving grounds are important.

The Teshekpuk caribou herd (TCH) is one of four large, barren-ground caribou herds that calve on the northern coastal plain of Alaska. First recognized as a distinct herd in the early 1970s (Silva *et al.*, 1985), the herd size has been estimated using photocensus techniques (Davis *et al.*, 1979) at 2–4 year intervals since 1984, with 45 166 counted in 2002 (Carroll, 2003). Studies using systematic-strip transects, satellite radio collars, and VHF radiotracking have all indicated fidelity to the calving area near Teshekpuk Lake, particularly to the area southeast, east, and northeast of the lake (Carroll, 1992; Philo *et al.*, 1993; Kelleyhouse, 2001; Prichard *et al.*, 2001; Carroll, 2003; Noel & George, 2003).

The annual range of the TCH contains the National Petroleum Reserve – Alaska (NPR-A), which is currently being leased for oil exploration and development. Planning for exploration and development included an extensive consultation process, resulting in the 1998 Northeast NPR-A Final Integrated Activity Plan/Environmental Impact Statement (IAP/EIS; BLM, 1998). As a result of this process, 3 protective areas were established in the area surrounding Teshekpuk Lake due to their value to wildlife resources, including caribou and waterfowl. These areas were termed "No Leasing Area," "No Surface Activity Area," and "Special Caribou Stipulation Area," and varied in their protective rigor (Fig. 1). The combined extent of these areas, termed the "protective boundaries" hereafter, were intended to protect large portions of the calving ground and insect relief areas (BLM, 1998). Revisions to the 1998 IAP/EIS are being considered, which might change the status of the protective boundaries (BLM, 2005).

In this paper, we evaluate the geographic adequacy of protective boundaries established in 1998 to protect the calving grounds of the TCH. We also describe some of the factors that influence calving site selection on an annual basis, and suggest how those factors should be accounted for when establishing long-term protective measures.

Study area

The study area included the portion of the coastal plain between the Colville River and the Chukchi Sea (Fig. 1). This area, north of the Brooks Range in Alaska, encompassed the area utilized by most radio-collared cows of the TCH during the calving period, which we defined as the first 16 days of June. This area is also delimited by the calving grounds of the Western Arctic Herd (WAH) to the southwest (Kelleyhouse, 2001; Dau, 2003), and the Central Arctic Herd (CAH) to the east (Wolfe, 2000). Vegetation on the TCH calving grounds is primarily composed of wet (54%) and moist (24%) sedge communities (Kelleyhouse, 2001), which are dominated by *Carex aquatilus* and *Eriophorum* species other than *E. vaginatum* (Muller *et al.*, 1999). The area contains thousands of thaw lakes and the riparian habitats of several major rivers. June temperatures in Barrow, 140 km northwest of Teshekpuk Lake, averaged 0.91 ± 2.75 °C during 1990–2002 (National Weather Service).

The low density of predators is a significant feature of the area. Bear density in low elevation (<800 m) areas of the western portion of the North Slope was estimated to be 0.5–2.0 bears per 1000 km^2, compared to 10–30 bears per 1000 km^2 in areas greater than 800 m in elevation (Reynolds, 1989). No wolves were seen during TCH calving surveys conducted during 1994–2003 (this study). Golden eagles (*Aquila chrysaetos*) have been seen occasionally during aerial surveys, but their numbers have not been quantified.

The TCH annual range overlaps with the annual ranges of the CAH (Wolfe, 2000) to the east and the WAH (Davis & Valkenburg, 1978; Kelleyhouse, 2001; Dau, 2003) to the southwest. During the snow-free period the TCH typically ranges across the Arctic Coastal Plain between the Colville River and the Chukchi Sea (Prichard *et al.*, 2001). The coastal plain is also used during the winter, although segments of the herd have occasionally made more dramatic movements, migrating to the foothills of the Brooks Range, the Seward Peninsula, and most recently, the mountains and coastal plain of the Arctic National Wildlife Refuge (ANWR) (Carroll, 1995, 1997, 2001, 2005).

Methods

In late June or early July 1990–2003 (except in 2002 when captures occurred in early Sep), caribou were captured within 50 km of Teshekpuk Lake and fitted with VHF radio collars or combined Platform Terminal Transmitter (PTT)/VHF collars (Telonics Inc., Mesa, Arizona, USA). A Hughes 500 helicopter, with a skid mounted net gun, or a Robinson-44 helicopter, with a hand-held net gun, were used during capture work. Once captured, we restrained caribou by placing a mask over their eyes and using hobbles and/or ropes to control their legs.

The number of active radio collars deployed in the herd gradually increased during the course of the study. We had 15–20 active radio collars on female caribou until 1995, 27–30 from 1996–1998, and 30–40 from 1999–2003. Satellite collars have been attached to 83 caribou since 1990, with a similar increasing trend in active collars per year. Summaries of movement patterns of satellite collared TCH caribou are summarized elsewhere (Philo *et al.*, 1993; Prichard *et al.*, 2001); here we report the results of VHF radiotracking surveys during the calving period.

VHF Radiotracking

VHF radiotracking surveys were based out of Umiat and Barrow, Alaska. The typical area surveyed each year was an area roughly bounded by the villages of Barrow, Wainwright, Umiat, and Nuiqsut (Fig. 1), although much of the flight time was concentrated around the Teshekpuk Lake area due to the greater number of collars found in the area.

Surveys were conducted from Piper Super Cub (PA-18), Bellanca Scout, or Cessna-185 aircraft. An ATS R4000 telemetry receiver connected to directional antennae was used to radiotrack collared caribou. Prior to 1996, locations were taken from the aircraft Global Positioning System (GPS). Since 1996, locations and flight paths have been recorded with a Garmin 12 XL hand-held GPS.

Weather permitting, we initiated calving surveys between 2 and 5 June, but started 8 June in 1995, and flew as frequently thereafter as weather and logistics would allow, usually every 1, 2, or 3 days. Surveys were terminated between 12 and 18 June when it appeared that all or nearly all the parturient collared cows had calved. We flew directly over each collared caribou and noted the location, presence or absence of a calf, and antler condition. When surveys were flown with a Piper Super Cub or Bellanca Scout we also attempted to establish udder condition. We assumed that cows with new, velvet-covered antlers did not conceive during the previous fall or lost the calf during pregnancy (but see Gagnon & Barrette, 1992), so we recorded their location and listed them as nonparturient. We continued to observe cows with hard antlers or no antlers through the calving period to determine if, when, and where they had calves (Gagnon & Barrette, 1992; Whitten, 1995). The first location a female was seen with a calf at heel was recorded as the approximate calving site (Fancy & Whitten, 1991), based on the limited mobility of calves shortly following parturition (Fancy *et al.*, 1989, Kelleyhouse, 2001; Griffith *et al.*, 2002; Ferguson & Elkie, 2004). The location recorded nearest to the middle of the calving period (8 Jun) was used for cows that were not seen with a calf. The estimated calving sites and locations of cows that were not seen with a calf were plotted using a Geographic Information System (GIS) (ESRI ArcView 3.3, Redlands, California, USA) to determine the location with respect to the protective boundaries.

On several occasions cows had calves at heel the first time we observed them. If the calves appeared to be very young, we assumed that they had been born shortly before we observed them and that observation was used as their calving location. In 2002 calving began earlier than normal and many of the cows already had calves on 2 June.

Snowmelt

To estimate relative spring phenology in the region for a given year, the date of snowmelt was obtained from the National Oceanic and Atmospheric Administration Global Monitoring of Climate Change (NOAA GMCC) site near Barrow (Dutton & Endres,

Table 1. Numbers of collared female Teshekpuk Herd caribou seen with a calf or never seen with a calf during calving season, 1994–2003; numbers of calving locations located inside the BLM protective boundaries (see Fig. 2); and the estimated dates of snowmelt in Barrow, Alaska (see Fig. 3).

Year	Cows with calf	Cows without calf	Total	Percent of collared cows with calf	Number calves inside	Percent inside	Snowmelt date
1994	10	6	16	63%	9	90%	11 Jun
1995	11	4	15	73%	9	82%	10 Jun
1996	24	4	28	86%	24	100%	30 May
1997	8	8	16	50%	7	88%	9 Jun
1998	15	12	27	56%	15	100%	1 Jun
1999	24	12	36	67%	23	96%	13 Jun
2000	23	4	27	85%	19	83%	14 Jun
2001	15	19	34	44%	13	87%	11 Jun
2002	22	8	30	73%	19	86%	25 May
2003	19	12	31	61%	17	89%	3 Jun
Total	171	89	260	66%	155	91%	
$\bar{x}$	17	8.9	26	66%	15.5	90.0%	6 Jun
SE	1.9	1.5	2.4	4.4%	1.9	2.1%	2.1 days

1991; Stone *et al.*, 2002; Dan Endres, pers. comm.). NOAA uses a threshold of 30% albedo, the ratio of upward to downward short wave irradiance, as an indicator of snowmelt. The date recorded was the first day the daily average was below 30%. A change from >75% albedo to <30% typically occurred over the course of only 2–3 days, making it a reliable and repeatable index of spring phenology from year to year. This index was measured at a location about 160 km northwest of the TCH calving ground. The occurrence of snow melt on the calving ground was assumed to be temporally correlated with snow melt in Barrow, based on the large scale meteorological factors influencing snow melt on the north slope (Stone *et al.*, 2002).

Geographic centers of distribution in relation to snowmelt date

The geographic center of the calving distribution for each year was estimated with the Weighted Mean of Points Extension in ArcView 3.3 (Jenness Enterprises, Flagstaff, Arizona, USA), which determined the average latitude and longitude of points in a given sample. The relationships between the coordinates of the distribution centers and snowmelt date were evaluated using simple linear regression. In addition, 2 maps were produced, one showing calving locations during years of earlier than average snowmelt (average snowmelt date 30 May) and one of later snowmelt (average snowmelt date 12 Jun).

Percentage of cows seen with a calf

We report the percentage of monitored VHF-collared cows, ≥3 years old, that were seen with a calf during the calving season because parturition rates were not always possible to estimate. During some time periods, only Cessna 185 aircraft were available for surveys, which made it difficult to determine whether cows had distended udders. In addition, during some years TCH caribou were so scattered at the beginning of calving season it was impossible to find many of them to determine whether they had a calf and lost it or were nonparturient. The annual percentages of cows with calves were compared with Barrow snowmelt dates using simple linear regression.

Movement rates from VHF radiotracking information

In 2002, movements of collared cows were monitored more closely than other years to estimate movement rates and direction of travel. Mean angular direction of travel was calculated from the net movement of individual cows during the calving period. Rayleigh's test was used to estimate whether the mean direction of travel differed from random (Zar, 1999). Daily rate of travel between the location the cow was first found (2 or 5 Jun) and the location on 12 June was calculated for cows seen with a calf versus cows that were not seen with a calf. Additionally, the movement rates of parous cows before and after being observed with a calf were estimated. We compared movement rates of parous cows before and after parturition with

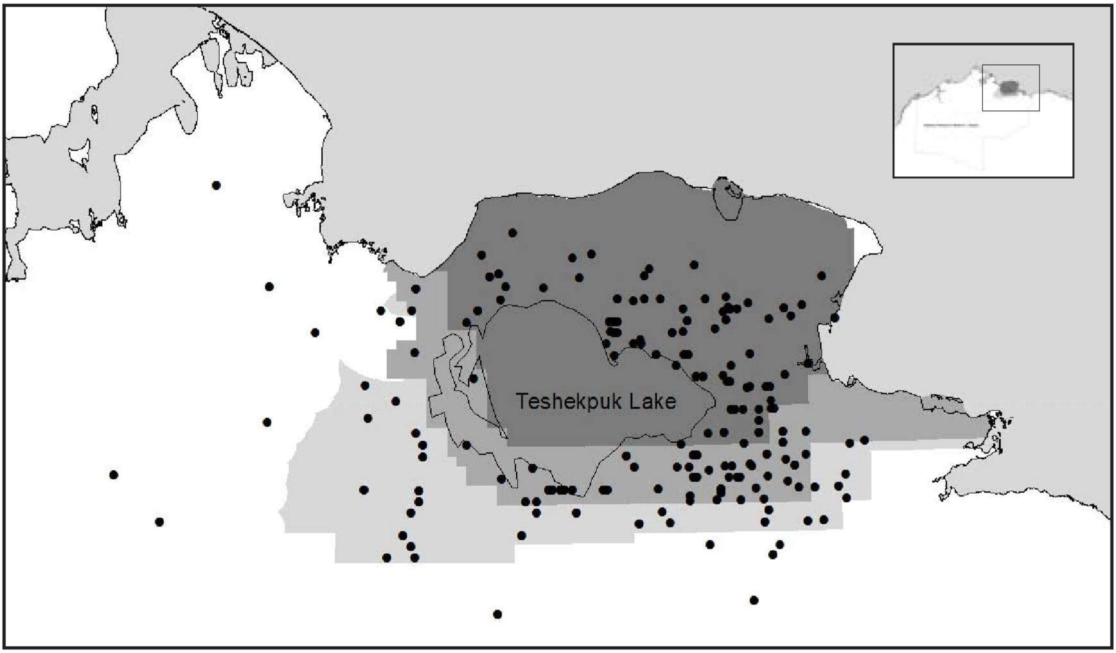

Fig. 2. Teshekpuk Lake area showing Teshekpuk caribou herd calving locations in relation to Bureau of Land Management Environmental Impact Statement protective boundaries from 1994 to 2003 (see Fig. 1). Note, there are 2 calving locations located farther west that are not shown on this close-up.

a paired *t*-test, and movement rates of cows that were seen with a calf versus cows that were not with an unpaired *t*-test (Zar, 1999).

Because re-location intervals differed slightly among individuals, average daily movement rates were calculated from the net distance moved and the number of days moved between relocations. Because the number of days between relocations was inversely related to the calculated rate of travel ($P = 0.03$) (suggesting that longer intervals between relocations were likely to underestimate the true daily rate of travel), rates were standardized, adding 497 meters per day between relocations to the estimated rate, based on the slope of the relocation interval and movement-rate regression.

Results

Calving distribution

BLM protective boundaries, as established in the 1998 EIS for the northeast section of the NPR–A, encompassed the area that received the highest use during the calving period (Fig. 2). Of 171 collared cows seen with a calf, 155 (91%) were located within the protective boundaries delineated in 1998. The mean annual percentage of collared cows with calves found within the protective boundaries was 90.0% (Table 1). In contrast, of the 89 cows that were not seen with a calf during the survey period, only 40 (44.9%) were within the protective boundaries at the middle of the calving period.

Yearly calving distributions in relation to snowmelt

Snowmelt date in Barrow ranged from 25 May to 14 June. Latitude of the center of the annual calving distribution was inversely related to the date of snowmelt ($P = 0.004$, $r^2 = 0.66$) (Fig. 3). When snowmelt dates were earlier, calving locations were farther north. The longitude of the distributional center of annual calving and snowmelt date were not correlated ($P = 0.62$). There was also no trend in calving site location over time ($P = 0.27$).

Percentage of cows seen with calves

The percentage of cows seen with calves during the calving period has ranged from 44% in 2001 to 86% in 1996 (Table 1). The 2 years that had the lowest percentage of observed calves were 2001 (44%) when late, deep snow conditions appeared to hinder the spring migration and 1997 (50%), when most of the herd migrated much farther south in winter than usual. There was no correlation however, between the percentage of cows seen with calves and snowmelt date in Barrow ($P = 0.59$).

Calving period movements

Of the 23 cows observed with calves in 2002, 7 were first observed before being seen with a calf, and 16

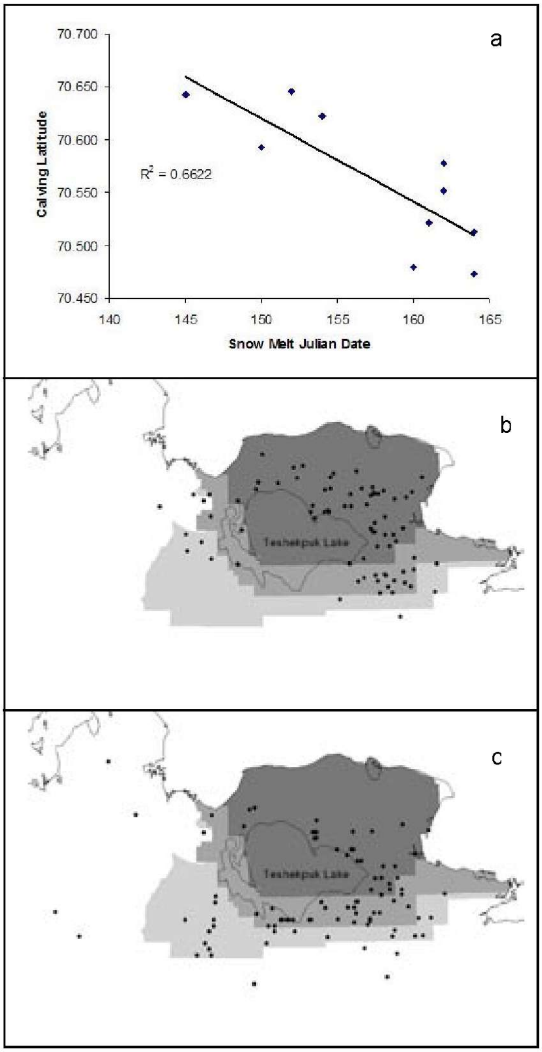

Fig. 3. Teshekpuk caribou herd calving distributions and snowmelt dates 1994 to 2003: (a) latitude of the center of annual calving distribution vs. Julian date of snowmelt, (b) calving distribution in years with earlier than average snowmelt, average date 30 May, (c) calving distribution in years with later than average snowmelt, average date 12 June.

were seen with a calf when first observed. For parturient cows, average standardized travel rate was significantly higher before being observed with a calf than after (7.25 vs. 3.89 km/d, $P = 0.02$, $n = 7$). The difference in net distance moved during the calving period for cows with calves versus cows without calves was marginally significant (1.09 vs. 3.97 km/d, $P = 0.058$, $n = 28$). Net movement direction of cows averaged 104 degrees, but was not significantly different from random (Rayleigh's $R = 4.57$, $n = 28$).

Discussion

Multiple previous studies have shown fidelity of the TCH to the calving area near Teshekpuk Lake (Carroll, 1992; Philo *et al.*, 1993; Kelleyhouse, 2001; Prichard *et al.*, 2001; Carroll, 2003; Noel & George, 2003). In order to protect this calving area and waterfowl habitat areas, BLM created protective boundaries in its 1998 IAP/EIS, which appear to adequately encompass annual variance in the preferred calving areas of the TCH. During our study, from 1994 through 2003, 171 collared cows were seen with a calf and 155 (91%) were located within the protective boundaries. Annually, the mean proportion of calving cows within the protected boundaries averaged 90 ± 2%. If development occurs within these protective boundaries in the future, this baseline measure could be compared to future averages as an indicator of displacement, absent any simultaneously occurring environmental changes.

Similar to other studies of telemetered female caribou (Fancy *et al.*, 1989; Kelleyhouse, 2001; Griffith *et al.*, 2002; Ferguson & Elkie, 2004), TCH females in our study moved at relatively slow rates during the calving period, and slowed even more following parturition, giving us confidence that the location where a cow was first seen with a calf was reasonably close to the calving site. We also found that cows, parturient or otherwise, were not moving in a consistent direction during the calving period, similar to findings by Fancy & Whitten (1991). This implies that there is no systematic directional bias in calving site estimation. We assume that the results of movement analyses from 2002 are consistent in other years, although it should be mentioned that 2002 was a year with very early snowmelt. Years with deep or persistent snow may lead to different patterns in calving period movement.

Annual variation in the distribution of TCH calving sites during most years appeared to be related primarily to time of snowmelt. During years when the snowmelt was earlier, calving sites tended to be farther north. Unlike bull caribou, which appear to track the northward progression of green-up during the spring (Whitten & Cameron, 1980; G. Carroll, ADF&G, unpubl. data), parturient cows in the CAH and TCH often arrive on the calving grounds before green-up has occurred (Whitten & Cameron, 1980; Kelleyhouse, 2001). Newly emergent and rapidly growing vegetation is high in soluble carbohydrates, nitrogen and phosphorus, which rapidly decline as the summer progresses (White *et al.*, 1975; Whitten & Cameron, 1980; Jorgenson *et al.*, 2002). By calving in areas just beginning to initiate new growth, the relatively immobile cow–calf pairs are able to take advantage of this green-up without having to follow this progression northwards, and this perhaps allows calves to initiate independent foraging with high quality, low bulk forage. This result supports the findings of Kelleyhouse (2001), who concluded that at the scale of the concentrated calving area versus the annual calving ground, the TCH consistently selected areas with high rates of biomass increase, as measured by the change in the Normalized Difference Vegetation Index (NDVI). The tendency for caribou to shift the distribution of the annual calving ground in response to the unique conditions encountered each year within the protective boundaries needs to be considered when establishing long-term protective measures. Specific areas within the protective boundaries may be more likely to be used in an average year than others, but the entire area is utilized, given enough variance in environmental conditions.

In addition to snowmelt date, distribution of female caribou during the calving periods, along with calf percentages, can be affected by factors such as where the caribou migrated the previous fall and unusual weather conditions. During winter 1996–1997 most of the herd migrated much farther south than usual, and in spring 2001 unusually deep, persistent snow throughout northern Alaska restricted spring migration (Lawhead & Prichard, 2002; Griffith *et al.*, 2002; Dau, 2003), resulting in fewer cows arriving at the traditional calving area during the calving period. The lowest percentages of collared cows with calves were recorded during spring 1997 (50%) and 2001 (44%), compared to a range of 56%–86% for other years. The low calf percentages during these 2 years may have been partially due to poor perinatal calf survival resulting from the unusually long migration in 1997; adverse snow conditions in 2001; and, possibly, because some parturient cows were hindered from getting to the preferred calving area. The condition of cows during the previous fall would have also had a substantial, but unknown, effect on the productivity of the herd (Cameron *et al.*, 1993, 1994).

While Teshekpuk caribou showed great fidelity to the calving area, it is unknown if development in the area would result in negative population size effects. In the neighboring CAH, concentrated calving in the western, developed portion, of the calving ground shifted to the south and southwest as infrastructure density increased, 1980–1995 (Wolfe, 2000; Cameron *et al.*, 2002). Although photocensus results from the Alaska Department of Fish and Game indicate that the herd has continued to grow through 2002 (Cameron *et al.*, 2002; Noel *et al.*, 2004), density of caribou in the developed area north of the "spine road" has decreased, particularly during calving, from 1978 to 2001 (Lawhead & Prichard, 2003; Noel *et al.*, 2004). Portions of the historical CAH calving grounds west of the Kuparuk River that have received the most use during the calving and postcalving periods in recent years (1993–2003) are south or southwest of the Kuparuk oilfield complex (Wolfe, 2000; Lawhead & Prichard, 2003). Although the CAH population size continued to increase (Cameron *et al.*, 2002) after the shift in concentrated calving away from the Kuparuk Development Area (Wolfe, 2000), lower parturition rates of cows calving in the more developed, western portion of the calving ground compared to those calving in the relatively undeveloped eastern portion of the calving ground were documented from 1988 through 1994 (Cameron *et al.*, 2002), and from 1998 through 2001 (E. Lenart, presented by the National Research Council [NRC], 2003). However, there were not similar differences in calf survival between the western and eastern portions of the calving ground (NRC, 2003).

Although we have shown that parturient TCH cows have demonstrated a historical fidelity to the calving area within the protected boundaries described in this paper, the potential for negative population size effects as a result of displacement due to forthcoming industrial development is a serious issue, and one that cannot be adequately addressed for the TCH at this time. Future research should be directed toward determining the fitness advantages derived from use of preferred, or concentrated calving areas versus peripheral areas, as well as determining baseline levels of calf survival and weight gain of cows and calves during the period that cow–calf pairs use the calving grounds.

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Two caribou mortality events in Northwest Alaska: possible causes and management implications

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Abstract: During fall and winter 1994–1995 and winter 1999–2000, caribou (*Rangifer tarandus granti*) from the Western Arctic Herd experienced high, localized mortality in northwest Alaska near Cape Thompson. Substantial numbers of caribou wintered in this area during 1986–1987, 2001–2002, and 2002–2003 without suffering high mortality. During the 1994–1995 event, 2000 to 3000 caribou died out of roughly 10 000 that wintered in this area. About 4000 caribou perished out of approximately 20 000 that wintered here during 1999–2000. During both mortality events, gross characteristics and tissue analyses indicated caribou in this area were malnourished. Weather near Cape Thompson during winter 1994–1995 was colder, windier, and had more snow than other years when caribou wintered in this area; in contrast, conditions during 1999–2000 were not unusually severe. Additionally, Cape Thompson experienced 2–5 occurrences of severe conditions during winter 1994–1995 while 1999–2000 experienced only 1 such occurrence at most. Several indicators suggested severe storms killed some caribou before starvation was fatal. Cape Thompson consistently experienced higher wind, lower ambient air temperature, and shallower snow cover than other portions of winter range used by this herd. Unlike years when caribou wintered in this area without experiencing high mortality, caribou were in relatively poor body condition during the autumn that preceded each die-off. Although these mortality events were inconsequential to size of this caribou herd, they raised local residents' concerns that contaminants had poisoned caribou and possibly jeopardized human health. Muskoxen *(Ovibos moschatus)* in this area were not affected by weather or snow conditions during either caribou mortality event.

Key words: caribou, malnutrition, mortality, *Rangifer tarandus*, snow, weather, windchill.

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Introduction

Most caribou (*Rangifer tarandus granti*) of the Western Arctic Herd (WAH) have wintered in southern portions of their range since the mid-1980s. However, during winters 1986–1987, 1994–1995, 1999–2000, 2001–2002 and 2002–2003, ≥30 000 WAH caribou wintered in the northwest portion of their range. During two of these winters (1994–1995 and 1999–2000) caribou wintering along the Chukchi Sea coast between Cape Lisburne and Cape Krusenstern experienced high, localized mortality. During both events the highest mortality was near Cape Thompson, an area characterized by chronic high wind and severe winter weather (Wilimofsky, 1966).

These die-offs concerned users and managers of the WAH for several reasons. The WAH last peaked at 242 000 caribou in 1970 and then declined to 75 000 caribou by 1976. From 1976 to 1990 the WAH grew 13% annually. It has numbered >400 000 caribou since 1990 and in 2003 numbered 490 000 caribou (Dau, in prep.). The total range of this herd encompasses ~363 000 km^2 (140 000 mi^2). In 2003, density of the WAH over its total range was 1.4 caribou/km^2 (3.6 caribou/mi^2). However, the 'functional density' (estimated number of caribou present on a seasonal range from telemetry data/area of seasonal range) individual caribou experienced on a daily basis has been much higher. For example, density on summer range reached 4.1 caribou/km^2 (10.7 caribou/mi^2) in 2003, and the maximum density observed on winter range was 10.2 caribou/km^2 (26.4 caribou/mi^2) in the Nulato Hills during 1990–1991 (Dau, 2003). These winter range densities are conservative because they do not include caribou from the Teshekpuk Lake Herd, Central Arctic Herd (CAH), or Seward Peninsula reindeer (*Rangifer t. tarandus)* that also use portions of WAH winter range. The sustained high WAH population level and high seasonal densities raise the possibility of another precipitous decline in the future.

Additionally, caribou are a critical source of meat for most residents of northwest Alaska and provide a vital link to the cultural identity of indigenous users. Recreational use of the WAH by nonconsumptive users is increasing as the availability of wild and remote areas declines worldwide. Similarly, use of the WAH by recreational hunters and commercial operators has increased as hunting opportunities in other portions of Alaska have been restricted. Finally, proximity of these mortality events to potential sources of environmental contaminants, e.g., radionuclides from the Project Chariot site and heavy metals from the Red Dog Mine, caused residents of this area to question whether caribou had been poisoned and, in turn, jeopardized human health.

This paper describes these caribou mortality events and examines the roles weather, snow, and severe storms may have played in causing them. It also describes management implications of both die-offs and contrasts behavioral and population responses of a resident muskox *(Ovibos moschatus)* population to WAH caribou.

Methods

Physical and biological systems near Cape Thompson have been previously described (Wilimofsky, 1966). Vegetation is largely decumbent and sparse on exposed ridge tops (Johnson *et al*., 1966).

After receiving reports from hunters of small numbers of dead and moribund caribou near Point Hope during winters 1994–1995 and 1999–2000, we searched the area within 15–25 km (10–15 mi) of the Chukchi Sea coast between Cape Krusenstern and Cape Lisburne during May and June 1995 and June 2000 using a Piper PA-18 airplane. Residents of Kotzebue, Kivalina, and Point Hope were hired as observers during these flights. We flew transects or contour lines depending on terrain to maximize search coverage. We searched for carcasses a total of 21.7 hr on 4 and 6–8 June 1995, and 23.2 hr during 3–5 June 2000. In both years, high wind prevented us from searching roughly 300 km^2 (115 mi^2) of the northernmost tip of the Lisburne Hills. In 1995 and 2000, search intensity was approximately 0.4–0.8 min/km^2 (1–2 min/mi^2) over elevated terrain (~1000 km^2 or ~400 mi^2) where most carcasses were located, and 0.2 min/km^2 (0.5 min/mi^2) over lowland tussuck tundra. Decumbent vegetation, sun-bleached hair and the presence of antlers on many bulls in 1995 made carcasses easily visible for up to 1 km (0.5 mi) from the airplane. We did not attempt to quantify a correction factor for carcasses missed during the surveys. Also, during aerial searches we did not attempt to distinguish males from females, or calves from adults, because too many carcasses were nondescript.

During June and early July 1995, a team consisting of a wildlife veterinarian/pathologist (J. Blake, University of Alaska Fairbanks), a veterinary toxicologist (T. O'Hara, North Slope Borough Department of Wildlife Management), two wildlife biologists (C. George, North Slope Borough Department of Wildlife Management and G. Carroll, Alaska Department of Fish and Game) and residents of Point Hope (E. Kingik & R. Koonuk) examined 101 caribou carcasses in the vicinity of Cape Thompson. Gross body characteristics were recorded during necropsies and tissue samples were collected to evaluate levels of heavy metals (arsenic, cadmium, copper, lead, zinc and iron; O'Hara *et al.*, 2003) and radionuclides (gross alpha and beta emissions as well as cesium-137, potassium-40, and strontium-90; O'Hara *et al.*, 1999). During 7–11 June 2000, 2 wildlife veterinarians (V. Woshner, North Slope Borough Department of Wildlife Management and C. Rosa, University of Alaska Fairbanks) necropsied 34 caribou carcasses in the vicinity of Cape Thompson using the same methods as in June 1995 (Woshner *et al.*, in prep.); however, radionuclide levels were not evaluated in 2000.

I purchased daily means of weather and snow parameters for Kotzebue, Barrow, Bettles, Nome, and Unalakleet from the National Oceanic and Atmospheric Administration (http://lwf.ncdc.noaa.gov). I estimated weather and snow conditions at Cape Thompson using Kotzebue weather data and monthly relationships reported by Allen & Weedfall (1966). For this paper, 'winter' is the period 1 October–15 April. I defined a severe storm as any day having a mean wind speed ≥15 mph (24 km/hr) and an average windchill ≤-60 °F (-51 °C): this corresponds to U.S. Department of Commerce (1998) criteria for issuing a 'weather warning.' I calculated windchill values using the recently revised formula provided by the National Weather Service (www.nws.noaa.gov/om/windchill):

$$\text{Windchill } (^\circ\text{F}) = 35.74 + 0.6215\,(T_a) - 35.75\,(W_{vel}^{0.18}) + 0.4275\,(T_a)\,(W_{vel}^{0.18})$$

T_a = ambient air temperature (°F)
W_{vel} = wind velocity (mi/hr)

Snow works together with wind and ambient air temperature to affect caribou. Although 'windchill' combines the latter two variables, there is no convention for integrating the effects of snow with windchill. Therefore, I calculated a daily index of environmental severity using mean values of standing snow depth and windchill:

$\text{Index}_{\text{daily severity}} = (-1 * \text{windchill} + 150) * (\text{daily snow depth} + 0.1)$

Units for this index are °F-inches

I multiplied windchill by -1 and added a constant (150) to make this value >0 for all days so that windchill and cumulative snow depth would complement rather than negate each other. I added a constant (0.1) to snow depth so that the index on days having no snow would not be reduced to 0 regardless of windchill.

Besides acting synergistically with other weather parameters, the effects of snow on caribou are also cumulative over the course of a winter. For example, 30 cm of snow that falls in October and persists through April has a greater effect on caribou than 30 cm of snow that falls in late March. Therefore, I calculated a cumulative index of environmental severity using daily values for windchill and cumulative snow depth at Ogotoruk Creek:

$\text{Index}_{\text{cumulative severity}} = (-1 * \text{windchill} + 150) * (\text{sum of daily snow depth} + 0.1)$

Units and constants for this cumulative index of environmental severity were identical to those used for the daily index. The only difference between these indices is that snow depth was summed by day to incorporate duration of snow cover for the cumulative index of environmental severity.

I used caribou winter distribution reported by Dau (2003) to identify years and weather stations for comparing weather and snow conditions. I attempted to separately estimate the number of days mosquitoes and oestrid flies were present on WAH summer range during 1994 and 1999 using relationships developed by Dau (1986) with weather data from Kotzebue and Barrow.

Beginning in 1995, fall body condition of caribou was evaluated in September during capture operations. The body condition of each caribou handled was subjectively ranked 1 (emaciated) - 5 (very fat) based on the presence of subcutaneous fat and prominence of ribs, scapula, and spine.

To evaluate the role weather may have played in these die-offs, I tested the following null hypotheses:

1. There was no difference in weather or snow conditions at Cape Thompson between winters of high mortality (1994–1995 and 1999–2000) and winters of typical mortality (1986–1987, 2001–2002, and 2002–2003).
2. For winters 1994–1995 and 1999–2000, there was no difference in weather or snow conditions between Cape Thompson and other areas where WAH caribou wintered.

I did not combine years to evaluate spatial differences in weather conditions among caribou wintering areas during 1994–1995 and 1999–2000 (hypothesis 2) because specific wintering areas changed annually. For these comparisons, I only considered portions of range having a winter density >0.8 caribou/km^2 (2.0 caribou/mi^2) in any individual year.

I used Statistix8 analytical software (www.statistix.com) to calculate indices of environmental severity; provide descriptive statistics (median, mean, variance, skewness, and kurtosis); plot distributions of weather parameters through time; and plot frequency distributions of temperature, snow depth, and windchill. I used Kruskall-Wallis tests for multiple pairwise comparisons of median weather values among caribou wintering areas and years, and considered *P*-values <0.05 statistically significant.

Results

Caribou mortality

1994–1995 mortality event

Snow obscured carcasses during three aerial searches in May 1995. In June 1995 we observed 1127 caribou carcasses. The carcasses were distributed over 4400 km^2 (1700 mi^2) within approximately 15–25 km (10–15 mi) of the Chukchi Sea coast (Fig. 1). This area comprises roughly 11% of 'WAH wintering area 9' defined by Dau (2003). The highest density of carcasses was within a 1000-km^2 (625 mi^2) area near Cape Thompson. We subjectively estimated up to 3000 caribou died during this event based on the proportions of areas searched at high intensity, low intensity or not searched at all. While conducting telemetry surveys I visually estimated roughly 10 000 caribou wintered in this area during 1994–1995.

Although caribou carcasses were distributed throughout the area, most were located on ridge tops or hillsides. We did not record the posture of intact carcasses but roughly 25–50% of them were sternally recumbent and curled as if asleep or, if on their side, had their head and neck curled back over their

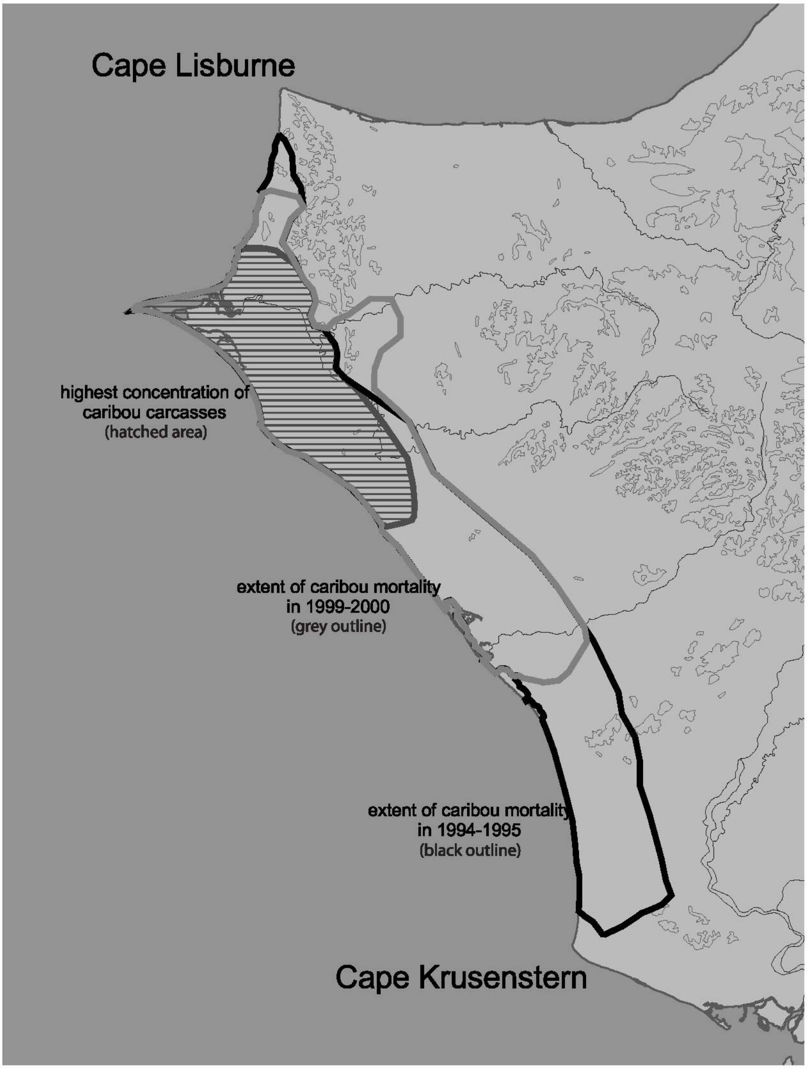

Fig. 1. Extent of caribou mortality and area of highest mortality during the 1994–1995 and 1999–2000 Western Arctic Herd mortality events in northwest Alaska.

body. Many carcasses were distributed in clusters of two to six individuals as if they had been part of a group and died within a brief time span. Many carcasses of mature bulls had 1 or both polished antlers attached to the skull. Mature WAH bulls typically begin casting their antlers during the last few days of October. The presence of hard antlers on these individuals suggests this mortality event began before mid-November 1994. Using the visual index scores developed by Neiland (1970), carcass femur marrow ranged from grade 2 (red, waxy, and filling the bone cavity) to grade 1- (deep red, mucous-like, and filling <50% of the bone cavity). The abundance of carcasses in the area overwhelmed large scavengers' capacity to consume them. Many carcasses remained virtually intact aside from loss of hair well into July, and some skeletons were still mostly articulated during summer 1996.

Necropsies of carcasses revealed extreme emaciation, serous atrophy of bone marrow, atrophy of the liver, and rocks and mineral soil in the abomasum. There were no lesions indicative of poisoning; likewise, laboratory analyses revealed no indication of poisoning by heavy metals (O'Hara *et al.*, 2003) or radionuclides (O'Hara *et al.*, 1999).

1999–2000 mortality event

As in 1995, snow obscured all carcasses during an aerial search conducted in May 2000. We observed 1878 caribou carcasses within a 3400 km^2 (1300 mi^2) area during 3–5 June 2000 (Fig. 1). This was roughly 8% of 'wintering area 9' defined by Dau (2003). During telemetry surveys I visually estimated roughly 20 000 caribou wintered in the mortality area during 1999–2000 and about 4000 caribou perished during this event. The area of highest mortality was virtually identical to that for the 1994–1995 event. Unlike 1995 however, we observed many carcasses on large ice-covered coastal lagoons in June 2000.

During late April 2000, I retrieved a radio collar from a female caribou that had died approximately 10 km (6 mi) northeast of Cape Thompson. The carcass was frozen on top of the snow and had not been scavenged by ravens (*Corvus corvax*) or foxes (*Vulpes vulpes* or *Alopex lagopus*). It appeared the cow had died two to four days before I located her. She showed no evidence of trauma and had no fluid discharge from any body orifice. The prominence of her hips, ribs and spine indicated the cow was emaciated at the time of death. Her frozen state precluded an internal examination. I broke metacarpal and metatarsal bones and her marrow was waxy and filled the bone cavity but was deep red and soft. This corresponds to a 'grade 2' visual marrow condition as reported by Neiland (1970). The deep red color of the marrow in this collared cow indicated depletion of fat reserves (Cheatum, 1949 as reported by Kirkpatrick, 1980) and was consistent with her general appearance. Nieland (1970) reported a mean marrow fat content of 42% for caribou in this grade. This suggests her fat reserves were not totally exhausted at the time of death. I speculate this cow, weakened by chronic malnutrition, died of exposure during a severe storm. Caribou fecal pellets were widely scattered over the snow surface in this general area and were <50% normal size, black, dry, and hard. Virtually all frozen urine in the area was dark brown and opaque, which could indicate caribou were catabolizing protein to stay alive.

Reports from hunters indicated a disproportionate number of calves died compared to adult caribou. Composition surveys conducted in April 2000 were consistent with these reports: we observed six 10-month-old calves:100 adult caribou within the mortality area compared to 20 calves:100 adults in other portions of winter range. During these surveys we occasionally saw caribou in the mortality area stagger as they attempted to flee the airplane. Many caribou that were lying down did not get up or show any response to the plane whatsoever.

As in 1995, gross characteristics of carcasses necropsied during June 2000 suggested caribou were malnourished. Laboratory analyses revealed no indication of heavy metal poisoning (O'Hara *et al.*, 2003; Woshner *et al.*, in prep.).

Winter weather at Cape Thompson during years of high vs. *normal mortality*

I rejected the null hypothesis of 'no difference among the five years when caribou wintered near Cape Thompson' for each weather parameter (Kruskall-Wallis tests, all n_i = 985 days, all $P<0.05$). Winter 1994–1995 was colder and windier with more snow than other years when caribou were present in this area (Table 1). While pairwise comparisons of years revealed many statistically significant differences for each weather parameter (Table 2), differences in median values for these variables seem too small to be biologically significant (Table 1). The statistical significance of these differences is probably an artifact of large sample sizes (n_i = 197 days for each weather parameter annually). A possible exception to this was snow depth; in 1994–1995, median snow depth at Cape Thompson was 28.2 cm (Table 1). While this is generally not considered severe for caribou, it was two to five times deeper than any other year when caribou wintered in this area. Maximum snow depth in 1994–1995 was only somewhat greater than other years. Median snow depth was high because snow fell early, it approached maximum levels by mid- to late November and remained deep beyond mid-April. Even so, maximum and median snow depths during 1994–1995 were modest compared to levels reported in other parts of WAH range where mortality was not elevated (Table 1). Median values of individual weather parameters at Cape Thompson during 1999–2000 were not particularly severe compared to other years when caribou wintered in this area.

The index of daily winter severity graphically revealed acute weather events that were not evident in median values of individual weather variables. This approach illustrated that harsh combinations of snow and windchills occurred earlier during winter, occurred more frequently, reached more severe levels and persisted longer during 1994–1995 than any other year when caribou wintered in this area (Figs. 2 and 3). In contrast, this index indicated snow and weather conditions during 1999–2000 were similar to the three years of normal mortality near Cape Thompson except that one bout of modestly severe conditions occurred in early February 2000. The maximum index of severity reached in February 2000 barely exceeded minimum levels of severity that persisted from mid-November 1994 through April 1995. Although the temporal pattern for the index of daily severity varied among years, only 1994–1995 was substantially different from other years in terms of magnitude and shape. Therefore, I only show this index for 2001–2002 (Fig. 3) as an example of a winter that did not have unusually severe weather.

Snow depth largely determined the general shape of the cumulative index of winter severity (Figs. 2 and 3). In all but 1994–1995, acute storms evident in the daily indices of severity were largely obscured by the effect of snow accumulation. In 1994–1995, though, the magnitude of windchills was such that five or six storms occur as spikes in the general trend of this index. Although it seems conceptually reasonable to meld duration with depth when trying to assess the effects of snow on caribou, the daily index of severity that ignored snow accumulation better reflected acute periods of severe conditions. A strength of the cumulative winter severity index is that it ascribes a higher value to a late winter storm than to one of equal strength that occurs in late fall or early winter. As with the daily index of severity, the shape and magnitude of the cumulative index of severity was substantially different only during winter 1994–1995. Therefore, in the interest of space, I only show this index for 2001–2002 (Fig. 3) as an

Table 1. Winter[a] weather and snow conditions near major Western Arctic Herd wintering areas during years of high caribou use of the Cape Krusenstern–Cape Lisburne area, northwest Alaska[b].

Year	Caribou wintering area	Weather station	Median air temp. (°C)	Median wind velocity (m/sec)	Median windchill (°C)	Median snow depth (cm)	# Days wind ≥11 m/sec (25 mph)	# Days wind ≥22 m/sec (50 mph)	# Days windchill ≤40 °C	# Days windchill ≤60 °C	# Severe storms
1986–1987	Lisburne Hills/Noatak/Wulik/Kivalina[c]	Kotzebue[d]	-14.8	8.7	-27.7	14.0	67	14	43	7	1
	Nulato Hills	Unalakleet	-5.0	6.2	-14.9	2.5	17	0	4	0	0
	Kobuk/Selawik/Buckland	Kotzebue	-13.0	4.5	-21.7	38.1	16	0	14	0	0
	North Slope	Barrow	-21.2	5.1	-34.4	22.9	2	0	62	0	2
1994–1995	Lisburne Hills/Noatak/Wulik/Kivalina[c]	Kotzebue[d]	-16.6	9.5	-30.7	28.2	81	17	60	8	2
	Nulato Hills	Unalakleet	-10.6	4.2	-17.9	12.7	9	0	8	0	0
	Kobuk/Selawik/Buckland	Kotzebue	-16.0	4.9	-26.0	91.4	14	0	20	0	0
	Seward Peninsula	Nome	-10.0	3.7	-16.8	101.6	1	0	0	0	0
1999–2000	Lisburne Hills/Noatak/Wulik/Kivalina[c]	Kotzebue[d]	-17.2	6.5	-28.7	7.8	52	6	32	0	0
	Kobuk/Selawik/Buckland	Kotzebue	-16.0	3.7	-23.2	15.2	6	0	8	0	0
	Seward Peninsula	Nome	-9.4	3.4	-16.1	10.2	1	0	2	0	0
	middle Koyukuk	Bettles	-14.4	2.6	-21.7	40.6	0	0	13	0	0
2001–2002	Lisburne Hills/Noatak/Wulik/Kivalina[c]	Kotzebue[d]	-16.6	7.9	-28.7	5.3	62	16	10	5	1
	Kobuk/Selawik/Buckland	Kotzebue	-14.0	3.9	-23.0	17.8	12	0	9	0	0
	Seward Peninsula	Nome	-10.0	3.2	-16.6	15.2	2	0	2	0	0
	central Brooks Range	Bettles	-16.1	2.0	-20.8	45.7	0	0	3	0	0
2002–2003	Lisburne Hills/Noatak/Wulik/Kivalina[c]	Kotzebue[d]	-12.6	7.5	-24.8	10.6	60	9	18	3	1
	Kobuk/Selawik/Buckland	Kotzebue	-11.0	4.1	-18.4	27.9	8	0	4	0	0
	Seward Peninsula	Nome	-6.1	3.9	-11.9	7.6	1	0	0	0	0
	central Brooks Range	Bettles	-13.9	2.2	-19.0	40.6	0	0	4	0	0

[a] 'Winter' defined as 1 Oct–15 Apr.

[b] Weather and snow parameters calculated from daily mean values reported by the National Oceanic and Atmospheric Administration.

[c] Includes area of high caribou mortality in 1994–1995 and 1999–2000 (Dau, in press)

[d] Weather and snow values for this area estimated from Kotzebue weather observations (Allen & Weedfall, 1966).

Table 2. Kruskall-Wallis test statistics for multiple pairwise comparisons of weather parameters estimated[a] for Cape Thompson during years when caribou wintered in this area; an italicized value indicates a statistically significant difference (all n_i = 197 days; all critical values = 80.46; all $P<0.05$).

		Year			
	Mean rank	1986–1987	1994–1995	1999–2000	2001–2002
Air temperature					
1986–1987	513.5				
1994–1995	435.7	77.73			
1999–2000	451.1	62.40	15.34		
2001–2002	469.9	43.53	34.21	18.87	
2002–2003	594.8	*81.35*	*159.08*	*143.75*	*124.87*
Wind velocity					
1986–1987	552.3				
1994–1995	546.2	6.08			
1999–2000	424.0	*128.22*	*122.14*		
2001–2002	459.4	*92.85*	*86.77*	35.37	
2002–2003	483.1	69.14	63.06	59.08	23.71
Windchill					
1986–1987	494.3				
1994–1995	413.7	*80.62*			
1999–2000	475.1	19.18	61.44		
2001–2002	479.3	15.00	65.62	4.18	
2002–2003	602.7	*108.42*	*189.04*	*127.60*	*123.42*
Snow depth					
1986–1987	467.9				
1994–1995	840.1	*372.20*			
1999–2000	427.3	40.58	*412.77*		
2001–2002	275.1	*192.81*	565.01	*152.23*	
2002–2003	429.4	38.46	*410.66*	2.11	*154.35*

[a] Values estimated from daily means of weather and snow depth measurements recorded in Kotzebue (Allen & Weedfall, 1966).

example of typical winter conditions.

Winter weather at Cape Thompson compared to other caribou wintering areas

During each of the five years when caribou were present near Cape Thompson most of the WAH wintered in other portions of its range as well (Table 3).

For each of the five winters I rejected the null hypothesis of 'no difference among wintering areas' for each weather variable (Kruskall-Wallis tests; all n_i = 197 days except for Unalakleet where n_i = 125 days; all $P<0.05$). In all years Cape Thompson experienced higher wind, less snow, lower ambient air temperature, and lower windchill temperature than other wintering areas except for the North Slope in 1986–1987. In each of the five years when caribou were present near Cape Thompson, wind velocity was significantly higher than in any other wintering area (Kruskall-Wallis pairwise comparisons, all $P<0.05$). The relatively deep snow at Cape Thompson in 1994–1995 (28.2 cm) was significantly less than on the Seward Peninsula (101.6 cm) or in the Kobuk–Selawik–Buckland drainages (91.4 cm) where substantial numbers of WAH caribou wintered (Kruskall-Wallis pairwise comparisons, both $P<0.05$).

In only one year (1986–1987) did a wintering area (North Slope) have more days of ≤-40 °C windchill than Cape Thompson. In four of five winters Cape Thompson was the only area that had any days with an average daily windchill ≤-60 °C. Similarly, Cape Thompson tended to experience one to two severe storms each winter based on U.S. Department of Commerce criteria. The North Slope was the only other wintering area that experienced a severe storm (one during 1986–1987). Ironically, the only year Cape Thompson did not experience at least 1 severe storm was 1999–2000. Compared to Kotzebue weather during nine years (1986–1987, 1987–1988, 1988–1989, 1991–1992, 1994–1995, 1995–1996, 1999–2000, 2001–2002, and 2002–2003) when density was >0.8 caribou/km^2 (2.0 caribou/mi^2) in the Kobuk/Selawik/Buckland drainages, winter 1999–2000 at Cape Thompson was not severe by any measure (Kruskall-Wallis multiple pairwise comparisons, all $P<0.05$).

Caribou body condition

Many WAH caribou were in relatively poor body

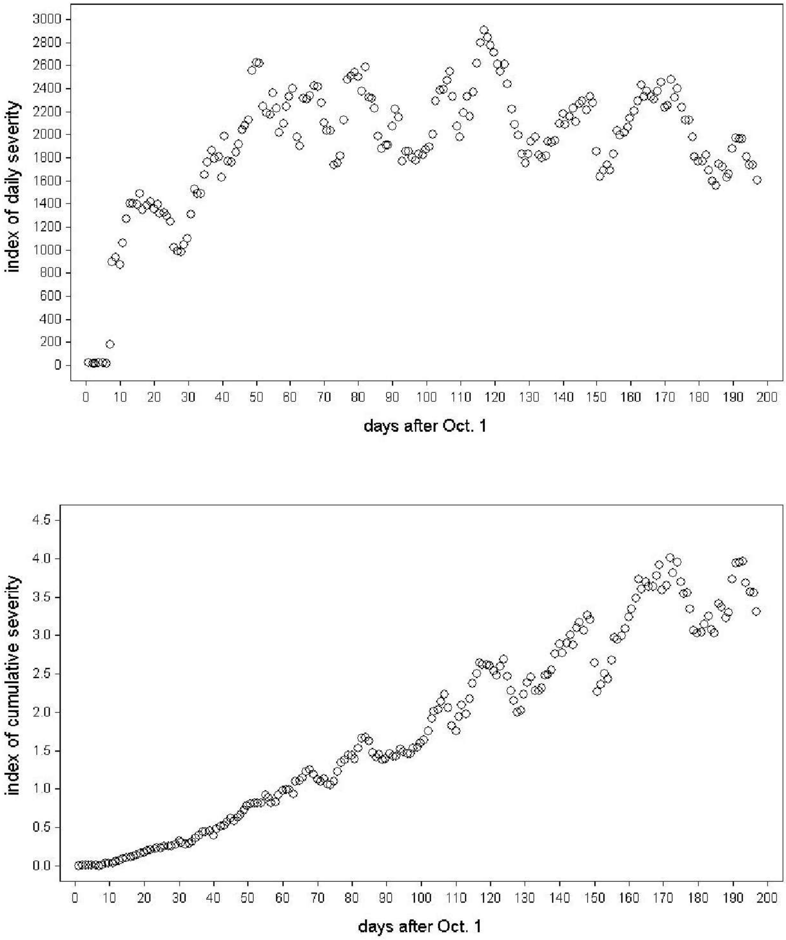

Fig. 2. Daily (top) and cumulative (bottom) indices of winter severity near Cape Thompson, Alaska, 1994–1995.

condition during the September preceding each mortality event. During WAH capture work at Onion Portage we did not begin recording body condition of individual caribou until September 1995. Indeed, the 1994–1995 die-off prompted us to begin recording this information during capture operations; however, we did note that many caribou were in poor condition during September 1994. Additionally, Valkenburg *et al.* (1996) reported body weights of female WAH calves collected in fall 1994 (71.5 lb) were lower than fall 1992 (89.2 lb) and fall 1995 (81.1 lb). Caribou captured at Onion Portage were in poor condition in September 1999 compared to other years (Fig. 4). Although we have no specific information regarding the fall body condition of caribou that wintered near Cape Thompson, there is no reason to believe their condition was substantially different from WAH caribou in other portions of their range.

Effects of winter conditions on muskoxen

Direct observations of muskox and their tracks during winters 1994–1995 and 1999–2000 revealed no unusual behavior: muskoxen were distributed on wind swept ridge tops and exhibited little movement or activity. We located only 1 muskox carcass following the 1994–1995 caribou mortality event, and none following the 1999–2000 event. During a muskoxen census between Cape Krusenstern and Cape Lisburne during June–July 2000, adult mortality appeared normal and calf production was the highest ever observed (30 calves:100 adults).

Discussion

Skoog (1968) noted that caribou are well adapted to northern climes and stated that weather conditions, other than icing events, are unlikely to affect the dynamics of mainland populations. Skoog (1968) further indicated coastal areas are most prone to icing from freezing rain or crusting by freeze-thaw cycles. Icing conditions are most common, and their significance to caribou most pronounced, during late winter and spring when caribou are migrating and females are carrying a near-term fetus. Similarly, Davis & Valkenburg (1985) reported there was no evidence that weather had directly influenced the population dynamics of the WAH since 1960. Reports of weather conditions substantially impacting caribou populations indicate these effects are mostly manifested through high calf mortality especially during parturition (Jackson 1900, 1904, 1906; Banfield, 1954; Kelsall, 1957; all as reported by Skoog, 1968). During a panel discussion regarding the effects of severe storms on caribou at the Tenth North American Caribou Workshop (Girdwood, Alaska, May 2004), each of the four panelists (with extensive experience as big game guides,

Table 3. Distribution of Western Arctic Herd caribou during winters when caribou were present between Cape Lisburne and Cape Krusenstern, northwest Alaska (Dau, 2003).

Year	Wintering area	% of WAH present	Caribou density #/km^2 (#/mi^2)	Approximate number of caribou present	Closest weather station
1986–1987	Lisburne Hills/Noatak/Wulik/Kivalina[a]	12	0.8 (2.0)	33 000	Kotzebue
	Nulato Hills[b]	38	2.9 (7.4)	107 000	Unalakleet
	Kobuk/Selawik/Buckland[c]	38	2.2 (5.7)	107 000	Kotzebue
	North Slope[d]	12	0.8 (2.0)	33 000	Barrow
1994–1995	Lisburne Hills/Noatak/Wulik/Kivalina[a]	8	0.8 (2.2)	36 000	Kotzebue
	Nulato Hills	55	6.7 (17.4)	250 000	Unalakleet
	Kobuk/Selawik/Buckland	26	2.4 (6.3)	119 000	Kotzebue
	Seward Peninsula[e]	6	0.8 (1.9)	30 000	Nome
1999–2000	Lisburne Hills/Noatak/Wulik/Kivalina[a]	9	1.0 (2.6)	43 000	Kotzebue
	Kobuk/Selawik/Buckland	42	4.1 (10.5)	199 000	Kotzebue
	Seward Peninsula	17	2.1 (5.4)	83 000	Nome
	middle Koyukuk[f]	12	1.7 (4.3)	56 000	Bettles
2001–2002	Lisburne Hills/Noatak/Wulik/Kivalina[a]	26	2.9 (7.6)	126 000	Kotzebue
	Kobuk/Selawik/Buckland	22	2.2 (5.7)	108 000	Kotzebue
	Seward Peninsula	30	3.7 (9.6)	148 000	Nome
	central Brooks Range[g]	9	1.3 (3.5)	43 000	Bettles
2002–2003	Lisburne Hills/Noatak/Wulik/Kivalina[a]	7	0.8 (2.2)	37 000	Kotzebue
	Kobuk/Selawik/Buckland	21	2.1 (5.5)	105 000	Kotzebue
	Seward Peninsula	42	5.1 (13.3)	205 000	Nome
	central Brooks Range	13	2.0 (5.2)	65 000	Bettles

[a] 42 841 km^2 (16 541 mi^2); includes area of high caribou mortality in 1994–1995 and 1999–2000.

[b] 37 343 km^2 (14 418 mi^2).

[c] 49 024 km^2 (18 928 mi^2).

[d] 42 419 km^2 (16 378 mi^2).

[e] 39 979 km^2 (15 436 mi^2).

[f] 33 901 km^2 (13 089 mi^2).

[g] 32 209 km^2 (12 436 mi^2).

a reindeer herder, subsistence hunters, and a retired biologist) noted that icing conditions were particularly hard on caribou.

The two mortality events reported here are consistent with the literature in that they occurred on the coast of northwest Alaska, and they did not affect the overall population dynamics of the WAH. Although it did not appear freeze–thaw crusts or rain-on-snow had contributed to either event, wind-hardened snow affected caribou as icing would by precluding access to some food and increasing the energetic costs of getting to food that was present.

Wind direction and velocity, and even ambient air temperature to a more limited extent, may change substantially and abruptly as weather fronts move across the earth's surface. Using daily median values to represent weather conditions near Cape Thompson probably underestimated the severity of winter conditions on caribou because they dampened short-term periods of severe conditions that could exceed thresholds for survival (Table 1). This dampening effect is even more pronounced for characterizations of winter severity that calculate an average index over the course of an entire winter.

Two interactions of weather variables probably affected caribou mortality in both events. The first was the interaction between wind and snow. Chronically high wind redistributed snow into valley bottoms where most vegetation was located and packed it to almost the hardness of ice. Compaction of snow by chronically high wind is probably more important to caribou in this area than snow depth. In fact, applying any single measure of snow depth to this area is difficult because exposed ridges are almost

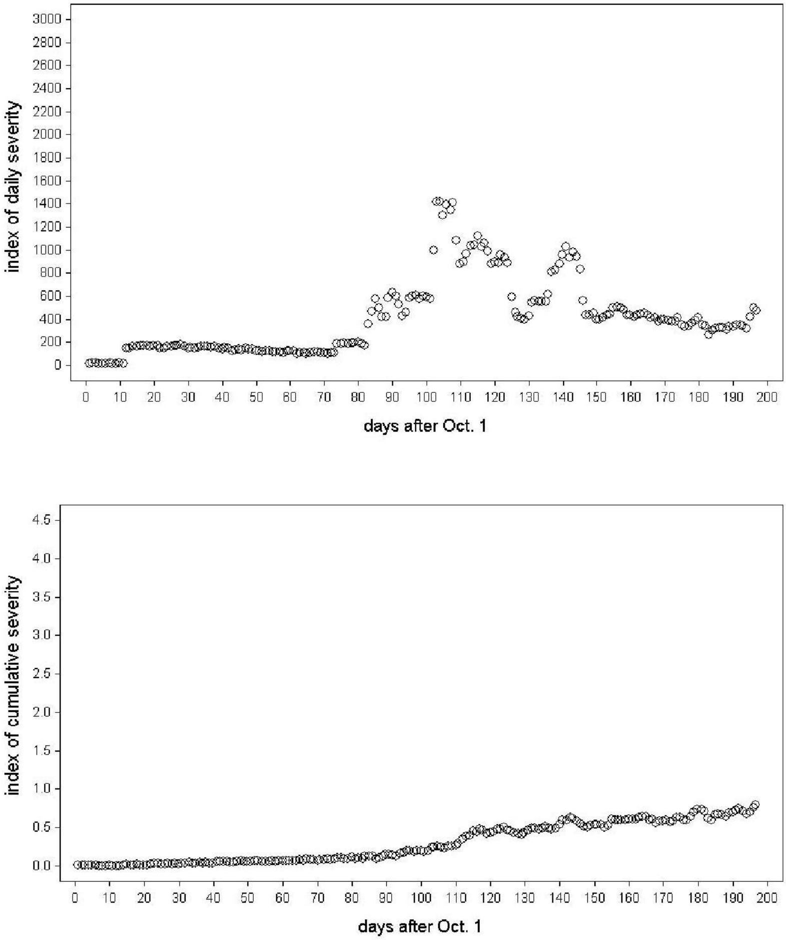

Fig. 3. Daily (top) and cumulative (bottom) indices of winter severity near Cape Thompson, Alaska, 2001–2002.

always blown snow-free while valley bottoms and the lee sides of hills are covered in deep, hard drifts almost regardless of how much snow has fallen. Wind-compacted snow reduces access to food and increases the energetic cost of cratering; its effects are chronic and cumulative. Unfortunately, unlike ambient air temperature and wind velocity that were measured through an automated device, no measure of snow hardness was available for these analyses. The second interaction of weather variables was wind and temperature: high wind with low ambient air temperature occasionally created very low windchills. Severely low windchills increase the energetic cost of thermoregulation and subject caribou to the acute effects of exposure.

Weather and snow conditions near Cape Thompson during winter 1994–1995 may have been severe enough to cause high caribou mortality regardless of their body condition. In addition to high median levels of wind and snow (Table 1), both the daily and cumulative indices of winter severity suggested weather variables acted synergistically to create brutal conditions on multiple occasions during this winter (Fig. 2). In contrast, winter 1999–2000 was not unusually severe by any measure. However, even average conditions near Cape Thompson are more severe than any other portion of WAH range.

The daily and cumulative indices of environmental severity (Figs. 2 and 3) were crude attempts to evaluate weather effects on caribou using a more comprehensive approach than provided by individual weather parameters. In 1994–1995, the daily index visually suggested five or six bouts of severe conditions occurred near Cape Thompson while only two severe storms were identified using U.S. Department of Commerce criteria (Table 1). I plotted each index of severity through time anticipating the cumulative index would be more revealing because it included duration of snow cover as a component of this variable. Surprisingly, neither index appeared clearly superior for evaluating winter severity. The daily index showed more day-to-day variability than the cumulative index because summing snow depth for the latter index tended to dampen the relative contribution of windchill to this value. When plotted through time, both indices at least visually revealed occurrences of severe conditions (as spikes on general trends) more clearly than temporal plots of individual weather parameters or windchill. Such indices may be useful for at least initial, qualitative assessments of winter conditions even if they are not suitable for statistical evaluation. Of course, lacking verification, it is uncertain whether either of these indices actually reflected the severity of weather on caribou.

Two possible explanations for the poor body condition observed during September 1994 and 1999 are

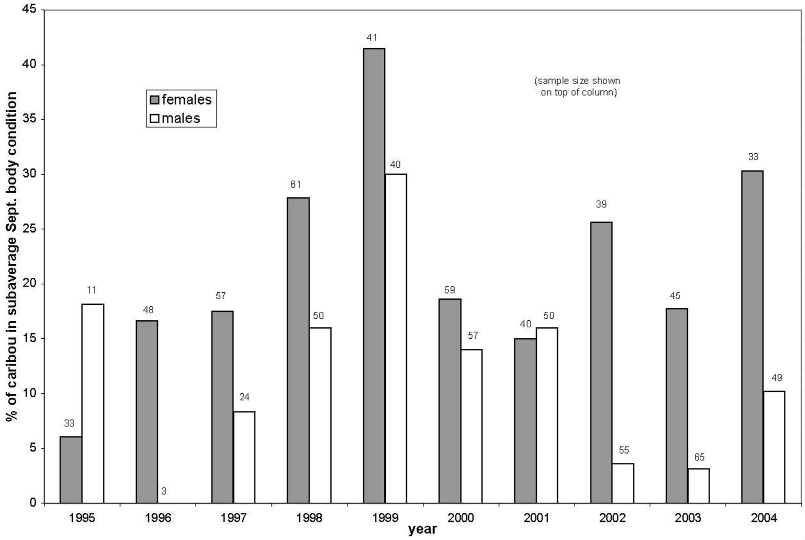

Fig. 4. Percent of Western Arctic Herd caribou in subaverage body condition in September.

1) some combination of food quality or quantity was limiting during each preceding summer (Finstad *et al.*, 2000; Finstad & Prichard, 2000) or 2) insect harassment during these summers prevented caribou from feeding and increased energy demands through avoidance behavior (Dau, 1986). Kelleyhouse (2001) reported that green-up on the WAH calving grounds (which are encompassed within summer range) began late and lagged well into summer during 1994. This likely contributed to the low fall 1994 body weights of female WAH calves reported by Valkenburg *et al.* (1996) compared to 1992 and 1995. During 1999, though, green-up was typical or perhaps even slightly early (Kelleyhouse, 2001). My attempts to model insect activity using Kotzebue and Barrow weather data only showed that these stations are not representative of WAH summer range. To my knowledge, there is no weather data for WAH summer range to evaluate levels of insect harassment. Of course, food limitation and insect harassment can act singly or in combination to influence caribou body condition during summer. Bulls and nonmaternal cows lag behind pregnant cows during the northward spring migration. Therefore, the effects of early summer range condition on body condition likely differ between maternal and nonmaternal caribou. Once mosquitoes (*Aedes* spp.), warble flies (*Hypoderma tarandi*), and bot flies (*Cephenemyia trompe*) emerge during late June, sexual segregation breaks down and most WAH caribou experience similar environmental conditions.

Weather and snow conditions made it virtually impossible to appreciate the magnitude of these mortality events as they were occurring. This is surprising given the number of caribou that died in an area hunted regularly by several communities and traversed multiple times daily by small, commercial airline flights. During each event only a few hunters reported seeing dead or moribund caribou to agency staff, and those who did never saw more than several carcasses per outing. Undoubtedly, drifting snow quickly covered carcasses until summer. Even after public reports alerted ADF&G to the possibility of the 1994–1995 event, it required substantial effort to confirm high mortality had occurred and several additional flights to determine its extent and magnitude. Caribou mortality events in remote portions of Alaska may occur more frequently than commonly thought.

The presence of fat in the bone marrow of some carcasses, the initiation of male mortality by mid-November (before the chronic effects of winter could accumulate) and the clustered distribution of many carcasses suggest exposure during severe storms killed some caribou before the chronic effects of malnutrition were fatal. Mild winters during recent years may partly account for the continued large size of the WAH. If so, several consecutive years of severe winters over the entire range of the WAH following a span of relatively mild weather could have devastating impacts on the size of the WAH especially if they follow poor summers.

Fall migratory movements for WAH caribou usually cease by mid- to late November regardless of where caribou are located on their range. Even so, why did caribou in poor body condition during fall initially settle in an area with relatively little food and harsh conditions rather than move to a better area before perishing? Part of the answer may lie with the 70–80% of caribou in this area that survived these die-offs. Caribou that died may have been unwilling to abandon the relative safety from predators and access to existing feeding craters provided by other caribou for the chance of finding better feeding conditions elsewhere. Rather than abandon a harsh, sparsely vegetated area, caribou wintering near Cape Thompson adopted a 'muskox' survival strategy by gravitating toward Cape Thompson where ridges were snow free. The problem with this strategy was that the ridges held little vegetation and the weather was unforgiving. Unlike muskoxen and the caribou that survived, caribou that died obviously lacked adequate fat to carry them through a period of low food intake. Although caribou have very warm winter fur it is probably not as warm as muskox fur based on the relationship between fur thickness and insulation value (Schmidt-Nielson, 1975); additionally, caribou body structure is probably not as conducive to heat retention as muskox. My observations during both die-offs suggest caribou in this area were more active than muskoxen as they searched for food.

Even though these mortality events were insignificant to the size or trend of the WAH population, they still had management implications. The North Slope Borough Department of Wildlife Management (NSB), ADF&G, University of Alaska and, in 2000, NANA/Teckcominco (which operates the Red Dog Mine) spent substantial time and money assessing the scope, magnitude, and causes of these mortality events which impinged on other work.

The most serious implications of these die-offs were social and focused on environmental contamination and trust rather than caribou mortality per se. During summer many caribou carcasses were visible to residents of Point Hope and Kivalina. Many people interpreted the high concentration of carcasses near Cape Thompson as evidence they had died of radiation poisoning from a controlled experiment in which soil was intentionally contaminated during Project Chariot (O'Neill, 1994). Some people were concerned that heavy metals from the Red Dog Mine had contaminated the Wulik River and poisoned caribou.

Although all evidence strongly suggested the caribou had starved (O'Hara *et al.*, 1999, 2003) and substantial effort was made to convey these findings to residents of the region, many people were convinced that contaminants had contributed to or caused these caribou die-offs and suspected results to the contrary were either inaccurate or misleading. Their concern was that the caribou they depend on for sustenance were unfit to eat. Residents of Point Hope and Kivalina have long held that the Atomic Energy Commission and other organizations associated with Project Chariot during the late 1950s and early 1960s were not forthright regarding potential effects of radiation on resources and people (see also O'Neill, 1994). This perceived deceit is now part of the regions' oral history. Additionally, the transition from traditional subsistence activities to the complex resource management system in place today did not engender local confidence in agency staff. Obviously, the good-faith response by agencies to investigate these mortality events was not enough to overcome the legacy of distrust local residents have harbored for decades regarding government agencies.

Conclusions

1. Environmental conditions at Cape Thompson were consistently harsher than other WAH wintering areas.
2. Winter 1994–1995 was unusually severe near Cape Thompson compared to other years when caribou wintered in this area. In contrast, winter 1999–2000 was not severe by any indication.
3. Many WAH caribou began winters 1994–1995 (see also Valkenburg *et al.*, 1996) and 1999–2000 in poor body condition. This probably predisposed them to high mortality under severe conditions. The 1999–2000 event suggested conditions were sufficiently harsh near Cape Thompson to kill caribou in poor condition even during a typical year.
4. During each event, snow densely compacted by chronically high wind and low windchills may have acted synergistically to kill caribou during severe storms before malnutrition was fatal.
5. Muskoxen behavior and mortality within the caribou mortality area appeared unaffected by winter conditions during 1994–1995 and 1999–2000.
6. Residents of the area were not convinced that caribou had starved during either mortality event despite gross characteristics of carcasses and laboratory analyses of tissues. Solid science was not enough to overcome long-held concerns regarding the veracity of management agencies.
7. Establishing remote weather stations on WAH summer and winter range would greatly facilitate understanding the effects of weather on the population dynamics of this herd. Besides improving our understanding of basic caribou biology and facilitating management, a more complete picture of weather conditions throughout the range of this herd could alleviate public concerns regarding environmental contaminants or other issues perceived to be important.
8. The effects of weather on caribou populations are difficult to quantitatively assess. Lags among seasons, and perhaps even years, between when weather occurs and when its effects are manifested on caribou confound results. Additionally, the effects of weather on caribou are cumulative and synergistic. Acute weather-snow conditions that may kill moribund caribou are not reflected in annual or perhaps even daily measurements of conditions. Indices of environmental severity, both on a daily and long-term basis, that integrate the effects of snow depth, duration of snow cover, snow

hardness, wind and temperature, would facilitate understanding the effects of weather on caribou.

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Where the wild things are: Seasonal variation in caribou distribution in relation to climate change

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Abstract: In this study, we develop a method to analyse the relationships between seasonal caribou distribution and climate, to estimate how climatic conditions affect interactions between humans and caribou, and ultimately to predict patterns of distribution relative to climate change. Satellite locations for the Porcupine *(Rangifer tarandus granti)* and Bathurst *(R. t. groenlandicus)* caribou herds were analysed for eight ecologically-defined seasons. For each season, two levels of a key environmental factor influencing caribou distribution were identified, as well as the best climate data available to indicate the factor's annual state. Satellite locations were grouped according to the relevant combination of season and environmental factor. Caribou distributions were compared for opposing environmental factors; this comparison was undertaken relative to hunting access for the Porcupine Herd and relative to exposure to mining activity for the Bathurst Herd. Expected climate trends suggest an overall increase in access to Porcupine caribou for Aklavik (NWT) hunters during the winter and rut seasons, for Venetie (Alaska) hunters during midsummer and fall migration and for Arctic Village (Alaska) during midsummer. Arctic Village may experience reduced availability with early snowfalls in the fall, but we expect there to be little directional shift in the spring migration patterns. For the Bathurst Herd, we expect that fewer caribou would be exposed to the mines during the winter, while more caribou would be exposed to the combined Ekati and Diavik mining zone in the early summer and to the Lupin-Jericho mining zone during the fall migration. If changes in climate cause an increased presence of caribou in the mining sites, monitoring and mitigation measures may need to be intensified.

Key words: development, hunting, *Rangifer tarandus granti, R. t. groenlandicus,* utilization density.

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Introduction

Numerous studies have documented the magnitude and trends of recent and projected climate change at the regional and continental scale (Zhang *et al.*, 2000; Zhou *et al.*, 2001; ACIA, 2004; Hinzman *et al.*, In Press). Knowledge of how caribou distribute themselves in relation to changing environmental conditions is crucial to our ability to project the future effects of climate change on caribou availability to user communities and the interaction of caribou with industrial development. While climate models have been developed to simulate how the environment may change over the next few decades, these models do not predict how living organisms will react and adapt to these changes. Furthermore, environmental assessment of the effects of proposed industrial development requires a good knowledge of the spatial and temporal movements of animals in relation to exposure zones. The better the knowledge of animal distribution, the more effective the mitigation measures will be.

Large migratory caribou herds in North America migrate from lichen-dominated, energy-rich winter-

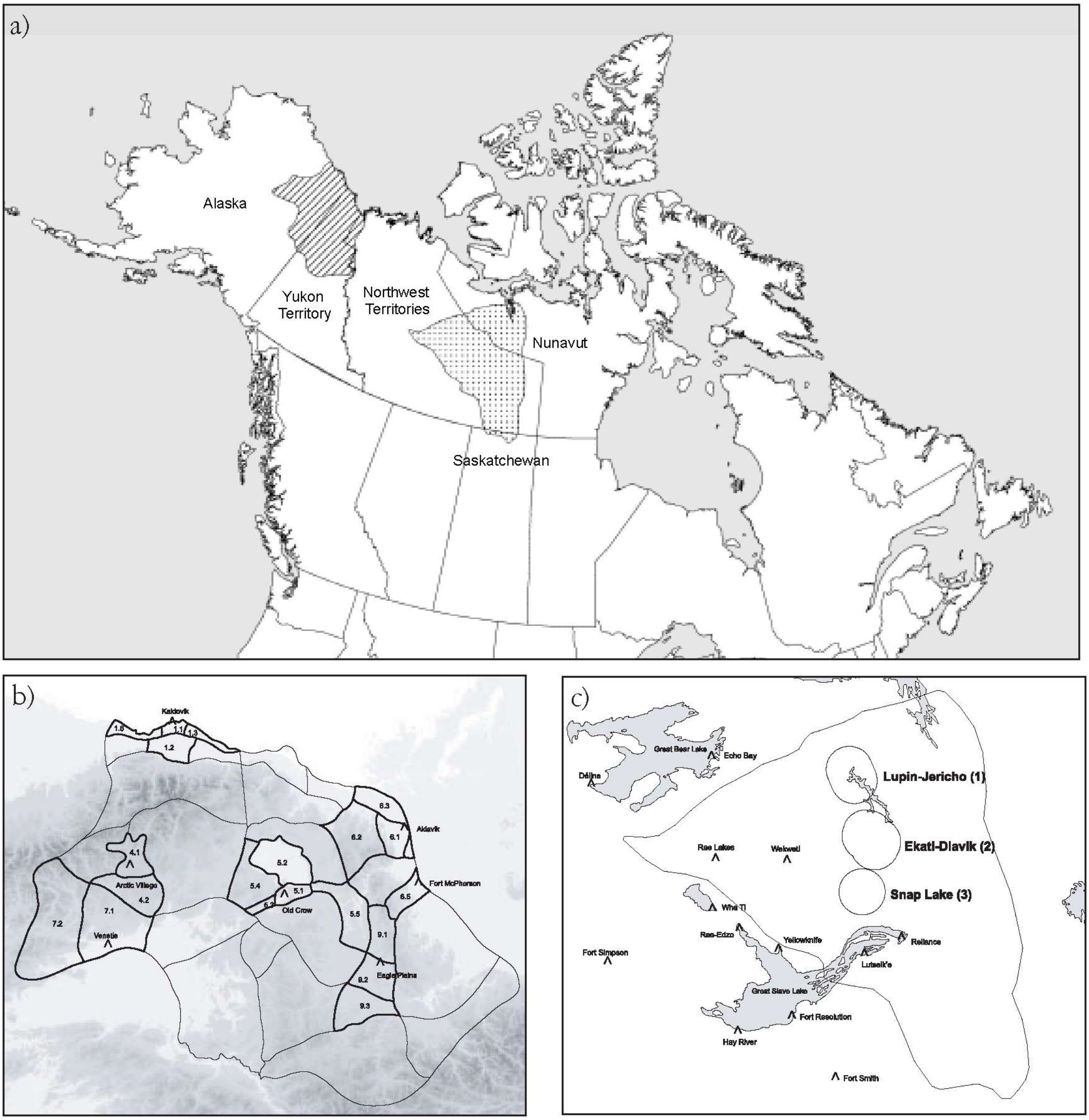


Fig. 1. a) Porcupine (stripes) and Bathurst (dots) caribou herd ranges; b) Porcupine caribou range with selected community access zones outlined in bold (see Table 2 for details); c) Bathurst caribou range with mining exposure zones (see Table 3 for details).

ing grounds south of the treeline to vascular plant-dominated, protein-rich calving and summer ranges along the arctic coast. The timing of calving generally coincides with the rapid growth of green vegetation, which is critical for the survival of newborn calves. After calving, the cows begin to form larger groups which are maintained due to insect harassment when warm, windless days persist into July. To avoid harassment, the herds will seek insect relief habitat such as coastal zones, windy mountain ridges or eskers, and snow patches.

By August, cool, freezing nights reduce insect activity. The dense aggregations disband while individuals forage intensively to replenish their body reserves in preparation for the rut and winter. From one year to the next, the herds may select quite different areas in which to winter, resulting in large cumulative wintering areas. The annual winter distribution appears to be a trade-off between favourable snow conditions and abundant lichen resources. There is some evidence that herds may also shift wintering areas periodically, perhaps in response to diminishing lichen biomass. Spring migration is first initiated by pregnant cows in late March or April.

If snow conditions are favourable, caribou may begin to drift north earlier and if unfavourable may delay movement either in their core wintering areas or along the migration routes (Eastland, 1991; Russell *et al.*, 1993).

The goal of our research was to improve our understanding of the relationship among caribou, human use of or effects on caribou, and climate. In this study, we estimate the effects of environmental factors on caribou distribution, provide predictions of caribou distribution relative to climate change scenarios, and consider the implications for hunting of caribou and use of caribou habitat. We achieve these goals by:

1. Estimating the seasonal patterns of distribution of the Porcupine and Bathurst caribou herds relative to key climate factors;
2. Predicting caribou distribution for given climate change scenarios;
3. Considering the implications of climate-related changes in caribou distribution for human activity.

Materials and methods

The study areas encompassed the annual ranges of the Porcupine caribou herd in the Northwest Territories, Yukon Territory and Alaska and the Bathurst caribou herd in Nunavut and the Northwest Territories (Fig. 1). During our study, the Porcupine caribou herd increased to 178 000 caribou in 1989, then declined to 123 000 by 2001. The Bathurst caribou declined from 350 000 animals in 1996 to 187 000 in 2003.

For the Porcupine caribou herd analysis, our primary objective was to assess the projected effects of climate change in relation to caribou availability to local communities for hunting. Through local knowledge interviews with community hunters, we delineated a

Table 1. Environmental classes and climate variables for eight seasons for the Porcupine (PCH) and Bathurst (BTH) caribou herds.

Season	PCH Date (mm/dd)	PCH Data Source	PCH Class	BTH Date (mm/dd)	BTH Data Source	BTH Class
1. Winter	12/1–3/30	1 Mar snow depth, Eagle Plains	Shallow snow <75 cm Deep snow >75 cm	12/6–4/14	Spring snow water equivalent, Snare & Yellowknife Basins	Shallow snow <200 cm Deep snow >200 cm
2. Spring migration	4/1–5/31	1 May snow depth–1 Mar snow depth, Old Crow	Early snowmelt >30 cm Late snowmelt <30 cm	4/15–6/2	30 Apr Snow on Ground, Lupin	Early snowmelt <20 cm[a] Late snowmelt >20 cm[a]
3. Calving	6/1–6/10	% Snow cover within extent of calving	Early snowmelt <20% Late snowmelt >20%	6/3–6/13	31 May Snow on Ground, Lupin	Early snowmelt = 0 cm[b] Late snowmelt >0 cm[b]
4. Post-calving	6/11–6/30	21 June NDVI–1 June NDVI, within extent of calving	Fast green-up >0.1 Slow green-up < 0.1	6/14–7/5	June Mean Temperature, Lupin	Fast green-up >7 °C Slow green-up <7 °C
5. Early Summer	7/1–7/15	Rank of total June precipitation & July mean max temperature, Old Crow	Few insects <20 Many insects >20	7/6–7/18	Rank of total June precipitation & July mean max temperature, Lupin	Few insects <9 Many insects >9
6. Mid to late summer	7/16–8/7	Rank of total June precipitation & July mean max temperature, Old Crow	Few insects <20 Many insects >20	7/19–8/22	Rank of total June precipitation & July mean max temperature, Lupin	Few insects <9 Many insects >9
7. Fall migration	8/8–10/7	Total September snowfall, Old Crow	Late snowfall <4.5 cm Early snowfall >4.5 cm	8/23–10/3	Total September snowfall, Yellowknife	Late snowfall <1 cm Early snowfall >1 cm
8. Rut/Late Fall	10/8–11/30	Total September snowfall, Old Crow	Late snowfall <4.5 cm Early snowfall >4.5 cm	10/4–12/5	Total September snowfall, Yellowknife	Late snowfall <1 cm Early snowfall >1 cm

[a] When April Snow on Ground was not available, January–April Total Snowfall and May Mean Temperature were used.

[b] When May Snow on Ground was not available, April Snow on Ground and May Total Snowfall were used.

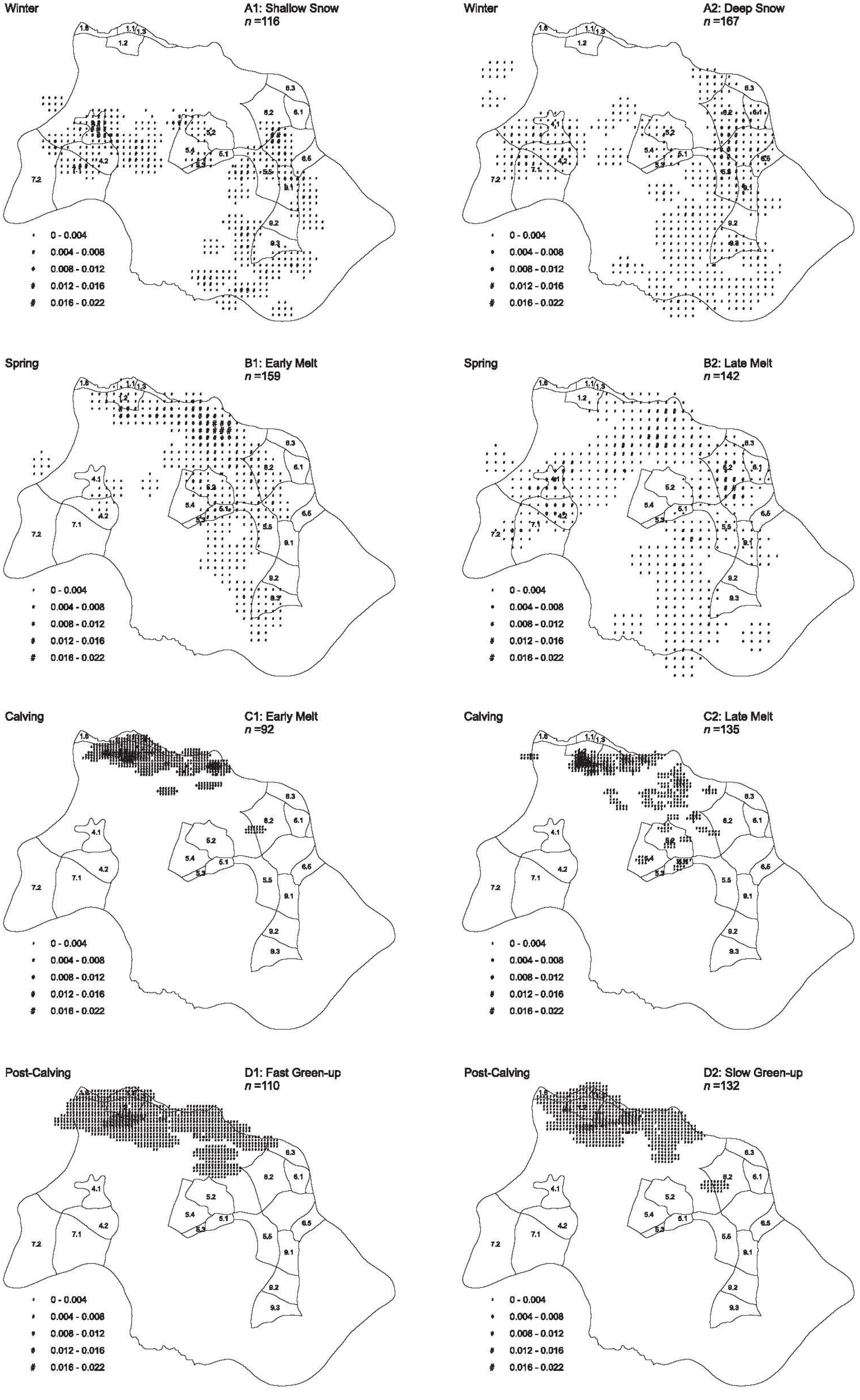
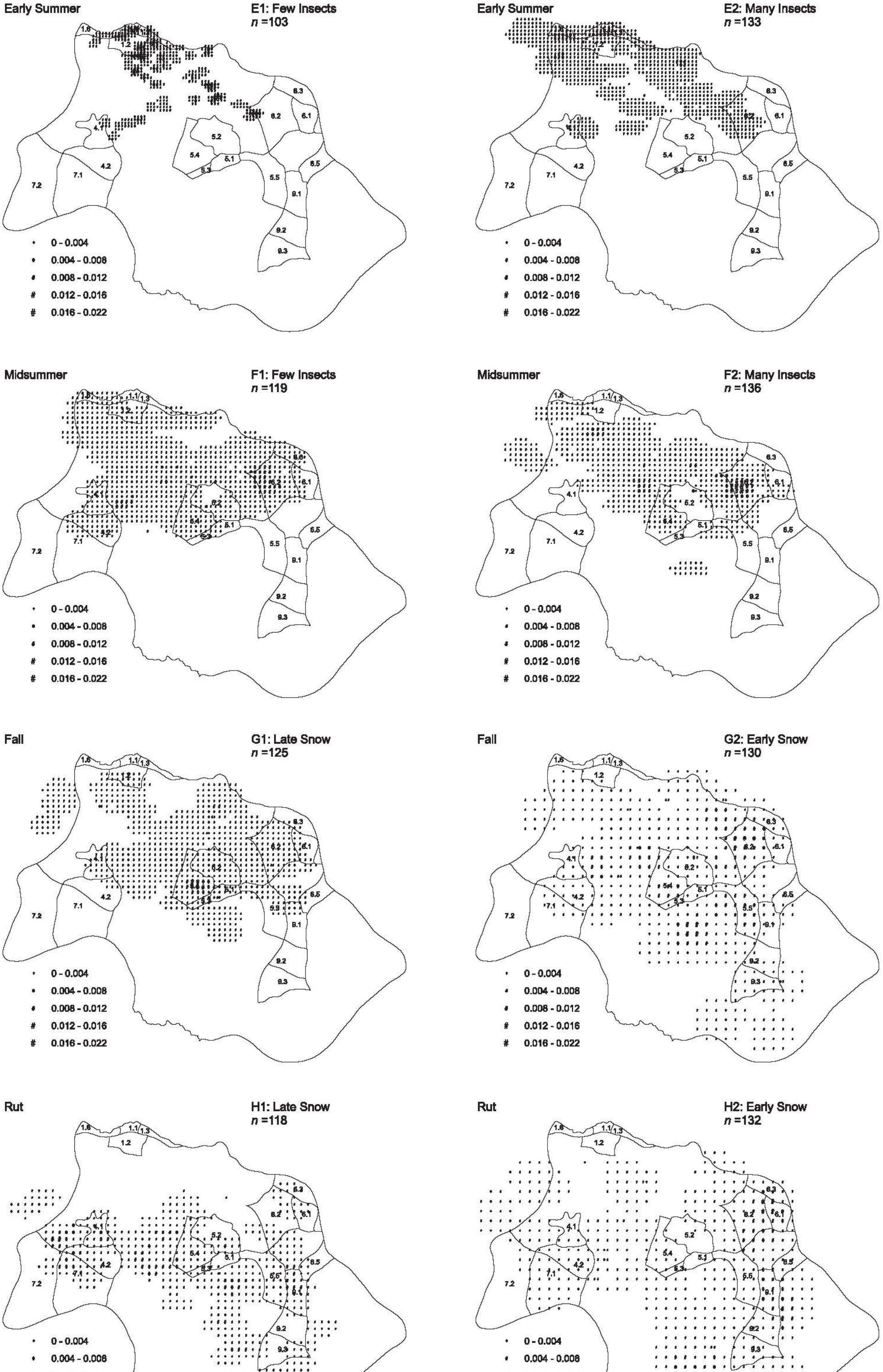


Fig. 2. Utilization densities of Porcupine caribou by season and environmental class with an overlay of the community access zones, 1985–2003. (Fig. 2 continues on next page).


Early Summer
E1: Few Insects
n =103
E2: Many Insects
n =133
Midsummer
F1: Few Insects
n =119
F2: Many Insects
n =136
Fall
G1: Late Snow
n =125
G2: Early Snow
n =130
Rut
H1: Late Snow
n =118
H2: Early Snow
n =132
1.1
1.2
1.3
1.6
4.1
4.2
5.1
5.2
5.3
5.4
5.5
6.1
6.2
6.3
6.5
7.1
7.2
9.1
9.2
9.3
0 - 0.004
0.004 - 0.008
0.008 - 0.012
0.012 - 0.016
0.016 - 0.022

set of community hunting zones within the range of the herd based on conditions affecting access to caribou (Fig. 2; Kofinas & Braund, 1998; Berman & Kofinas, 2004). Designations of "near" and "far" for each zone indicate the overall accessibility by hunters from the communities. "Near" indicates areas that are accessible within a day in normal conditions for each season whereas "far" refers to hunting areas that involve overnight travel and hence are less accessible to those people with employment. To simplify our initial analysis, we have not included the full set of hunting zones for each community, and instead focus specifically on a subset of zones.

For the Bathurst Herd, we explored a method for assessing effects of industrial development on caribou. We created 50 km buffer zones around the 4 potential or operational mines within the range of the herd (the potential Snap Lake mine and the operational Ekati, Diavik, and Lupin-Jericho mines; Fig. 3). We based the 50 km buffer on a preliminary analysis which suggested that satellite-collared cows spent less time than expected within 50 km of the Ekati mine. We include the proposed Snap Lake mine as a baseline site that can be used to note changes as human activity increases in the area.

Satellite locations from collared cows from the Porcupine (1985–2003) and Bathurst (1996–2003) caribou herds were compiled in a geographic information system (GIS). The data were analysed using Arcview 3.2a (Environmental Systems Research Institute Inc., 1992), SAS 8.2 (SAS Institute Inc., 1999) and Kernel HR (Seaman *et al.*, 1998), based upon the following steps.

We divided the annual cycle into eight seasons based upon caribou activities (Porcupine Caribou Technical Committee, 1993) and for each season selected a single environmental factor that may affect movement (Table 1). We then divided the years into two classes (e.g., early/late snowmelt; few/many insects) per season based on rankings of the environmental factor (Table 1). For the Bathurst Herd, Snow-on-Ground data were not available for all years. To determine which years classified as early or late snowmelt, we used January to April Total Snowfall and May Mean Temperature for spring migration and April Snow on Ground and May Total Snowfall for calving. These climate data were used in conjunction with the available Snow on Ground data to rank all years. Two to three random locations per caribou per class per season were selected to ensure that no animal was overrepresented. Two thousand eighty-two sample locations of 18 979 were selected for the Porcupine Herd and 928 sample locations were chosen from the 6015 Bathurst locations. These locations represented 68 animals for the Porcupine Herd and 48 animals for the Bathurst Herd.

We subsequently conducted a kernel analysis to create utilization density grids for the 16 different classes and calculated the proportional use of human use zones (e.g., hunting territories, development buffers) to analyse caribou movements relative to human activity. Finally, we performed a jackknife analysis to estimate the variance of the proportional use of the zones. For each season and environmental class, we sequentially deleted a single year of data and repeated the kernel analysis and used the results to calculate the variance and 95% confidence intervals on the proportional use of each human use zone (Smith, 2001). Pairs of environmental states within seasons were considered significantly different if the pairs had non-overlapping 95% confidence intervals, a very conservative assessment of significance (Payton *et al.*, 2003).

Results

Porcupine caribou herd

Shallow snow in the winter corresponded to two main distributions around zones 4.1 and 6.2 (Fig. 2-A1). Overall, caribou were more concentrated in those zones than in years with deep snow (Fig. 2-A2) but winter distributions were similar under both sets of conditions.

During spring migration, annual differences in movement patterns were distinguishable. With an early snowmelt (Fig. 2-B1), caribou were distributed further north and west along the North Slope than in late snowmelt years (Fig. 2-B2). There were two main migration routes when snowmelt was late; however animals that followed the Brooks Range from zone 7.1 northeast through zone 4.1 (Fig. 2-B2) may have simply been further along the route in years of early melt.

Caribou distributions during the calving season were more concentrated at the lower elevations towards the coastal plain in years of early snowmelt (Fig. 2-C1). Late snowmelt years (Fig. 2-C2) exhibited distributions further south of zones 1.2 and 1.3 in the Brooks Range as well as numerous pockets to the southeast.

Distributions during the post-calving period were very similar under both sets of environmental conditions. In years with faster green-up (Fig. 2-D1), caribou tended to form concentrations further west into Alaska and were less diffuse than in years of slow green-up (Fig. 2-D2).

Early summer distributions were concentrated in small dense pockets when the insect harassment level was low (Fig. 2-E1). Caribou were much more widely dispersed during years with many insects (Fig. 2-E2).

In midsummer caribou were scattered under both sets of conditions (Figs. 2-F1 and 2-F2). There was a main concentration located in zone 6.2 during years with many insects (Fig. 2-F2).

Distributions in the late summer/fall migration season (Figs. 2-G1 and 2-G2) differed in latitude; in years with an early arrival of snow (Fig. 2-G2), caribou were located further south. The use of the area in years of early snowfall was also more diffuse.

During the rut/late fall season, the caribou distribution in years of late snowfall (Fig. 2-H1) was characterized by a band running east–west across the middle portion of the range with pockets of concentration and a few animals present in the southern tip of the range. During years when snow arrived early (Fig. 2-H2), the dominant distribution was north–south from zone 6.3 to the southern tip of the range. The distributions were more concentrated in years with late arrival of snow (Fig. 2-H1).

Based on the community access zones (Table 2) for the Porcupine caribou herd (Berman & Kofinas, 2004), we considered the implications of changes in caribou distribution on hunting. The effects are by no

Table 2. Proportion of zone (by area) occupied by the mean utilization density distribution for the Porcupine caribou herd. Data are presented by community hunting zone by season and environmental factor; * indicates that caribou were significantly more accessible during that condition. Only zones relevant to community access are shown so columns do not total 1.0.

Community Access	Zone	Winter		Spring Migration		Calving		Post-Calving		Early Summer		Midsummer		Fall Migration		Rut – Late Fall	
		Snow Depth		Snowmelt		Snowmelt		Green-Up		Insects		Insects		Snowfall		Snowfall	
		Shallow	Deep	Early	Late	Early	Late	Fast	Slow	Few	Many	Few	Many	Late	Early	Late	Early
Kaktovik	1.1 Near			0.002		0.008*		0.007	0.023	0.047	0.049	<0.001					
	1.2 Far			0.028*	0.001	0.344*	0.171	0.189	0.139	0.095	0.041	0.008	0.002	0.013*	<0.001		
	1.3 Far			0.003	<0.001	0.031	0.002	0.004	0.013	0.036	0.035	0.001					
	1.6 Far			0.001		0.005		0.031	0.023	0.021	0.073	0.006	0.001				
Arctic Village	4.1 Near	0.102*	0.020	0.005	0.054*					0.005	0.004	0.021*	<0.001	0.016	0.004	0.026*	0.004
	4.2 Far	0.023	0.055*	0.007	0.047*							0.018*		0.002	0.021*	0.034	0.027
Venetie Old Crow	7.1 Near	0.049	0.053	<0.001	0.039*							0.001*			0.005*	0.045	0.027
	7.2 Far	0.010	0.020		0.014*											0.012	0.002
	5.1 Near	0.004	0.008	0.025*	<0.001		0.016*					0.001	<0.001	0.016	0.008	0.003	<0.001
	5.2 Far	0.014	0.019	0.037*	0.003		0.022*					0.008	0.005	0.046	0.031	0.023*	0.001
	5.3 Far	0.009	0.001	0.001								0.001	<0.001	0.002	0.008	0.005	0.002
Aklavik	5.4 Far	0.028*	0.006	0.005			0.008*					0.032	0.040	0.145*	0.058	0.069*	0.006
	5.5 Far	0.028	0.084*	0.028	0.011							<0.001	0.007*	0.014	0.068*	0.033	0.019
	6.1 Near		0.016*	<0.001	0.008*							0.002	0.007	0.007	0.010	0.004	0.042*
Fort McPherson	6.2 Far	0.025	0.060	0.051	0.095	0.014	0.005		0.014*	0.028	0.066	0.193	0.223	0.097	0.112	0.013	0.079*
	6.3 Far		0.002	<0.001	0.001			0.001				0.010*	<0.001	0.002	0.017*	0.005	0.019
	6.5 Near	0.003	0.009	<0.001	0.001									0.001	0.002	0.008	0.011
	9.1 Near	0.035	0.045	<0.001	0.006									0.006	0.011	0.046	0.056
	9.2 Far	0.002	0.001	<0.001	<0.001										0.002*	0.005	0.021*
	9.3 Far	0.008	0.029	0.017*	0.003										0.007*	0.011	0.006

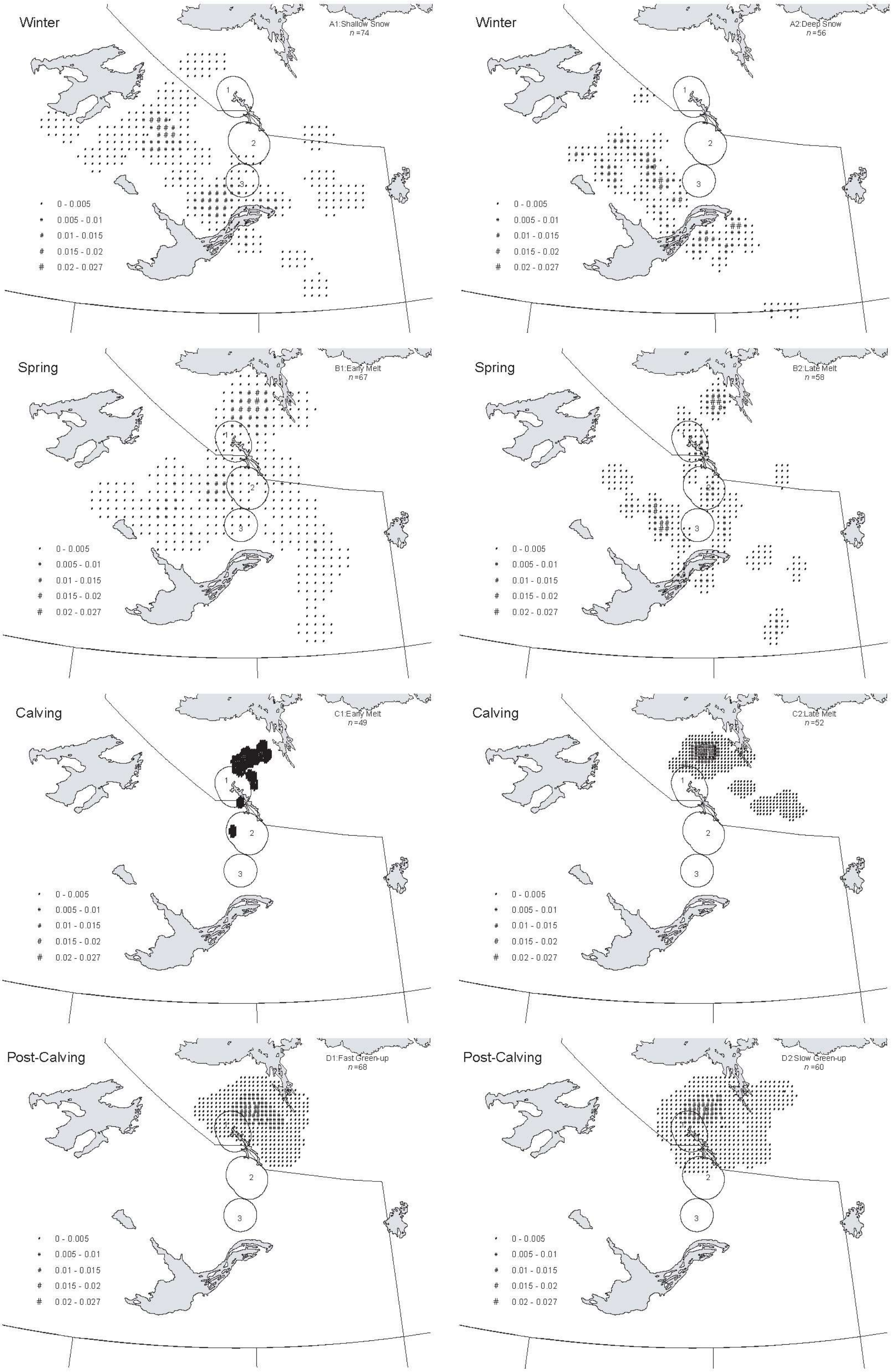
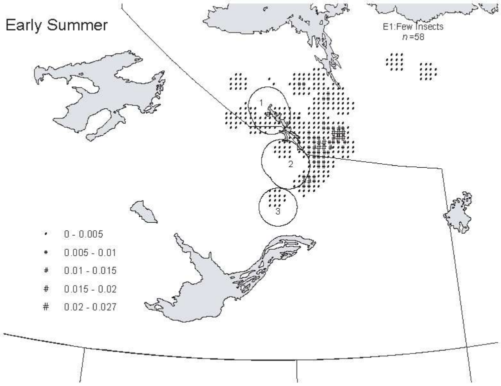
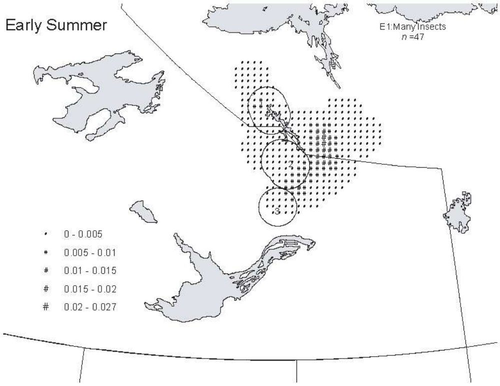
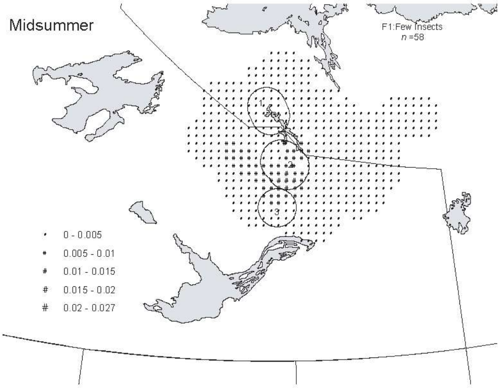
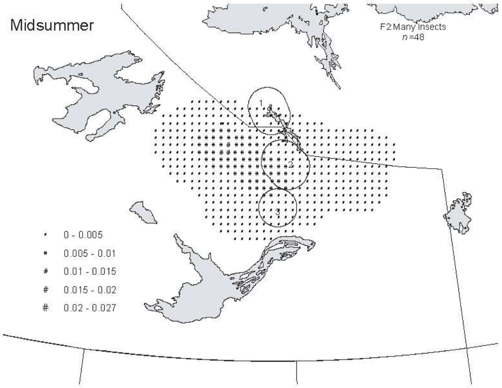


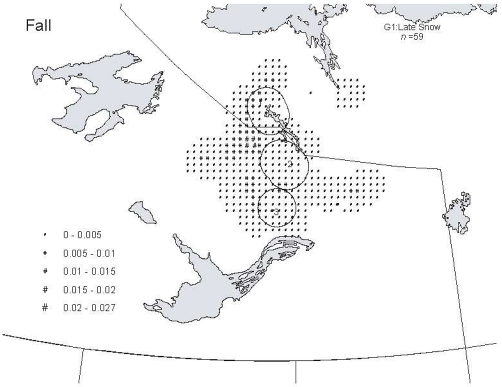
Fig. 3. Utilization densities of Bathurst caribou by season and environmental class with respect to mine sites (50 km buffer zones), 1996–2003. The mine zones are 1 Lupin Jericho, 2 Ekati-Diavik, and 3 Snap Lake. (Fig. 3 continues on next page).

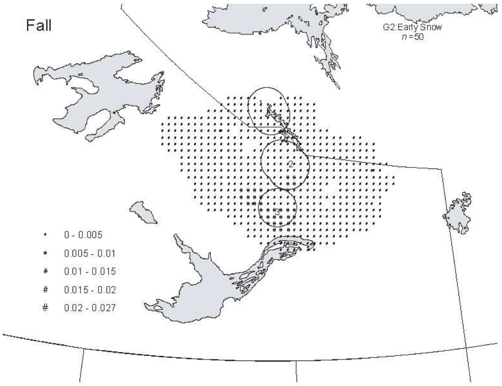

Early Summer
E1:Few Insects
n =58
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027

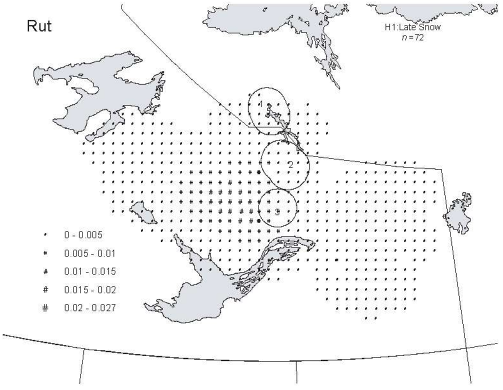

Early Summer
E1:Many Insects
n =47
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027

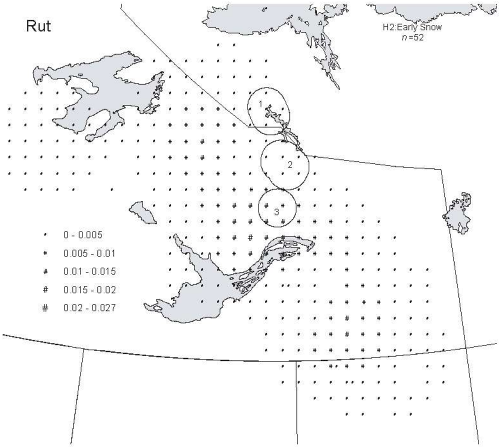

Midsummer
F1:Few Insects
n =58
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027


Midsummer
F2:Many Insects
n =48
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027


Fall
G1:Late Snow
n =59
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027


Fall
G2:Early Snow
n =50
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027


Rut
H1:Late Snow
n =72
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027


Rut
H2:Early Snow
n =52
1
2
3
0 - 0.005
0.005 - 0.01
0.01 - 0.015
0.015 - 0.02
0.02 - 0.027

means clear-cut. For example, with respect to near hunting zones, only Arctic Village had improved access during winters of shallow snow, while Aklavik hunters had improved access to caribou during winters of deep snow. Spring migration allowed Kaktovik hunters some access to the herd but despite the more northerly distribution of caribou in years with early snowmelt, the animals were still located too far south to significantly improve Kaktovik access within the near hunting zone. Old Crow benefited from early snowmelt but Arctic Village, Venetie and Aklavik hunters all had better access in years with late snowmelt.

During calving, early snowmelt provided increased access for Kaktovik residents while late snowmelt benefited Old Crow hunters, which was likely due to delayed northbound migration. The environmental conditions during the post-calving and early summer seasons did not significantly affect community access to caribou. In midsummer, the Alaskan communities of Arctic Village and Venetie had greater access to caribou when the insect harassment level was low. During fall migration, only Venetie hunters experienced greater caribou access when snow arrived early. In the late fall, early snowfall increased access for Aklavik residents but decreased access for Arctic Village hunters (Table 2).

Bathurst caribou herd

For the Bathurst caribou, shallow snow years in winter (Fig. 3-A1) were characterized by a broad range encompassing areas further to the north, west and east than the distribution in deep snow years (Fig. 3-A2). Caribou were most concentrated southeast of Great Bear Lake in shallow snow years whereas in deep snow years, caribou were concentrated in areas near Great Slave Lake. In deep snow years, caribou were located as far south as the Saskatchewan border.

Spring migration showed similar concentrations west of Bathurst Inlet for both early (Fig. 3-B1) and late (Fig. 3-B2) snowmelt. However, the early melt distribution included terrain further to the west as well as an area east of Great Slave Lake to Saskatchewan. In late melt years, the distribution was comprised of smaller isolated pockets and included terrain close to Great Slave Lake.

Calving distributions were focussed in the area west of Bathurst Inlet. During early melt (Fig. 3-C1), some cows were further south and within the mining zones while in late melt years (Fig. 3-C2) the focus area was broader with some caribou located further to the southeast. Those cows further south were nonbreeders who then caught up to the breeding cows by early postcalving.

Post-calving distributions (Figs. 3-D1 and 3-D2) were also very similar between the slow and rapid green-up. In years exhibiting slower green-up (Fig. 3-D1), the area extended to both the south and east, closer to the mining zones.

During early summer, the main difference between distributions was a more continuous distribution in years with many insects (Fig. 3-E2) than in years with few insects (Fig. 3-E1). However, the same area was used under both sets of conditions and the same area contained the greatest densities of caribou.

Into midsummer, the distributions (Figs. 3-F1 and3-F2) remained similar. The few insect years had a broad diffuse coverage (Fig. 3-F1), with greater use of Nunavut (northeast of the mining zones).

During autumn, the densest concentration of caribou was found northwest of zone 2 for years with late arrival of snow (Fig. 3-G1). There was also a small concentration at the southern tip of Bathurst Inlet. During years with early snow (Fig. 3-G2), the densest concentration was located within north of zone 3 and the coverage extended further west and south than in late snow years. The distribution during years of early snow had two gaps in the centre.

During the rutting period, late snowfall (Fig. 3-H1) occurred with a continuous distribution north of Great Slave Lake with a few isolated patches to the east of the lake. During years with early snow arrival (Fig. 3-H2), the distribution was much broader. Range use included a band of coverage from Great Bear Lake southeast to Saskatchewan.

For the Bathurst caribou herd, zones of exposure to mines were analysed for differences in caribou distribution between pairs of conditions (Table 3). During the winter season, more caribou were located outside the mining zones when the snow was deep and fewer caribou were exposed to the Snap Lake mining zone than in years of shallow snow. During spring migration, more caribou remained outside the mining zones when the snow melted early compared to when snowmelt was late. Significantly more caribou were located within the Ekati–Diavik zone in years of late melt. During calving, significantly more caribou were exposed to the Lupin–Jericho and the Ekati–Diavik mining zones when snowmelt was early and fewer caribou were outside of the mining zones during early snowmelt. There was no significant difference in caribou distribution during the post-calving season.

During early summer, Bathurst caribou were 3.5 times more likely to be located within the Ekati–Diavik mining zone when the insect harassment level was high. There was no significant difference in distributions either during midsummer or during rut. During the fall migration period, more caribou were

Table 3. Proportion of zone (by area) occupied by the mean utilization density distribution for the Bathurst caribou herd. Data are presented by mine site (50 km buffer zone) by season and environmental factor; * indicates that caribou were significantly more accessible during that condition. Column totals for zones 0 through 3 total 1.0.

Mining exposure	Zone	Winter		Spring migration		Calving		Post-calving		Early summer		Midsummer		Fall migration		Rut – Late fall	
		Snow depth		Snowmelt		Snowmelt		Green-up		Insects		Insects		Snowfall		Snowfall	
		Shallow	Deep	Early	Late	Early	Late	Fast	Slow	Few	Many	Few	Many	Late	Early	Late	Early
No Exposure	0	0.961	0.999*	0.921*	0.809	0.885	0.983*	0.888	0.804	0.883	0.707	0.676	0.775	0.758	0.734	0.842	0.942
Lupin–Jericho	1			0.033	0.095	0.095*	0.017	0.112	0.189	0.052	0.085	0.032	0.013	0.076*	0.020	0.012	0.005
Ekati–Diavik	2	0.006		0.039	0.090*	0.027*			0.008	0.051	0.168*	0.216	0.156	0.093	0.107	0.074	0.007
Snap Lake	3	0.032*	0.001	0.007	0.006					0.015	0.040	0.075	0.057	0.073	0.139	0.073	0.046

exposed to the Lupin–Jericho mining zone with a late arrival of snow.

Discussion

Changes in caribou distributions can be predicted in response to climate change. Over the past 50 years, climate trends have been towards warmer wetter winters and springs in both caribou ranges (ACIA, 2004). Within the Porcupine range, the summers have been warmer and the autumn seasons have been cooler and wetter (Zhang *et al.*, 2000). For the Bathurst caribou herd, the summers have become slightly warmer and wetter and the autumn seasons have become wetter (Zhang *et al.*, 2000). Current climate models predict warmer temperatures in both ranges for all seasons, but no changes to the spring snowmelt. The models predict widely varied precipitation changes from 30% decreases to 46% increases; however the majority of the models predict some increase in total precipitation (Canadian Institute for Climate Studies, 2004).

Given warmer and wetter conditions, our analysis suggests more years with deep snow in the winters across the ranges of both herds, more insects in the summer, and fall seasons with later snowfalls. Changes in the spring seasons are projected to be small with a one °C increase in temperature, with no change in snowmelt (Canadian Institute for Climate Studies, 2004). However, frequency and severity of icing events may be better indicators of changes in caribou distribution.

These expected climate trends suggest an overall increase in access to Porcupine caribou for Aklavik hunters during the winter and rut seasons, for Venetie hunters during midsummer and fall migration and for Arctic Village during midsummer. Generally, the primary hunting seasons for communities are the autumn and spring migration seasons with little to no hunting occurring during the calving and rutting periods (Kofinas, 1998). Arctic Village may experience reduced availability with early snowfalls in the fall, but we expect there to be little directional shift in the spring migration patterns. In recent years many elders have observed increased variability in conditions affecting caribou movements, and commented that they cannot predict the weather or the movements of these two herds as they did in years past. (Kofinas *et al.*, 2002; Thorpe *et al.*, 2002). Climate change may alter the ideal timing of hunts and if communities continue with traditional hunting times and locations, they may be less successful than in the past.

For the Bathurst Herd, with more years with deep snow in winter, more insects in the summers and fall seasons with later snowfalls, we would expect that fewer caribou would be exposed to the mines during the winter, while more caribou would be exposed to the Ekati–Diavik mining zone in the early summer and to the Lupin–Jericho mining zone during the fall migration. It is unclear whether the distribution within the Ekati–Diavik zone in early summer represents a selection or avoidance strategy. It is possible that caribou avoided the mining zone in years with few insects but were forced into the mining zones when insect levels were elevated. There is also the possibility, however, that the mining zone exhibited characteristics which provided insect relief. If changes in climate cause an increased presence of caribou in the mining sites, monitoring and mitigation measures may need to be intensified.

The analysis presented here is preliminary and will undergo further modification; the intent is to present our methods for understanding caribou–climate–human relationships. To date, our procedure does not account for serial correlation among seasons. For example, there is a correlation between shallow winter snow and late spring melt within the Porcupine caribou annual range, indicating that the spring caribou distributions may be a result of winter snow depths rather than spring melt. Currently, we are also analysing NDVI data to use green-up and snow cover to classify the data during the Bathurst calving and post-calving seasons. Furthermore, we are investigating the possibility of using Snow Water Equivalent data from satellite data to inventory the winter conditions (Derksen *et al.*, 2003), rather than relying on climate data from a single station within the range of the herd.

Due to the limited number of years of data, thirteen years for the Porcupine caribou and eight years for the Bathurst caribou, a dichotomy of environmental conditions was used. A division of the seasonal data into three categories ("normal" years, "good" years, and "bad" years) would have resulted in a loss of statistical power, with too few samples. Thus, some data were separated into opposing classes even though the climatological conditions did not differ greatly. With a long-term set of satellite and climate data, separating the data into normals and extremes may provide a clearer picture of the relationship between caribou distribution and climate.

Another limitation to this approach is the sparse number of collared animals in any given year (8–24 females per year for the Porcupine Herd; 8–17 females per year in the Bathurst Herd). Patterns of caribou distribution ascertained from these satellite locations provide valuable information, in spite of the acknowledged fact that the current number of collars does not capture all movements within the herds. For example, hunters may be able to access caribou even if the satellite locations do not indicate the presence of caribou in a specific zone. Nonetheless, these preliminary results do help to construct testable hypotheses that can be explored with more rigour in the future. One option for exploring the validity of our caribou distribution analysis is to compare our conclusions with the community monitoring data of the Arctic Borderlands Ecological Knowledge Co-operative (Kofinas *et al.*, lecture, 10th NACW). The analysis here also assumes that the climatic condition does not affect hunters' access to caribou hunting grounds. For example, while our analysis may determine that caribou are in closer proximity to a user community during a year of early spring melt, it does not account for the fact that early spring melt may severely restrict river travel by hunters, and thus result in an overall decrease in successful harvesting. This limitation suggests the need to integrate this analysis with more socio-economically sensitive travel-cost models developed for the Porcupine region (Berman *et al.*, 2004).

With further refinement, this methodology will increase our understanding of human–caribou relations. The methodology and assumptions developed here are applicable to other caribou herds as we were easily able to adapt the initial procedures from the Porcupine caribou to the Bathurst Herd. The success of the application depends upon the availability of sufficient years of satellite collar data and the completeness of the climate records for stations within the herd range. We also require knowledge of the herd ecology to designate meaningful seasons. The use of satellite data for NDVI and, potentially, Snow Water Equivalent data may assist in ranges where climate data are incomplete or where climate stations are sparse. To date, we do not have a satellite measure for insect harassment, however, temperature and moisture information are available from satellite data.

Conclusion

This methodology has provided hypotheses for validation as well as insights into the effects of climate change on caribou distribution and the resulting effects on availability of caribou to local communities and the exposure to industrial development sites. The protocol is flexible enough to be expanded to other herds and other human activities. Zones can be created in a GIS to consider roads, railways, forestry, oil and gas activities and infrastructure and ultimately the cumulative effect of all human activities could be analysed. Furthermore, the methodology provides the opportunity for discussion by managers and resource users and for reanalysis when additional data become available.

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Conservation of Peary caribou based on a recalculation of the 1961 aerial survey on the Queen Elizabeth Islands, Arctic Canada

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Abstract: The estimate of 25 845 Peary caribou (*Rangifer tarandus pearyi*) on the Queen Elizabeth Islands (QEI) in the Canadian High Arctic in summer 1961 is the only nearly range-wide 'benchmark' for the past number of caribou. No variances or confidence intervals were calculated for this estimate and no estimates were calculated for Peary caribou on the three major islands of Ellesmere, Devon, and Axel Heiberg. We reexamined the 1961 raw data by grouping the QEI into five island-complexes ('eco-units') and calculating, for each unit, the estimated number of caribou and the standard error, and the 95% confidence interval of the estimate, using a 'bootstrap' technique with 100 000 replications. Our goal was to provide an ecological basis for evaluating subsequent changes in numbers rather than relying on single-island evaluations. Our bootstrap reanalysis produced an estimate of 28 288 ± 2205 SE with a 95% CI of 20 436–37 031 Peary caribou on the QEI in summer 1961. Substantial differences in density were apparent among the five eco-units, with about a 50-fold difference from 0.01 caribou • km^{-2} in the Eastern eco-unit to 0.5 caribou • km^{-2} in the Northwestern eco-unit. The 1961 findings, with our subsequent reexamination, are crucial to any evaluation of trends for the number of Peary caribou on the QEI and the relative importance of individual eco-units for these animals. These findings also allow a more accurate evaluation of the magnitude of the subsequent decline of Peary caribou on the QEI during the last four decades and may help predict future potential levels for caribou in each of the five eco-units.

Key words: Canadian High Arctic Islands, conservation, distribution, management, numbers, *Rangifer tarandus pearyi*.

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Introduction

Tener (1963) estimated there were 25 845 Peary caribou (*Rangifer tarandus pearyi*) on the Queen Elizabeth Islands (QEI) in summer 1961. This initial, range-wide, systematic aerial survey of Peary caribou has never been repeated. Tener found that the distribution of caribou among the QEI was markedly uneven: based on island sizes he used, 94% (24 363) were on western QEI (WQEI), which makes up 24% of the total island landmass, and the remaining 6% (1482) were on eastern QEI (EQEI), with 76% of the landmass (Fig. 1).

Before 1961, the only information on distribution and numbers of Peary caribou across the QEI came from a few interested geologists in the mid- and late 1950s. After Tener's 1961 survey, only three composite multi-island caribou surveys were conducted in WQEI with adequate temporal separation (Miller *et al.*, 1977a; Miller, 1987a, 1987b, 1988, 1989; Gunn & Dragon, 2002). There have been no range-wide systematic aerial surveys for Peary caribou on the EQEI or on any major portion of that region since 1961. Only parts of Ellesmere Island were subsequently aerially surveyed (Riewe, 1973; Case & Ellsworth, 1991; Gauthier, 1996; Manseau *et al.*, 2004).

The 1961 survey of the three largest islands—Ellesmere, Devon and Axel Heiberg—was hindered by persistent bad weather in some sections (Tener, 1963). Survey coverage was low and fragmented. As a result, Tener (1963) did not quantitatively estimate the total number of caribou on those islands and his "intuitive guesses" for them were exceedingly small. The mean overall density of 0.003 caribou • km^{-2} was but a tiny fraction of what the usable range on those three islands could support (62% of the total usable range on the QEI occurs on these three islands).

Subsequent development of aerial survey techniques and statistical analyses allow us to reevaluate the 1961 data to determine standard errors and confidence intervals. We emphasize that the application of these statistical methods in no way betters Tener's original 1961 data set. The benefits of our approach are: 1) it refines Tener's (1963) estimate of abundance; 2) it permits more detailed comparisons with subsequent aerial surveys; and 3) it identifies five eco-units to serve as the best standard for evaluating future changes in Peary caribou numbers, distributions, and movements. Our statistical analyses may also satisfy those individuals who place an unfounded degree of reliance on probability testing and statistical significance instead of evaluating results in terms of biological significance (e.g., Yoccoz, 1991; Johnson, 1999; Steidl *et al.*, 2000; Anderson *et al.*, 2001). Our objective is to recalculate caribou numbers and densities using recently available accurate measures of island size, to place confidence intervals on those estimates using raw data in a bootstrap simulation, and to provide an ecological basis for the conservation of Peary caribou on the QEI.

Materials and methods

Animals and study area

The Canadian High Arctic Islands form the northern apex of the North American continent and collectively comprise a landmass of 419 061 km^2 (Fig. 1). The QEI are those islands entirely north of ca. 74°N latitude. Although there are 2126 islands in total, only 34 of them each exceed 136 km^2 in size and are considered 'large' islands. The 22 islands surveyed in 1961 differ in size from 412 km^2 to 196 236 km^2 and total 410 765 km^2 or 98% of the entire QEI. The largest is Ellesmere Island, the tenth largest island in the world. The 12 large islands not surveyed in 1961 had a collective landmass of 5975 km^2.

We divided the QEI into western (WQEI) and eastern (EQEI) zones (Fig. 1). We further subdivided the QEI into five island-complexes, which we termed 'eco-units' (Fig. 1). The two major zones and the five eco-units are based on their relative differences in numbers of caribou estimated in 1961, and caribou numbers, distribution, and movements or migrations, as measured between 1961 and 1997 (e.g., Tener, 1963; Miller *et al.*, 1977a, 1977b; Miller, 1990a, 1990b, 1998, 2002; Gunn & Dragon, 2002), climate differences (Maxwell, 1981, 1997), and vegetation differences (Edlund & Alt, 1989; Bliss, 1990; Edlund, 1990). The collective landmass of the relatively large islands within the five eco-units is 416 740 km^2. The portion of the 1961 survey area that we judge to be usable by Peary caribou is 301 978 km^2 or about 72% of the entire QEI. The 2092 small islands (defined as each having an area <137 km^2) with a total landmass of 2321 km^2 are not included in any calculations for the five eco-units. A few caribou do live on these small islands: usually only seasonally, but sometimes even year-round (Miller, 1995a, 1997, 1998).

1961 Aerial survey

Macpherson's (1961) summary of wildlife observations by geologists in the mid- and late 1950s was available as an internal report in 1960 and provided some factual information about the numbers and distributions of Peary caribou or other animals on the QEI. However, Tener (1963: 8) believed that those surveys were "not detailed enough in their animal sightings to be of real value in selecting the method of survey." Discussions with P. Larkin (University of British Columbia) led Tener to choose systematic sampling as the best design for obtaining both distributions and numbers. Although systematic surveying on the Canadian Arctic Archipelago has become a method used by most biologists for aerial surveys of caribou and muskoxen (*Ovibos moschatus*), Tener (1963) did not apply any statistical analysis to his 1961 survey results because he and P. Larkin concluded that a useful statistical approach was not available at the time.

The survey transect flights in 1961 employed two survey crews, each operating with a Piper Super Cub aircraft. The planes were equipped with large, low-pressure tires ('tundra tires') to allow them to take-off and land on unprepared ground. When possible, the crews flew the surveys at about 152 m (500 ft) above ground level and 137 km • h^{-1} (85 miles • h^{-1}) air speed. The single observer in each plane sat directly behind the pilot and limited his observations to the right side of the aircraft. Transect width was about 402 m (0.25 mi). On each island, the first transect was selected at random and drawn on a survey map; additional transects were then drawn parallel to it at fixed intervals.

Aerial coverage varied by island and was small, averaging 4% (see Tener, 1963: Table 1). The interval between transects was determined by the chosen sampling intensity. Tener (1963) based his survey intensity on the belief that using a large number of small samples was better than using only a few large ones and that a large number of systematically spaced transects probably ensured adequate representation

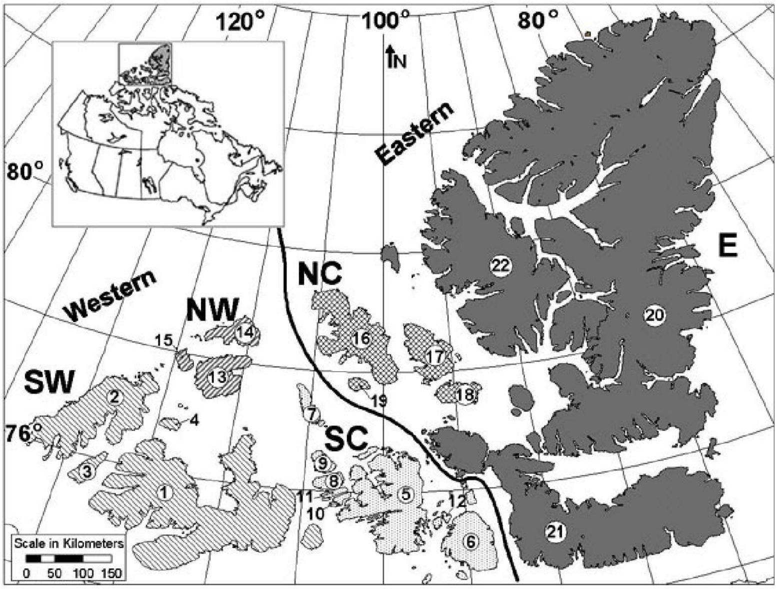

Fig. 1. Queen Elizabeth Islands split into two major zones, western and eastern Queen Elizabeth Islands; and five eco-units, Southwestern (SW), South-central (SC), Northwestern (NW), North-central (NC), and Eastern (E): islands surveyed by Tener in 1961, (1) Melville, (2) Prince Patrick, (3) Eglinton, (4) Emerald, (5) Bathurst, (6) Cornwallis, (7) Lougheed, (8) Vanier, (9) Cameron, (10) Alexander, (11) Massey, (12) Little Cornwallis, (13) Mackenzie King, (14) Borden, (15) Brock, (16) Ellef Ringnes, (17) Amund Ringnes, (18) Cornwall, (19) King Christian, (20) Ellesmere, (21) Devon, and (22) Axel Heiberg.

of range types and the geographical distribution of the animals within them.

Observers used previously prepared forms to record animals within the survey strip as being 'on-transect' and those seen beyond as being 'off-transect.' Tener (1963: 9) believed that the selected transect width and flight altitude facilitated the sighting of all animals on each transect and accurate identification of them by sex and age classes. The exception to this was on parts of Devon Island where, to take advantage of the good weather while the Piper Super Cubs were not ready for service, he used a deHavilland Beaver aircraft. They surveyed two transects each about 805 m (0.5 mi) wide by flying the Beaver aircraft at about 305 m (1000 ft) above ground level.

During the 70-d period between 10 June and 18 August 1961, prevailing weather at the time permitted survey flights on only 34 (49%) days. The Piper Super Cubs flew about 500 h and the Beaver flew about 100 h, but only about 205 h were on survey transects.

Reexamination of 1961 data

Our approach

We relied on the observations plotted and transect lines drawn on the original 14 field survey maps, as the original data forms no longer exist (J. S. Tener, pers. comm., 2001). During his initial analysis, Tener plotted his observations on the maps from the data forms, but after he completed the survey. We compared our raw data tabulations from those maps to the text, tables and figures in Tener (1963). To reconcile minor discrepancies between data on the maps and Tener (1963), Frank L. Miller and Samuel J. Barry each independently tabulated observations of Peary caribou from each data map. They repeated this process four more times over the course of several months, leaving sufficient time between repetitions to decrease 'remembering' their previous interpretation. They then did one joint count to confirm that their reasoning on each observation was the same. Finally, they compared the totals for each island and for each smaller survey land unit (stratum) used by Tener (1963) on those islands.

Calculation of estimated numbers and confidence intervals

We now know that many, perhaps most, caribou on the QEI make seasonal inter-island migrations (e.g., Miller *et al.*, 1977a, 1977b; Miller, 1990a, 1995a, 2002). The objective of this evaluation of the 1961 aerial survey findings (Tener, 1963) was to recalculate the estimates by grouping the 22 individual islands in a more ecologically sound manner into five island-complexes and to attach a measure of variability and confidence to the estimates. At the level of our five eco-units, we used a 'bootstrap' procedure (Krebs, 1999) to estimate the number of caribou, standard errors, and confidence intervals. We then summed the eco-unit statistics to obtain values for WQEI, EQEI, and the entire QEI.

Our bootstrap procedure is as follows. Using only those observations of caribou seen on-transect, we simulated a 'resurvey' of each island 100 000 times. On each resurvey we selected the same number of transects that Tener had flown in 1961 randomly and with replacement from the set of transects for that island. For each of these 100 000 resurveys we summed the number of caribou 'observed' and the area 'surveyed' from the randomly selected transects. For each of these resurveys, we calculated the number of caribou within each eco-unit by first pooling these island results (caribou observed and area surveyed) among the islands in the eco-unit then multiplying the resulting caribou density (total pooled caribou observed divided by total pooled area surveyed) by the area of usable range within the eco-unit. Our bootstrap estimate of caribou for each eco-unit is the mean of 100 000 of those estimates. We measured bootstrap variability for each eco-unit as the variance of the bootstrap estimates (reported as standard error) and our bootstrap 95% confidence interval as the 2.5th and 97.5th percentiles of the distribution of all bootstrap estimates of caribou numbers. Hereafter, 'caribou' is synonymous with 'estimated caribou' in all cases.

Although Tener (1963) used the best information available at the time for the sizes of the 22 islands he surveyed, the areas of those 22 islands have been recalculated recently (http://atlas.gc.ca/english/facts/islands.html) and the reported sizes for 21 of them have changed. Only Little Cornwallis Island, the smallest island surveyed in 1961, remained at its 1961 measured size of 412 km^2. Therefore, we used sizes for 13 of 21 islands that were smaller than the values used by Tener (1963) by 1% to 44% and for the eight islands that were larger by 1% to 22%. Thus, our estimates of numbers of caribou reflect these changes in island sizes, which cause some deviation from Tener's (1963) original 1961 estimates.

Ellesmere, Devon, and Axel Heiberg islands have large glaciated areas and high elevations that are not suitable caribou range. Additionally, Melville Island has a small west-central permanent ice field. Tener (1963) excluded these areas from his calculation of caribou numbers (but his calculations were based on different island sizes). We recalculated the size of permanently glaciated areas using GIS-based 1:250 000 topographic maps with 150-m elevation contours and the recently revised island sizes (Table 3). As a result, we excluded all land > 750 m above mean sea level (amsl) and the glaciated areas < 750 m amsl from the land area we used for computing estimates for the number of caribou present. This removed all large areas of unsuitable range including all permanent snow and ice fields. We also excluded areas on Axel Heiberg and Ellesmere islands that received no aerial coverage.

Results

We tallied 393 observations of 1583 caribou on-transect on the QEI from Tener's 1961 field maps. Caribou in groups of two or more individuals constituted 78% (306) of the observations and the remaining 87 (22%) were individual caribou. By our calculations, Tener flew 27 872 km of transect lines and surveyed 11 213 km^2 (*ca.* 4%) of the usable range within the 1961 survey area. The 100 000 estimates of caribou numbers formed by randomly resampling transect counts within each eco-unit yielded 28 288 ± 2205 SE and a 95% CI of 20 436–37 031 Peary caribou on the QEI in summer 1961. Our estimate for the QEI is nearly 9% greater than Tener's (1963) original estimate (Table 2). Calves made up 20% of all caribou observed throughout the QEI.

Two major zones

Our recalculation suggests that 90% of Peary caribou on the QEI occurred on the WQEI and only 10% on the EQEI in summer 1961 (Table 2). The number of caribou on WQEI is only 4% greater than the original number estimated there by Tener (Table 2). Tener (1963) did not calculate an estimate for the islands surveyed in the Eastern eco-unit but used only "intuitive guesses"— collectively 650 caribou. When that 650 is combined with the 832 caribou estimated by Tener (1963) on the four islands in the North-central eco-unit there are 1482 caribou on the EQEI in 1961. Therefore, our estimate is 95% greater than the original 1961 collective island estimate plus guesses, although our 95% CI includes Tener's 1961 combined estimate for the EQEI (Table 2). The WQEI and the EQEI represent 24% and 76% of the collective landmass of the 22 islands surveyed in 1961 and 32% and 68% of the potential range for caribou, but the WQEI held nine times as many caribou as the EQEI. Caribou exhibited a strong preference for WQEI with a density 18-fold greater than that on the EQEI in summer 1961.

Five eco-units

Southwestern

There are five islands from 549 to 42 149 km^2 in size that make up this eco-unit (Table 1; Fig. 1). However, Byam Martin Island (1150 km^2) was not surveyed in 1961. Therefore, the eco-unit estimate is based on the other four islands minus 159 km^2 for ice fields on western Melville Island (Table 1). There was a strong preference for Peary caribou in this eco-unit, most (58%) of the caribou on the QEI and 64% of those on WQEI occurred there (Table 2).

South-central

There are 12 islands from 412 to 16 042 km^2 in size that make up this eco-unit (Table 1; Fig. 1). The four smallest islands, Helena (326 km^2), Baillie–Hamilton (290 km^2), Griffith (189 km^2), and Lowther

Table 1. Statistics compiled from 14 observation maps for the 1961 aerial survey of Peary caribou (Tener, 1963) and the most recent values for the 22 islands in the 1961 aerial survey, Queen Elizabeth Islands, Canadian Arctic Archipelago.

Eco-unit	Total length of transects (km)	Area surveyed (km^2)	Caribou observed on-transect	Area used for calculating estimates (km^2)[a]	Overall size of land unit (km^2)[b]
(Western QEI)	(14 410)	(5797)	(1470)	(96 067)	(98 651)
Southwestern	8163	3284	894	59 928	61 237
South-central	5221	2100	363	27 858	28 808
Northwestern	1026	413	213	8281	8606
(Eastern QEI)	(13 462)	(5416)	(113)	(194 535)	(318 089)
North-central	1929	776	30	19 553	19 553
Eastern	11 533	4640	83	174 982[c]	298 536

[a] Includes only potentially usable range for Peary caribou.

[b] Island sizes available from http://atlas.gc.ca/english/facts/islands.html.

[c] Excludes 11 376 km^2 of usable range that did not receive aerial coverage.

Table 2. The 1961 estimates of Peary caribou from Tener (1963) compared to the new estimates, associated standard errors, and confidence intervals calculated from the distribution of 100 000 bootstrap replications for each of five eco-units, Queen Elizabeth Islands, Canadian Arctic Archipelago.

Eco-unit	1961 estimate of Peary caribou	1961 estimated % calves	N[a]	Bootstrap estimates of caribou from this study			Mean density of estimated caribou (caribou • km^{-2})
				Mean	SE	95% CI[b]	
(Western QEI)	(24 363)	(21)	(286)	(25 401)	(2109)	(19 060–32 287)	(0.264)
Southwestern	15 418	20	173	16 315	1779	12 969–19 936	0.272
South-central	4933	21	89	4826	833	3283–6538	0.173
Northwestern	4012	21	24	4260	767	2808–5813	0.514
(Eastern QEI)	(1482)	(15)	(208)	(2887)	(642)	(1376–4744)	(0.015)
North-central	832	21	38	760	293	269–1405	0.039
Eastern	650[c]	12	170	2127	571	1107–3339	0.012

[a] N equals number of aerial survey transects flown.

[b] 95% CI based on the 2.5th and 97.5th percentiles of 100 000 bootstrap estimates of caribou numbers.

[c] Estimates for Ellesmere, Devon, and Axel Heiberg islands were not calculated in 1961 but based only on "intuitive guesses" by Tener (1963).

Table 3. Vertical relief divisions of the three mountainous islands of Ellesmere, Devon, and Axel Heiberg, within the Eastern eco-unit, eastern Queen Elizabeth Islands, Canadian Arctic Archipelago.

Island	Size of island (km^2)	% Area (km^2) in 150-m bands						% Area of ice/ snow	% Usable range
		0–150	151–300	301–450	451–600	601–750	> 750		
Ellesmere	196 236	10	13	15	13	12	37	43	57
Devon	55 247	12	19	15	38	5	11	20	80
Axel Heiberg	43 178	20	19	15	11	9	26	30	70
Totals	294 661	12	15	15	18	10	30	37	63

($145\ km^2$) were not surveyed in 1961. Therefore, the eco-unit estimate is based on the collective landmass of Bathurst, Cornwallis, Lougheed, Vanier, Cameron, Alexander, Massey, and Little Cornwallis islands (Table 1: Tener's (1963) "Bathurst Island" included Bathurst and the islands of Vanier, Cameron, Alexander, and Massey). Caribou within this eco-unit made the second largest contribution to the estimate for the QEI (Table 2: 17%).

Northwestern

There are three islands from 764 to 5048 km^2 in size that make up this eco-unit (Table 1; Fig. 1). Thus, the eco-unit estimate is based on the collective landmass of Mackenzie King, Borden, and Brock islands, excluding 325 km^2 from Brock Island due to fog (Table 1). Caribou within this eco-unit made the third largest contribution to the estimate on the QEI (Table 2: 15%). Although the number of caribou contributed from this eco-unit to the QEI estimate was only moderate, the density was exceptionally high (Table 2).

North-central

There are four islands from 645 to 11 295 km^2 in size that make up this eco-unit (Table 1; Fig. 1). All four islands were surveyed in 1961: Ellef Ringnes (11 295 km^2), Amund Ringnes (5255 km^2), Cornwall (2358 km^2), and King Christian (645 km^2). Caribou within this eco-unit contributed the least to the QEI estimate (Table 2: 3%). The density of caribou within this eco-unit was markedly low (Table 2).

Eastern

There are 10 islands from 137 to 196 236 km^2 in size that make up this eco-unit (Table 1; Fig. 1): Ellesmere (196 236 km^2), Devon (55 247 km^2), Axel Heiberg (43 178 km^2), Graham (1378 km^2), Meighen (955 km^2), North Kent (590 km^2), Coburg (344 km^2), Stor (313 km^2), Hoved (158 km^2), and Buckingham (137 km^2). Only the three largest islands of Ellesmere, Devon, and Axel Heiberg were surveyed in 1961. Aerial coverage was low and fragmented due to poor weather. The potential range for caribou on the three islands is 63% of their collective landmass because 108 303 km^2 are covered by glaciers (Table 3). Only 27% of the land area on the three islands is <300 m amsl; in contrast, about 90% of the entire WQEI lies below the 300-m amsl level (Table 3; Miller *et al.*, 1977a). More importantly, about 60% of the landmass within the Eastern eco-unit is at higher elevations than those found anywhere else on the QEI. Caribou within this huge eco-unit composed only 7% of the total in the QEI, but 74% of the caribou in the EQEI (Table 2). The density of caribou within this eco-unit was exceptionally low, based on usable range for caribou (Table 2). Calves were appreciably lower in this eco-unit than in the other four eco-units (Table 1: $\chi^2 = 21.55$, 4 df; $P < 0.005$).

Discussion

Tener was greatly limited in any interpretation or evaluation of his results, with almost no on-site background information to draw from. In 1961, it appeared that there was a relatively large number of Peary caribou available on the QEI to support the establishment of Inuit settlements there. Unfortunately, that condition has not persisted and Peary caribou on the QEI are now 'Endangered' (Gunn *et al.*, 1981; Miller, 1990b; Miller & Gunn, 2003a, b). Peary caribou populations on the WQEI now occur as mere remnants of their 1961 sizes (Tener, 1963; Miller *et al.*, 1977a; Miller, 1995b, 1998; Gunn *et al.*, 2000; Gunn & Dragon, 2002). With the benefit of 4 decades of fragmentary information, we can extend our assessment of the 1961 findings.

In summer 1961 the relative mean densities and distribution of Peary caribou populations on the QEI indicated strong preferences for the Northwestern, Southwestern and South-central eco-units, low occurrence in the North-central eco-unit, and extremely low occurrence in the Eastern eco-unit. Since then only the Southwestern and South-central eco-units have served as 'heartlands' for Peary caribou.

Two major zones

In summer 1961 there were 18-fold more Peary caribou per unit area of usable range on the WQEI than on the EQEI (Fig. 1). Subsequent aerial surveys suggested that the highest estimates of Peary caribou were still in the Southwestern and the South-central eco-units (e.g., Miller *et al.*, 1977a; Miller, 1990b; Gunn & Dragon, 2002). The high numbers of caribou estimated in summer 1961 within the Northwestern eco-unit and on Lougheed Island in the South-central eco-unit have not been observed again (Miller *et al.*, 1977a; Miller, 1990b; Gunn & Dragon, 2002).

We believe the observed distribution of Peary caribou on the WQEI in 1961 reflected a summertime redistribution of the relatively high density of caribou in the Southwestern eco-unit beyond the eco-unit boundaries to 'out islands' in the Northwestern eco-unit. Thus, the relatively high density of caribou in the Northwestern eco-unit only reflects temporary ingress from elsewhere, not a persistent year-round state. It is also most likely that summer range extended in 1961 to Lougheed Island, with some spillover to the North-central eco-unit islands.

Whether this summertime redistribution involved caribou from both the Southwestern and South-central eco-units is not clear, but Lougheed Island appears to be more closely linked over time with changes in caribou numbers and distributions within the South-central eco-unit than with changes in the Southwestern eco-unit. Lougheed Island could not support caribou at a density of 1.1 • km^{-2} year-round for more than a few years without overutilization of the range. The same applies to Borden Island at 0.6 • km^{-2} and Mackenzie King Island at 0.5 • km^{-2}, where much of the range is on the poorly vegetated Beaufort Formation (Tener, 1963; Edlund & Alt, 1989). However, surveys in winter have shown that sparsely vegetated but wind-blown range on the Beaufort formation can be important to the survival of Peary caribou (Miller *et al.*, 1977a).

Five eco-units

Southwestern

After Tener (1963) completed his analyses, we learned that many, if not most, caribou within this eco-unit make seasonal inter-island migrations, moving from summer ranges on eastern Melville and Byam Martin islands to winter ranges on Prince Patrick and Eglinton islands (Miller *et al.*, 1977a, 1977b). Western Melville Island appears to be important to Peary caribou only during times of high numbers, such as in summer 1961. The small size of Emerald Ile apparently relegates it to transitional range for some few caribou, mainly during spring and autumn.

Inter-island movements within this eco-unit must have persisted over time, as Parry (1821) noted Peary caribou moving off eastern Melville Island in autumn. Therefore, multi-island surveys of at least Melville and Prince Patrick islands are necessary to estimate the number of caribou and any changes in the number of caribou there over time. Ideally, Byam Martin, Eglinton, and Emerald islands should be included in those surveys.

South-central

Caribou within this eco-unit also make seasonal inter-island migrations (Miller, 1995a, 1998, 2002); however, some remain year-round on Bathurst Island (Miller & Barry, 2003) and on other smaller islands (Miller, 1997, 1998). The primary linkage appears to be among Bathurst, Alexander, Marc, Massey, Vanier, and Cameron islands. Ile Marc was not surveyed in 1961: it is small (56 km^2) but important caribou summer range, lying between Alexander and Massey islands. There is some evidence of movement between Bathurst and the other lesser satellite islands as well as Cornwallis and Lougheed islands (Miller, 1997, 1998).

This eco-unit is of particular importance because it is readily accessible by hunters. The Inuit settlement of Resolute Bay on Cornwallis Island was established in the mid-1950s. Bathurst Island became a primary hunting area and remained so until the major die-off of caribou there in winter and spring 1973–74 (Parker *et al.*, 1975; Miller *et al.*, 1977a). Caribou abundance had apparently been adequate to satisfy annual harvest needs from at least the time of settlement until 1973, when they were already decreasing in number. Based on the past, this eco-unit could once again support a harvestable number of caribou, but probably only if the hunters from Resolute Bay give them time to recover. The three most recent annual die-offs between 1994 and 1997 saw the number of caribou reduced from about 3000 to < 100 (Miller, 1998; Gunn & Dragon, 2002; Miller & Gunn, 2003a).

Northwestern

This eco-unit is particularly remote from human settlement and the prevailing weather does not favor systematic aerial surveys. Mackenzie King, Borden, and Brock islands all lie beyond the northern limit of prostrate shrubs, and sedges and vascular plants are sparse, completely herbaceous, and least diverse of the QEI (Edlund & Alt, 1989; Edlund, 1990). This eco-unit has served on occasion as a 'spillover area' for caribou from the Southwestern eco-unit and possibly the South-central eco-unit when the caribou on one or both eco-units uncommonly reached a relatively high density. However, it is the smallest of the five eco-units and there is no reason to believe that it could sustain anything more than a relatively small low density 'reservoir area' for Peary caribou.

North-central

This eco-unit lies mainly in the environmentally stressful northern zone of plant growth (Edlund & Alt, 1989; Edlund, 1990). The ability of this range to support a large number of caribou year-round is highly questionable given its moderate size and meager flora. In all likelihood, this eco-unit serves mainly as a rarely used 'spillover area' for caribou from the Southwestern eco-unit and possibly the South-central eco-unit when caribou on one or both eco-units infrequently reach relatively high densities. This eco-unit should be viewed as a low density reservoir that can help foster the long-term persistence of Peary caribou on the QEI. The islands are not readily accessible to Inuit hunters and could never provide any appreciable level of sustained annual harvest.

Eastern

It is a mystery why there are not many more Peary caribou in this eco-unit. Its vastness makes Tener's

(1963) "intuitive guess" of only 650 Peary caribou there in 1961 appear ultra-conservative. This is especially true as there are at least 186 000 km^2 of potential range within this eco-unit. Our estimate of 2127 ± 571 SE requires only 0.01 caribou • km^{-2} and our estimate minus 1 SE (1556) would require, on average, only 0.008 caribou • km^{-2} of usable range.

Based on the 1961 results and subsequent limited information, we view the Eastern eco-unit as a huge, low-density reservoir for Peary caribou. In the foreseeable future, caribou there can make only a relatively small contribution to annual harvests of Peary caribou on the QEI. However, because of the Eastern eco-unit's large and rugged land base, it has great benefit to the persistence of Peary caribou on the QEI. Also, given the paucity of data for the three major islands in this eco-unit and their large size, there is a chance that this area may have more caribou than anyone is aware of.

Ironically, when the scenarios of 'global warming' are considered, we could speculate that the Eastern eco-unit may become the most important region for Peary caribou on the entire QEI. Because of the ruggedness of its terrain and its elevation relief (Table 3), many micro niches will be available that could foster Peary caribou survival in that region compared to survival in the relatively low-lying WQEI and the North-central eco-unit of the EQEI. If global warming advances as predicted by some, this change could occur within the next century. Even more importantly, it is possible that virtually only the Peary caribou on the Eastern eco-unit may survive the transitional phase of greater snowfall and more frequent icing events during global warming. The probability of this may be tied to the rapidity of warming processes which may cause micro niches to become critically important to the caribou's long-term survival on the QEI.

Management and conservation implications

Future aerial surveys of Peary caribou on the QEI should be at the eco-unit level to maximize both the accuracy of the estimated number of caribou and the probability of detecting real changes in caribou numbers and distribution over time. Surveys should be flown in July, at three-year or shorter intervals as long as the number of caribou remains small and especially if they are being harvested annually. Regardless of when the last survey was carried out, a July survey should be flown in the summer immediately after a winter or spring with exceptionally severe weather to determine the impact, if any, on the overwinter survival of caribou and the production and early survival of calves. Once adequate aerial surveys indicate that the number of caribou has increased to a size where the annual level of harvest would not exceed 5% (cf. Kelsall, 1968), based on the mean estimate minus 1 SE, minus the percentage of calves present, the interval between surveys could be extended to 5 years. In all cases, however, an aerial survey still should be carried out following any winter or spring with exceptionally severe weather to prevent a major decline in number going undetected.

The past and current status of Peary caribou in the EQEI remains debatable. No current information exists for caribou in the North-central eco-unit. In the Eastern eco-unit, recent information from northern Ellesmere Island suggests a stagnant condition with a minimum of only 45 Peary caribou estimated there between 1988–2002 (Manseau *et al.*, 2004). However, recent information from Inuit hunters from Grise Fiord on southern Ellesmere Island suggests that caribou are increasing there, based on sightings of a low number of caribou in places where they have been absent for several decades. Both M. Raillard, Canadian Wildlife Service, and J. England, University of Alberta, believe that while conducting other field activities they have seen numbers of caribou on parts of Ellesmere and Axel Heiberg islands in summers 1999–2001 that suggest increases are probably occurring on some relatively well-vegetated sections. The accuracy of island-wide extrapolations of caribou numbers from such casual observations cannot be measured with confidence. Thus, such extrapolations form a poor basis for making decisions regarding rates of annual harvest, particularly for an 'Endangered Species.' Only prescriptions for annual harvest that are based on actual counts of caribou that yield a total minimum number adequate to sustain desired harvests should be employed. Even then, following exceptionally severe weather years, harvest of Peary caribou may have to be temporarily halted by emergency action through cooperation with Inuit hunters.

The vastness and concomitant prohibitive costs of aerial surveys on the Eastern eco-unit require a different approach. We recommend the establishment of at least five permanent survey plots, 100 km by 100 km on areas of known importance to Peary caribou and where annual harvests are most likely to occur. These plots should be flown in early July when weather is most stable, and should be flown each time as close as possible to the same days of this month to record the percentage of calves, and ideally yearlings, present and the phenological state of plants for comparisons among years. This procedure would provide a relative estimate of the number of caribou, calving success, yearling recruitment, and annual variation in new plant growth within those 'food patches' that would allow the setting of flexible maximum annual harvest levels. Accurate calf and yearling counts should be made, as a measure of performance to eventually provide a measure of their trend over time to better prescribe the maximal allowable level of annual caribou harvest, especially when annual harvest appears high. After the first year of plot surveys, both the previous number of animals counted and the size of the desired future annual harvest would dictate the needed frequency of those aerial searches. In the absence of a better measure, a maximum of a 5% annual harvest should be adhered to, especially as long as Peary caribou remain an 'Endangered Species.'

It is most unlikely that the concepts of 'carrying capacity' and 'sustained yield' have any real application to Peary caribou on the QEI. To date, everything suggests that the caribou on the QEI function in a 'nonequilibrium grazing system' where abiotic factors, mainly snow and ice, control their fate through infrequently occurring, sporadic and unpredictable 'exceptionally hard weather years' (Caughley & Gunn, 1993; Behnke, 2000; Miller & Gunn, 2003a, b). At such times, extremely unfavorable snow and ice conditions prevent the animals from getting to food or cause caribou to use more energy accessing it than they recover in forage intake. In years when such snow and ice conditions are prolonged and widespread, a large number of caribou (and muskoxen) will die from starvation. This happens because the carrying capacity of those caribou ranges will change, both quickly and unpredictably, with the prevailing severity of the snow and ice cover in each year. The more severe the snow and ice conditions and the longer they persist, the greater the loss of animals regardless of their densities or nutritional state at the beginning of the die-off period. Once the snow and ice melts, the carrying capacity of the range instantly experiences a many-fold increase—the absolute forage supply is still there and is once again readily available to the animals.

Therefore, caribou range in early winter that could support several thousand animals under favorable snow and ice conditions can be rapidly reduced to one that will support only several hundred or fewer animals. Then, following snowmelt, it will return immediately to a relatively favorable state. Such capricious range conditions will not allow a predictable fixed sustainable level of annual harvest of any appreciable size for more than a short series of years, if that. The lack of adequate periodic monitoring programs and the uncertainty of 'climate change' leave the fate of Peary caribou on the QEI unpredictable. Intervals of > 5 years between estimates of caribou on the QEI could run the risk of merely documenting serious declines after the fact, especially if continual annual harvests had been at relatively high levels. Although there is no evidence that harvesting has caused Peary caribou declines on the QEI, it could have accelerated and deepened them in some instances.

Conclusions

The Peary caribou on QEI is a unique part of Canada's High Arctic natural heritage and is recognized as an 'Endangered' form of wildlife in Canada. The number of caribou now on the QEI is a vestige of the number estimated there in 1961; yet, Peary caribou continue to be considered a usable renewable resource! Our recalculation of the 1961 aerial survey is the best benchmark for subsequent evaluations of changes in numbers, distributions, and movements of Peary caribou on the QEI. The division of the entire QEI into five eco-units provides a standard for evaluating the above changes over time on an ecologically sound basis for prescribing and assessing conservation measures for Peary caribou on the QEI.

Continued annual harvesting of Peary caribou—an 'Endangered Species'— requires that special safeguards and an adequate monitoring program be established. Cooperation among wildlife agencies and Inuit hunters is essential, because precautionary measures will require the participation of Inuit users in setting the restrictions and complying with them. No more than a few Peary caribou should be taken from any island within any eco-unit without first obtaining actual counts to determine that enough caribou exist there to sustain the desired level of annual harvest. Otherwise, we run the risk of being found negligent in our stewardship responsibility to this unique resource.

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Sea-ice crossings by caribou in the south-central Canadian Arctic Archipelago and their ecological importance

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Abstract: The islands of the Canadian Arctic Archipelago lie immediately north of mainland North America in the Arctic Ocean. They are surrounded by ice for most of each year. Caribou (*Rangifer tarandus*) cross the sea ice in seasonal migrations among the islands and between the mainland and Arctic Islands. We compiled observations of 1272 discrete caribou crossings on the sea ice of northeastern Franklin Strait, Bellot Strait, Peel Sound and Baring Channel in the south-central Canadian Arctic Archipelago during four May–June search periods from 1977 to 1980. We clustered the 850 caribou trails found on the sea ice of northeastern Franklin Strait and on outer Peel Sound as 73 sea-ice crossing sites. We investigated whether caribou at the origin of a sea-ice crossing site could see land on the opposite side at the potential terminus. We measured the straight-line distance from where the caribou first came onto the ice (origin) to the first possible landfall (potential terminus). Potential termini were geodetically visible to caribou from elevated terrain near 96% of the origins of the 73 sea-ice crossing sites and still visible at sea-level at the origins on 68%. Caribou are able to take advantage of seasonal use of all of the islands and the peninsula by making sea-ice crossings, thereby helping to increase the magnitudes and durations of population highs and reduce their lows. Knowledge of these alternative patterns of use made possible by sea-ice crossings is necessary to fully understand the population dynamics of these caribou and the importance of possible future changes in ice cover.

Key words: Canadian Arctic Islands, inter-island and mainland-island seasonal migrations, *Rangifer tarandus*.

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Introduction

The Canadian Arctic Archipelago is the northernmost extension of the North American continent (Fig. 1). It lies in the Arctic Ocean, spanning 22° of latitude (61–83°N) and nearly 65° of longitude (61–126°W), with a maximum north–south extent of *ca.* 2400 km and a maximum east–west breadth of *ca.* 2700 km. The archipelago has a collective island-landmass of >1.3 million km^2 (one-seventh of the land area of Canada), with >18 000 islands north of the Arctic Circle. However, only 70 of those islands each have a landmass ≥137 km^2 (http://atlas.gc.ca/english/facts/islands.html). The weather is highly variable and often extreme, especially on the High Arctic Islands (Maxwell, 1981, 1997). Throughout the entire archipelago, only tundra vegetation occurs: bryophytes, cushion plants, graminoids, herbs, lichens, and prostrate shrubs, with dwarfed or low erect shrubs occurring on some areas of southern islands (Edlund & Alt, 1989; Bliss, 1990; Edlund, 1990; Thomas *et al.*, 1999).

The islands of the Canadian Arctic Archipelago are surrounded by ice for ≥9 months each year, and the northern fringe of the Queen Elizabeth Islands remains virtually ice-bound all year. This condition allows caribou (*Rangifer tarandus*) to make seasonal migrations and sporadic movements across the sea ice virtually throughout the Canadian Arctic Archipelago and between the southern islands and the mainland. At various times in the past, caribou have reached every or almost every island.

We consider all caribou sea-ice crossings reported herein to have been a component of their habitual

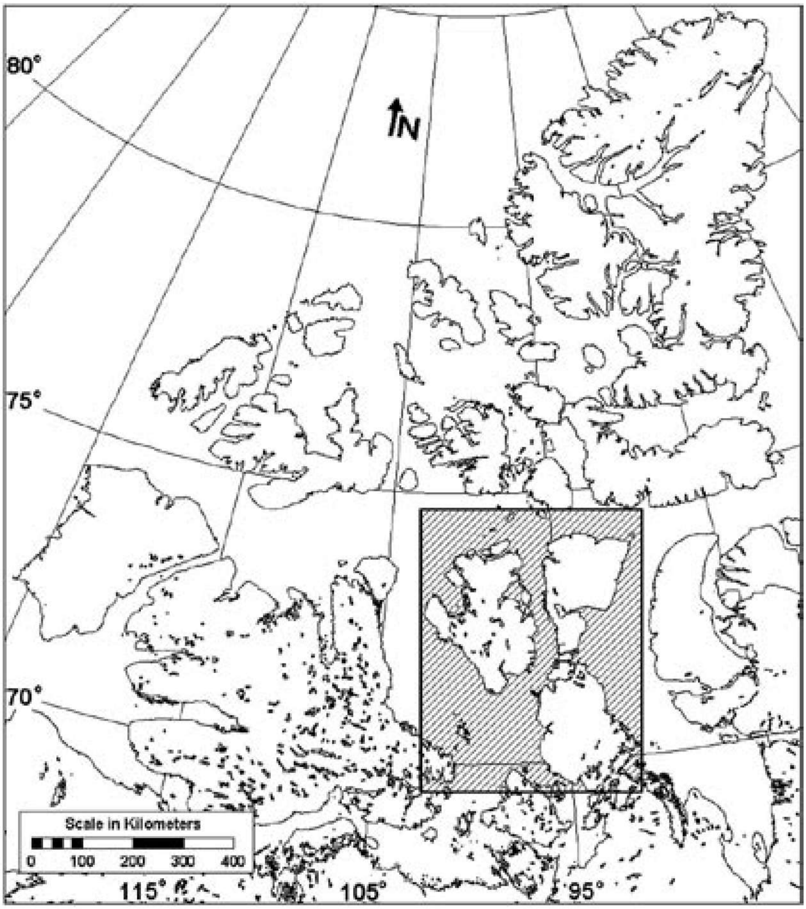


Fig. 1. Canadian Arctic Archipelago and the most northerly extension of mainland North America. Shaded area indicates Prince of Wales Island–Somerset Island–Boothia Peninsula Complex study area.

pattern of movement (seasonal migration) made during the late winter and spring within the Prince of Wales Island–Somerset Island–Boothia Peninsula Complex (PSBC) by the majority of caribou in this "geographic population." The actual trails on the sea ice or on land are not necessarily fixed migration routes used every year—but they are indicative of a broad migration path or zone that the caribou use to get from winter ranges to calving areas and summer ranges. The caribou return to winter ranges to the east and south in an early winter migration sometime after freeze-up and repeat the round-trip each year. Although the early winter migration after freeze-up has not been systematically documented, it is well-known among Inuit hunters from Resolute Bay, Cornwallis Island (G. Eckalook, pers. comm., 1980). It is also known that caribou from Prince of Wales Island together with caribou from Somerset Island occur regularly in winter on Boothia Peninsula. For example, caribou that summered on southern Somerset Island in the 1920s and 1930s moved annually to winter ranges on Boothia Peninsula, returning in spring to Somerset Island (A. Ooyukuluk via M. A. D. Ferguson, pers. comm., 2000). Inuit hunters see caribou from "Kingailak" (Prince of Wales Island) on Boothia Peninsula in winter, and select them because their meat is preferred to meat from mainland caribou (A. Buchan, pers. comm., 2000). The temporal pattern of these migrations within the PSBC (e.g., Miller & Gunn, 1978, 1980; Miller *et al.*, 1982; Miller, 1990a) is similar to seasonal migrations by caribou in other parts of the Canadian Arctic Archipelago and between the archipelago and the mainland: Queen Elizabeth Islands (Miller *et al.*, 1977a, 1977b; Miller, 1990a, b); and Dolphin and Union herd (Manning, 1960; Gunn *et al.*, 1997; Gunn & Fournier, 2000a, b). These late winter–spring migrations from winter range to calving areas and summer range and return to winter range in early winter are on a smaller scale but similar in purpose to those performed by caribou on the mainland (e.g., Kelsall, 1968; Skoog, 1968).

Our objectives were (1) to describe the seasonal migrations of caribou between and among the islands and peninsula within the PSBC, (2) to document the north–south extent of sea-ice crossings in northeastern Franklin Strait and Peel Sound, (3) to document that caribou move directly from Boothia Peninsula to Prince of Wales Island, (4) to evaluate whether caribou could see the opposite side of the sea-ice crossing sites, and (5) to assess whether caribou need visual reference points before making sea-ice crossings. We also discuss possible mechanisms that allow *R. tarandus* to make long-distance sea-ice crossings. In doing so, we hope to provide a better understanding of the various patterns of island and peninsula use of seasonal and annual ranges available to caribou within this region. We believe these movements also have general application to virtually all of the archipelago, and understanding these movements is important to the development of needed conservation and management efforts.

Methods

We selected the PSBC in the south-central Canadian Arctic Archipelago (Fig. 1) where caribou exhibit several intricate patterns of annual and seasonal use of islands and a mainland peninsula. Caribou sea-ice crossings on northeastern Franklin Strait, Bellot Strait, Peel Sound, and Baring Channel were included. We emphasized northeastern Franklin Strait and Peel Sound because they are wide and bisect the PSBC, with Prince of Wales Island (33 339 km^2) to the west and Boothia Peninsula (32 331 km^2) and Somerset Island (24 786 km^2) to the east. The entire study area encompasses about 212 000 km^2, including *ca.* 93 000 km^2 of land.

We used information from Inuit hunters, aerial and ground searches, and satellite telemetry reported in published articles, internal project reports, and unpublished data to summarize the seasonal dynamics of the annual distribution of caribou within the PSBC. We reviewed the evidence for inter-island and mainland-island movements and migrations of caribou over the sea ice within the PSBC, and other island complexes in the archipelago and between islands and adjacent mainland areas (e.g., Manning, 1960; Banfield, 1961; Manning & Macpherson, 1961; Fischer & Duncan, 1976; Miller *et al.*, 1977a, 1977b, 1982; Miller & Gunn, 1978, 1980; Miller & Kiliaan, 1980a, b, 1981; Thomas & Everson, 1982; Gunn & Miller, 1983; Gunn & Ashevak, 1990; Miller, 1990a, b, 1995, 1998, 2002; Gunn & Dragon, 1998; Gunn *et al.*, 1997, 2000a; Gunn & Fournier, 2000a, b).

We place our emphasis on observations made within the PSBC between 1977 and 1980 by Miller & Gunn (1978, 1980) and Miller & Kiliaan (1980a, 1981). A Bell 206B helicopter was used in all 4 years of those studies as the main search aircraft. It was flown at 10–25 m above mean sea level (amsl) and 96 km • h^{-1} in 1977 with three observers plus pilot, then at 20–60 m amsl (usually <40 m amsl) and at an airspeed of 130 km • h^{-1} in 1978–80 with two observers plus pilot. When a trail was encountered, it was circled, hovered over, or the helicopter landed by the trail so that the observers could determine the direction the caribou were traveling.

In 1978, a deHavilland Twin Otter also was used in the searches. It was flown at 25–60 m amsl and at 220 km • h^{-1}, with an observer in the copilot seat and the pilot also acting as an observer. In 1979, snowmobile-mounted observers reported trails to the helicopter crew, who subsequently overflew any trails that had not already been recorded. The entire course of 40% of the 1272 trails recorded was flown, but each of the other 60% was either directly flown or crisscrossed only as far as necessary to determine its course, usually about halfway across the frozen water body. The direction of travel by caribou was determined for all trails seen in 1977, 1979, and 1980. In 1978, the direction of travel along 111 trails seen from the Twin Otter could not be verified with confidence. These included 5% of trails on outer Peel Sound, 16% of those on inner Peel Sound, and 29% of those on Baring Channel.

We produced a schematic illustration of sea-ice crossing sites representing multiple trails used by caribou while in migration, as springtime inter-island or mainland-island routes within the PSBC. The schema shows approximate locations of caribou crossing sites across the frozen water bodies. We clustered the 850 trails found on northeastern Franklin Strait between Boothia Peninsula and Prince of Wales Island and on Peel Sound between Somerset Island and Prince of Wales Island as 73 sea-ice crossing sites. To determine crossing distances, we measured the straight-line distance at sea-level where the caribou first came onto the ice (origin) to the nearest possible landfall (potential terminus), rather than to the point at which caribou actually left the ice. We investigated whether caribou at the origin could possibly see land at the potential terminus. We then determined the highest ground ≤10 km from each origin and potential terminus. Caribou crossing sites on inner Peel Sound between and among the satellite islands and Prince of Wales Island, on Baring Channel, and on Bellot Strait are not considered in detail because of the relative narrowness of those water bodies.

All locations were approximations and are reported to the nearest 0.1° (6 min) of latitude and longitude for reference purposes only. All elevations were in meters amsl. Elevations were taken either from values indicated on maps (verified Geodetic Survey of Canada benchmarks or less exact (±) unverified elevations) or from contour lines. All distances were recorded as kilometers in a straight-line along a horizontal plane. We used both 1:250 000–scale topographical maps and Geographical Information System computer-generated maps for this task.

We investigated whether land at the terminus was visible to caribou on the sea ice at the origin of each crossing site by calculating whether the geodetic horizon impedes visibility of the potential terminus from the origin. We did this by computing the distance to the "visible horizon" from an elevated origin by the following standard formula (The American Practical

Table 1. Sea-ice crossings by caribou within the Prince of Wales Island–Somerset Island–Boothia Peninsula Complex, south-central Canadian Arctic Archipelago, May–June 1977–1980.

Year	Search days (dates)[a]	Caribou trails	Caribou[b]	Search vehicle	Data source
1977	4 (12–18 June)	158	0	helicopter	Miller & Gunn (1978)
1978	20 (16 May–30 June)	422	53	helicopter, Twin Otter	Miller & Gunn (1980)
1979	10 (21 May–22 June)	107	25	helicopter, snowmobiles	Miller & Kiliaan (1980a)
1980	4 (14–22 June)	588	15	helicopter	Miller & Kiliaan (1981)

[a] For example: "4 (12–18 June)" equals 4 days of searching took place within the 7-day interval between 12 and 18 June 1977.

[b] Number of live caribou seen walking in trails on the sea ice during that search period.

Navigator, 2002), adjusted for refraction (http://www.sailingissues.com/vier/mathproof2.html):

$$d = \sqrt{\frac{h(1+2r)}{\rho}}$$, where

h = height (m)
r = radius of earth – 6378137 m
ρ = 0.8279 is the coefficient of atmospheric refraction
d = distance to visible horizon (m).

Using this formula, we calculated the maximum distance that two points could be separated and still be visible to each other over the curvature of the earth.

Results

Search effort during May–June 1977 through May–June 1980 varied markedly in terms of timing, duration, and areas searched (Table 1). The greatest search efforts were made where the greatest numbers of trails were found. Therefore, these data do not accurately indicate the proportional occurrence of caribou trails on the sea ice among the various search areas, but instead provide a qualitative guide to where most sea-ice crossings took place (Table 2; Fig. 2).

Those 4 years of limited aerial searches documented 1272 caribou trails on the sea ice within the PSBC (Tables 1–3; Fig. 2). Ninety-four percent (142) of the 151 trails found on northeastern Franklin Strait between Boothia Peninsula and Prince of Wales Island were from east to west. The remaining 6% (9), all in 1979, were made by caribou traveling west to east. Ninety-two percent (645) of the 699 caribou trails seen on Peel Sound between Somerset Island and Prince of Wales Island or the satellite islands in Peel Sound were also from east to west. The direction of travel of caribou on 5% (35) of the 699 trails could not be verified from the Twin Otter. The other 3% (19) of the trails on Peel Sound went from west to east: 18 in 1979 and one in 1980.

Elevations on the high ground ≤10 km from the origins and termini of the 73 crossing sites varied by 188 and 282 m, respectively (Table 3). The length of 26 crossing sites between Boothia Peninsula and Prince of Wales Island ranged from 39–84 km between the elevated points. The 47 caribou crossing sites between Somerset Island and Prince of Wales Island ranged from 30–57 km. The longest distance we recorded for caribou traveling on the sea ice without making a landfall was 109 km. The last 25 km were, however, on sea ice in a bay where land was ≤5 km to the side of them. Thus, the animals could have left the ice at any point after reaching the 84-km potential terminus.

In good weather, caribou on an elevated position ≤10 km from the origin of a trail could have seen the terminus on the far side at 96% (70) of the 73 crossing sites on northeastern Franklin Strait and Peel Sound (Table 2; Fig. 2). If the visibility was adequate, the termini of the sea-ice crossing sites could still be seen for 68% of the 73 sites even when the caribou were standing on the sea ice (from 1 m amsl) at the origins (Tables 2–4). Caribou could see potential termini on Prince of Wales Island from most (88%) elevated positions near origins on Boothia Peninsula and from 100% of the origins on Somerset Island (Table 2). However, once on the sea ice, caribou could see Prince of Wales Island from origins of only 38% of crossing sites on northeastern Franklin Strait and from origins of 85% of crossing sites on outer Peel Sound (Table 2). Prince of Wales Island could be seen from sea level (1 m amsl) at all of the origins for the crossing trails on inner Peel Sound and on Baring Channel.

Seventy-nine percent (550) of the 699 trails found on Peel Sound went directly between Somerset Island and Prince of Wales Island (Fig. 2). The remaining 21% (149) went between Somerset Island and one of the four satellite islands off the east coast of Prince of

Table 2. Numbers of caribou crossing sites on northeastern Franklin Strait and Peel Sound presented in relation to whether the terminus could be seen from the high ground ≤10 km before the origin of the crossing site, south-central Canadian Arctic Archipelago, May–June 1977–80.

Water body crossed (latitudinal zone)	Crossing sites[a]	Trails seen	Length of crossing sites (km)		Elevation of terminus visible from ≤10 km of origin (m amsl)				Terminus not visible at origin
			Minimum	Maximum	1	5–20	25–40	110–115	
Franklin Strait (71–72° N)	26	151	39	84	10	7	4	2	3
South Peel Sound (72–73° N)	19	450(106)[b]	30	51	17	2			
North Peel Sound (73–74° N)	28	249(214)[b]	31	57	23	5			

[a] Caribou crossing sites representative of distribution of 1170 caribou crossing trails on northeastern Franklin Strait and throughout Peel Sound; the sites on Bellot Strait and Baring Channel are not included in this analysis.

[b] Values in parentheses are for trails on inner Peel Sound among the east-central satellite islands of Pandora, Prescott, Vivian, and Lock and between those islands and Prince of Wales Island.

Wales Island. The 88 crossing sites between the satellite islands and Prince of Wales Island were 15–29 km long. The 232 crossing sites between and among the 4 satellite islands were only 1–7 km long. The crossing sites on Baring Channel also were only ≤ 7 km long. Bellot Strait, only 1–4 km wide, had the narrowest crossing sites. It was searched only once, in 1979, because it was common knowledge that caribou crossed it. Although only four complete caribou trails were found on that occasion, the numerous broken trails on both the south and north shores indicated that many caribou had crossed recently from Boothia Peninsula to Somerset Island, then continued northward along the west coast of Somerset Island.

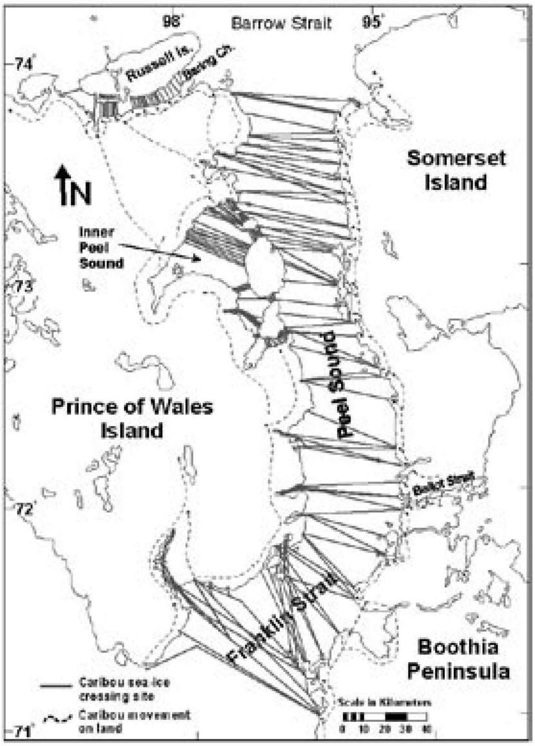


Fig. 2. Seventy-three crossing sites representing 850 caribou trails on northeastern Franklin Strait and Peel Sound, south-central Canadian Arctic Archipelago, May–June 1977–1980.

Discussion

Importance of seasonal use of islands

Caribou trails across the sea ice effectively joined all neighboring land areas for most of each year (Fig. 3), making it possible for caribou to range throughout the complex. Thus, the potential annual home range expanded from a single major land unit of roughly 25 000–33 000 km^2 to >90 000 km^2 among all three major land units, while the satellite islands would add another 3000 km^2 to the maximum overall range. This greatly increased the collective landmass available seasonally compared to what was available if caribou within the PSBC remained on a single island or Boothia Peninsula.

No evidence was obtained during this study for caribou crossing from Prince of Wales, Russell, or Somerset islands to islands north of 74.5°N latitude or vice versa. Also, no additional evidence for such caribou crossings between the PSBC and those more northerly islands was obtained during aerial searches as part of studies in the Bathurst Island complex from 1989 to 1996 (Miller, 1998).

In summer and early autumn, the food supply was adequate and readily accessible throughout the PSBC (e.g., Fischer & Duncan, 1976; Russell *et al.*, 1978; Miller *et al.*, 1982). Calving occurred annually on Prince of Wales Island, Russell Island, Somerset Island, and on lesser satellite islands (e.g., Fischer & Duncan,

Table 3. Elevation of high ground ≤10 km of origins and termini of 73 caribou crossing sites, south-central Canadian Arctic Archipelago, May and June 1977–1980. (see Table 2).

Water body	*n*	Elevations (m amsl) Minimum	Elevations (m amsl) Maximum
Origins			
Franklin Strait	26	61	238
South Peel Sound	19	90	210
North Peel Sound	28	50	110
Termini			
Franklin Strait	26	46	234
South Peel Sound	19	110	328
North Peel Sound	28	61	349

Table 4. Distance to visible horizon (km) from various land elevations (m amsl).

Elevation of origin	Elevation of terminus or potential terminus								
	1	30	60	100	150	200	250	300	350
1	8								
30	25	42							
60	34	51	59						
100	42	59	68	77					
150	51	68	77	85	94				
200	58	75	84	93	101	109			
250	65	82	90	99	108	115	121		
300	70	87	96	105	113	121	127	133	
350	76	93	102	110	119	126	132	138	144

1976; Miller & Gunn, 1978, 1980; Miller *et al.*, 1982; Gunn & Fournier, 2000b). The Prince of Wales Island and Somerset Island seasonal resident caribou returned to calve and summer on those islands along with the year-round residents (Miller & Gunn, 1980; Miller *et al.*, 1982). As soon as freeze-up occurred in early winter, the annual cycle of migrations over the sea ice was renewed and the PSBC caribou returned to their winter haunts. Caribou found on Boothia Peninsula in summer were not part of the PSBC geographic population, but were either year-round residents or migrants from the mainland further south (Gunn & Ashevak, 1990; Gunn & Dragon, 1998; Gunn & Fournier, 2000b; Gunn *et al.*, 1997, 2000a).

Winters on Boothia Peninsula are slightly shorter and, in general, less harsh than on the Arctic Islands. Most importantly, more of the forage on Boothia Peninsula should be accessible in winter because plant growth is more erect and taller there than on the Arctic Islands. We speculate that caribou moving from Prince of Wales and Somerset islands to winter on Boothia Peninsula would reduce overwinter grazing pressure on forage plants on their island summer ranges. Range rotation would allow faster recovery and better growth of forage plants on summer range during the following growing season and this would lessen grazing pressure. This could allow the caribou population to increase more than if it was restricted to a single island (Fig. 3). Of course, this is all conditional on the absence of exceptionally severe weather years, heavy predation, or unsustainable levels of annual harvesting.

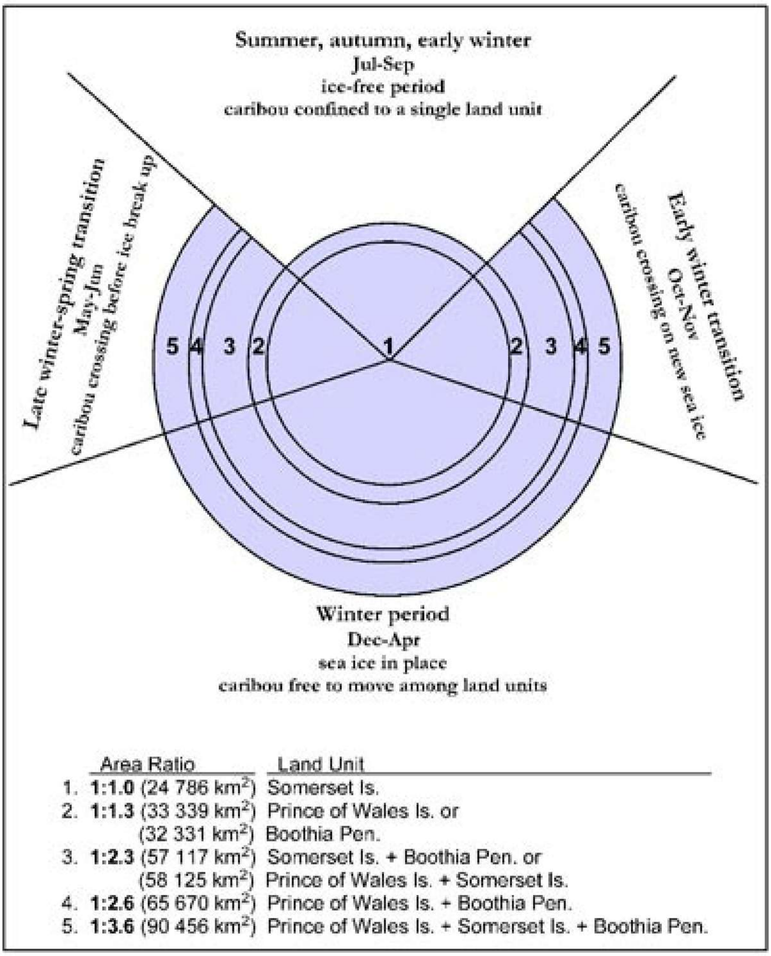
Do caribou need visual aids for sea-ice crossings?

Caribou could see the potential terminus from elevated positions at the trail origin of all but the three longest sites, 84 km from the trail origin, which were the most southerly trails on Franklin Strait. Potential termini for these three crossing sites were slightly beyond what was geodetically visible, but distant land forms were visible in other directions, and may have been used for guidance.

The influence of the curvature of the earth on the distance to the horizon from an elevated point of land determines the visibility under a given set of conditions (Table 4). In the Arctic, however, this relationship can be markedly altered by the common occurrence of mirages. Mirages can effectively elevate the coast lines of low-lying islands many times above their true height, making it possible to see low-lying landmasses at much greater distances than the values in Table 4 indicate. Conversely, persistent fog is common and together with occasional blizzards would hinder or prevent the use of visual guidance by caribou migrating between or among the islands or the mainland and an island.

There is no indication that higher origins or termini were used preferentially by caribou in migration; seemingly, elevations at crossing sites just reflect the variation in heights of high ground found along the coasts. The lack of preference for high origins or termini is supported by the fact that crossing sites were distributed rather evenly from 71–74°N (Fig. 2), regardless of the length of the sea-ice crossing site or the elevation at its origin or terminus.

Other authors have reported that reindeer and caribou are capable of making sea-ice crossings over great distances well beyond the sight of land. The longest reported distance traveled over the sea ice without any possible landfall and well out of sight of any land was recorded for a reindeer marked by natives on Novaya Zemlya that then crossed 380 km of sea ice to Kong Karls Land, then 340 km to Franz–Josef Land, plus a further 90 km to Edgeøya



	Area Ratio	Land Unit
1.	**1:1.0** (24 786 km²)	Somerset Is.
2.	**1:1.3** (33 339 km²)	Prince of Wales Is. or
	(32 331 km²)	Boothia Pen.
3.	**1:2.3** (57 117 km²)	Somerset Is. + Boothia Pen. or
	(58 125 km²)	Prince of Wales Is. + Somerset Is.
4.	**1:2.6** (65 670 km²)	Prince of Wales Is. + Boothia Pen.
5.	**1:3.6** (90 456 km²)	Prince of Wales Is. + Somerset Is. + Boothia Pen.

Fig. 3. Schematic ratio representation of annual expansion (nearly quadrupling) of annual caribou home ranges made possible by seasonal inter-island, mainland-island, and island-mainland late winter–spring and early winter migrations across the sea ice within the Prince of Wales Island–Somerset Island–Boothia Peninsula Complex, south-central Canadian Arctic Archipelago.

in Svalbard before being killed there (Banfield, 1961; Hakala *et al.*, 1985). Banfield (1961) also notes records of reindeer crossing from the New Siberian Islands to Bennet Island, a distance of 125 km. Manning & Macpherson (1958) report that caribou are known to cross from Banks Island to Cape Bathurst on the mainland, a distance of about 185 km. Other examples of long-distance movements by *R. tarandus* over the sea ice are reported in Miller (1990a). Thus, it appears that while caribou might often cross frozen water bodies at sites where a visual terminus exists on the far side, such visual cues are not necessary.

Mechanisms for sea-ice crossings

Although we know little about their methods, the navigational prowess of *R. tarandus* is well known. For caribou and wild reindeer, seasonal migrations are accomplished through "learned traditions" incorporating innate behavior (Ortstreue: Wynne Edwards, 1962). It is most likely that the odoriferous materials produced by their interdigital scent-glands and secondarily by tarsal and caudal scent glands and in urine and feces (e.g., Quay, 1955; Lewin & Stelfox, 1967; Andersson *et al.*, 1975; Muller-Schwarze *et al.*, 1978) facilitate long-distance migrations by reinforcing the coherence of the different groups in migration and directionality during daily travels (e.g., Miller, 2003).

The caribou's habit of walking single-file when moving or migrating and often stepping in exactly the same spot is well known. This behavior would concentrate scent deposits from the interdigital glands and greatly intensify the scent markings that guide visually separated trailing animals. Lapp herders have long believed that the interdigital glands serve in layering an odor track on the ground (Muller-Schwarze *et al.*, 1978). It is quite possible that odorous material such as a long-lasting pheromone in the tracks of the first caribou to make a sea-ice crossing would be detectable by following caribou for some time afterwards. This could be true even after the tracks have been obliterated by snow and even after no visual or tactile stimulus could be transmitted from footprints in the snow pack.

If the caribou choose to retreat back along their trail, they have a strong scent trail (including a "trail pheromone": Muller-Schwarze *et al.*, 1978) to guide them, even if the trail has been obliterated by new snowfall or wind action. No other form of guidance would be necessary to allow them to return to land. Most importantly, once a few or possibly just one caribou crosses successfully, all other caribou can follow the scent trail without additional guidance. On two occasions, F. L. Miller observed caribou on previously established trails on Peel Sound coming onto northeastern Prince of Wales Island in fog and low overcast that at times allowed only about 1 km forward visibility.

Caribou would also add to their scent trail with urine and feces. When caribou urinate on snow in subzero weather, the urine freezes into a "urine cone." On the High Arctic Islands, these urine cones are often 15–20 cm high with a base 6–10 cm wide that tapers upward to only 2–4 cm in width where the hot urine first penetrated the snow pack. Foraging caribou often deliberately sniff and are seen to lick such frozen urine deposits; it seems reasonable that urine cones in the snow cover, or frozen pooled urine on a hard surface would serve as "sign posts" for migrating caribou. If they needed any further guidance, scent from feces obviously could aid caribou in migration and general body odors and the smell of the land may provide additional aids. Visual, tactile, and auditory aids may be useful on occasion but are not necessary for caribou to travel over long distances along a particular course.

Potential impacts of climate change

If climate change advances as predicted, the caribou will experience radical changes in their environment and the ultimate result might be restriction to a single island or to the mainland. Changes due to climate warming are predicted to occur first and most severely in the Arctic (Maxwell, 1997; Weller, 2000). Climate change at its most drastic may test thousands of years of caribou evolution in this region and throughout the Arctic.

Recent trends suggest that the seasonality and characteristics of sea ice cover surrounding the Arctic Islands and particularly the sea ice linking the islands to the mainland may greatly change in the near future (Comiso, 2002). Increases of 1–3 months in the duration of the ice-free season are predicted, suggesting that freeze-up could be delayed well into November, that the melt could begin in May, and that sea-ice break-up could occur in early June. If such changes occur, they would seriously alter the timing and, perhaps, the opportunity for seasonal migrations across the sea ice. The timing of these migrations is linked to annual life history phases of caribou. Thus, many of the benefits to caribou derived from migration between land areas could be severely reduced or virtually lost due to later freezing or earlier melting of sea ice. A series of years with extremely short periods of ice cover could cause caribou to alter or lose their tradition of inter-island or mainland-island seasonal migrations. Loss of these migrations could seriously reduce the ability of the region to support viable populations of caribou.

Delayed freeze-up would lead to increased mortality of caribou attempting to migrate over sea ice that was still too weak to support them (e.g., Miller & Gunn, 1986). Already in recent years, there have been reports of the drowning of a large number, perhaps several hundred, of the Dolphin and Union caribou herd during their autumn migration from Victoria Island to the mainland (Gunn *et al.*, 1997, 2000b; A. Gunn, pers. comm., 2005).

Ship traffic through the ice-covered channels among the Arctic Islands and especially between those islands and the mainland would be another impediment to caribou seasonal migrations (Miller, 1990a, b). Five shipping lanes through Arctic waters have been proposed in initial scenarios and as many as 20 ships a day have been forecast to pass through the Northwest Passage (*ca.* 74–75°N latitude): an average rate of one ship every 1.2 hours. At that rate, it is most unlikely that the shipping track could refreeze sufficiently to support caribou crossings between ship passages. Although caribou can easily swim open-water ship tracks, the ice shelf and the ice-block rubble pushed-up along the edges of the track could be a death-trap, especially for the small-bodied calves, yearlings, and 2-yr olds, but in some instances for any caribou that enters the water.

The economic enticement for heavy use of shipping lanes in Arctic waters is great. Nationally, this shipping is focused on the extraction of nonrenewable resources (oil, liquefied natural gas, and mineral ores) from the Canadian Arctic islands and the coastal mainland. All-season shipping will bring greatly increased exploration and development activities for nonrenewable resources and the associated human-induced novel stimuli could be detrimental to the long-term well-being of caribou populations in the Canadian Arctic Archipelago and on the coastal mainland (e.g., Miller & Gunn, 1979). Internationally, the greatest benefit from shipping through Arctic waters arises from the 11 000 km that would be cut off the Europe–Asia route through the Panama Canal and the 19 000-km reduction for the trip around Cape Horn for supertankers unable to use the canal (Kerr, 2002). Thus, the continued feasibility of caribou making seasonal inter-island migrations, and especially migrations between the mainland and the Arctic Islands, is questionable. When and if climate warming and heavy shipping traffic come to pass, those caribou now prospering from seasonal migration over the sea ice would be forced to face the rigors of life imposed on a "single-island dweller." For at least some and possibly many islands, extirpation of caribou would be the result.

Conservation and management implications

Although the search efforts from 1977 through 1980 were limited, a large number of caribou sea-ice crossing trails were documented (Tables 1 and 2; Figs. 2 and 3). These migrations over the sea ice allow marked expansions of caribou use of different land units on a seasonal basis for about nine months of each year (Fig. 3). The importance of these intricate seasonal movements over the sea ice cannot be ignored when planning conservation efforts or making management prescriptions for these caribou.

We demonstrate that while caribou could see 96% of the termini from elevated positions, once on the sea ice they could see only 68% of the termini (Table 2). Prince of Wales Island can be seen from sea level (1-m amsl) at all of the origins for the crossing trails on inner Peel Sound and Baring Channel (Table 2). Information from the literature shows that caribou and reindeer travel great distances on the sea ice well beyond any possible sight of land. This, in itself, rules out the supposed necessity that caribou or reindeer be able to see land on the opposite side before beginning a migration or movement over the sea ice.

The majority of caribou on Prince of Wales and Somerset islands (and their satellite islands), apparently functioned as an intricate geographic population with several calving areas and rutting areas, with different segments exhibiting different seasonal and annual patterns of island and peninsula use. However, some caribou stayed year-round on either of the two major islands and could be considered as at least two separate local populations with different annual patterns of single-island use. If they were, in fact, functioning as discrete ecologically meaningful local populations, then they may be a "metapopulation" or part of one. The extensive movements among the islands and the peninsula suggest that, for purposes of conservation and management, it would be best to treat the entire PSBC as one unit.

The caribou's ability to move freely over the sea ice for most of each year makes it ecologically invalid to view caribou on the Canadian Arctic Archipelago as compulsory single-island dwellers. This is particularly true in terms of the greater environmental limitations that could be imposed on caribou restricted to a single Arctic island for their entire lifetime. Important exceptions, when no great benefits are derived from inter-island movements, are the years with exceptionally severe widespread snow and ice conditions that lead to major winter die-offs. These occur infrequently and sporadically and thus unpredictably on a widespread and sometimes range-wide basis (Miller *et al.*, 1977a; Miller, 1998; Gunn *et al.*, 2000b; Gunn & Dragon, 2002; Miller & Gunn, 2003a, b).

In all likelihood, annual inter-island and island-mainland migrations represent the most important behavioral tradition held by caribou on most of the Canadian Arctic Archipelago, as they greatly expand the available land base. This includes the caribou in the PSBC, and the Dolphin and Union herds that calve and summer on Victoria Island and winter on the mainland. Migrations allow all caribou to greatly expand their annual home range through seasonal movements to different islands or onto the adjacent mainland. Inter-island, island-mainland, or mainland-island movements can take the form of seasonal migrations, sporadic environmentally-forced responses, and chance events. More specifically, migration across the sea ice can reduce caribou grazing pressure on the forage through expansion of annual range by using different seasonal ranges. This should reduce grazing pressure per unit area and markedly increase the magnitudes and durations of population highs and reduce the depths and lengths of their lows (e.g., Miller, 1990a).

In the Canadian Arctic Archipelago, possibly only Baffin Island (the fifth largest island in the world at 507 451 km^2) is an exception to the restrictions imposed on a single-island dweller. Although caribou on Baffin Island experience population highs and lows along with range shifts (Ferguson & Messier, 2000), the island's huge size and varied terrain negate the need for caribou to use more than one island for seasonal ranges. Nevertheless, even the Baffin Island caribou might benefit, at times, from using summer ranges on nearby islands to reduce the year-round grazing pressure on some ranges on Baffin Island. It is possible that caribou on Victoria Island (the 9th largest island in the world at 217 291 km^2) and Ellesmere Island (the 10th largest island in the world at 196 236 km^2) would also not need to move to other islands. Infrequent major die-offs could occur, however, on large sections of those two islands if the caribou do not shift their range or emigrate when they are subjected to exceptionally severe and prolonged snow and ice conditions.

It is critical for both ecologically sound conservation and biologically sound management of these caribou to document the full repertoire of seasonal migrations among the islands and the peninsula within the PSBC. Most importantly, this information should be used in conservation and management efforts for these caribou. Knowledge of these alternative patterns of use made possible by sea-ice crossings is necessary to truly understand the population dynamics of these caribou and the importance of possible future changes in ice cover.

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Putting the environmental impact assessment process into practice for woodland caribou in the Alberta Oil Sands Region

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Abstract: Since 1985, woodland caribou (*Rangifer tarandus caribou*) have been designated as a threatened species in Alberta. Populations studied since the 1970s have been stable or declining, with no population increases documented. Resource expansion into previously undeveloped areas and associated increases in access have been implicated as possible causes for the declines. To facilitate development on caribou ranges, while ensuring the integrity and supply of caribou habitat, standing committees have been formed. The primary role of the committees is to act as advisory bodies to the government and to search for effective and efficient industrial operating guidelines. Recent research has been conducted on the responses of woodland caribou ecotypes to increased human and predator access. Based on this research, operating guidelines have been refined and implemented through Caribou Protection Plans. I discuss how the current operating guidelines are put into practice and linked to the Environmental Assessment process within the Oil Sands Region of Alberta. In particular, I discuss the origination of impact predictions, specific mitigation measures to reduce impacts and monitoring.

Key words: Caribou Protection Plans, Environmental Impact Assessment, mitigation, monitoring, oil sands, operating guidelines, *Rangifer tarandus caribou*.

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Introduction

Woodland caribou are listed as a threatened species in Alberta (Alberta Wildlife Act 2000) and nationally in Canada (COSEWIC, 2003). Since 1991, populations of woodland caribou in Alberta have been stable or declining, and no population increases have been documented (Dzus, 2000; McLoughlin *et al.*, 2003). Concurrently, resource-based industries have expanded at a rapid rate into previously undeveloped areas, and associated increases in access have been implicated as possible causes for declines of caribou populations (Edmonds, 1988). To sustain industrial activity on caribou ranges, while ensuring the integrity and supply of caribou habitat (Alberta Department of Energy, 1991), multi-stakeholder standing committees were formed throughout the province. The primary role of the committees is to advise the government and to search for effective and efficient industrial operating guidelines (Rippin *et al.*, 1996). Currently, two guideline documents are applied to industrial activities occuring within woodland caribou ranges in the province (Boreal Caribou Committee [BCC], 2001; West-Central Alberta Caribou Standing Committee, 1996).

Current operating guidelines address habitat targets and activity targets within caribou ranges, range planning, adaptive management initiated through on-going research, and best operating practices. The best operating practices are industry-specific and are applied through each developer's annual Caribou Protection Plan (CPP). The CPPs provide a tool for land managers to make decisions on proposed activities within each caribou range and provide a venue for cooperation among developers to utilize common access corridors and other infrastructure in an effort to minimize cumulative disturbances to caribou.

Research to date

A primary objective of the industrial guidelines is to apply adaptive management initiated through

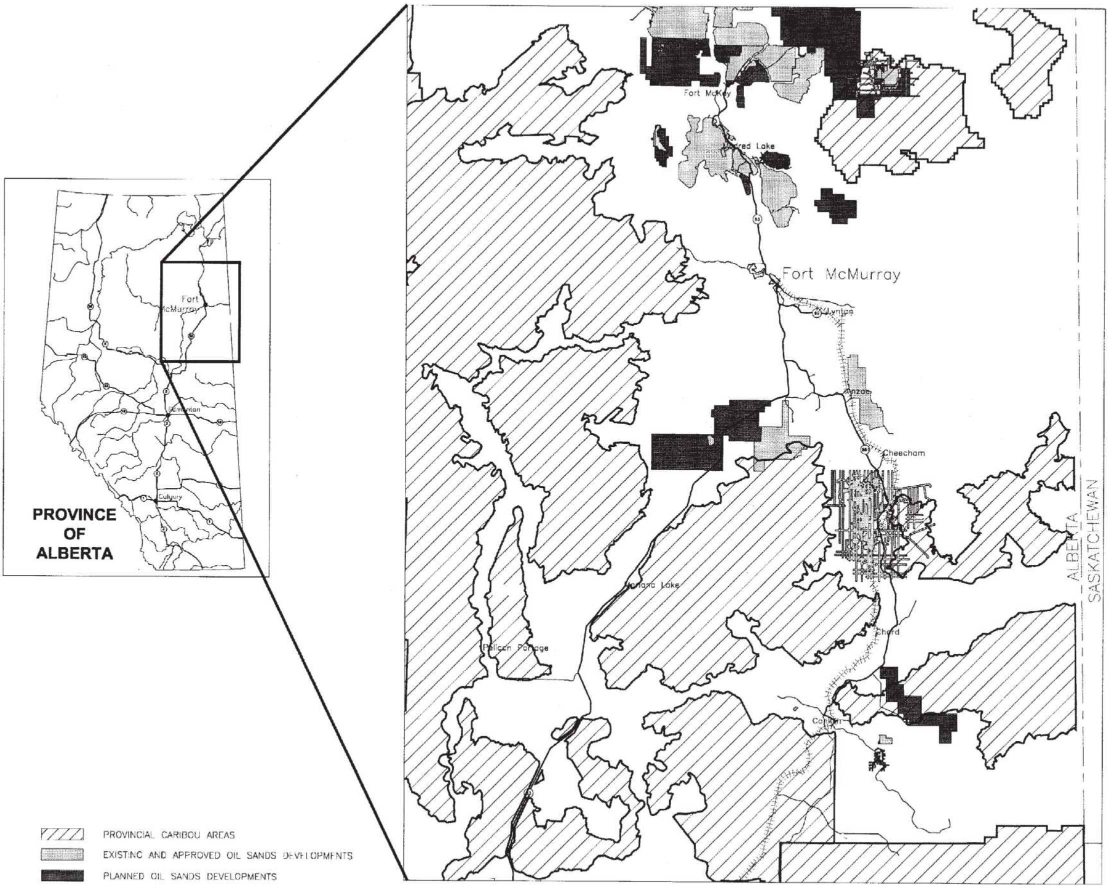

Fig. 1. Location of caribou areas in association with existing and planned oil sands developments in the Oil Sands Region. (Diagonal lines indicate caribou range, shaded blocks are proposed or active oil and sands developments).

on-going research. Research has focused on increased human and predator access within caribou ranges. Caribou response to instantaneous human activity, increased predation risk resulting from linear corridors (e.g., roads, seismic lines), indirect habitat loss associated with caribou avoidance of industrial development, roads and cutlines as barriers to movement, and the influence of fire on habitat use have been examined in an effort to refine the industrial guidelines.

Caribou response to "instantaneous" human activity (i.e., simulated seismic programs) appears to be short term, with caribou moving away from areas of human activity but returning once activity has been terminated (Bradshaw *et al.*, 1997). Wolf distribution and kill site locations have been studied in the context of caribou avoidance and potential increased predation as a result of disturbances. James (1999) found that woodland caribou demonstrated a pattern of habitat selection that differed from that of moose and wolves. Caribou tended to occur further from linear developments, while wolves and their kill sites were closer than random to linear developments (James, 1999; James & Stuart-Smith, 2000). In addition, wolves use linear developments as travel routes and have been documented travelling up to 2.8 times faster on linear developments than in surrounding forest (James, 1999), which may improve their predation efficiency. Human-caused mortalities have also been documented closer to linear corridors (James & Stuart-Smith, 2000).

Although woodland caribou utilize land near industrial development, use is less than expected and varies depending on the season and the type of development. Dyer (1999) reported that the density of caribou locations was significantly lower than expected in areas closer to roads, wellsites and seismic lines. Such avoidance patterns will reduce the useable habitat available to caribou. In addition, these linear developments may form barriers to the free movement of caribou between patches of undisturbed habitat (Dyer *et al.*, 2001; Dyer *et al.*, 2002).

Avoidance of seismic lines by boreal woodland caribou appears to be greater during the late winter when seismic lines may act as winter roads on frozen ground (Dyer, 1999). Conversely, radio locations of mountain woodland caribou (mountain ecotype) do not appear to be influenced by the distribution of seismic lines. However, research on the mountain ecotype occurred on caribou ranges with considerable natural reforestation on older seismic lines and all newer seismic lines were developed using low impact seismic techniques (Oberg, 2001).

As fire is the dominant natural landscape influence in the boreal forest, Dunford (2003) examined the response of woodland caribou to habitat loss and alterations associated with fire. Large-scale distribution patterns of caribou appeared to have little relationship to the loss of lichens due to wildfires, and changes in forage availability resulting from wildfires did not alter caribou distribution or range fidelity (Dunford, 2003). Caribou avoidance of burned areas declined as the areal extent of burned areas increased, possibly because caribou were selecting unburned patches within burned areas in their home ranges. Large home ranges appear to allow caribou to meet their forage requirements even when lichen availability is reduced as a result of fire.

Based on the research to date, operating guidelines have been refined and implemented at a local scale by industrial developers through the use of best operating practices as outlined within the current guidelines (BCC, 2001; WCACSC, 1996).

Putting process into practice

Alberta's Oil Sands Region

The Oil Sands Region (OSR) of Alberta encompasses almost the entire northeastern portion of the province. This boreal forest region has experienced a rapid expansion of industrial development, including oil sands extraction (open-pit mining and Steam-Assisted Gravity Drainage [SAGD] in-situ operations), gas extraction and processing, forestry activities and peat mining. These developments are associated with infrastructure such as roads, pipelines (above and below ground), utility corridors and seismic exploration programs. Specific impacts from the oil sands extraction developments include the direct loss of habitat from large-scale open pit mines, and multiple well-pads with aboveground pipelines from in-situ operations. Current projects that have been approved or planned in the OSR overlie a number of woodland caribou (boreal ecotype) ranges (Fig. 1). Assessment of the impacts from oil sands developments is required under the Alberta Environmental Protection and Enhancement Act (AEPEA 110/93). Assessments must include a baseline (Baseline Case), project (Application Case) and cumulative effects assessment (CEA Assessment) for species of concern, including woodland caribou.

In this paper, I discuss how the multi-stakeholder Boreal Caribou Committee's operating guidelines and research results are incorporated into an Environmental Impact Assessment (EIA) for woodland caribou in the OSR of Alberta. In particular, I discuss the origin of impact predictions, specific mitigation measures to reduce impacts and long-term monitoring programs.

Baseline case

The baseline case provides a summary of wildlife observations and habitat found within a local study area (LSA). Woodland caribou are classified as a Priority 1 Key Indicator Resource (KIR) species within the OSR (Westworth, 2002) as a result of their status in the province and traditional value for indigenous people (First Nations). Because of their ecological and traditional importance, baseline surveys completed prior to the completion of an EIA focus on identifying the presence of caribou and their relative density and habitat use within the LSA. Aerial surveys, winter track count surveys, pellet surveys and historical database searches (e.g., Biodiversity/Species Observation Database [BSOD] and caribou range maps [Dzus, 2000]) are completed at a local scale to determine baseline conditions for caribou within the LSA. Historical data at the regional scale are also compiled to determine caribou locations and important habitat areas (e.g., historical calving locations). If caribou are present within the LSA, planning for the location of the development footprint (e.g., plant site, camp location, wellpads) considers caribou location information (e.g., calving sites, potential movement corridors and range boundaries) to minimize the overall impact of the project on caribou within the LSA.

Application case

The purpose of the Application Case is to assess specific effects on wildlife, identify strategies to minimize potential project-related effects, and to discuss the potential to return wildlife habitat within the LSA to predisturbance conditions. Oil sands development activities affect woodland caribou through several pathways including habitat loss and alteration, direct and indirect mortality (e.g., vehicle–wildlife collisions, implications of physiological stress from sensory disturbance on calving and recruitment), and changes in access and use.

In the OSR, direct habitat loss results from clearing and is greatest during the site clearing phase of a development. Indirect habitat loss results from

Table 1. Zones of influence (ZOI; m) and disturbance coefficients (DC) for 3 types of disturbance likely to affect woodland caribou in the Alberta Oil Sands Region.

Access (roads)		Facilities and development		Utility corridors[a]	
ZOI	DC	ZOI	DC	ZOI	DC
100	0	250	0.5	100	0.5
250	0.25				
500	0.50				
1000	0.75				

[a] Seismic lines, powerlines, pipelines.

fragmentation, changes in hydrology (e.g., drainage of peatlands), barriers to movement, sensory disturbance and air emissions. Indirect habitat loss occurs when habitat is still physically present, but caribou choose not to, or may not be able to, use habitat as a result of barriers to movement, fragmentation, sensory disturbance and air emissions (i.e., reduction in lichen). Indirect habitat loss also includes habitat which has reduced effectiveness for caribou due to its proximity to a development feature (e.g., roads, seismic lines, well site) and the reduced use by caribou (Dyer, 1999). Direct habitat loss and initial fragmentation are closely associated with the construction phase of developments, while indirect habitat loss is more closely associated with the operational phases.

To determine the magnitude of direct and indirect habitat loss, Habitat Suitability Index (HSI) models are generated for assessing quantity and quality of caribou habitat (see Petro-Canada, 2001 for model description). The HSI models are research driven, derived from research results on woodland caribou habitat use (e.g., Anderson, 1999; Schneider *et al.*, 2000; Stuart-Smith *et al.*, 1997) and the effects of disturbance on caribou use of habitat (e.g., Dyer, 1999). Using a Geographic Information System (GIS), habitat quantity and quality are examined under the Baseline Case, the Application Case and the CEA Case. For example, habitat loss calculations for the Application Case are based on the direct and indirect removal of habitat in the LSA as a result of the development. Indirect habitat loss is quantified by buffering the development footprint by Zones of Influence (ZOI). A ZOI is the estimated maximum distance to which a disturbance (e.g., noise) influences caribou habitat use. A Disturbance Coefficient (DC) is applied to the ZOI. The DC is the effect a disturbance has on habitat use within a ZOI. For example, a DC of 0.5 represents a 50% reduction in habitat effectiveness for caribou and can be characterized as all caribou using a ZOI 50% of the time or 50% of the caribou using ZOI all the time. Different ZOI and DC coefficients are applied for each development activity type for caribou (Table 1). Indirect habitat loss is quantified by multiplying the area within ZOIs with appropriate DCs. Total habitat loss as a result of the development (the Application Case) is the sum of all direct and indirect habitat loss within the LSA. Changes in hydrology and impacts to terrestrial lichen abundance predicted from air emissions (i.e., acid deposition) are also added to the indirect habitat loss for caribou using the habitat modelling results overlaid with an isopleth for the predicted hydrology drawdown areas and an isopleth for the predicted potential acid input in excess of the critical load values adopted for use in Alberta (CASA, 1999).

Fragmentation indices are measures of the change in the forest landscape from extensive and continuous forest. Because caribou prefer large tracts of uninterrupted habitat, or a "well-connected" landscape, fragmentation indices are generated for caribou HSI habitat classes (low/moderate/high). To determine changes in landscape composition and structure, indices for the number of habitat patches and mean patch size are generated. Mean nearest neighbor distance is used to assess changes in landscape connectivity. For caribou, fragmentation is considered to be a negative impact when a proposed development is predicted to result in fewer, larger patches and high nearest neighbor distances.

Empirical data collected from the baseline surveys, as well as from wildlife surveys completed for other Oil Sands projects are used to test the predictions of HSI models. Once the HSI modelling is complete, the quantity of low, moderate and high quality caribou habitat which will be both directly and indirectly affected by the development are summarized.

Indirect mortality may result from sensory disturbance from construction and operations. Direct mortality may result from changes in human and predator access. Increased human and predator access may lead to increased predation, illegal and legal (First Nations) hunting, and the potential for increased vehicle–wildlife collisions. These effects are primarily a result of construction and operation activities. Professional judgment is used for assessing the magnitude of indirect and direct mortality. For caribou, research results (e.g., James, 1999), traditional knowledge (i.e., on the approximate amount of native harvest) and road mortality data from government agencies are used to form the assessment.

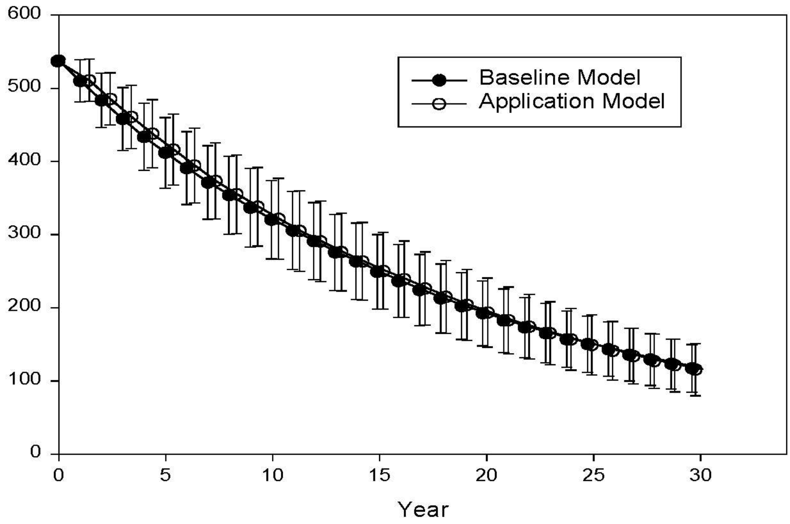

Fig. 2. Predicted change in caribou population from cumulative disturbance (modified from Petro-Canada, 2001)

CEA case

The CEA Case predicts the effects of a particular project plus existing, approved and planned developments on caribou at a regional scale, the Regional Study Area (RSA). Similar to the Application Case, the effects of the CEA Case on caribou habitat availability and effectiveness are determined through the use of HSI models in the RSA.

In addition to assessing direct and indirect habitat loss in the RSA, the cumulative impacts of development on caribou populations are assessed using a Population Viability Analysis (PVA) model (i.e., RAMAS GIS). The PVA incorporates both demographic rates and environmental variation to simulate population trajectories through space and time. The PVA is ultimately used to estimate the probability of a population becoming extirpated (Soulé, 1987; Shaffer, 1990), but also provides a tool for identifying those variables that are driving changes in population size. RAMAS® GIS is a PVA program that links habitat changes to population models (Akçakaya, 1998). Landscape data are used to calculate species HSI values and given a set of rules, RAMAS determines the patch structure and the number of potential populations (i.e., metapopulations) within the RSA. HSI models are used to generate estimates of carrying capacity and initial population size for both the baseline and cumulative effects development scenarios. Carrying capacity and initial population size are input into a population model that includes density dependence and the effects of environmental stochasticity on fecundity and survival rates. By changing carrying capacity of the landscape and initial population size, while keeping all other population parameters constant, we can quantitatively assess the cumulative effects of habitat change on the probability of woodland caribou declining below a particular threshold value. For example, results from the assessment of the Petro-Canada Meadow Creek Project indicated that the cumulative changes in habitat caused by future developments did not statistically alter the caribou population trajectory, or the risk of decline below a threshold value (Fig. 2). Rather, the models predicted a population decline that was strongly dependent on the current estimates of demographic rates for woodland caribou in Alberta and North America (Petro-Canada, 2001; Fig. 2). This conclusion was similar to that of Stuart-Smith *et al.* (1997), who predicted that with no change in growth rate, the caribou population in northeastern Alberta (adjacent to and overlapping the RSA used in our analysis) will decrease by 55% during the next 10 years.

Mitigation

During the EIA, mitigation measures to preclude or minimize potential project-related effects are provided for each impact. Mitigation measures for woodland caribou in the OSR focus on the current operating guidelines, best practices, and specific range plans developed through the multi-stakeholder caribou committees (BCC, 2001). Prior to development, environmental protection planning assists in minimizing or avoiding potentially negative impacts to caribou during construction and subsequent operation phases. Use of common corridors, route selection, low-impact seismic exploration techniques (reduced width and line of sight) and facility siting are the primary means of minimizing the impacts of habitat loss. Timing constraints (e.g., to activity during calving periods) and/or buffer zones for construction may minimize the impacts of sensory disturbance. Prompt reclamation of disturbed areas (i.e., progressive reclamation) ensures that habitat is disturbed for as short a period as possible. Reclamation and revegetation methods within caribou areas focus on minimizing the creation of suitable habitat for other ungulate species (e.g., deer [*Odocoileus* spp.], moose [*Alces alces*]) and maximizing the restoration of suitable caribou habitat. For linear developments, on-going research through the multi-stakeholder committees on caribou habitat restoration (Szkorupa, 2002) is incorporated into project mitigation.

Additional mitigation may include aboveground pipeline crossing structures and gaps in snow berms and other barriers to movement (CNRL, 2000), education and awareness programs for employees and contractors, human access control measures (e.g., signs, reduced speed limits, manned gates, prohibition of recreational vehicles, busing employees to the site), and predator access control measures (e.g., tree felling). Once mitigation measures for a project have been determined, the residual impacts (i.e., postmitigation) are evaluated and discussed within the EIA.

Monitoring

Monitoring programs are incorporated throughout the life of a project to ensure that mitigation measures are effective and improved where necessary and to verify impact predictions. For example, the location and design of aboveground pipeline crossing structures, implemented to reduce barriers to movement from SAGD operations, are still in their infancy. Track count surveys and remote camera monitoring provide data on active game trails and are helping to identify proper placement of crossing structures. These data also provide evidence for use of the crossing structures by caribou (e.g., Golder, 2004). Regular aerial surveys (e.g., Bentham & De La Mare, 2003) employee sighting cards (e.g., Golder, 2004), caribou incident reports (e.g., vehicle collisions) and regular reporting of monitoring results to regulators provide a record on the distribution and conservation of caribou in relation to on-going development activities. The results from long-term monitoring programs trigger developers to modify mitigation measures when necessary to ensure caribou conservation, and will ultimately provide data on reclamation success as developments enter the closure phase.

Caribou Protection Plans

To assist provincial caribou conservation goals, the Alberta Energy and Utilities Board (1994) requires an annual CPP for all activities occurring within caribou areas (EUB IL 94-22). CPPs are used to assist the provincial government in predicting the level of activity and habitat disturbance that will occur in each caribou range. CPPs for each winter's work must be submitted to the regional Alberta Sustainable Resource Development (ASRD) office by 15 October annually. The value of the CPPs is in identifying where resource users can combine footprints and work together to help achieve effective habitat in caribou ranges.

A CPP strategy is outlined within each EIA to cover the construction, operation and reclamation activities of each project. The strategy is based on the impact assessment, mitigation and monitoring as outlined within the EIA. Each CPP reports on the results of the caribou protection strategy and any monitoring activities from the previous year. The "Strategic Plan and Industrial Guidelines for Boreal Caribou Ranges in Northern Alberta" (BCC, 2001) are incorporated into the protection measures outlined in the CPP strategy. As research on woodland caribou is conducted within the province, best practices for industry can be updated to reflect research results. Annual CPPs will incorporate these updates as well as report on development activities of the past year, results of caribou protection planning and monitoring from the past year, development plans for the upcoming year, and protection measures for the upcoming year. Additionally, once specific range plans are developed, range planning protection measures and habitat targets (e.g., BCC, 2003) will also be incorporated into the CPPs.

Conclusion

The ongoing research, current operating guidelines and caribou protection strategies provide a framework to achieve caribou conservation in Alberta. However, the success of the caribou standing committees and the operating guidelines depends upon the commitments of individual developers in the OSR. As illustrated in this paper, commitment begins during the EIA process where research findings are used to refine and improve impact predictions, impact predictions are linked to cumulative effects and regional caribou populations, mitigation measures are implemented and refined through long-term monitoring programs (e.g., Golder, 2004), and CPPs are used to document protection planning and to help identify areas for collaboration among industries throughout the life of a project (e.g., CNRL, 2000; Opti, 2000; Suncor, 2000; Petro-Canada, 2001).

Considering the rapid rate of development within the OSR of Alberta, industries recognize that they will have to work in partnership to minimize impacts to woodland caribou and to stabilize caribou populations. The success of the caribou committees and the multi-stakeholder partnerships have also provided a framework for collaboration on a number of other wildlife issues in the OSR. Proposed initiatives include additional research for species of concern (e.g., caribou, Canadian toads [*Bufo hemiophrys*]), developing effective aboveground pipeline crossing structures, and the creation of regional wildlife movement corridors. These are good news stories, with industries taking the benefits of being involved in the caribou committees and using this as a framework to work together to do the right thing for caribou, and for other species of concern in the OSR.

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Mountain pine beetles and emerging issues in the management of woodland caribou in Westcentral British Columbia

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Abstract: The Tweedsmuir–Entiako caribou (*Rangifer tarandus caribou*) herd summers in mountainous terrain in the North Tweedsmuir Park area and winters mainly in low elevation forests in the Entiako area of Westcentral British Columbia. During winter, caribou select mature lodgepole pine (*Pinus contorta*) forests on poor sites and forage primarily by cratering through snow to obtain terrestrial lichens. These forests are subject to frequent large-scale natural disturbance by fire and forest insects. Fire suppression has been effective in reducing large-scale fires in the Entiako area for the last 40–50 years, resulting in a landscape consisting primarily of older lodgepole pine forests, which are susceptible to mountain pine beetle (*Dendroctonus ponderosae*) attack. In 1994, mountain pine beetles were detected in northern Tweedsmuir Park and adjacent managed forests. To date, mountain pine beetles have attacked several hundred thousand hectares of caribou summer and winter range in the vicinity of Tweedsmuir Park, and Entiako Park and Protected Area. Because an attack of this scale is unprecedented on woodland caribou ranges, there is no information available on the effects of mountain pine beetles on caribou movements, habitat use or terrestrial forage lichen abundance. Implications of the mountain pine beetle epidemic to the Tweedsmuir–Entiako woodland caribou population include effects on terrestrial lichen abundance, effects on caribou movement (reduced snow interception, blowdown), and increased forest harvesting outside protected areas for mountain pine beetle salvage. In 2001 we initiated a study to investigate the effects of mountain pine beetles and forest harvesting on terrestrial caribou forage lichens. Preliminary results suggest that the abundance of *Cladina* spp. has decreased with a corresponding increase in kinnikinnick (*Arctostaphylos uva-ursi*) and other herbaceous plants. Additional studies are required to determine caribou movement and habitat use responses to the mountain pine beetle epidemic.

Key words: natural disturbance, *Rangifer tarandus caribou*, terrestrial lichens, winter range.

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Introduction

Five woodland caribou (*Rangifer tarandus caribou*) populations are found in Westcentral British Columbia (BC): Tweedsmuir–Entiako, Telkwa, Itcha–Ilgachuz, Rainbow and Charlotte Alplands (Northern Caribou Technical Advisory Committee, in prep.). Much of the area consists of low elevation flat to gently rolling terrain, gradually rising to mountainous plateaus of the Itcha, Ilgachuz, Rainbow, Fawnie and Quanchus ranges, and to the Coast Mountains in the west. Low elevation forests consist primarily of lodgepole pine (*Pinus contorta*) with hybrid white spruce (*Picea glauca* x *engelmanni*) and subalpine fir (*Abies lasiocarpa*) on moist sites. Woodland caribou in the area typically calve and summer in mountainous habitat and winter primarily in lower elevation forests or on windswept alpine slopes, and to a lesser extent, in subalpine forests (Cichowski, 1993; Telkwa Caribou Standing Committee, 1999; Young & Roorda, 1999; Young *et al.*, 2001).

Fire and forest insects are the main natural disturbance factors affecting forest dynamics in the region, while forest harvesting is the primary anthropogenic disturbance (Cichowski *et al.*, 2001a,b). For the past 40–50 years, fire suppression has been effective in minimizing the area burned by wildfire and forest insects have played a relatively minor role in forest renewal, except for a mountain pine beetle (*Dendroctonus ponderosae*) epidemic that affected ~500 000 ha in the area south of the Itcha and Ilgachuz Mountains in the early to mid-1980s (Garbutt, 1996). In the early 1990s, mountain pine beetles were detected in and adjacent to northern Tweedsmuir Park. Currently, >1 000 000 ha have been moderately or severely attacked by mountain pine beetles in Westcentral BC, including most of the Tweedsmuir–Entiako caribou winter range, and a large portion of the Itcha–Ilgachuz caribou winter range.

There is an increasing body of literature on the effects of forest harvesting and fire on caribou and terrestrial lichens (Schaefer & Pruitt, 1991; Snyder & Woodard, 1992; Harris, 1996; Kranrod, 1996; Thomas *et al.*, 1998; Goward, 2000; Smith *et al.*, 2000; Coxson & Marsh, 2001; Miège *et al.*, 2001a, 2001b; Sulyma, 2001, 2003), but little has been published on the effects of mountain pine beetles or other major forest insect pests on caribou or lichens. Mountain pine beetles are unlike fire or forest harvesting in their effects on woodland caribou and lichens. All 3 types of disturbance result in changes to canopy structure, but fire and forest harvesting result in an abrupt change whereas mountain pine beetles cause a more gradual change, with standing dead trees persisting for up to 20 years. Surface and crown fires in lodgepole pine forests usually consume much of the forest floor including terrestrial lichens, which are highly flammable and are often important in carrying surface fire in these forest types (Cichowski *et al.*, 2001a). Forest harvesting can also result in significant disturbance to the forest floor, but low impact forest harvesting practices such as harvesting during winter and using low impact equipment reduce the amount of disturbance (Sulyma, 2003). Mountain pine beetle attack does not result in disturbance to the forest floor unless it is followed by salvage logging. Therefore, effects of mountain pine beetles on caribou and lichen ecology cannot be inferred from studies on the effects of fire or forest harvesting alone.

Climate change models predict increases in average annual and winter temperatures (Cubasch & Meehl, 2001; Ministry of Water, Land and Air Protection, 2002). In BC, mountain pine beetles are found in the southern two-thirds of the province with most of the activity occurring in the southern half (Garbutt, 1996). With increased average winter temperatures and fewer cold weather extremes predicted, there is potential for a northern migration of mountain pine beetles as winter temperatures become insufficient to maintain populations at endemic levels (Ministry of Water, Land and Air Protection, 2002).

Mountain pine beetles attack and kill mature lodgepole pine trees (Safranyik *et al.*, 1974). Adult beetles select larger trees that provide adequate food resources for overwintering progeny. At epidemic levels, mountain pine beetles also attack smaller trees, where progeny survival is much lower. Although mountain pine beetles can affect hundreds of thousands of hectares at epidemic outbreak levels, not all susceptible trees are killed. Overwinter mortality resulting from very cold temperatures is the only known factor that can limit or reduce mountain pine beetle numbers under epidemic conditions (Safranyik *et al.*, 1974).

Current mountain pine beetle epidemic

In the early 1990s, mountain pine beetle activity increased in the area east of northern Tweedsmuir Park (Garbutt & Stewart, 1991; Garbutt, 1996). In 1993, the Canadian Forest Service detected mountain pine beetle spot attacks within a 720 ha area in northern Tweedsmuir Park (Garbutt, 1994). A prescribed burning program was initiated in 1995 where small burns (~500 ha) were to be conducted over a 3-year period in areas subject to mountain pine beetle attack, with prescribed burns conducted in September when risk of escape was lower. In 1995, 650 ha were burned and in 1997, 260 ha were burned (Cichowski *et al.*, 2001a). Although less area was burned than planned, high intensity burns were found to be effective in reducing mountain pine beetle numbers within the burned area (Safranyik *et al.*, 1996). Weather conditions caused cancellation of prescribed burns in 1996 and reduced the efficacy of prescribed burns in 1995 and 1997. In 1998, the BC Ministry of Forests and BC Parks revised the prescribed burning strategy to conduct a series of 3 large burns (1500–2000 ha each) in August under more favorable burning conditions. Again, prescribed burns were not conducted because of inadequate weather conditions. By 1999, the area attacked included 29 000 ha of moderate and severe attack in Entiako Park and Protected Area and 41 000 ha of moderate and severe attack in northern Tweedsmuir Park, and the strategy of prescribed burning in protected areas and forest harvesting in commercial forests for mountain pine beetle management was abandoned (Cichowski *et al.*, 2001a; 2001b). A series of mild winters since beetles were first detected in the early 1990s provided ideal conditions for increasing mountain pine beetle numbers. By 2003, >270 000 ha in northern Tweedsmuir Park and Entiako Park and Protected Area had been attacked by mountain pine beetles.

Tweedsmuir–Entiako caribou population

The Tweedsmuir–Entiako caribou population summers in mountainous terrain in the northern Tweedsmuir Park area and winters mainly in low elevation forests in the Entiako area (Cichowski, 1993). Caribou travel through the East Ootsa area (east of northern Tweedsmuir Park) during spring and fall migration and occasionally winter there. Initially, the mountain pine beetle-attacked area affected a small portion of the Tweedsmuir–Entiako caribou summer range and migration area. As the epidemic progressed, beetle attack increased in the Tweedsmuir–Entiako caribou winter range. Currently, most of the winter range has been affected by the mountain pine beetle epidemic.

In this paper we discuss implications of the current mountain pine beetle epidemic in Westcentral BC to the Tweedsmuir–Entiako caribou population and other caribou populations that use pine-lichen ranges, and preliminary results from a study recently initiated on the effects of mountain pine beetles on terrestrial forage lichens.

Methods

We used the current literature to identify potential effects of epidemic mountain pine beetle levels on woodland caribou ecology. Because terrestrial lichens are an important component of caribou ecology, we developed methods to assess the effects of mountain pine beetles on terrestrial lichen abundance. In addition to measuring change in terrestrial lichen abundance, we examined annual growth rates of forage lichens (*Cladina* spp.) and their main competitors, kinnikinnick (*Arctostaphylos uva-ursi*) and red-stemmed feathermoss (*Pleurozium schreberi*), and soil moisture conditions under trees, in forest gaps and in cutblocks.

In 2001, we established 80 permanent sample plots, each with an 8-m radius, in the Tweedsmuir–Entiako area (Williston & Cichowski, 2002). Within each plot we recorded stand structure characteristics, documented downed-wood along 2 transects, and took 10 photographs of permanently marked photoplots (75 cm × 75 cm) containing colonies of *Cladina* spp., the dominant forage lichen in the region. We used image analysis software (Gap Light Analyzer Version 2; Canham, 1988) to calculate the area of lichen cover within each photoplot. These photoplots were revisited in 2003 and reanalyzed to document changes in the coverage of lichens in beetle affected forests and cutblocks after 2 growing seasons. This approach is also being used in related studies by independent researchers (Sulyma, 2003). At each of the 80 plots we also took hemispherical photographs of the canopy and analyzed light transmission using Gap Light Analyzer Version 2 (Canham, 1988, Frazer *et al.*, 2000).

To determine growth rates we selected 15 shoots each of kinnikinnick, feathermoss and lichen under 3 canopy classes: under the canopy, in a forest canopy gap, and in a cutblock. We measured the growth rate of kinnikinnick by recording the length of the longest shoot from the annual bud scar. For both feathermosses and forage lichens, we tied a piece of black nylon thread to each shoot exactly 10 mm from the apex and determined the annual growth rate of these organisms using subsequent measurements from the nylon to the apex and subtracting 10 mm.

We determined forest floor and soil moisture under the same 3 canopy classes (beneath the canopy, canopy gaps, and cutblocks) by comparing the weight of wet to the weight of oven-dried samples. Values represent averages of 6 cumulative samples (each with 5 forest floor or soil subsamples) per canopy class.

Results and discussion

The mountain pine beetle epidemic is expected to impact woodland caribou through effects on terrestrial lichen abundance, effects on caribou movements and habitat use, mountain pine beetle management activities (principally forest harvesting), and mountain pine beetle range expansion associated with climate change.

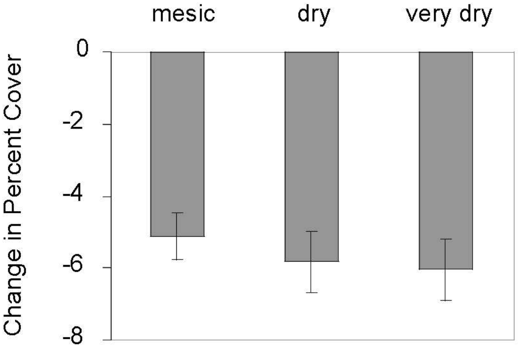

Fig. 1. Changes in lichen cover in the Entiako area after canopy mortality due to mountain pine beetle, from 2001 to 2003 (Mesic: *n* = 50; Dry: *n* = 50; Very dry: *n* = 42; error bars indicate standard error).

Terrestrial lichens

Caribou forage lichens are most abundant on nutrient poor sites where the success of potential competitors is limited (Ahti, 1961). Although these lichens are

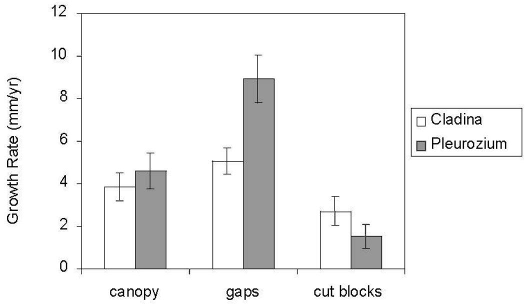

Fig. 2. Growth rates of caribou forage lichens (*Cladina* spp.) and feathermoss (*Pleurozium schreberi*) in cut-blocks, canopy gaps, and under the forest canopy (n = 15 each; error bars indicate standard error).

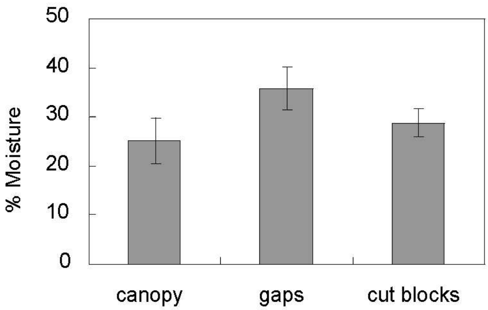

Fig. 4. Average forest floor moisture (% water) in gaps, under canopy trees, and in clearcuts (n = 6 each; error bars indicate ± 1 standard deviation).

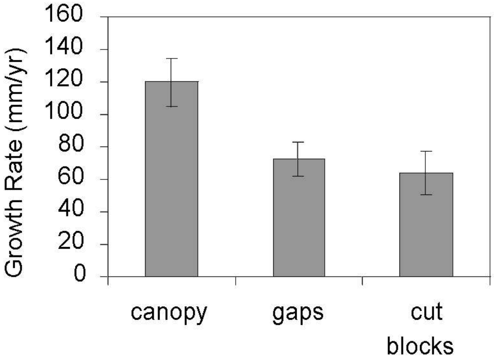

Fig. 3. Growth rates of kinnikinnick (*Arctostaphylos uva-ursi*) in cutblocks, canopy gaps, and under the forest canopy in the (n = 15; error bars indicate standard error).

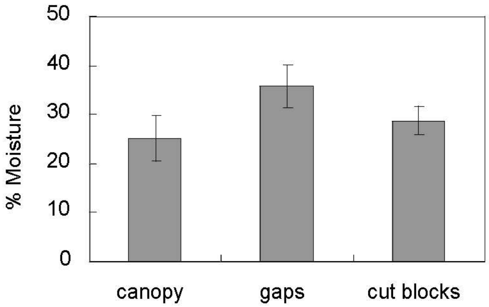

Fig. 5. Average mineral soil moisture (% water) in gaps, under canopy trees, and in clearcuts (n = 6 each; error bars indicate ± 1 standard deviation).

physiologically capable of inhabiting moist, rich sites (and often grow larger on those sites than on drier ones), they tend to be uncommon on rich sites because of competition from mosses and vascular plants (Ahti, 1961; Johnson, 1978). In the Tweedsmuir–Entiako area, the main competitors with terrestrial lichens are kinnikinnick and red-stemmed feathermoss. Mountain pine beetles affect the distribution and abundance of terrestrial lichens largely through changes in the distribution and abundance of competitors as they respond to increased light penetration and changes in forest floor conditions, specifically moisture and temperature.

Preliminary results suggest that abundance of terrestrial lichens has decreased in response to mountain pine beetles, primarily due to increased growth of kinnikinnick and to a lesser extent, feathermoss. For example, in mesic, dry and very dry sites in Entiako Park and Protected Area, the total forage lichen cover declined between 5 and 6% in 2 years (Fig. 1; data from Williston & Cichowski, 2004). Kinnikinnick grows approximately 10 times more rapidly than lichens (Figs. 2 & 3), and is able to respond quickly to the increase in light (and possibly nutrient) availability created by beetle-induced canopy tree mortality.

Feathermoss responds positively to greater moisture and is generally not light limited in the forest understory of the study area (Busby *et al.*, 1978). With sufficient moisture, feathermosses outgrow forage lichens. Our data shows that canopy gaps support higher forest floor and soil moisture than beneath live crowns (Figs. 4 & 5). This pattern suggests that forest floor moisture may increase in beetle affected stands in response to reduced canopy interception and reduced canopy tree evapotranspiration. The wetter soils should favor feathermosses, although this will take time to detect because of the relatively slow growth rate of mosses (Fig. 2).

Our preliminary results show that lichen colonies appear to be in decline in beetle affected stands, and are being replaced by kinnikinnick and feathermoss. We are not certain whether the patterns reported here will continue or how caribou will respond to declining abundance of terrestrial lichens. Because winter forage is currently not a limiting factor for the Tweedsmuir–Entiako caribou, other factors important to caribou discussed below may result in overriding cumulative effects.

Caribou movements and habitat use

Mountain pine beetles may affect caribou movement at stand and landscape levels. At the stand level, increased snow depths resulting from decreased canopy interception, and eventual blowdown of beetle-killed trees could impede caribou movement. As not all trees are killed by, or are susceptible to, mountain pine beetle attack, the number of live trees remaining in each stand will depend on the resistance of individual trees to attack, the size of the lodgepole pine trees, and the number of trees present from other species. Changes in snow depth and amount of blowdown will depend on the original stand density and the number of trees killed in the stand. Snow accumulation tends to be greater in more open stands (Gary & Troendle, 1982; Teti, 2003). Caribou typically forage in open pine stands with lower tree densities, so small increases in snow depth may not impede foraging in individual stands. However, increased sunlight penetration in the winter may increase crusting conditions in late winter. Cichowski (1993) found that caribou in Westcentral BC increased their use of arboreal lichens in late winter as snow penetrability decreased. If snow conditions affect the ability of caribou to crater for terrestrial lichens, they may increase their reliance on arboreal lichens on their low elevation winter ranges. For blowdown, if initial stand density is low, the level of blowdown may not be sufficient to impede movements.

At the landscape level, the distribution of mountain pine beetle-killed trees will affect how caribou move through their range. If enough stands contain tree species other than lodgepole pine, or support lower overall levels of mountain pine beetle attack, caribou may continue to travel across the landscape through these stands. At mountain pine beetle levels that impede caribou movement throughout the range, caribou may be forced to abandon preferred habitats and ranges and use other areas where predation and other risks may be higher. Alternatively, caribou may abandon lower elevation winter ranges and concentrate in the higher elevation subalpine and alpine portions of their range.

Mountain pine beetle management/salvage harvesting

Management activities associated with mountain pine beetles may also affect woodland caribou. When mountain pine beetles are at endemic levels, management focuses on individual tree treatments such as felling and burning. As beetle numbers increase, mountain pine beetle management focuses on sanitation logging, where large areas are harvested in an attempt to remove infested trees prior to the next beetle flight. At epidemic levels when sanitation logging is no longer effective, salvage logging is conducted as soon as possible to harvest beetle-killed trees before wood quality deteriorates. Recently, the Allowable Annual Cut was doubled for 2 Timber Supply Areas in central BC (Pedersen, 2004a, 2004b) and increased substantially for a third (Pedersen, 2004c) to accommodate salvage harvesting of mountain pine beetle-killed stands.

For the Tweedsmuir–Entiako caribou population, much of the winter range is in Entiako Park and Protected Area where forest harvesting is not permitted. However, for caribou populations without large portions of the winter range protected, sanitation and salvage logging could override guidelines designed for caribou management, and result in increased road networks. In Alberta, woodland caribou avoided portions of their winter range that were fragmented by logging (Smith *et al.*, 2000) and faced higher predation risks along and near linear corridors (James, 1999; James & Stuart–Smith, 2000).

Climate change

Mountain pine beetle range is expected to expand northward as average winter temperatures increase and survival-limiting low temperatures become less frequent due to climate change (Cubasch & Meehl, 2001; Ministry of Water, Land and Air Protection, 2002). As a result, woodland caribou pine-lichen winter ranges in northern BC, Alberta and the Yukon that were free from mountain pine beetles in the past, may start experiencing mountain pine beetle attack in the future.

Conclusions

The size of the current mountain pine beetle epidemic in Westcentral BC is unprecedented in recorded history and its potential influence on contemporary woodland caribou ranges is considerable. Preliminary studies suggest that there has been an initial reduction in terrestrial lichen abundance as a result of mountain pine beetle attack. It is not known how the mountain pine beetle epidemic will affect caribou movement and whether caribou will continue to use their winter range in response to expected changes in snow depth and snow condition, and increased blowdown. Historically, woodland caribou may have avoided mountain pine beetle killed portions of their ranges by switching to alternate ranges. However, with a combination of shrinking ranges and increased industrial activity, fewer alternate ranges are available to caribou. Currently, many woodland caribou populations in the southern portion of BC are experiencing some level of mountain pine beetle attack. With climate change models predicting increases in average annual temperatures, there is potential for a northern migration of mountain pine beetles. Cumulative effects of mountain pine beetles, mountain pine beetle management harvesting and salvage, and climate change may result in increased risks to woodland caribou populations associated with pine winter ranges in western North America. A greater understanding of the interactions among mountain pine beetles, vegetation, and the Tweedsmuir–Entiako caribou herd may have far-reaching applications for woodland caribou management throughout their range.

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Distribution and relative abundance of caribou in the Hudson Plains Ecozone of Ontario

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Abstract: To determine past distribution and relative abundance of caribou (*Rangifer tarandus caribou*) in the Hudson Plains Ecozone (HPE) of Ontario, we reviewed past HPE-wide winter systematic aerial surveys, partial winter systematic surveys, summer photographic surveys, incidental observations of caribou, and other sources of information from the period 1950–2003. We conducted new HPE-wide aerial surveys in February 2003 and 2004 to evaluate current distribution patterns. From this information, we defined 9 core wintering areas in the HPE and differentiated between 3 categories of relative abundance. Wintering areas for the January–March period have changed relatively little over the past 45 years. Summer distribution of caribou along the Hudson Bay coast apparently shifted or expanded from the area west of the Severn River to the central and eastern portions of the coast since the 1980s, and caribou observations have become much more common in the area east of the Winisk River since 1998. Because major resource development activities in the HPE are proposed and some are imminent, we recommend additional caribou surveys to document current caribou population identity, size, and distribution, and research projects to better define caribou wintering areas, calving areas, and movement patterns in the HPE.

Key words: aerial surveys, historical review, Hudson Bay, James Bay, Omushkego Cree, photographic surveys, *Rangifer tarandus caribou*, systematic surveys, summer aggregations, wintering areas.

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Introduction

In Ontario, the term Hudson Plains Ecozone (HPE) refers to an ecological region lying south of Hudson Bay and west and south of James Bay (50–59°N, 76–96°W; Fig. 1) (Ecological Stratification Working Group, 1996). Historically, the term Hudson Bay Lowland has been used to refer to a physiograhic region of Ontario that corresponds to the area covered by the HPE. The HPE is subdivided into 3 ecoregions: Coastal Hudson Bay Lowland, Hudson Bay Lowland, and James Bay Lowland. Because the term Hudson Bay Lowland is used for the name of an ecoregion in the HPE as well as for the entire physiographic region, we will refer to our study area as the HPE to avoid confusion, even though many of the references cited in this paper use the term Hudson Bay Lowland when referring to the entire region.

As early as the 1700s caribou were documented inhabiting the Hudson Bay coast in Ontario east as far as Cape Henrietta Maria (Banfield, 1961 citing Jérémie, 1720 and Hearne, 1795). At that time, caribou observed along the coast were thought to migrate seasonally, spending the winter in wooded interior regions of what is now Manitoba and migrating southeastward in summer along the narrow tundra belt bordering the Hudson Bay coast in Manitoba and Ontario. Lytwyn (2002: 84) stated that "caribou did not migrate as far south as the Albany River during the fur-trade period. The most southerly destination was Akimiski Island, where large numbers spent the summer on the tundra of the island's northern shore." Caribou no longer occur on Akimiski Island. An elder Attawapiskat resident who has hunted and trapped on Akimiski Island all his adult life reported seeing caribou on the island for the last time in the 1940s (M. Kataquapit, pers. comm.). Lytwyn (2002: 229), quoting from a 1948 unpublished report by the Department of Northern Affairs and National Resources, wrote "The brush caribou (locally called 'deer') ('hatik'), once fairly plentiful along the west coast of James Bay, has all but disappeared from the country." Other historical references to caribou in the eastern HPE south of the Ekwan River indicate that caribou occurred in small, widely scattered groups (Brokx, 1965 citing the following: Bell, 1886; Dowling, 1904; de Vos & Peterson, 1951). Banfield (1961, citing Tyrrell, 1913) and Lytwyn (2002) reported that heavy kills of caribou to provision the Hudson Bay Company fur-trading posts rapidly reduced the size of the migratory caribou population by the late 1700s and may have changed the population's migratory patterns. Lytwyn (2002) reviewed Hudson Bay Company meat trade records and reported that caribou numbers began to increase again by the late 1800s.

Cringan (1956) contributed more recent information on distribution and abundance of caribou in Ontario based on data collected from trappers and hunters. However, systematic surveys of caribou in the HPE were not begun until 1957, when the Ontario Department of Lands and Forests [reorganized into the Ontario Ministry of Natural Resources in 1973 and hereafter referred to as OMNR regardless of the year] began winter aerial surveys of caribou over large areas of Ontario. Simkin (1965) and Brokx (1965) summarized the results of systematic winter surveys through 1964. Simkin (1965) also reported summer observations of caribou in the northern portion of the HPE collected while doing ground surveys of vegetation in July and August 1960–1962, and an aerial survey in August 1963. From 1967 through 1979, OMNR personnel periodically conducted additional winter aerial surveys in limited areas of the HPE, and in 1982–1984 they carried out a broad-scale systematic winter survey. In an unpublished report, Thompson (1986) summarized the results of the OMNR winter caribou surveys in the HPE from 1959–1984 and Thompson & Abraham (1994) summarized caribou observations from the northwestern HPE for the period 1958–1990. Biologists and others working in coastal areas continued to record incidental observations of caribou along Hudson Bay and in the southeastern portion of the Hudson Bay Lowlands along James Bay. These observations are archived by OMNR.

Using radiotelemetry, Abraham & Thompson (1998) followed the movements of caribou in northwestern Ontario (Pen Islands caribou herd) from 1987 through 1990 and determined that the collared caribou made seasonal movements from wintering areas in the forested interior of northeastern Manitoba and northwestern Ontario to the Hudson Bay coast in spring, and then back again in the fall and early winter. The only other telemetry study of caribou in the HPE was in the southeastern portion near the Quebec border (Brown *et al.*, 2003).

Historically, the HPE in Ontario was occupied by the Hudson Bay Lowland Cree (Muskekowuck Athinuwick) living in dispersed bands (Lytwyn, 2002). Today, the human population (approx. 10 000) is largely concentrated in 7 coastal villages—Fort Severn, Peawanuck, Attawapiskat, Kashechwan, Fort Albany, Moosonee, and Moose Factory (Fig. 1). Hunting, trapping, fishing, and tourism dominate the local economies (Berkes *et al.*, 1994; Berkes *et al.*, 1995; Abraham & Keddy, in press). While patterns of harvesting activities have changed markedly, the geographic extent of land use continues to reach far beyond the settlements (Berkes *et al.*, 1995). The HPE remains essentially roadless, with only winter ice roads connecting some of the more isolated communities. One rail line penetrates the HPE in Ontario, and surface access to interior regions is primarily by boat along major rivers and streams in summer and by snowmachine in winter. However, in recent years there has been increasing use of all-terrain vehicles along coastal areas in summer. Commercial forestry does not currently occur in the HPE and mining is in its infancy. However, there are a number of pending or planned resource development projects that will affect the area and potentially caribou populations in the region, including forestry along the southern edge (OMNR, 2001) and development of diamond resources (AMEC, 2004), primarily in the James Bay Lowland. Winter roads have been proposed to develop the mining claims near Attawapiskat (AMEC, 2004). In view of these developments and others that may follow, it is important to develop baseline information on caribou populations in the Ontario HPE and monitor the effects of resource development on caribou numbers, distribution, and movements. Loss of historical range

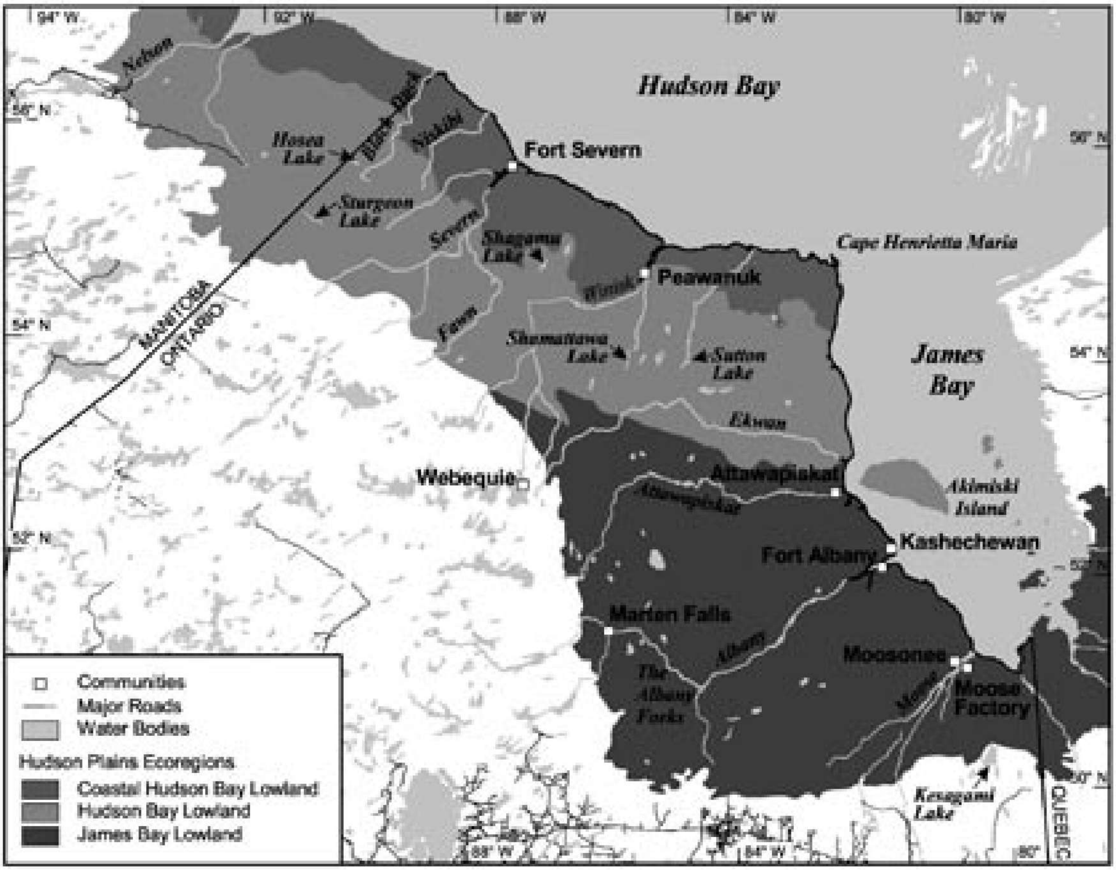


Fig. 1 The Hudson Plains Ecozone (HPE) of Ontario and its 3 ecoregions.

of caribou in the southern half of the province since 1880 (Racey & Armstrong, 2000; Schaefer, 2003) highlights the vulnerability of caribou to changes in human land use patterns and emphasizes the need for knowledge about the status of northern caribou populations before there are appreciable changes in land use in this region of Ontario.

For this paper, we have 3 objectives:

1 Summarize unpublished information on systematic winter surveys and incidental observations of caribou,
2 Discuss patterns of caribou distribution and relative abundance over time, and
3 Recommend future directions for documenting caribou distribution and relative abundance in the Hudson Bay Lowlands in light of impending changes in human land use.

Study area

The study area (Fig. 1) comprises the portion of the HPE that lies within Ontario. Detailed descriptions of each ecoregion in the HPE are provided in *A National Ecological Framework for Canada* (Ecological Stratification Working Group, 1996).

The climate of the HPE is characterized by short, cool summers and cold winters. Ecoregional climates vary from high subarctic along the Hudson Bay coast (cooler and drier) to midboreal around southern James Bay (wetter and warmer). From Fort Severn to Cape Henrietta Maria, 50% of offshore waters can remain ice-covered into late July in some areas (Rouse, 1991). Rowe (1972) described the area as a poorly drained region of unconsolidated glacial and postglacial deposits underlain by Palaeozoic limestone over Precambrian rock, abounding in bogs and shallow lakes. Abraham & Keddy (in press) provide a detailed description of the HPE, with emphasis on the wetland features of the region.

The forested areas of the Coastal Hudson Bay Lowland are characterized by very open stands of stunted black spruce (*Picea mariana*) and tamarack, with secondary quantities of white spruce (*Picea glauca*). In the Hudson Bay Lowland, stands are denser and trees are larger. In both ecoregions, the shrub layer consists of dwarf birch (*Betula nana*), willow (*Salix* spp.), and ericaceous shrubs, and the ground cover is dominated by sedges (*Carex* spp.) and cottongrass (*Eriophorum* spp.) or moss and lichen (*Cladonia* spp., *Alectoria* spp., *Cetraria* spp., and others). Dry sites in the Hudson Bay Lowland ecoregion support open stands of white spruce with an ericaceous shrub layer and a ground cover of lichen. Poorly drained sites in both ecoregions are characterized by sedge and cottongrass tussocks or sphagnum moss. The James Bay Lowland ecoregion is a transition zone between the coniferous and mixed forests of the clay belt to the south and the tundra to the north. Most of the area is poorly drained and dominated by sedge, mosses, and lichen with or without stunted black spruce and tamarack. In the southern portion of the ecoregion and along the parallel rivers draining east into James Bay, forests are composed of balsam fir (*Abies balsamea*), white and black spruce, trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) (Ecological Stratification Working Group, 1996).

Riley (1982) catalogued the wetland types and Riley (2003) provided details of the flora of the HPE. Ahti & Hepburn (1967) provided detailed descriptions of the lichens and noted that lichens used by caribou were most abundant in the Hudson Bay Lowland. Brokx (1965) categorized 25 ecological zones based on physiographic and vegetational characteristics important to caribou in the region north of 52°N.

Methods

Data sources

We used the following data sources to identify past and present distribution patterns and relative abundance of caribou in the HPE of Ontario:

1 HPE-wide systematic surveys—Since 1959 there have been a number of systematic winter surveys of caribou carried out in the HPE using aircraft to fly transects and record the locations of caribou, their tracks, and their feeding craters (caribou sign). These surveys were designed to cover a large proportion of the HPE over a relatively short time period and occurred in 3 periods separated by about 20 years. We used unpublished reports and data from OMNR to summarize the results of the earlier surveys and carried out a new survey in 2003–2004. We compared the results from these 3 survey periods:
   - The first survey period was 1959–1964 (hereafter referred to as the 1960s survey). The results of the surveys are summarized in Simkin (1965) and Brokx (1965). Surveys were carried out in January and February and transects were either 6 km or 13 km apart, depending on the density of forest cover within the survey unit; more intensive coverage occurred where tree cover was dense. Caribou tracks were followed off transect until the caribou were located. Using the original survey data (see Table 1 for references to the original survey reports), Simkin (1965) and Brokx (1965) estimated caribou density using the number of caribou counted within the transect area.
   - From 1982 through 1984, OMNR conducted systematic surveys (hereafter referred to as the 1980s survey) in the HPE from January through March using 171 transect lines spaced 5 km apart (Thompson, 1986). We located the original survey maps showing the locations of caribou sign. Caribou tracks were followed off transect until the caribou were located. Thompson (1986) estimated caribou densities using caribou numbers counted within the transect area.
   - In February 2003 and 2004, we conducted coarse-scale surveys (hereafter referred to as the 2000s survey) for caribou in the HPE as part of a more comprehensive survey of carnivores and ungulates in northern Ontario. We divided the study area into 1000-km^2 hexagons and established flight lines through the centers of the hexagons. Distance between flight lines was usually 34–60 km, with most flight lines in the eastern portion of the HPE separated by 34 km. The survey aircraft (2 Piper PA-18 Super Cubs) were not required to stay on a set GPS track but could deviate up to 2 km from the flight route to check open areas for carnivore and ungulate tracks as long as the aircraft passed through the centers of the hexagons. We recorded caribou sign and counted caribou when they were visible, but we did not follow fresh tracks to count caribou and did not estimate caribou density.

2 Partial systematic surveys—Between 1967 and 2003, OMNR carried out additional surveys in portions of the HPE, including caribou surveys and moose surveys that included observations of caribou. These surveys used the same transect method that was used in the 1960s and 1980s surveys, although transect width differed somewhat between surveys. Unpublished reports on these surveys were reviewed for information on caribou distribution and abundance.

3 Telemetry studies—Two telemetry studies of caribou in the HPE provided locations of caribou in the northwestern (Thompson & Abraham, 1994) and southeastern (Brown *et al.*, 2003) portions of the HPE. Only winter locations were available for the northwestern area, but winter and summer locations were available for the southeastern area.

Table 1. Results of caribou surveys in the Hudson Plains Ecozone (HPE) from 1959 to 1964, referred to as the HPE-wide 1960s survey. Caribou counted on transects are expressed as caribou per 100 km^2 of transect area.

Fig. 4 survey area	Survey report[a]	Caribou on transects	Caribou off transects	Number of groups on transects	Total transect length (km)	Transect area (km^2)	Caribou per[b] 100 km^2
1	Simkin (1959)	7	Not reported	Not reported	1261	3061	0.2
2	Simkin (1960)	99	Not reported	9	1888	2611	3.8
3	Simkin (1964)	294	256	35	4624	5102	5.8
4	Simkin (1962a)	61	104	24	2938	3999	1.5
5	Simkin (1961)	140	11	16	2493	3064	4.5
6a	Simkin (1962b) Simkin (1965)	66	Not reported	Not reported	957	1054	6.2
6a+6b	Simkin (1962b) Brokx (1965)	66	Not reported	Not reported	2250	2186	3.0
7a	Goddard (1961) Simkin (1965)	72	Not reported	Not reported	1675	1585	4.5
7b	Goddard (1961) Simkin (1965)	23	Not reported	Not reported	2854	2797	0.8
7a+7b+7c	Goddard (1961) Brokx (1965)	86	Not reported	Not reported	5907	5737	1.5
8	Gagnon (1962) Simkin (1965)	36	0	3	3430	3367	1.1
9	McLellan (1962) Simkin (1965)	45	Not reported	4	5645	6775	0.7

[a] Reference to the original survey report, except for Simkin (1965) and Brokx (1965), which are summaries of the surveys from 1959–1964 (1960s HPE-wide systematic survey). In some cases, data for this table were only available from these summaries. Simkin (1965) separated survey area 6 into 2 parts and calculated density separately for area 6a after finding no caribou in area 6b; Brokx (1965) calculated density for the entire area. Simkin (1965) separated survey area 7 into 3 areas and calculated density separately for 7a and 7b; Brokx (1965) reduced the size of the original survey area (Goddard, 1961) to include only those areas within the HPE and calculated density for the entire area within the HPE.

[b] Density of caribou within the transect area.

4 Incidental summer observations—We used observations of caribou in the HPE, archived by OMNR, to digitize summer locations of caribou from the 1950s to 2003. These sightings were reported by individuals involved in radiotracking caribou, conducting wildlife surveys for other species, and doing vegetation studies as well as by the public.

5 Summer photographic surveys—Photographic surveys of caribou in coastal tundra habitat during summer (Apr–Sep) began in 1986 and ended after 1997. The search area was between Fort Severn and the Nelson River in Manitoba, covering the known summer range of the Pen Island caribou herd (Thompson & Abraham, 1994; Abraham & Thompson, 1998). All aggregations encountered along flight lines parallel to the coast in open tundra habitat were photographed. No sizable caribou groups were noted east of Fort Severn during this period, so the area was not included in the summer photographic surveys, although incidental observations of caribou were recorded.

Analyses

We examined trends in caribou distribution separately for winter (Jan–Mar) and summer (Apr–Sep), because winter data were derived from systematic surveys over broad areas of the HPE, while those from summer were collected nonsystematically, primarily along the coast of Hudson Bay. Flights in March only occurred during the 1980s survey and only 15% of caribou locations were found during the March flights. We believe the March data can be combined with January and February data, because 80% of the March locations were clustered with the January and February locations.

We used ArcView GIS software to digitize locations of caribou sign from incidental observations in summer and from the 1980s and 2000s systematic winter surveys. Because we could not locate original survey maps from the 1960s survey north of 52°N, we were unable to digitize locations of caribou sign from that survey. Instead, we used locations of caribou sign provided by Brokx (1965: Fig. 36) to determine where caribou were distributed north of 52°N

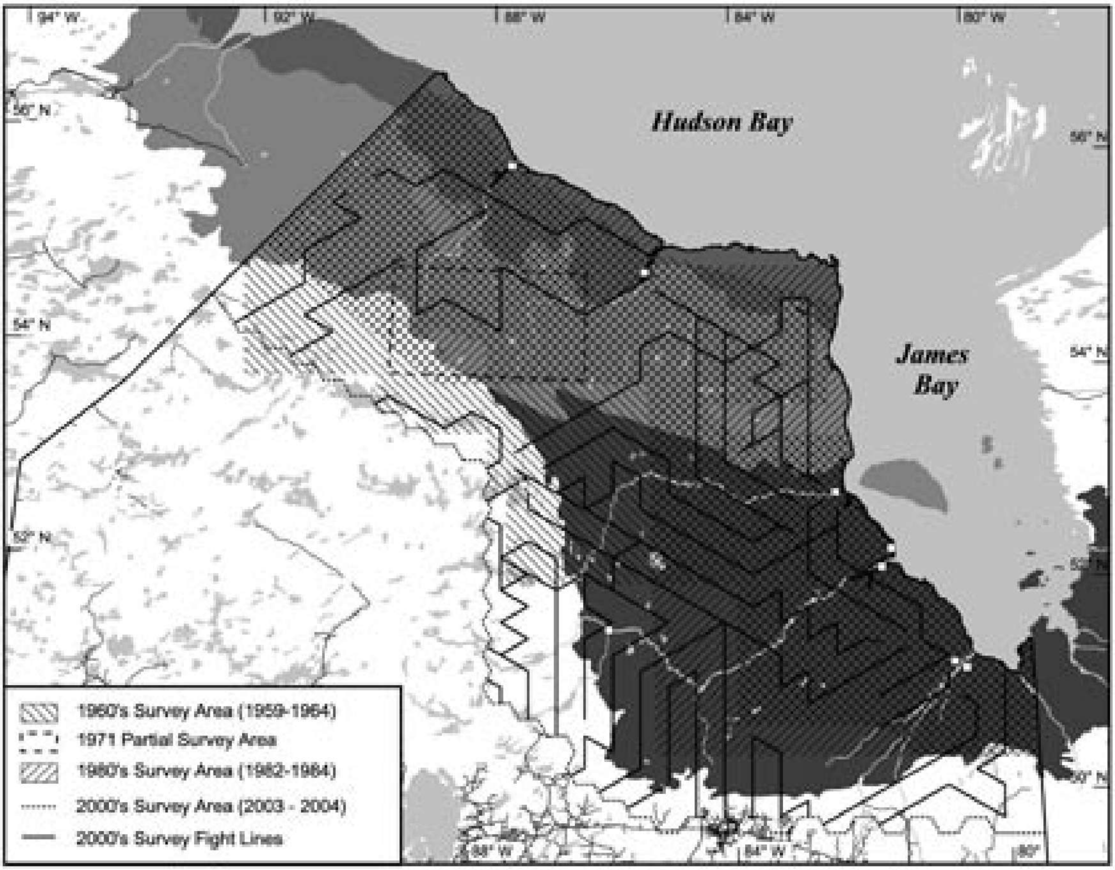


Fig. 2. Coverage of the Hudson Plains Ecozone (HPE) of Ontario by 3 systematic aerial surveys for caribou from 1959 to 2003

(southern boundary of Brokx's study area) during the 1960s survey. South of 52°N we digitized locations provided by OMNR.

Comparing systematic surveys conducted over a 45-year timespan presented challenges that we acknowledge here. Survey conditions, methodologies, and boundaries of survey areas changed over time, and the rigor of data analysis, interpretation, and reporting varied among the surveys. In the earlier surveys, the number of caribou counted along transects (within a given distance from the transect center) were used to calculate a density for caribou within the area covered by the transects. For some of the later surveys, standard errors and confidence limits were provided for the density estimates, but the usefulness of these figures for comparing caribou densities between areas is questionable at best. Caribou were distributed in a clumped pattern during the winter surveys, sample sizes of caribou groups were usually small, and the boundaries of wintering areas and survey areas changed from year to year.

With no consistency in survey areas and no measure of sampling error, the density estimates cannot be used to compare the number of caribou between survey areas or survey periods. Moreover, because there is no information on caribou subpopulations in the HPE or the extent of their winter ranges, there is no way to know what proportion of the population or subpopulations were included in the surveys. However, we believe that information gathered on caribou numbers during the surveys should not be disregarded despite sampling problems. The density estimates reflect not only the number of caribou seen on transects but also the area covered by transects. As such, the density estimates are the only available and comparable measure of relative abundance of caribou in the HPE for the time period we examined. We used the density estimates only as a means of delineating broad areas of relative abundance. The estimates should not be used to compare population size between areas or evaluate changes in population size in the HPE over time.

We plotted summer distribution in coastal areas along Hudson Bay using incidental observations

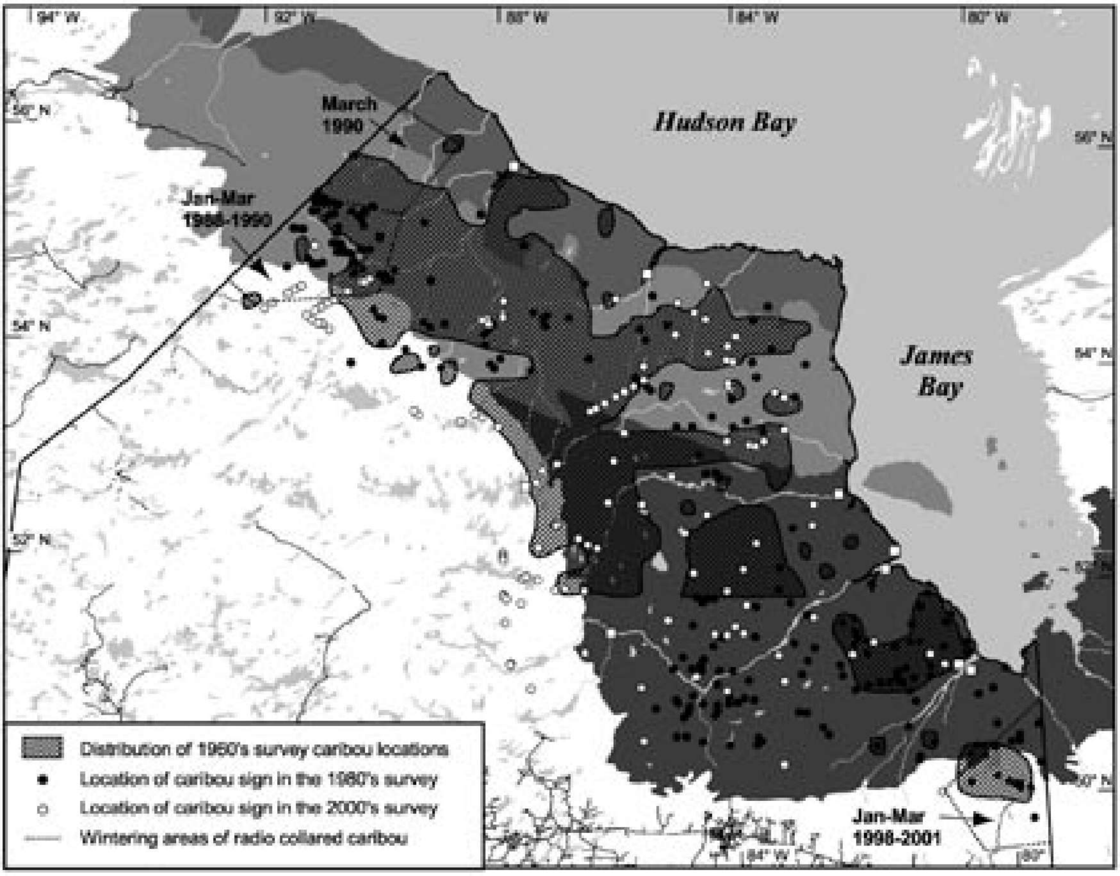


Fig. 3. Areas where caribou and their tracks were located during 3 systematic aerial surveys in the Hudson Plains Ecozone (HPE) of Ontario from 1959–2003. Point locations for the 1960s caribou distribution can be found in Brokx (1965). The arrows point to areas where radiocollared caribou in 2 study areas were concentrated in winter (Jan–Mar) during 1988–1990 (Thompson & Abraham, 1994) and 1998–2001 (Brown *et al.*, 2003).

and the results of photographic surveys, however, summer locations in areas away from the coast were generally not available. We plotted summer locations by time period and the approximate number of animals per group.

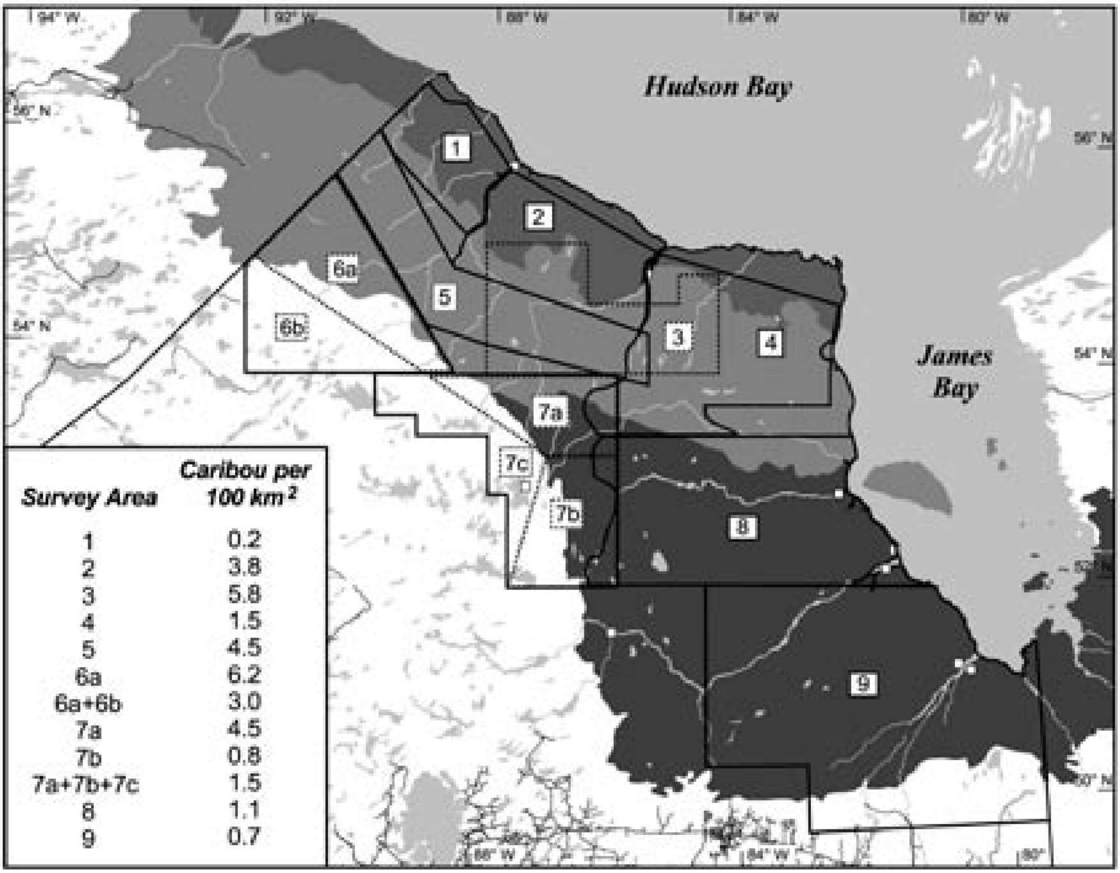
Results and discussion

Comparing the systematic survey coverages

The areas covered in the HPE-wide systematic surveys are shown in Fig. 2. In all 3 surveys, some portions of the HPE were not surveyed or some data were missing from the original surveys. Also, some portions of the HPE were surveyed more than once during the 1960s survey (Brokx, 1965: Fig. 33). The portion of the HPE lying south of 54°N and west of 85°20'W was not covered in the 1980s systematic survey nor was the small portion of the HPE south of 50°30'N. In the 2000s survey, distances between transects were greater than in previous surveys and coverage was particularly light between Shamattawa Lake and the Fawn River.

Winter distribution

During the 1960s survey, signs of caribou were detected over large areas of the HPE, primarily within the Hudson Bay Lowland and the western third of the James Bay Lowland above 52°N (Fig. 3). Below 52°N, caribou were recorded west and north of Moosonee and near Kesagami Lake. Caribou were not surveyed in the western portion of the HPE near The Albany Forks. Unlike subsequent surveys, the 1960s survey detected caribou tracks in the Coastal Hudson Bay Lowland, mainly east of Fort Severn (Brokx, 1965: Fig. 36). Most caribou from the 1960s survey north of 52°N were concentrated in 5 areas: between Sturgeon Lake and Hosea Lake near the Manitoba border, around Shagamu Lake north of the Winisk River, around Shamattawa Lake, in the area



Survey Area	Caribou per 100 km²
1	0.2
2	3.8
3	5.8
4	1.5
5	4.5
6a	6.2
6a+6b	3.0
7a	4.5
7b	0.8
7a+7b+7c	1.5
8	1.1
9	0.7

Fig. 4. Location of caribou surveys in the Hudson Plains Ecozone (HPE) of Ontario from 1959 to 1964, referred to as the HPE-wide 1960s survey (details in Table 1). Caribou counted on transects are expressed as caribou per 100 km^2 of transect area (see Table 1 for references to the original survey reports).

of Sutton Lake, and between the Winisk and Ekwan Rivers northeast of Webequie.

The 1980s survey (Thompson, 1986) also located concentrations of caribou in the Sturgeon Lake area (532 caribou in 67 aggregates observed), however, most caribou in the 1980s were located southeast of where Brokx (1965: Fig. 36) reported concentrations of animals in the 1960s (Fig. 3). Thompson & Abraham (1994) verified that radiocollared caribou from the Pen Islands Herd also used this area during winters 1988–1990 (Fig. 3). During the 1980s survey, caribou were also scattered from the Severn River east to about 83°30'W and south of 54°N as far as the Attawapiskat River. Thompson (1986) reported a concentration of caribou between the Ekwan and Attawapiskat Rivers (108 caribou in 10 aggregates observed) and another concentration in the Shamattawa Lake area (46 caribou in 5 aggregates), which was a smaller number of caribou than he expected based on earlier survey results. Few caribou were located between the Attawapiskat River and 52°N. Thompson (1986) referred to a "second major concentration area" [relative to the one near Sturgeon Lake] near The Albany Forks, a relatively small area where 78 caribou in 12 aggregates were observed. Unfortunately, Brokx's (1965) study area did not include The Albany Forks, so we cannot compare the results of the 1980s survey with the 1960s survey for this area. However, OMNR personnel reported a "large" caribou concentration northwest of The Albany Forks during winter 1962 (Gagnon, 1962). In the 1980s, small groups of caribou and caribou tracks were scattered east of The Albany Forks from about 83°W to Moosonee, and additional animals were located near Kesagami Lake, as they had been in the 1960s.

Although the 2000s survey was coarse-scale relative to earlier surveys, especially in the northwestern portion of the HPE, we found similar patterns in caribou distribution with some minor differences. The center of concentration for caribou in the Sturgeon Lake area was south of where it had been in the 1960s and 1980s (Fig. 3). The center of concentration

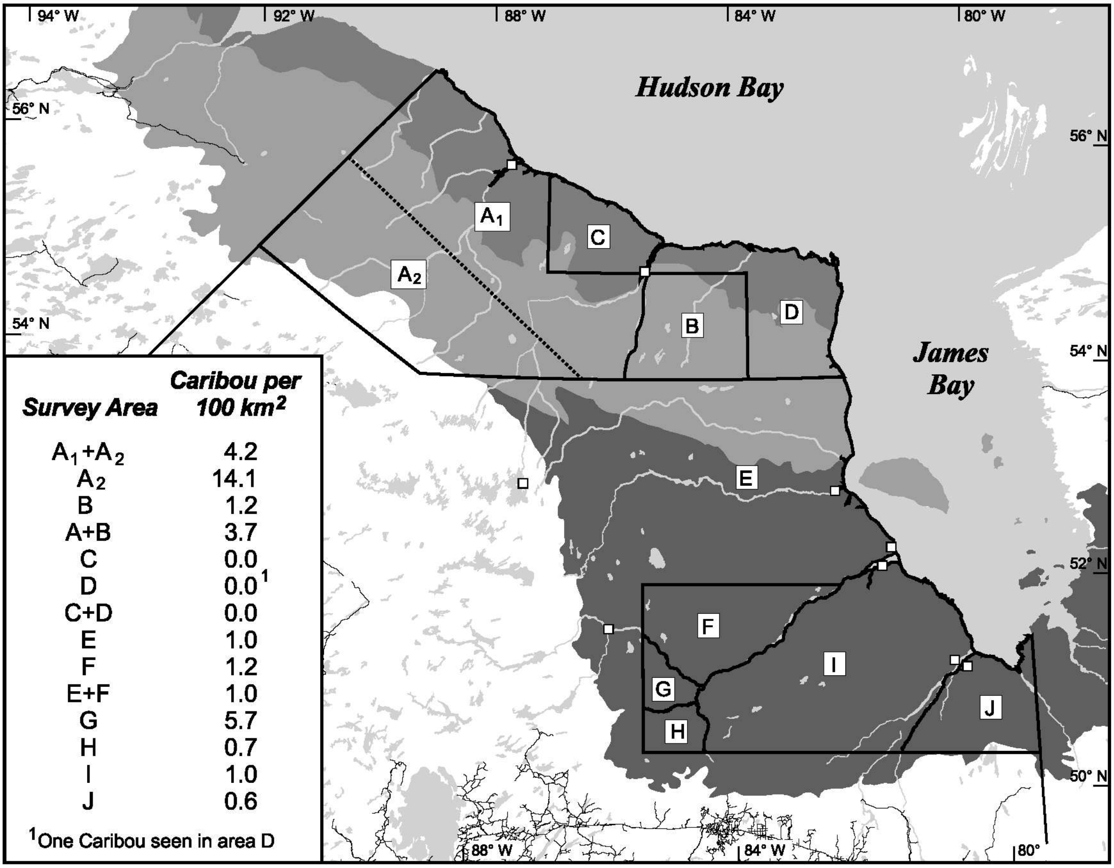


Fig. 5. Location of caribou surveys in the Hudson Plains Ecozone (HPE) of Ontario in 1978 (area A2) (details in Hamilton, 1978) and from 1982 to 1984, referred to as the HPE-wide 1980s survey (details in Thompson, 1986). Caribou counted on transects are expressed as caribou per 100 km^2 of transect area.

for caribou between the Fawn and Winisk Rivers was southwest of where it had been in the 1960s survey (see Brokx, 1965: Fig. 36). Finally, despite greater distance between survey transects, more caribou observations were recorded in the 2000s survey between 52°N and the Attawapiskatt River than were recorded in that area during the 1980s survey.

Relative abundance of caribou in wintering areas

Using the distribution maps of caribou locations from the 3 HPE-wide systematic surveys (Fig. 3 and Brokx, 1965: Fig. 36) and the caribou density estimates provided in OMNR reports (Figs. 4 & 5), we designated 3 areas of relative abundance for caribou in the HPE: high, moderate, and low (Fig. 6). Areas of high relative abundance had caribou present during the 3 systematic surveys and at least 4 caribou counted per 100 km^2 of transect area. Areas of moderate relative abundance had caribou during the 3 systematic surveys, but less than 2 caribou counted per 100 km^2 of transect area. Areas of low abundance were nearly devoid of caribou during the winter surveys. As we discuss below, it was not possible to define relative abundance more specifically or determine if relative abundance changed over time based on the available data. However, we believe the clumping of the highest density estimates in the northwestern portion of the HPE reflects actual regional differences in the abundance of caribou in the HPE during winter for the period of study.

In the 1960s, the highest reported caribou densities were in the Hudson Bay Lowland, particularly in the west around Sturgeon Lake and in the central portion of the ecoregion surrounding Shagamu, Shamattawa, and Sutton Lakes (Fig. 4: areas 6a and 3, respectively). The only area within the James Bay Lowland with comparable reported densities in the 1960s was north of Webequie between the headwater tributaries of the Winisk River (Fig. 4: area 7a). The lowest estimated caribou densities from the 1960s survey were from the Coastal Hudson Bay Lowland (Fig. 4: area 1) and the James Bay Lowland (Fig. 4:

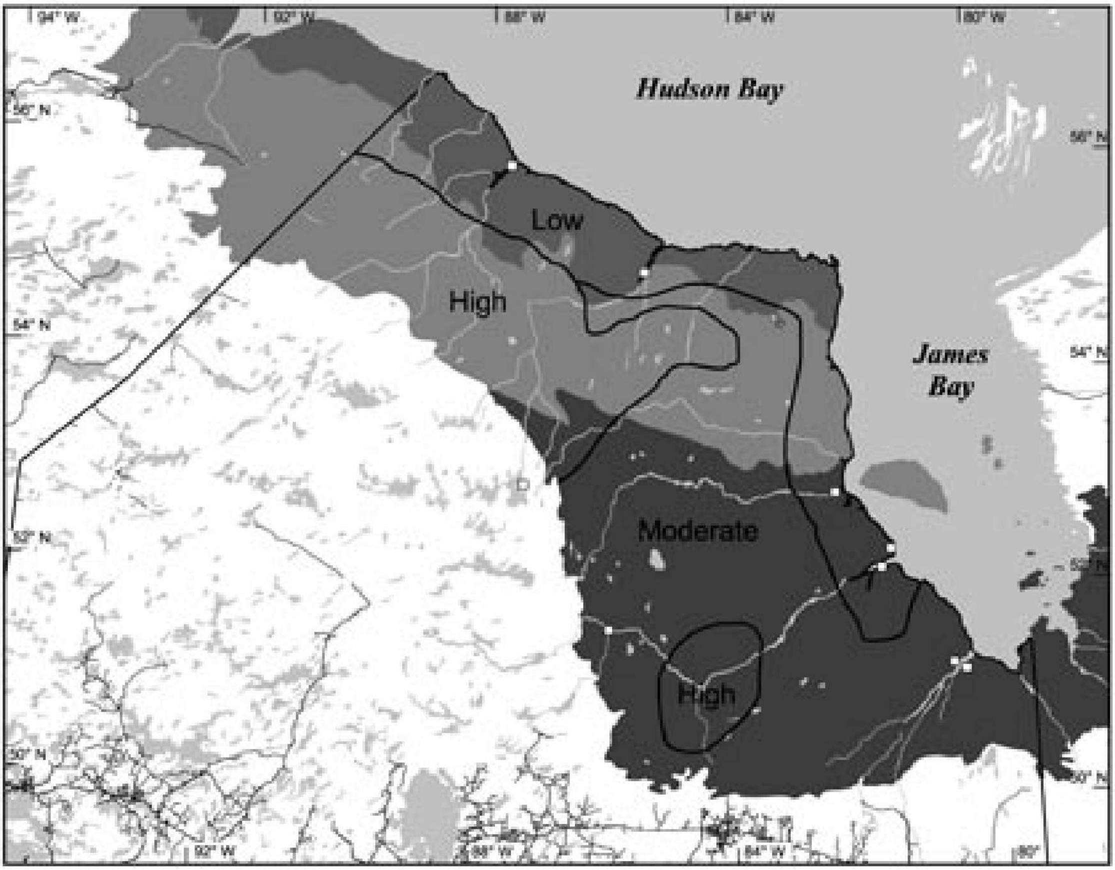


Fig. 6. Relative abundance of caribou in winter (Jan–Mar) in the Hudson Plains Ecozone (HPE) of Ontario based on the results of systematic aerial surveys from 1959 to 2003.

areas 7b, 8, & 9). In Figure 4, areas 2 and 4 had very few caribou in the areas that did not overlap with area 3. In the 1980s survey, reported caribou densities were highest west of the Shamattawa River (Fig. 5: area A) and in a very small area near The Albany Forks (Fig. 5: area G). As in the 1960s survey, caribou density estimates from the 1980s survey were generally low in the James Bay Lowland, except for The Albany Forks.

Changes in caribou numbers and/or shifts in concentration areas may have occurred in portions of the HPE between survey periods, but evaluating such changes was not possible, particularly because survey boundaries usually changed between surveys. However, between the 1960s and the 1980s surveys, 2 partial surveys of the Hudson Bay Lowland were conducted in the same central portion of the Hudson Bay Lowland ("1971 partial survey area" in Fig. 2). Simkin (1967) surveyed this area in 1967 and found about 2 caribou per 100 km^2 of transect area (transects 6 km apart and 914 m in width). The number of caribou counted (including those off-transect) was 477. In 1971, Buss (1971) resurveyed the area and found about 4 caribou/100 km^2 of transect area (transects 6 km apart and 1097 m in width) and counted 929 caribou. When we examined the data from the 1980s survey and determined the number of caribou seen in this same area, we found that only 61 caribou were counted (transects 5 km apart and 1000 m in width in 1982).

The size of survey areas and the location of survey boundaries relative to core caribou wintering areas affected survey results. In 1978, a portion of the Hudson Bay Lowland near the Manitoba border was surveyed (Fig. 5: A$_2$) as part of a more comprehensive survey for moose and caribou in the West Patricia Planning Area (Hamilton, 1978). Distance between transects in 1978 was 10 km and transect width was 600 m. Estimated caribou density (14 caribou/100 km^2) was more than twice that of any other area surveyed during the 1960s or 1980s. We believe this estimate was high, at least in part, because the 1978 survey area captured most of the wintering area of the Pen Islands caribou herd and included

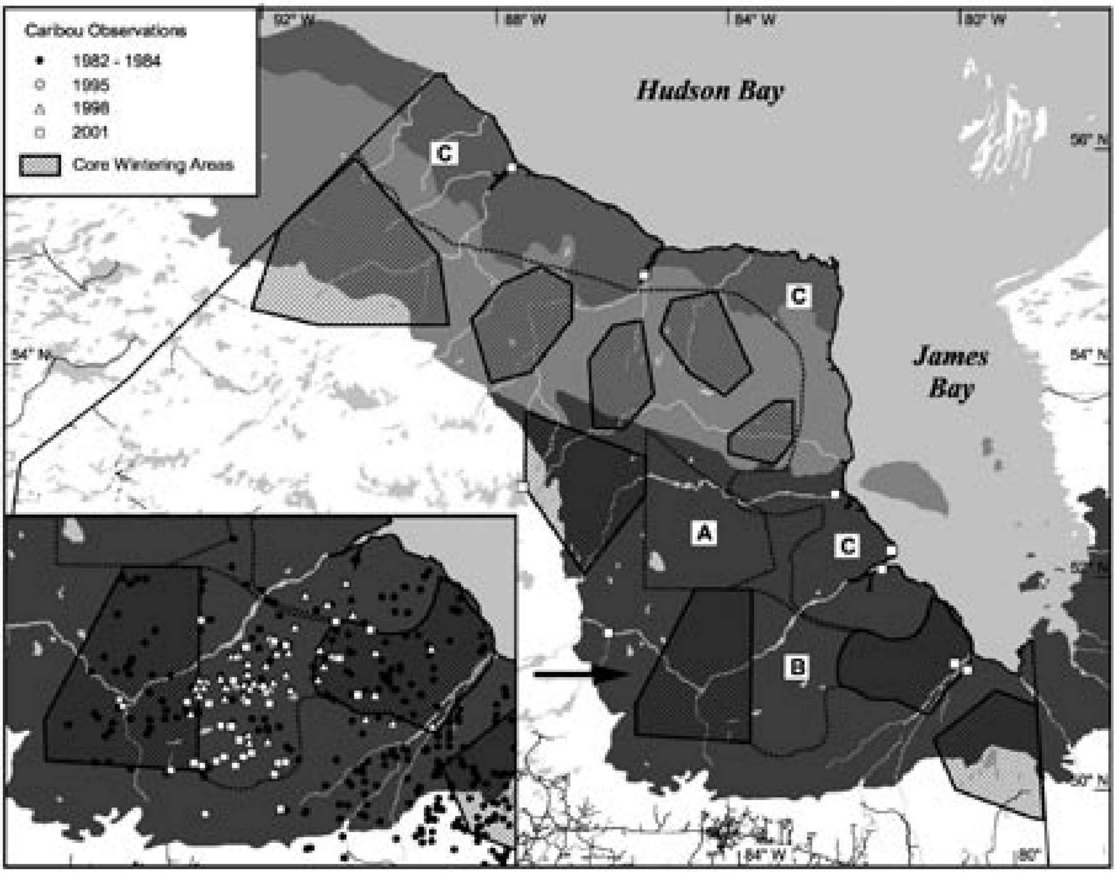


Fig. 7. Core wintering areas used by caribou in the Hudson Plains Ecozone (HPE) of Ontario from January–March 1959–2003 based on the locations of caribou and their tracks from 3 HPE-wide systematic aerial surveys. A, B, and C are areas referred to in the text.

the southern portion of the core area for caribou wintering immediately east of there as well (Fig. 6; also, see discussion of core wintering areas below). The density estimate from the 1980s survey did not center on the wintering range of the Pen Islands herd and included a much larger area than in 1978 (Fig. 5: areas $A_1 + A_2$), resulting in a density estimate of only 4 caribou/100 km^2, despite the fact that the number of caribou from the Pen Islands Herd using the area west of the Severn River may have increased between 1978 and 1982 when the 1980s survey was done (Abraham & Thompson, 1998).

The James Bay Lowland in general had lower density estimates than the Hudson Bay Lowland. Within the James Bay Lowland, however, there were some relatively small areas where caribou densities were estimated at 4–6 caribou/100 km^2 (Fig. 4: area 7a; Fig. 5: area G). Stewart (1977) estimated 5 caribou/100 km^2 for the portion of the HPE north of Kesagami Lake (roughly area J in Fig. 5), commenting that the estimate has "extreme confidence limits" because 66% of caribou on transects were in just 2 herds. In 2000, the estimate for this area was also about 5 caribou/100 km^2 (Gauthier & Hildebrandt, 2000). Caribou in this area may winter south of the HPE and across the provincial border in Quèbec, so density estimates can be highly variable depending on movement patterns of caribou between years.

Changes in wintering areas confound the interpretation of survey results between years. From 1986 to 2001 there have been 6 systematic winter surveys in a portion of the James Bay Lowland (roughly area I in Fig. 5) with density estimates for caribou ranging from <1 to 6/100 km^2(Chenier, 2001), with the highest density estimates in 1998 and 2001. In surveys carried out in January of 1995, 1998, and 2001 in the southern HPE, a relatively large number of caribou were located in the central part of the area (Fig. 7: area B) compared to the 1960s and 1980s surveys. No caribou were reported in this area in the 1960s (late Jan–early Feb) and only a few in the 1980s (Jan) compared to the areas east and west of area B for those periods. We could not locate the original 1960s survey maps to verify that caribou were absent from area

B during that period. See Figure 3 for the distribution of caribou locations in the 1960s and 1980s surveys. A more thorough discussion of Figure 7 is provided below in the section on core wintering areas.

In summary, based on the available information on the relative abundance of caribou in the HPE over a 45-year timespan, we concluded that caribou were most abundant in the western and central Hudson Bay Lowland during January–March and possibly in a small area of the James Bay Lowland near The Albany Forks. Caribou were largely absent in areas bordering Hudson Bay and James Bay (Fig. 6). For most of the James Bay Lowland, caribou occurred in small, scattered groups during winter, except in The Albany Forks area and possibly east of The Albany Forks to about 82°W in some years.

The relative abundance of caribou in different regions of the HPE support the conclusion of Ahti & Hepburn (1967) that the Hudson Bay Lowland is the most important of the 3 ecoregions in the HPE for caribou wintering habitat. They referred to these regions as the Coastal Tundra Belt (=Coastal Hudson Bay Lowland), the Northern Boreal Lichen Belt (=Hudson Bay Lowland), and the Eastern Swamp Region (=James Bay Lowland). The authors found the Coastal Hudson Bay Lowland to be rich in lichens, especially on the edge of the tundra, and considered the region to be excellent summer range for caribou, but too windswept in winter to supply important winter range. In contrast, they believed the Hudson Bay Lowland comprised year-round caribou range because of extensive lichen growth, more forest cover for shelter, and *Carex* spp. and *Scirpus* spp. in the tamarack swamps and sedge fens. The authors considered the James Bay Lowland poor winter range, but speculated that sedges, shrubs, and forbs in the swamps and fens supplied good summer range. Although we concur that the James Bay Lowland likely provides less winter habitat on the whole than the Hudson Bay Lowland, systematic winter surveys have shown that caribou nevertheless find winter range in this region of the HPE. Apparently, only the tamarack fens bordering the area along the west coast of James Bay are largely devoid of caribou in winter.

Core caribou wintering areas in the HPE

We defined a core wintering area as an area where concentrations of caribou sign were located during the HPE-wide systematic surveys. The core areas had multiple locations of caribou sign during all 3 survey periods, with the exception of The Albany Forks area, which was not part of the 1960s systematic survey but was known to have a concentration of wintering caribou in 1962 (Gagnon, 1962), and the area near Webequie (Fig. 5: area 7a), which was not surveyed in the 1980s but had a large amount of caribou sign in the 1960s survey (Brokx, 1965: Fig. 36). Based on this definition and using the location data in Figure 3 and in Brokx (1965: Fig. 36), we delineated 9 core wintering areas, 5 in the Hudson Bay Lowland and 4 in the James Bay Lowland (Fig. 7), that were used during the survey periods. The sizes of the core areas are not proportional to the number of caribou that were surveyed in those areas. Some areas are relatively large because the center of use changed from one survey to another or, in the case of the area near Webequie, data from the 1980s was not available to more narrowly define the core area. While the core areas had the highest concentrations of caribou during the surveys, caribou were found outside the core areas as well. In fact, caribou harvested by First Nations people outside the core areas appeared to make up a larger proportion of the harvest in the HPE than caribou harvested within the core areas (Brokx, 1965; Simkin, 1965; Thompson, 1986). A key harvesting location for Attawapiskat residents, for example, is south of the Attawapiskat River (Victor Project TEK Working Group, 2004) where no core wintering areas were identified.

Because we could not locate the original 1960s survey maps to verify caribou location data, we are uncertain of the boundaries of the core areas between The Albany Forks and Moosonee (Fig. 7: area B). Data from OMNR files indicated that caribou locations south of 52°N (n = 15) were located near Moosonee and Kesagami Lake during the 1960s survey (Fig. 3), at least in the area east of the Albany Forks for which the data were compiled. It is surprising that not one location was recorded in area B (Fig. 7) during the 1960s survey, considering the spread of caribou locations from The Albany Forks to Moosonee in later surveys (Fig. 7). Surveys in this area from 1995, 1998, and 2001 located relatively large numbers of caribou in area B (Fig. 7) and relatively few near Moosonee. These more recent surveys suggest that caribou, if indeed absent from area B (Fig. 7) in the 1960s and distributed mainly east and west of area B in the 1980s, have increased in numbers and/or distribution in recent decades. The relatively high density estimates for 1998 and 2001 support the argument for an increase in numbers, but the variation in movements of caribou during the winter months could alone account for the differences. Unless surveys are carried out over a large enough area to cover all possible wintering areas for caribou that use this portion of the HPE, it will not be possible to differentiate between changes in numbers and changes in winter distribution.

Unfortunately, there is no way to determine whether the changes in the amount of caribou sign detected

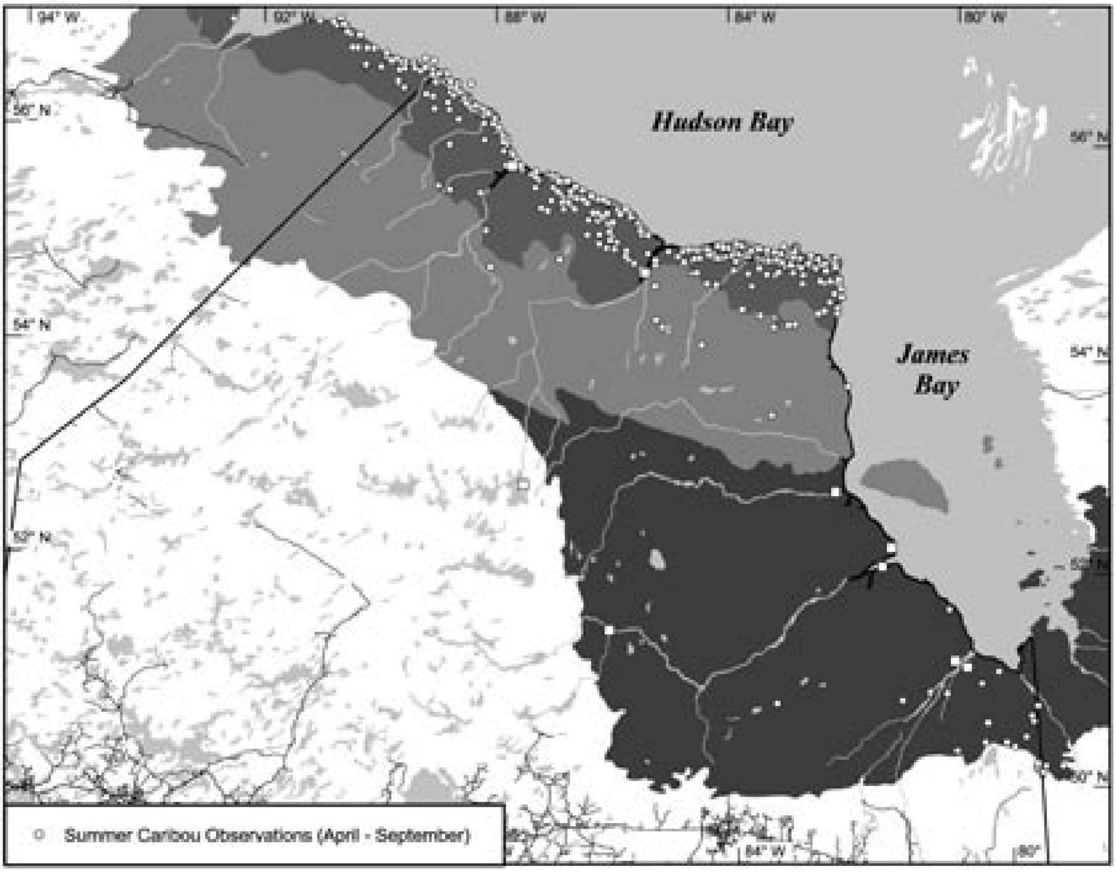


Fig. 8. Summer locations of caribou groups in the Hudson Plains Ecozone (HPE) of Ontario based on incidental observations and photographic surveys from 1950 to 2003.

during the systematic surveys are due to changes in caribou distribution, abundance, or survey design. However, there is reason to believe that there have been changes in distribution and/or abundance of caribou in portions of the HPE in recent years. There was no sign of caribou recorded for the 9000-km^2 area in the northcentral James Bay Lowland (Fig. 7: area A) in the 1980s survey (Fig. 3). In contrast, caribou sign in this area during the 1960s was not uncommon (Brokx, 1965: Fig. 36) and in the 2000s survey, we located caribou sign in 7 of 9 survey hexagons and saw 4 groups of caribou averaging 5.5 caribou per group in 4 different hexagons, even though transects were spaced much farther apart in the latter survey and we did not follow tracks to count caribou numbers. Furthermore, during the 1960s survey caribou sign was uncommon just north of the Ekwan River, but by the 1980s and 2000s surveys, caribou were fairly evenly distributed east of Shamattawa Lake and north of the Ekwan River (Fig. 3). In 1996 there was an unusual movement of relatively large numbers of caribou through the community of Peawanuck in November 1996. The herd was estimated at about 2000 animals and was much larger than any known caribou concentration in the area for more than a decade (Scholten & Chenier, 1996). Our interviews with residents of Peawanuck in August 2004 indicated that, since about the mid-1990s, winter caribou harvesting opportunities have increased substantially for hunters from Peawanuck. Residents reported that caribou used to winter in discrete pockets "until the last 5–10 years," when they now appear to be "everywhere south of the treeline" (i.e., south of the Coastal Hudson Bay ecoregion within the Hudson Bay Lowland).

Summer distribution

Summer locations of caribou from incidental observations and photographic surveys are presented in Fig. 8. Very little is known about the summer distribution of caribou in the HPE, except for the Coastal Hudson Bay Lowland (Thompson & Abraham, 1994) and the area south of James Bay where Brown *et al.* (2003) conducted a study of caribou using satellite

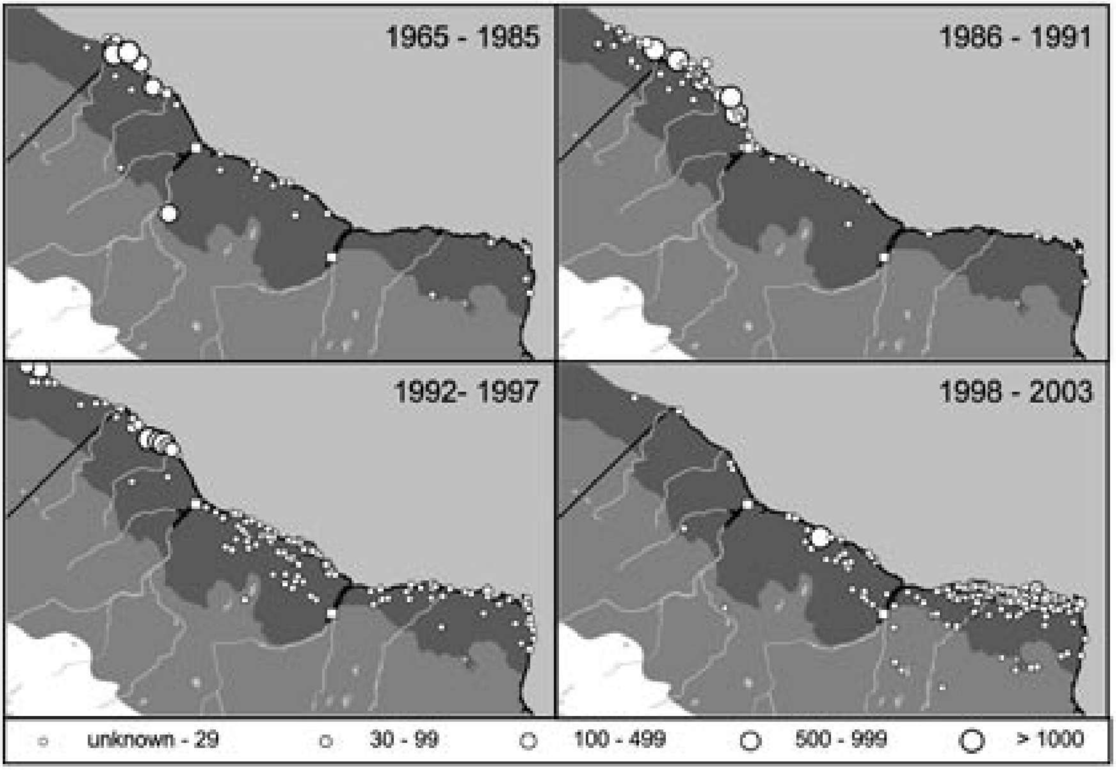


Fig. 9. Summer locations of caribou along the Hudson Bay coast during 4 periods from 1965 to 2003 based on incidental observations and photographic surveys.

collars. While the low number of caribou locations in the interior portions of the HPE most likely results from few observers in that area in summer, the lack of caribou observations along the coast of James Bay compared to Hudson Bay reflects actual caribou distribution in coastal areas in summer. Biologists working on the Hudson Bay coast in summer traveled from Moosonee to Hudson Bay along the James Bay coast and they rarely observed caribou along James Bay.

We divided the summer observations along the Hudson Bay coast by decade and caribou group size to show changes in distribution along the coast over time (Fig. 9). Simkin (1965) reported that caribou were seen all along the Coastal Hudson Bay Lowland in summer, although the largest group he reported was 41 animals east of the Winisk River (early 1960s). He did note a high concentration of caribou tracks near the mouth of the Niskibi River to the west. However, Simkin and others could easily have missed seeing caribou groups along portions of the coast during that period because of the relatively restricted areas of the coast where they spent time during the summer. In the early 1970s evidence began to accumulate that caribou were using the coastal areas in larger numbers than in the past. As many as 2300 animals were photographed at the mouth of the Black Duck River on 6 July 1979 at the Ontario–Manitoba border (Abraham & Thompson, 1998). This was the summer following the 1978 winter survey mentioned previously (Hamilton, 1978) that produced an unusually high density estimate (Fig. 5: area A2), and Hamilton (1978) estimated that approximately 4500 caribou used the wintering area near the Manitoba border that winter. In 1986, large summer aggregations of the Pen Islands Herd were photographed just on the Ontario side of the border, with one group well to the east. Regular photographic counts of aggregations on the coast in the late 1980s and early 1990s suggested a relatively large and increasing herd (e.g., 10 798 animals photographed in 1994) distributed across the border of Ontario and Manitoba (Abraham & Thompson, 1998). Most of the caribou photographed were in large mixed groups, averaging about 1000 animals and ranging from about 200–2000 animals. This pattern appears to have changed beginning in the mid-1990s, with more but smaller groups of caribou scattered along the coast of Hudson Bay and becoming more common in areas east of Fort Severn.

The last photographic survey of the Pen Island Herd occurred in 1997 and incidental observations west of Fort Severn declined after 1997, likely because fewer field studies occurred there by the late 1990s. However, goose banding has occurred annually in the area in mid- to late July since the late 1970s, and in recent years banders have reported fewer encounters with caribou than previously (D. Byers, pers. comm.). In 2002, a dedicated search for caribou was made from Fort Severn west into Manitoba; no aggregations and virtually no caribou were found (D. Sutherland and M. Obbard, OMNR, pers. comm.). The search was in early July when in the 1980s and 1990s postcalving aggregations would have been peaking in size and occurrence (Thompson & Abraham, 1994). Similar results were obtained on a vegetation survey in mid-July 2000 by K. Abraham and during a 2-week ground expedition to the Pen Islands in July 2004 during the period of peak aggregations; no postcalving aggregations and only a few scattered individuals were observed (D. Sutherland, pers. comm.). However, it is possible that aggregations, even large ones, could have been missed west of the Winisk River. In contrast, from 1998 to 2003, many groups of caribou were recorded east of the Winisk River by observers engaged in studies of geese, polar bears (*Ursus maritimus*), and breeding birds, although these aggregations did not appear to be as large as those of the Pen Island Herd in the 1980s and early 1990s. This increase of caribou in the area east of Fort Severn since the early 1990s was real, not simply an artifact of observer distribution. Annual goose banding, mid-July photographic goose surveys, breeding bird surveys, and polar bear research all took place during in the 1980s and early 1990s as well, but incidental observations of caribou in the coastal zone east of the Winisk River during that period were minimal (Fig. 9). Reasons for the change in summer distribution are unknown.

Interpreting the information available on summer distribution of caribou in the HPE is problematic. Data on caribou numbers and distribution during summer were not collected systematically, and radiotelemetry was not used to find animals that were outside the major coastal aggregation areas. Most summer incidental observations were confined to the areas of the coast where biologists were working on projects unrelated to caribou, so even coastal aggregations were likely missed in some years. Photographic surveys were confined to the western portion of the coast and were discontinued after 1997. Finally, a system for routinely documenting the locations of all caribou sighted in the HPE by biologists working in the area was not put in place until the 1990s. We concluded from our limited information, however, that 1) relatively large numbers of caribou began using the western coastal area of the HPE in Ontario sometime in the 1970s, 2) by the 1980s the coastal area west of the Severn River in Ontario was used by relatively large aggregations of caribou, 3) caribou numbers were low along the coast east of the Winisk River in the 1980s, 4) summer aggregations, although smaller than those of the western coastal area in the 1980s, began to appear in the eastern coastal area in the 1990s, and 5) large summer caribou aggregations largely disappeared from the western coastal area sometime between 1997 and 2000.

The dramatic change in summer distribution along the Hudson Bay coast and the decline in the size of the coastal aggregations calls into question the current range, distribution, and size of the Pen Islands Herd, which is often included in the total population estimate of caribou in Ontario. Up to 52% of the population estimate for the province has been attributed to this herd (Cumming, 1998; Harris, 1999), even though the herd resides partly in Manitoba. The disappearance of large summer aggregations along the coast west of Fort Severn suggests the herd may no longer occupy its past range in Ontario in numbers comparable to the 1980s. On the other hand, reasons for the increase in the number of caribou aggregating on the coast east of the Winisk River in recent years are not known; perhaps the Pen Islands caribou herd has shifted its summer range to the east. Lytwyn (2002) reviewed Hudson Bay Company records to determine the seasonal hunting patterns of the "Lowland Cree" and found evidence that caribou crossed the Severn River in large numbers ("many thousands") in the spring and the fall; a favorite crossing place where caribou were traditionally hunted was about 35 km upstream of Severn House (present-day Fort Severn) (Lytwyn, 2002: 104). He noted that some of the Severn River Lowland Cree moved eastward when hunting the migrating caribou in summer, and the Albany River Lowland Cree traveled north to meet the migrating herds (Lytwyn, 2002: 96). "The main caribou calving grounds were reported to be east of the Severn River in the vicinity of Cape Henrietta Maria, but some caribou spent the summer between York Factory and Severn House" (Lytwyn, 2002: 97). An alternative explanation for the increase in the number of caribou aggregating along the coast east of Fort Severn in summer is a change in the numbers and/or distribution of caribou, not associated with the Pen Islands Herd, that winter in the Hudson Bay Lowland between the Severn River and James Bay.

Conclusions and recommendations

The results of our synthesis of information on caribou in the HPE have shown that over the 45-year period since systematic surveys were initiated, caribou distribution patterns in winter have largely remained the same, although the centers of some core wintering areas may have shifted. Summer use of the Hudson Bay coast west of Fort Severn by the Pen Islands caribou has declined while use of the coastal area east of Fort Severn has increased, although with smaller aggregations. Changes in population size for caribou in the HPE may have occurred over this period as well, but data are insufficient to detect these changes.

Use of satellite collars placed on caribou in the core wintering areas and on those that aggregate along the Hudson Bay coast in summer would greatly improve our understanding of the distribution and movements of caribou in the HPE and would help to determine if caribou using different core wintering areas in the region belong to distinct groups of caribou. Once subpopulations of wintering caribou are identified, future surveys to derive population estimates could encompass entire wintering areas to produce more accurate population estimates that are comparable between years and provide information on annual changes in winter distribution.

Large changes in caribou distribution and numbers in the HPE will have direct effects on the people and ecosystems of the region, yet no comprehensive programs are in place to monitor changes in caribou distribution, abundance, or harvest. The challenges in monitoring caribou in such remote regions of Ontario are daunting, but identification of important wintering areas, summer calving areas, and movement corridors is crucial to conservation of caribou in the HPE as modern, industrial-scale resource development and associated infrastructure expand into this region for the first time.

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Climate change and woodland caribou in Northwestern Ontario: a risk analysis

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) range occupancy and populations have declined in northwestern (NW) Ontario over the last 100 years primarily due to human-induced factors. Recovery efforts are underway to halt this decline by reducing risk factors. Climate forecasts suggest a 4–5 °C increase in May–August mean temperature over the next century with little change in precipitation. Resulting increases in extreme weather events and increased fire weather severity will likely increase the amount of forest burned, reduce the area of older forest, alter distribution and abundance of forest tree species and plant communities, and increase abundance of alternate prey. The reduced amount of older forest preferred by caribou will be in greater demand by the forest industry leading to more conflict over ecological and economic values. Most of these factors will increase risk to caribou survival. Although forests may experience enhanced productivity, forest management practices will try to adapt harvest, regeneration, silviculture and fire management practices to both maintain economic benefits and increase the ability of forests to sequester carbon. The interaction of climate-induced forest change and forest management practices adds uncertainty to caribou conservation efforts at the southern edge of its current range. This uncertainty reinforces the need for a precautionary approach to forest management, increased research and monitoring effort, sustained emphasis on caribou recovery, and careful rationalization of restoration efforts where greatest opportunities for success may be realized.

Key words: boreal, climate change, forest-dwelling, forest management, *Rangifer*, recovery, weather.

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Introduction

Over the past 100 years, the range occupied by woodland caribou (*Rangifer tarandus caribou*) in NW Ontario has receded northward (Racey & Armstrong, 2000). This decline has been attributed to many factors (Bergerud, 1974; Darby *et al.*, 1989; Cumming, 1998; Racey & Armstrong, 2000), most of which are direct or indirect effects of human activity and development. These factors include logging, land clearing, fire, disease and parasites associated with white-tailed deer (*Odocoileus virginianus*) range expansion, predation, hunting and human disturbance. Predation risk, as influenced by multiple biological and physical factors, is considered by many biologists to be the most important ecological variable in all seasonal distributions of caribou rather than forage supplies (Bergerud, 1996). There is certainly interaction among factors contributing to caribou decline (Racey & Armstrong, 2000).

The Committee on the Status of Endangered Wildlife in Canada officially listed Woodland Caribou - Boreal Population as a Threatened species in May 2000 (Thomas & Gray, 2001). Ontario has taken steps to officially designate forest-dwelling woodland caribou as a threatened species based on recommendations in a provincial status report (Harris, 1999). These designations impose responsibility for recovery planning to ensure forest-dwelling woodland caribou do not become endangered (National Recovery Working Group, 2001). Recovery planning is underway in Ontario, incorporating policy, education, research, and management objectives.

Since the 1980s, the government of Ontario has supported efforts to understand and modify forest management practices to mitigate adverse consequences for caribou (Cumming, 1992; Racey & Armstrong, 1996; Greig & Duinker, 1997; Armstrong, 1998; Euler, 1998; OMNR, 1999a; Racey *et al.*, 1999). Ontario's Crown Forest Sustainability Act (Statutes of Ontario, 1994) and Ministry of Natural Resources strategic direction statement (OMNR, 2000) set ecological sustainability as a cornerstone for all other resource management objectives. Sustainable resource management planning has generally not regarded climate as a factor despite recognition that weather patterns and climate influence forest pattern and composition (Thompson *et al.*, 1998; Flannigan & Weber, 2000) and likely caribou distribution and abundance (Thompson, 2000). Despite significant efforts to minimize risk by increasing the number and size of protected areas (OMNR, 1999b), emulating natural disturbance patterns (OMNR, 2001), conserving habitat value for caribou, (Racey *et al.*, 1999) and trying to ensure natural processes important to caribou continue to operate; climate change may alter the very natural processes we are attempting to emulate and conserve.

The connection between caribou and climate is obscure and managers and policy-makers question how climate change will impede recovery efforts. They also express concern that even if climate change effects are real, measurable impacts on caribou populations, range occupancy or habitats may only be detectable over decades. More important, climate change may affect the nature, magnitude and consequences of the interaction between physical and biological variables, changing the ecological context of caribou habitat and the entire approach to caribou conservation and recovery efforts. Climate change scenarios also add uncertainty by creating an environment substantially different from that under which current scientific knowledge was generated and applied.

Climate change context

Climate projections based on General Circulation Models (GCMs) (Boer *et al.*, 1992; McFarlane *et al.*, 1992) suggest NW Ontario will experience mean increases in air temperature of 4–5 °C with no significant change in growing season precipitation (Parker *et al.*, 2000). The largest reduction in precipitation will occur from north of Lake Superior west to Manitoba. Temperature differences (Table 1) will be more pronounced in spring and early summer (Wotton *et al.*, 2003). Higher temperatures will increase evapotranspiration and lead to drier soils (Parker *et al.*, 2000). Extreme weather events are expected to be more frequent (Frances & Hengeveld, 1998; Parker *et al.*, 2000) and will likely be expressed as heavier but less frequent rainfall events and severe thunderstorms. These less frequent but heavier rainfall events will be less efficient at recharging soil moisture than lighter more frequent rainfall events (Francis & Hengeveld, 1998). The severe weather projections include a 30% increase in lightning activity (6% for every 1 °C rise in average temperature), increased moisture moving to the higher latitudes with potential increases in mid-latitude winter snowfall, and the potential for an increase in extreme wind events associated with storm activity (Frances & Hengeveld, 1998).

Table 1. Monthly temperature differences (ΔT) and precipitation ratios (P_{2090}/P_{2000}) for northwestern Ontario GCM grid cells for 2 future decades using the year 2000 (1995–2004) as a baseline (adapted from Wotton *et al.*, 2003).

Month	Northwestern Ontario 50.1°N by 93.75°W			
	2040		2090	
	ΔT (°C)	P2040/ P2000	ΔT (°C)	P2090/ P2000
April	3.0	1.19	6.5	1.60
May	2.1	1.08	6.2	1.05
June	2.9	0.79	6.5	0.87
July	2.5	1.00	4.4	0.83
August	2.4	0.94	4.3	0.80
September	1.8	0.93	4.2	1.07

Climate change projections suggest the most pronounced increase in fire weather severity is expected in the extreme northwest and south-central regions of Ontario (Parker *et al.*, 2000). Assuming current fire management efforts, Ontario may experience a 30% increase in number of escaped fires by 2040 and a 80% increase by 2090, largely attributed to increased receptivity of fuels to ignition sources (Wotton *et al.*, 2003), a higher frequency and severity of drought years (Simard, 1997) and an extension of the fire season by as much as 25 days (Wotton & Flannigan, 1993). In addition to lightning-caused fires, an estimated 26% increase in human-caused fires is anticipated (Wotton *et al.*, 2003). Overall, by 2090 a conservative estimate of an 80% increase in the average annual area burned (Wotton *et al.*, 2003) is expected in the zone of intensive fire management (Fig. 1d).

A 3.5 °C mean temperature increase may shift the climatic range of species 100–500 km to the north (Parker *et al.*, 2000). Major shifts in forest species and plant communities have occurred in the past (DeHayes *et al.*, 2000). However, there is a tendency for plant species to migrate singly rather than as intact plant

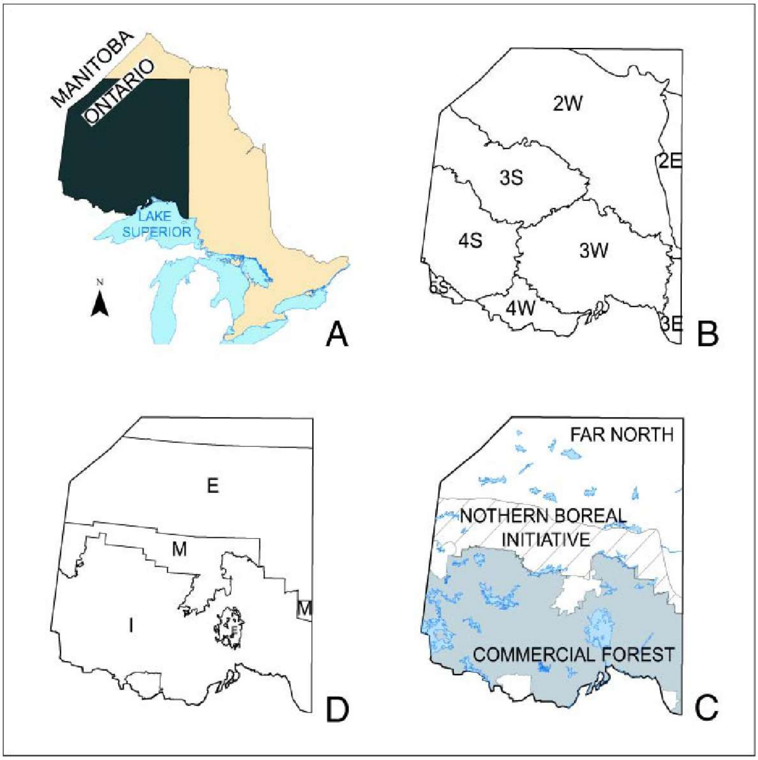

Fig. 1. Administrative and ecological context of the northwestern Ontario study area: a) study area within Ontario; b) ecoregions of Ontario; c) forest management context; and d) major fire management zones prior to 2004 (extensive [E], Intensive [I], measured [M]).

communities (Peters, 1990). If anticipated climate changes are realized, trees that begin growing in the next decade will mature in a climate substantially different from today (Parker *et al.*, 2000). The forest prairie ecotone of NW Ontario will see some of the largest relative changes in vegetation, and in regions where fire is expected to increase in frequency, fire adapted tree species will be favored (Parker *et al.*, 2000). In the extreme case where the fire interval is shorter than the age to sexual maturity of tree species, jack pine forests in NW Ontario may be replaced by grasslands or aspen parklands (Schindler, 1998). With increases in extreme storm events and heavier snowfalls (Francis & Hengeveld, 1998) there is an associated potential for increases in snow and wind damage. Forest disturbance caused by insects and disease may increase in frequency or intensity due to climate trends. Outbreaks of spruce budworm (*Choristoneura fumiferana* Clem.), jack pine budworm (*Choristoneura pinus pinus* Freeman), and forest tent caterpillar (*Malacosoma disstria* Hubner) are likely to increase in areas with warmer, drier growing seasons like NW Ontario (Fleming & Volney, 1995).

The focus of forest management is expected to adjust to changing climate and its associated environmental stresses. Forest management practices intended to increase carbon storage could become a critical component of national efforts to reduce greenhouse gas emissions and slow the rate of climate change (Parker *et al.*, 2000). Additional effort will likely be applied to the management and regeneration of declining stands (Parker *et al.*, 2000) and extensive artificial regeneration efforts to assist migration of tolerant genotypes (Mackey & Sims, 1993). Forest management for carbon sequestration may encourage longer rotation periods (balanced against fire interval), planting of fast growing genotypes, partial cutting systems, artificial rather than natural regeneration, control of competing vegetation to make more light, nutrients and water available, thinning and fertilization (Parker *et al.*, 2000).

Some authors forecast an expansion of white-tailed deer range and reduction in caribou and moose (*Alces alces*) range associated with climate change (Thompson *et al.*, 1998). Meningeal worm (*Parelaphostrongylus tenuis*) infection rates will most likely increase as a result of warmer summers and lengthening of the frost-free period in autumn, combined with a documented northward extension of deer range and altered range and abundance of terrestrial gastropods (Greifenhagen & Noland, 2003).

This report is a synthesis of existing climate change literature pertinent to NW Ontario and central Canada augmented by a limited modelling exercise. I examine current and projected climatic trends as they might affect risk factors associated with woodland caribou survival. I speculate how these changes might influence the prospects for caribou persistence on the landscape and how managers may adapt their approach to caribou conservation.

Study area

The NW Ontario study area (Fig. 1a) is characterized mainly by provincial ecoregions 4S, 3W, 3S and 2W (Crins, 2000) (Fig. 1b) of the boreal shield ecozone. Each ecoregion has a set of climatic, physical and

Table 2. Modelled (150 yr) change in forest composition and caribou habitat availability (with forest management) under 3 projected levels of wildfire. Forest response in terms of older (≥ 80 yr) jack pine (Pj old), black spruce (Sb old), and mixed upland conifer (Conmx old). Caribou refuge (caribou habitat) and winter habitat availability were estimated based on forest composition and age class. The third model run (80% increase) was only able to find a feasible solution through elimination of most environmental constraints such as maintenance of 10% old growth.

Analysis area	Forest unit class	Change (%) 30% increase in area burned per yr	Change (%) 50% increase in area burned per yr	Change (%) 80% increase in area burned per yr
4S	Pj old	12	-9	-91
	Sb old	-22	-24	-69
	ConMx old	-45	-49	-36
	Caribou habitat	-8	-12	-89
	Caribou winter habitat	-3	-8	-94
3W & 3S[a]	Pj old	7	-1	-98
	Sb old	-5	-16	-99
	ConMx old	-4	-17	-99
	Caribou habitat	0	0	-96
	Caribou winter habitat	1	2	-95

[a] Models for this analysis area only captured the northern portion of 3W and made available for harvest only those forests currently licensed for forest management.

biological properties that help distinguish them from other ecoregions. Ecoregions reflect forest vegetation soil and climate relationships and are used to stratify the land for biodiversity conservation, and land use planning. There is a strong relationship between these ecoregions and major climatic gradients. Within these ecoregions, forest and wetland plants are organized in well-defined community types (Sims *et al.*, 1989; Harris *et al.*, 1996; Racey *et al.*, 1996), many of which are directly associated with habitat value for caribou, deer or moose (Racey *et al.*, 1989).

Administratively, the study area consists of 3 zones: the most southerly is subject to commercial forestry and reflects most of the human presence in NW Ontario; the far north has no anticipated forest management activity and in between is an area where new economic development opportunities are sought under the Northern Boreal Initiative (NBI) (Fig. 1c). Fire management effort varies among these zones and prior to 2004 this effort was termed intensive (each fire receives initial attack and sustained suppression effort), measured (fires receive initial attack and escaped fires are assessed for their potential impacts and appropriate suppression actions are formulated within program capacity), and extensive (fires only monitored and no suppression action taken unless life or property is at risk) (Fig. 1d).

Historically, the forests and associated flora and fauna of NW Ontario have developed under a natural fire regime (Heinselman, 1971; 1981). Fire cycles, within the current management environment are estimated at 248 yr (4S), 389 yr (3W), 120 yr (3S) and 154 yr (2W) (Frech, 1998). Forest management recognizes the historic and natural forest condition within these ecoregions as a benchmark against which sustainability is assessed (OMNR, 1996).

Methods

I examined existing literature describing recent weather trends, projected climate change and associated impacts in NW Ontario and central Canada to extract inferences and arguments pertaining to risk factors relevant to woodland caribou. I analysed these risk factors within a framework based on a functional definition of habitat, i.e., habitat provides refuge from predation and disease while also providing essential resources for survival and reproduction. I then tabled potential changes and impacts under categories of forest attributes, disease, predation pressure, compensatory forest management practices and thermal stress. I assumed that risk to caribou increased if the refuge value of habitat was reduced.

I used Ontario's Strategic Forest Management Model (OMNR, 2002a) to examine the potential impact of a predicted increase in annual area burned by wildfire as a result of climate change. I modelled 2 forest management - succession scenarios, assuming factors such as forest succession and non-fire disturbance agents remain relatively constant. I then used

Table 3. Modelled (150 yr) forest composition change under 4 levels of fire, and without forest management on all or part of ecoregions 3S, 3W, and 4S. Forest response is reported for older jack pine stands ≥ 100 yr (Pj old), older black spruce stands ≥ 110 yr (Sb old), and older mixed conifer stands ≥ 110 yr (Conmx old).

Analysis area	Forest unit class	Change (%) 30% increase in area burned per yr	Change (%) 80% increase in area burned per yr	Change (%) Gradual increase[a]
3S	Pj old	-16	-40	-40
	Sb old	-26	-55	-43
	Conmx old	-27	-57	-48
3W	Pj old	+36	-17	-18
	Sb old	-22	-48	-37
	Conmx old	-22	-49	-37
4S	Pj old	-9	-28	-22
	Sb old	-26	-55	-41
	Conmx old	-23	-50	-43

[a] Modelled under a gradual increase from 0% (yr 1–50) to 30% (yr 51–70) to 80% (yr 71–150).

the model outputs to quantify changes in forest cover attributes relevant to habitat quality.

Modelled forest composition with forest management
Existing forest models featuring forest dynamics, harvest, fire and silviculture were obtained from the provincial *Forest Resource Assessment Project*. These models have been used to assess forest resources for the *State of the Forests* report (OMNR, 2002b). The 2 models, corresponded approximately to provincial ecoregions 4S, and upper portions of 3W and 3S. In these models, forest harvest was fixed at levels agreed under the *Ontario Forest Accord*. A 150 yr simulation was run, within which the only change from the base models was the area burned by wildfire which was adjusted to correspond approximately to 2040 and 2090 projections made by Wotton *et al.* (2003). For each model run the percent change in older conifer forest types was determined as well as the approximate area represented as preferred caribou habitat and winter habitat (Racey *et al.*, 1999).

Modelled forest composition without forest management
Three existing, generalized natural dynamics forest models featuring only forest dynamics and fire for ecoregions 3S, 4S, and 3W were used to estimate potential changes in forest composition with increased occurrence of fire assuming no forest management takes place. These base models were used to estimate modelled bounds of natural variation in NW Ontario (Ride *et al.*, 2004). A 150 yr simulation was run, within which the only change from the base models was the area burned by wildfire which was adjusted to correspond approximately to 2040 and 2090 projections made by Wotton *et al.* (2003). For each model run, 12 in all, the number of hectares of forest types by age class at the end of the modelling period was recorded.

Results

Modelled forest composition showed a substantial reduction in older conifer forest types with (Table 2) and without (Table 3) forest management. In the presence of forestry and fire management, stands with desirable attributes for caribou habitat were reduced 8–12% in 4S but did not change in the northern portions of 3W and 3S where a large portion of the modelled forest was not considered available for harvest. The *Forest Resource Assessment* models were unable to find a feasible solution in trying to meet wood supply commitments and environmental constraints with an 80% increase in area burned per year (Table 2). In this case, the constraints on maximum silvicultural investment and 10% old growth maintenance had to be eliminated along with other assumptions in order to maintain wood products flow resulting in virtual elimination of older forest components and caribou habitat potential. Therefore, results of a 50% increase in annual area burned was recorded for comparison purposes. In the absence of forest and fire management and within the most realistic gradual increase scenario, best estimates of changes in forest composition suggest an 18–48% reduction in older conifer forest depending on species and ecoregion (Table 3).

A risk-analysis framework (Table 4) applied to direct and indirect consequences of climate change suggests that most will tend to increase risk to woodland caribou survival in the study area. Of the 14 risk categories assessed, 10 clearly increased risk, 1 reduced risk, 1 was uncertain, and 2 are assumed to increase risk but may actually reduce risk if alternate assumptions are more important than currently

Table 4. Risk analysis framework to examine the potential impacts of climate change on risk to woodland caribou in northwestern Ontario; mechanisms and risk are synoptic and have value primarily for supporting future debate, investigation and analysis.

Category	Factor	Factors affected directly by climate	Theoretical mechanism for impact on woodland caribou	Risk[a]
Forest Attributes	Proportion of older forest	Wildfire frequency	Reduced area in large patches of older, conifer dominated forest reduce ability of caribou to separate themselves spatially and temporally from predators.	++
	Proportion of conifer forest	Wildfire frequency and intensity		++
	Size of patches of older forest	Wildfire frequency		++
	Forest community distribution	Growing season length, growing season precipitation drought frequency	Relative distribution and abundance of browse producing stands influences alternate prey species abundance or distribution.	?
	Forest stand mortality	Insect infestation rates and frequency of severe wind or snow events	Blowdown and breakage of trees impedes travel and visibility while increasing fire risk.	+
Disease	Distribution of alternate hosts and carriers	Winter severity, snow depth, snow-free period (deer range expansion)	If extreme winter weather frequency is enough to minimize deer range expansion and fire frequency, fire intensity and drought cycles are significant enough to depress gastropod populations, *P. tenuis* may not increase risk in study area. Otherwise risk increases.	+/-
Predation Pressure	Numbers of alternate prey	Suitable habitat for moose, white-tailed deer	Increased area covered by early successional forests increases moose and deer numbers inducing a functional response by wolves and coyotes (increased predator numbers).	+
	Distribution of Alternate prey	Wildfire frequency and distribution, winter severity, winter temperatures, snow depth, extreme weather events	Fire will increase early successional habitats beneficial to moose and deer but will reduce older forest components necessary for coping with extreme winter weather events. Deer and moose both respond to severe winter weather conditions concentrating in most suitable habitats. Caribou refuge habitats with low abundance of alternate prey will become smaller and less abundant.	+
	Predator efficiency	Winter severity, winter temperatures, snow depth, extreme weather events	Extreme weather favors caribou more than moose and deer. Heavy snow years may also concentrate deer and wolves that prey on them yielding a spatial separation from caribou. Longer growing season and increased forest disturbance could increase black bear abundance and caribou encounters.	+
Compensatory Forest Management Practices	Harvest levels	No direct climate effect	If wood flow is maintained despite increased fire losses, there will be increased pressure on older forest components	+
	Age of stands harvested	No direct climate effect	Shorter rotations for upland stands will reduce effective time period for larger areas of older forest to provide for caribou habitat	+
	Intensified silviculture activities	No direct climate effect	Increased forest productivity may reduce terrestrial lichen abundance and distribution in mature and developing stands. Increased road construction and maintenance may support predator mobility across landscape. Competition control to enhance conifer crop tree growth may enhance refuge value	+ /-
	Fire Suppression Effort	No direct climate effect	Increased fire suppression efforts to maintain wood supply may also help maintain older conifer forest components important for maintaining caribou. Resources available for managing wildfire activity may or may not change proportionate to fire risk.	-
Thermal Stress	Thermal stress	Spring and summer temperature extremes	Despite increased ambient temperatures, caribou have abundant access to environments with water-moderated temperatures and ready access to water for consumption.	+

[a] ++ large increase in risk, + higher risk, - lower risk, ? unknown change in risk, +/- increased risk assumed but may be reduced risk if alternate assumptions are more important than presently thought.

thought. These projections, generated by inference from findings in published literature, are intended as testable hypotheses for future debate, investigation and analysis. There is no implied level of accuracy or precision.

Discussion

Modelled climate change projections are generalized over large areas and demonstrate substantial continental variation. They suggest northeastern Ontario may not warm as dramatically as NW Ontario, and the climate may become drier towards the Manitoba border (Parker *et al.*, 2000). The size, location, unique biophysical landscape and projected climate response of NW Ontario justifies its role as a unique study area for examining the implications of climate change on woodland caribou.

Conservation of woodland caribou depends on maintaining risk factors at levels compatible with maintaining range occupancy. The objective for conserving caribou landscapes subject to forestry is to maintain a continuous supply of suitable, mature, year-round habitat distributed both geographically and temporally across the landscape in such a manner as to ensure permanent range occupancy (Racey *et al.*, 1999). This objective recognizes that woodland caribou have evolved to cope with a naturally dynamic boreal forest that includes predators. The premise behind this objective is that the overall forest landscape provides refuge from predators and disease. The landscape provides a context for relative abundance and distribution of predators, availability and distribution of alternate prey species, escape opportunities and separation from disease agents. It also provides a context for caribou forage opportunities. Factors that change the forest landscape in a manner that increases risk, reduce the likelihood that caribou range occupancy can be maintained. Considerable interaction among factors is expected, and this interaction is likely to be complex. It is also likely that some factors have both positive and negative implications for caribou. Speculation on relative importance of one factor over another and the consequences for caribou survival can only be made within the context of existing, incomplete scientific understanding supplemented by logical inferences to "fill-the-gaps."

Forest attributes

Forest modelling results

Forest modelling suggests a major shift in forest composition leading to a future forest with less area in older, conifer dominated forests which currently characterize landscapes that contain woodland caribou. These older conifer forest types are an important component of both winter and summer caribou habitat. The reduction in older forest usually results in a landscape dominated by younger stands of hardwoods and jack pine. This general shift in age class structure and forest species composition is presumed to increase risk by reducing the refuge value of the landscape. However, spatial arrangement or pattern of forest types is generally recognized as important for refuge value (Racey *et al.*, 1999). Especially important are large contiguous areas of relatively old conifer forest associated with lichen-rich woodlands, shallow-soil dominated forests and forested peatland complexes. Although the model results are not spatially explicit, an increase in number of escaped fires will not only change the proportion of young and old forest, it will also likely reduce the number and extent of large contiguous tracts of older conifer dominated forest. It is anticipated that the reduction in availability of older forest will increase public pressure for social and economic trade-offs with caribou conservation, due to the need to maintain flow of wood to the forest products industry. These trade-offs will likely result in increased forest fragmentation because forest companies will have to apply greater selectivity to access wood in specific age classes (the forest models suggest most stands must be harvested at 65–75 years of age to maintain wood flow), and with high-quality fiber attributes. Collectively, the potential reduction in the proportion of larger tracts of older conifer forest, and an increase in forest landscape fragmentation could result in a biologically significant reduction in caribou refuge value across the landscape.

In ecoregions 3S and upper 3W, the reductions in conifer forest were not as great as ecoregion 4S, attributed in part to the fact there was no expectation for the models to "generate" wood from the NBI area. Under this scenario, there was a minor increase in caribou habitat availability. However, in the foreseeable future, there will be demand for wood products from this area and the projections for caribou habitat and older conifer forest may be more similar to the results for 4S. As this area represents the "heart" of current occupied caribou range, the potential combined impacts of forest harvest and increase in area burned might have substantial negative impacts on forest types that serve to provide caribou with refuge from predators. The combined effects of increased fire under an 80% increase in area burned scenario and the effects of a forest products driven management system essentially eliminated the older conifer forest and virtually all caribou habitat potential. If such a scenario actually occurs and there are no dramatic changes in forest product demand or economic expectations, managers will have to make the tough choice between caribou survival and the maintenance of the forest industry as we now know it. However, if sustainable forest management adapts thoughtfully to the changing climatic and ecological context, a suitable balance may be struck among harvest levels, natural disturbance and habitat values that could sustain caribou on a managed landscape. A comprehensive ecosystem-based approach to management of the forest landscape may be essential for the survival of both caribou and the forest industry.

Inferences should be tempered with caution. Many factors, singly and in combination, contribute to the fire regimes demonstrated in NW Ontario (Li, 2000). The estimates of change in forest cover and age class presented here are considered conservative, recognizing the crude fire-change estimates of Wotton *et al.* (2003) which did not account for increased lightning activity and other weather pattern phenomena that would also contribute to increased fire activity. Estimates of the increase in area burned are for northern Ontario, but the increase for NW Ontario is expected to be greater than northeastern Ontario. In addition, these estimates were for the zone of intensive fire management that represents only a portion of the caribou range in NW Ontario. The remainder of the forest might be expected to exhibit even greater increases in area burned. Risk to caribou would increase at least in proportion to, and possibly exponentially with the amount of area disturbed by fire and logging.

The general relationship between forest cover, age class and caribou is thought to be fairly well understood (Racey *et al.*, 1999). Wildfire has a direct impact on temporal expression and use of habitat by woodland caribou (Schaefer & Pruitt, 1991). However, indirect implications of climate change for habitat relationships may be reflected in successional relationships (Kenkel *et al.*, 1998) and silvicultural practices (OMNR, 1997) that are likely to respond to ecologically and commercially significant changes in the composition and productivity of forests (Reed & Desanker, 1992).

Forest community types and distribution

Changes in forest plant communities are difficult to forecast because they relate to a multitude of factors and interactions such as frequency and intensity of wildfire, rates of nutrient cycling, growing season length and growing season precipitation. The greatest risk to caribou, independent of changes to the broad forest cover and age class distribution, is a general increase in shrub or herb richness of sites. Greater occurrence of desirable moose browse species in mature forest communities may make the landscape more desirable for moose, leading to an increase in abundance of alternate prey for wolves.

Generally, forest conditions sampled in ecoregion 3S (Racey, 2001), home to some of the healthiest populations of woodland caribou in NW Ontario (Racey & Klich, 2003), suggest a higher proportion of low-diversity vegetation community types. Among the species most conspicuous in their absence are beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), balsam fir (*Abies balsamea*) and pin cherry (*Prunus pensylvanica*), which tend to be major contributors to browsable biomass for moose elsewhere in NW Ontario (Rempel *et al.*, 1997a). A possible explanation for the reduced occurrence of some of the more herb and shrub rich vegetation types as described by (Sims *et al.*, 1989) is the aggressive fire regime exhibited within the ecoregion (Racey, 2001), particularly on shallow or deep sandy soils. While increased growing season length may favor herb and shrub growth, the potential increase in fire frequency and intensity may discourage these species at the landscape level. Climate change may also disrupt the expected occurrence and structure of vegetation types due to the tendency for species to migrate singly rather than as intact plant communities (Peters, 1990). If, at the landscape level, climate change favors the development of browse producing species, an increase in mixed forest conditions and a reduction in the frequency and distribution of low-diversity stands normally used by caribou, increased risk would be expected. On the other hand, if increased fire frequency, intensity and drought cycles maintain the proportion of lower-diversity forest types exhibited, then the level of risk associated with abundance and distribution of forest community types may not change much.

Disease

The primary disease agent of concern with climate change is *P. tenuis*. This parasite is fatal to caribou (Trainer, 1973), is carried by white-tailed deer and uses terrestrial gastropods as intermediate hosts. Deer range in NW Ontario has fluctuated widely over the past 70 years, most likely due to among-year variation in winter severity. In the study area, white-tailed deer range in 2003 approximates range extent in the 1940s (J. Van den Broek, pers. comm.) but was greatly reduced between the late 1960s through to the 1980s. These range expansions correspond to 2 general warming trends separated by a cooling trend. Biologists speculate that white-tailed deer range will continue to expand under a warmer climate. But winter severity is a major limiting factor for white-tailed deer (Hepburn, 1959) partly attributed to over-winter condition but mostly due to their susceptibility to predation (DelGiudice *et al.*, 2002). Climate change scenarios for increased snowfall and bigger storm events especially in middle and higher latitudes (Francis & Hengeveld, 1998), combined with a reduction in the proportion of older conifer forest suggest that white-tailed deer may continue to be limited by sporadic severe winter conditions.

Little is known of the ecological requirements of the gastropod intermediate hosts for *P. tenuis.* However, in Newfoundland, Ball *et al.* (2001) found that infection rates of *Elaphostrongylus rangiferi* in caribou had a positive correlation with mean annual minimum temperature, and a negative correlation with mean summer temperatures. The risk of infection increased with moderate summer temperatures suitable for the activity and infection of gastropod intermediate hosts and by mild winters with little snow that extended the transmission period. It is possible that hotter, drier conditions and severe fire events projected with climate change, particularly on the very shallow, sandy soils common in NW Ontario may not be conducive to either the abundance or the activity of intermediate host gastropods.

As white-tailed deer populations are able to recover more quickly than caribou when suitable conditions prevail, and as there is great uncertainty regarding the response of terrestrial gastropods, I suggest that risk to caribou may increase provided terrestrial gastropod populations are not significantly inhibited by the occurrence of drought, intense fire, and shallow and dry soils in the study area.

Predation

Ontario caribou managers believe that direct and indirect causes of increased predation pressure, as described by Bergerud (1974; 1996), Bergerud *et al.* (1984) and Seip (1992) are a highly significant factor in caribou decline. Caribou cope with predators through range use and habitat selection at various spatial scales (Rettie & Messier, 2000; 2001; Johnson *et al.*, 2002). We assume predator numbers in existing woodland caribou-occupied forest ecosystems will respond to increased availability of alternate prey such as white-tailed deer or moose. Increased predator numbers will place caribou at risk. The degree of risk will depend on the size of increase in predator numbers in response to the available ungulate prey and the increase in predator efficiency. It is the number and distribution of alternate prey that is expected to respond to climate-induced environmental changes.

In the absence of hunting, moose respond positively to younger forest resulting from both logging and natural disturbances (Rempel *et al.*, 1997b). The frequency of forest disturbance and area of disturbed forest is expected to increase under the modelled climate change scenario and the proportion of older forest is expected to decrease. However, even with lower hunting pressure in northern wildlife management units, moose populations have not responded in the more northern portions of the managed forest in Ontario (McKenney *et al.*, 1998).

Increased proportion of younger forests as a result of increased fire activity may favor some aspects of moose habitat quality. However, moose may actually decline in some parts of their range because of changes in landscape structure (Thompson *et al.*, 1998). Cursory examination of forest stand composition and structure in the NBI area suggests that the aggressive fire regime experienced in the past may actually maintain forest conditions less desirable to moose because of a reduction in some preferred browse species such as white birch (*Betula payrifera)*, red-osier dogwood (*Cornus stolonifera)*, mountain maple, and serviceberry (*Amalanchier* sp.) (Racey, 2001). It is uncertain if increasing the intensity and frequency of fires in this system will reduce or enhance the quality of moose habitat in the manner described by Rempel *et al.* (1997b), but I suggest that it is more likely that moose browse production will increase through an increase in younger, hardwood and shrub–dominated forest types. The increased proportion of disturbed forest, shrub-rich forest, and a longer growing season may also increase mast availability for black bears *(Ursus americanus*) and increase the length of time black bears are active. Increased activity periods may increase encounter rates with caribou calves.

An additional factor may be the incidence of heat stress imposed by increasing frequency of hot spring and early summer conditions. Moose begin to experience thermal stress at 14 °C with full open-mouth panting at 20 °C (Renecker & Hudson, 1986; 1990). This may be particularly significant in spring and early summer when the greatest increases in temperature are expected and may increase the number of days each year when moose are exposed to heat sufficient to depress foraging activity and weight gain as described by Renecker & Hudson (1986). Increased spring and summer temperatures would be expected to add stress to moose populations at the southern edge of their range. This may provide a small mitigating factor affecting some alternate prey within caribou range.

Winter habitat selection tends to be associated with larger contiguous tracts of older conifer forest and major wetland complexes (Racey & Klich, 2003), likely in response to lower risk of predation (Rettie & Messier, 2000). Modeled forest composition shows a decline in older conifer forest which may increase the evenness of moose distribution, and reduce the size and extent of old forest patches that provide limited refuge for caribou. Even if the absolute increase in alternate prey and predators is lower than forecast, the reduction of refuge and more even distribution of predators may increase risk to caribou by increasing encounter probabilities. I believe this is a very important risk factor unless countered by an increase in winter severity.

Deep snow, crusting conditions and severe weather may negatively impact white-tailed deer populations by concentrating wintering herds, increasing susceptibility of deer to predation (Fuller, 1991) and imposing nutritional constraints (DelGiudice *et al.*, 2002). The degree to which white-tailed deer contribute to abundance of alternate prey may not be significant if wintering herds are highly concentrated or if they are subject to periods of increased predator or weather-related mortality. It is unlikely that white-tailed deer winter habitat overlaps substantially with the forest types described by Ahti & Hepburn (1967) or Racey *et al.* (1989).

Compensatory forest management practices

Forest management practices are expected to adapt to increased fire frequency, increased forest disease, altered nutrient cycling and to maximize carbon storage in the boreal forest. Parker *et al.* (2000) suggest that managing species on relatively short rotations may be preferable for upland tree species. They also suggest the potential use of partial cutting systems, greater emphasis on artificial regeneration, and further analysis of the net benefits of thinning and fertilization. Shorter rotations would combine with fire to reduce the amount of older forest on the landscape. Efforts to increase forest or site productivity may have negative impacts on terrestrial lichen availability on shallow or sandy soils that normally support abundant terrestrial lichen communities (Sims *et al.*, 1989; Racey *et al.*, 1989) by increasing canopy closure of crop trees and herbaceous species thus reducing exposure to sunlight, one of the most important requirements for lichen establishment and growth (Ahti & Hepburn, 1967; Johnson, 1981). Some resource managers are concerned that the increased road networks and road maintenance periods associated with more harvesting activity or intensified silvicultural approaches may also increase the movement or effectiveness of predators in caribou range thus increasing risk in a manner similar to that suggested by Dyer *et al.* (2001) or James (2000). With the exception of increased fire protection effort, most compensatory forest management practices will increase expected risk to caribou.

Thermoregulation

Experimental evidence on caribou shows measured physiological response to heat at temperatures of 35 °C and above (Yousef & Luick, 1975). With the increasing frequency of warm days, the number of days per year caribou might have to devote to minimizing heat stress will also increase. Rosenmann & Morrison (1967) suggested that caribou have good capacity for heat resistance when water is available. The abundant lakes, rivers and wetland complexes associated with summer habitats in NW Ontario offer abundant free water, aquatic refuge and water-cooled environments to assist caribou in coping with heat stress. Risk to caribou may increase if high temperatures are combined with human or predator disturbance, causing caribou to remain active during warm weather.

Conclusions

Climate change as described in current projections will almost certainly increase risk to woodland caribou survival in NW Ontario. Many of the factors that contribute to increased risk likely apply similarly to other jurisdictions such as Manitoba and northeastern Ontario. Much uncertainty remains, not only in the projections for climate change, but in the response of forest and wildlife communities to climate change. At the same time as our appreciation of this uncertainty grows, land use and resource management decisions (wood supply commitments, forest harvest, regeneration efforts and desired future forest condition in terms of forest pattern and composition) are being made under current assumptions of forest dynamics and wildlife habitat relationships. The time frame for climate change to have an impact on current assumptions is probably less than the time required to realize the outcomes of our current management decisions. If we are to maintain our commitment to conserve woodland caribou in NW Ontario, a sustained emphasis on caribou recovery conservation efforts must be precautionary, practical, responsive and visionary.

Precautionary

We must live with the uncertainty of modelled projections and recognize that they may be wrong. But we must err on the side of caution and develop management responses to higher-risk scenarios. Conversely we should develop plausible management alternatives for high risk caribou populations under the assumption that our climate change evaluation may be incorrect.

Practical

Management approaches based on the "best science" and augmented by precautionary assumptions need to be designed and implemented across the managed landscape. These approaches must be integrated across the disciplines of forestry, wildlife management, and sociology. Practical solutions must not pit caribou against all other development opportunities which, in a "take-it-or-leave-it" alternative may not favor caribou. The ultimate survival of both caribou and the forest industry may depend on a reasoned and adaptive ecosystem-based approach to management of the forest landscape.

Responsive (adaptive)

Measurable indicators of success for woodland caribou conservation, and indicators of desired future forest condition need to be established. Suitable measures of woodland caribou population health should be regularly monitored in order to determine, at the earliest opportunity, if conservation efforts have been successful or if additional or modified mitigation measures are required. Effectiveness should be evaluated at the landscape or "ecosystem" scale consistent with caribou range use in a dynamic boreal forest. Rigorous scientific investigation of the changing ecological context of caribou conservation is crucial.

Visionary

Bold approaches may be required to manage the relationship between various ecological, social and economic values represented in Ontario's boreal forest. These approaches may have to seriously examine societal response to threatened species, the role of the forest industry, and the notion of forest sustainability under plausible climate change scenarios. Managers have never before faced prospects of such systematic and far-reaching changes in the ecological context for the renewable resources and social benefits they try to sustain. Risk-taking is an important component of any visionary approach, including sustained recovery efforts on high-risk populations and the possible abandonment of populations that have no hope of maintenance even if climate change predictions and their negative impacts are wrong.

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Caribou recovery and coexistence with introduced feral reindeer on the Nuussuaq Peninsula (70–71°N), West Greenland

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Abstract: The small native caribou population (*Rangifer tarandus groenlandicus*) of Nuussuaq Peninsula was supplemented in 1968 with 10 semi-domestic reindeer (*Rangifer tarandus tarandus*). Hunting was prohibited in the early 1990s, but resumed with a quota of 100 animals in 1996 after the population was estimated to be around 400. Despite local criticism that herd size had increased, managers kept the estimate unchanged and permitted similar quotas for the next 5 years. To ascertain current status of the population, a late winter ground survey for minimum count, recruitment and distribution was done in April 2002 employing local hunters. Data collected included group size, location and animal sex/age. Only two age classes were used; calf (<1 year) and "adult" (>1 year). The 2002 ground survey observed 1164 individuals and a calf percentage of approximately 30%. The bull to cow ratio was 0.32. This data did not allow a calculation of population size, because areas where maximum animal numbers were expected were preferentially sampled. Spatial segregation of these two subspecies is suggested, given the observed and unexpected dissimilar behavior, phenotype and spatial distribution. If true, then by 2002 feral reindeer had established a successful population, while native caribou had recovered to number several hundred. Genetic sampling is necessary to examine this hypothesis. At current late winter recruitment rates animal density could increase rapidly making both range expansion and genetic mixing likely in future. Since the total non-ice covered area available is about 6000 km^2, greater caribou/reindeer densities may not be compatible with sustainable range use. Harvest quotas were increased in 2002 and 2003, and may reduce densities and preserve caribou range for the future.

Key words: density, distribution, phenotype, population, *Rangifer tarandus groenlandicus, Rangifer tarandus tarandus,* recruitment, sex ratio, status, survey.

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Introduction

The Nuussuaq Peninsula (70–71°N; 49–55°W) in West Greenland is isolated by topography and distance from other *Rangifer tarandus* populations in Greenland. Prior to 1968 only native wild caribou (*Rangifer t. groenlandicus*) were present and just 15–25 individuals were presumed remaining (Meldgaard, 1986). Therefore 10 semi-domestic reindeer (*Rangifer t. tarandus*) were introduced in 1968. These animals originated from the Greenland Godthåbsfjord's Itivnera/Kapisillit reindeer herding district (64.2°N; 50.5°W), which was established in 1952 with a shipment of reindeer from northern Norway, (Cuyler, 1999). The 10 semi-domestic reindeer were released into the eastern portion of the Nuussuaq Peninsula in the vicinity of the lake, Boyes Sø (Fig. 1).

These semi-domestic reindeer were never intended for animal husbandry, but were to become feral, possibly mix with the native caribou, and ultimately provide the region's hunters with a meat resource for future harvests. Semi-domestic reindeer typically rut and calve about two or three weeks earlier than their caribou counterparts. Because the latitude of the Nuussuaq Peninsula matches the extreme northern limit for semi-domestic reindeer in Scandinavia, the success of this introduction was uncertain. Still, neither wolves (*Canis lupus*) nor any other potential

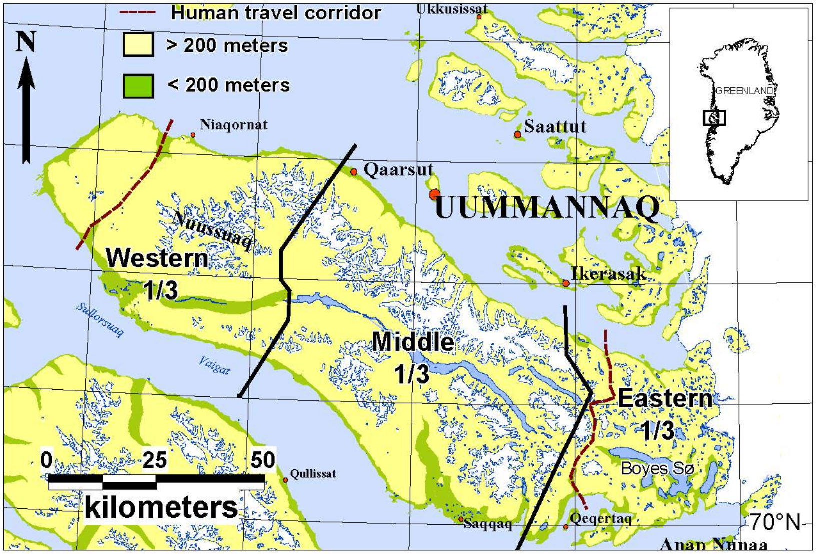

Fig. 1. West Greenland's Nuussuaq Peninsula (70–71°N) divided into rough thirds: Western, Middle, and Eastern. Approximately 6000 km^2 non-ice covered. Shading indicates elevation.

predator have existed in West Greenland for several hundred years (Dawes *et al.*, 1986). Harvesting by local hunters, however, was unregulated by quotas until 1987 (Fig. 2).

In 1991, following an aerial survey, which observed only 44 animals, the decision was made to prohibit hunting for 10 years (Greenland Institute of Natural Resources [GN] file 28.63.02/15 Nuussuaq). Another survey in 1995 observed 161 animals, which included 11% calves (age <1 year), and population size was estimated to be 400 (Ydemann & Pedersen, 1999). Thus, despite the decision to prohibit hunting until 2001, a quota of 100 animals was permitted in 1996. Harvesting continued with little variation in quota into 2001. Managers assumed population size remained unchanged since the 1995 estimate of 400 animals, however by 2001, locals insisted that caribou numbers had risen and wanted the harvest quota increased. As a result, this study was initiated to ascertain a current minimum count, calf recruitment and the distribution of *R. tarandus* on the Nuussuaq Peninsula in 2002.

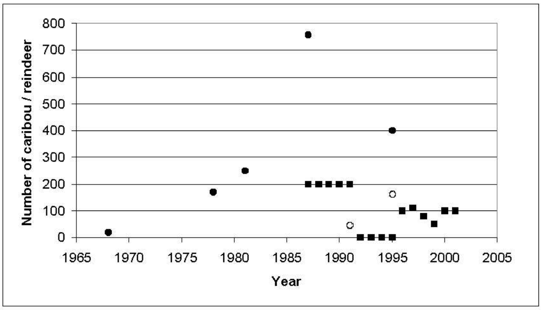

Fig. 2. Population estimates (●), numbers observed (○) and harvest quotas (■) for *Rangifer tarandus* on the Nuussuaq Peninsula, West Greenland, between 1968 and 2001. (Unpubl. data from the Greenland Institute of Natural Resources and Greenland Ministry of Fisheries, Hunting and Agriculture.)

Methods

Study area

The Nuussuaq Peninsula (70–71°N; 49–55°W) roughly follows an east–west orientation, with the Greenland Ice Cap forming its eastern border. It encompasses an area of about 7150 km^2. If the numerous alpine ice caps and glaciers are deleted, however, the remaining area is about 6000 km^2 and most is above 200 meters elevation.

Minimum count ground survey

This ground survey sought a minimum count of *R. tarandus* and the percentage of calves from the previous spring 2001. The minimum count is the number of animals observed and was not intended to be a population size estimate. This data did not allow a calculation of population size, because areas where maximum numbers were expected were preferentially sampled. Minimum counts, if repeated, could

Table 1. Late winter *R. tarandus* herd structure observations on the Nuussuaq Peninsula, West Greenland, April 2002.

Caribou/Reindeer	Observations	Percentage
Adult female	443	38.1%
Adult male	143	12.3%
Adult sex unknown	167	14.3%
Calves (both sexes)	324	27.8% (30.1%[a])
Unknown age	87	7.5%
Total	1164	100%

[a] True calf percentage, 30.1%, calculated using animals of known age; adult (753), calf (324).

be expected to provide indices of abundance and recruitment, and indicate population changes.

The Nuussuaq Peninsula was surveyed by snowmobile for minimum count and calf recruitment in late winter 2002 (21–29 Apr). Local knowledge on where animals were likely to be concentrated was obtained through several meetings with the Uummannaq community, which also chose survey routes and local participants. The survey included seven participants: four local commercial hunters and one hunting officer from the Uummannaq Municipality, and two staff from the Greenland Institute of Natural Resources. Six snowmobiles were used, and the total distance of survey routes was about 1000 kilometers.

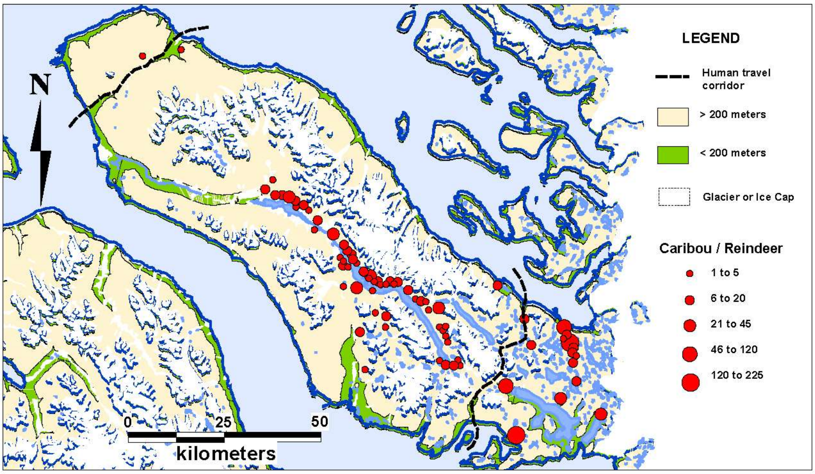

Fig. 3. Locations of *Rangifer tarandus* observations on the Nuussuaq Peninsula, West Greenland, April 2002.

The observers drove together as a group and counted all animals seen using 10×30 Leica binoculars or 60× Leica telescopes, which made it possible to observe animals even from several kilometers distance. Since caribou/reindeer can be expected to move in the terrain, to prevent the possibility of "double-counting" animals, routes taken were surveyed once only and as quickly as weather and snow conditions permitted. Animals were sexed and aged. Sex was determined by presence or absence of a vulva and/or urine patch on the rump. This reliably indicated a female on both adults and calves. No other method was 100% certain, e.g., antler size, shape, presence/absence were not used. There were two age categories, calf (<1 year) and adult (>1 year). Age was determined by body size. Calves of both sexes were smaller than all others.

Snow depth and type were noted. Area of survey coverage was calculated using MapInfo Professional Version 7.0 (Copyright©1985–2002 MapInfo Corporation) regions. Significance testing and predictability were tested using 2 tailed *t*-tests (2 sample assuming unequal variances).

Results

Variations in snow and ice cover

In the western third of the peninsula a ground ice layer occurred, and this was overlain by 70 cm of hard packed snow. The thick ground layer of ice was caused by an unusual and heavy December 2001 rainstorm, which was followed by below freezing temperatures for the rest of the winter. The ground ice ended abruptly at the western most edge of the middle third. Snow in the middle third was often a deep (60–90 cm) loose powder, with no ground layer of ice. The situation was similar in the eastern third, except snow conditions also included extremely windblown areas of either stone-hard snow or rocky expanses blown bare of snow. South facing aspects had a thinner snow layer and relatively large patches of bare ground.

Status and distribution

In late April 2002 animals were observed over the entire peninsula, however, the western third was scarcely used (Figs. 3 and 4). The greatest concentrations were in the middle third and specifically the eastern third of the peninsula. In both, valley bottoms were the primary habitat, followed by valley slopes or elevated plateaus. All animals in the middle third were observed at elevations above 200 meters and reaching to about 500–600 meters. Most in the eastern third occurred below 200 meters. Few animals were observed at elevations over 600 meters. Most of the animals and feeding craters were on south facing slopes and plains, where snow was thin and large patches of bare ground were available. Macro-lichens preferred by caribou/reindeer (*Cladina* spp., *Cetraria* spp.) were present on the south-facing slopes and being grazed.

The ground survey area coverage was ca. 25% of the 6000 km^2 of non-ice covered terrain and observed a minimum count of 1164 individuals, which included 324 calves (age <1 year; born in 2001), for an overall calf percentage of 27.8% (Table 1). However, 87

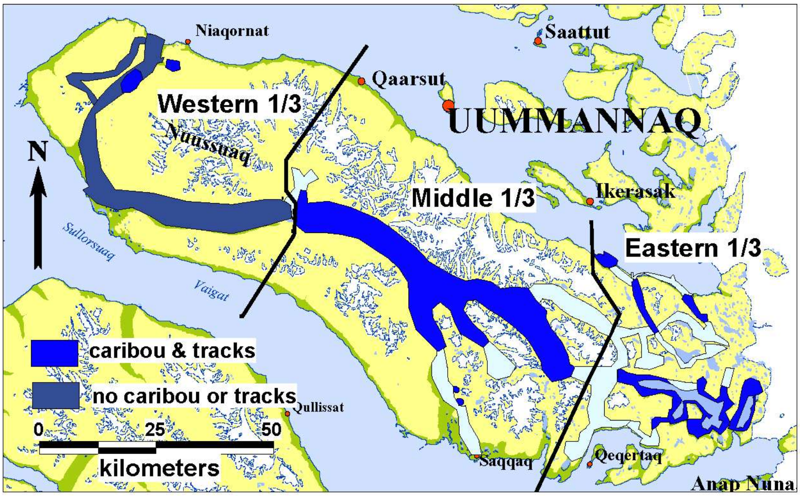

Fig. 4. Survey area coverage and the presence or absence of *Rangifer tarandus* in the areas surveyed on the Nuussuaq Peninsula in April 2002, West Greenland.

of the animals could not be aged due to within group animal movement, which confounded identification, combined with too great a distance between observer and animals. All 87 were in an area where observations included primarily females with calves. Given the known numbers of adults (753), the true late winter calf percentage was 30.1% and calf recruitment was 43 calves per 100 adults, or similarly, 73 calves per 100 cows (443). Given the known number of bulls (143) and cows (443), there were just over 3 females for every bull for a bull to cow ratio of 0.32. Average group size was small in the middle third of the peninsula (Table 2), but large in the eastern third, which included tightly cohesive groups of 63, 206 and 212 animals. Similarly, density was greatest in the eastern third. Body condition was subjectively ascertained as prime. All animals appeared well rounded and not a single animal showing ribs was observed.

Phenotypic variation

Average group size and density were not the only notable differences between the animals inhabiting the middle versus the eastern third of the peninsula. Adult females in the eastern third possessed antlers, and even many female calves were antlered (Table 3). Whether single or paired, antlers were well formed, with no raggedy remnants of velvet. Antlers among females in the middle third were not common. Further, the animals in the middle third were always a pale gray-white color. In contrast, the animals in the eastern third were typically dark, with some being a deep brown. Further, calves in the middle third were noticeably smaller than those observed in the eastern third. The latter were almost adult in size and often possessed paired antlers with several tines.

Discussion

Distribution

Caribou/reindeer were concentrated in the middle and eastern portions of the Nuussuaq Peninsula. This may be the typical late winter distribution, however, it is possible that 2002 was an exception. Given the ground ice layer and deep hard snow covering the western third of the peninsula in April 2002, it was not surprising to find so few animals present, since obtaining food would have required large energy expenditure.

Although most of the Nuussuaq Peninsula is above 200 meters elevations, most animals were observed in valley bottoms. South facing slopes and plateaus also received high utilization, likely due to the thinner snow layer and abundance of bare patches. Obtaining food from these locations would require a minimum of energy expenditure. Whether the vegetation at these locations differed from others, e.g., north-facing slopes, is currently unknown, but differences are suspected.

Status

Body condition was subjectively ascertained as prime. Although late winter, animals appeared round and fat, when some individuals in other Greenland populations of *Rangifer tarandus* may clearly show backbone and ribs (C. Cuyler, pers. obs.).

During the ground survey in late April 2002, observers counted a minimum of 1164 animals. A population estimate was not possible. The late winter calf percentage was high at ca. 30%, and the recruitment was 73 calves per 100 cows. Since these calves were almost 1-year of age, at which time their mortality rate becomes similar to mature animals, this was a high rate for an ungulate population. Studies from North America and Scandinavia report late winter recruitments of 20, 22 and 41 calves per 100 cows (Dzus, 1999; Parker, 1972; Fancy *et al.*, 1994, respectively), but these populations have predators. The Southhampton Island Herd, like Greenland, has no predators, and late winter recruitment varies between 22 and 77 calves per 100 cows and is likely dependent on climate (Heard & Ouellet, 1994).

The sex ratio of bulls to cows, 0.32, was low, and likely the result of selective hunting of bulls (estimated to be 90% of the harvest) (Loison *et* *al.*, 2000). Persistent male-skewed harvesting carries risks for the population dynamics and genetics of a population (Ryman *et al.*, 1981; Ginsberg & Milner-Gulland, 1994). On the Nuussuaq Peninsula, however, there is opportunity for crossbreeding between caribou and reindeer, which would likely tend to increase genetic variation in the population. Still, the Nuussuaq population would benefit if the preference for males were reduced and harvesting females encouraged. A female dominated population with good body condition and a high recruitment rate can rapidly become too large for the range to support, potentially resulting in long-term degradation of the range and ultimately a population crash.

Table 2. *Rangifer tarandus* group size and density on the Nuussuaq Peninsula, West Greenland, based on ground survey minimum counts of late April 2002.

Area	Survey area (km^2)	Numbers observed	Known adult (calf)[a]	Calf %	Average group size	Density/ km^2
Western third	≈ 390	4	4 (0)	--	1–3	≈ 0.01
Middle third	≈ 726	449	449 (137)	30.51	8 ± 8 SD	≈ 0.6
Eastern third	≈ 420	711	624 (187)	29.97	40 ± 64 SD	≈ 1.8
Total	≈ 1506	1164	1077	30.08	15 ± 34 SD	≈ 0.8

[a] Number of calves among the total number observed is given in parentheses.

Table 3. Phenotypic and behavioral differences in *Rangifer tarandus* observed between the animals inhabiting the middle and eastern third's of the Nuussuaq Peninsula, West Greenland, April 2002.

	Middle third	Eastern third
Group size	Small	Large
Pelt coloration	Pale gray-white	Dark to deep brown
Antlers on females	Uncommon on adults; never on calves	Common adults and calves
Antler size on females	Few tines	Many tines
Antlers on calves[a]	Seldom	Common
Antlers size on calves[a]	Few or just a single peg	Many tines
Calf size	Smaller than animals >1 year	Similar to animals >1 year
Occurrence	Elevations >200 meters	Elevations <200 meters

[a] Calves male or female.

Possible spatial segregation

Observations of the morphology and behavior of the animals surveyed in April 2002 suggests that the two subspecies have remained relatively segregated since the reindeer were introduced in 1968. This was unexpected. Animals in the middle third of the peninsula were similar in appearance and behavior to native wild caribou in West Greenland. In contrast, among animals in the eastern third of the Nuussuaq Peninsula semi-domestic reindeer characteristics were common, e.g., group cohesion and large aggregations were prevalent, dark brown coloration, females with well developed antlers, antlered female calves, and large calf size. The latter suggests calves are born in May, which is typical of semi-domestic reindeer, rather than June, typical for the native caribou. The extra weeks allow for greater growth in reindeer calves during their first summer, range conditions permitting. Group cohesion and large aggregations are not typical for native West Greenland caribou, where average group sizes are 3–6 animals, regardless of density or population size (Cuyler & Linnell, 2001; Cuyler *et al.*, 2002, 2003). Further, female caribou with antlers are unusual, while polled females are common, and almost all female caribou calves lack antlers and are noticeably smaller than adults. In addition, the late winter pelt of caribou is always pale gray-white (C. Cuyler, pers. obs.). Possible contributing factors to the suggested segregation would include, low initial animal numbers and the hunting pressure and/or disturbance associated with the human travel corridor, which separates the middle and eastern areas. There is also the possibility of voluntary segregation, if reindeer and caribou are behaviorally incompatible.

Caribou recovery and successful establishment feral reindeer

It appears that today both wild native caribou and feral reindeer inhabit the Nuussuaq Peninsula in West Greenland. If the behavioral and morphological differences truly reflect subspecies segregation, then in April 2002 a minimum of 449 native wild caribou *(R. t. groenlandicus)* inhabited the middle portion of the Nuussuaq Peninsula, while a minimum of 711 feral reindeer *(R. t. tarandus)* lived in the eastern portion in close proximity to the Ice Cap. In future, however, if both populations continue to increase in abundance, then genetic mixing may be expected.

Almost three times the number of animals was observed in 2002 than had been assumed present on the peninsula, and the late winter calf percentage was excellent. The few remaining native caribou from 1968 appear to have recovered. Also, the 1968 introduction of 10 semi-domestic reindeer has successfully established a feral population, which is currently providing a meat resource for locals. Greenland managers increased the harvest quota in 2002 to 350 animals and to 400 animals in 2003.

Future surveys

Random transects used elsewhere in Greenland are not recommended for the Nuussuaq Peninsula. The feral reindeer exhibit tight group cohesion. This results in an extremely clumped distribution of large numbers of animals. The native caribou, although more evenly spread throughout the terrain in small groups, were still more common in valley bottoms. Both distributions would likely make population estimates highly inaccurate if based on aerial surveys using random transects. An index of abundance is possible if the ground survey for minimum count is repeated, preferably annually, using the same routes and time period. Although vegetation maps, terrain models or NDVI maps are not yet available for this region, in future such maps could be used to stratify the census area. Then, an index of caribou density could be calculated for the various habitat types encountered on the survey route. Further, an objective documentation of snow and ice cover will better allow comparison of count data from different years.

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Movement pathways and habitat selection by woodland caribou during spring migration

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) are a threatened species throughout Canada. Special management is therefore required to ensure habitat needs are met, particularly because much of their current distribution is heavily influenced by resource extraction activities. Although winter habitat is thought to be limiting and is the primary focus of conservation efforts, maintaining connectivity between summer and winter ranges has received little attention. We used global positioning system data from an interprovincial, woodland caribou herd to define migratory movements on a relatively pristine range. Non-linear models indicated that caribou movement during migration was punctuated; caribou traveled for some distance (movement phase) followed by a pause (resting/foraging phase). We then developed resource selection functions (RSFs), using case-controlled logistic regression, to describe resting/foraging sites and movement sites, at the landscape scale. The RSFs indicated that caribou traveled through areas that were less rugged and closer to water than random and that resting/foraging sites were associated with older forests that have a greater component of pine, and are further from water than were random available locations. This approach to analyzing animal location data allowed us to identify two patterns of habitat selection (travel and foraging/resting) for caribou during the migratory period. Resultant models are important tools for land use planning to ensure that connectivity between caribou summer and winter ranges is maintained.

Key words: AIC, Alberta, British Columbia, GIS, habitat selection, mixed effects models, non-linear modeling, *Rangifer tarandus caribou*, resource selection functions, validation.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations are declining in west-central Alberta, and the species is classified as threatened in both Alberta and British Columbia, and is listed federally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Factors recognized as threats to population persistence are habitat alteration and loss, climate change, and predation, although predation is often considered to be a proximate contributor to caribou declines (Thomas & Gray, 2002). Caribou have evolved in dynamic landscapes, and shift their ranges in response to forest succession (Schaefer & Pruitt, 1991; Thomas & Gray, 2002). However, current rates of landscape change associated with industrial activities (primarily logging) are high and extensive (Schneider, 2002) and caribou ranges are being compressed (Smith *et al.*, 2000), such that range shifting may no longer be a viable option. In some areas, increased industrial activities have resulted in the direct loss of habitat and the displacement from calving and foraging areas (c.f. Nellemann & Cameron, 1998). In addition, indirect threats exist due to increased predation risk as a result of increased predator (wolf; *Canis lupus*) access to caribou habitat (James & Stuart-Smith, 2000) and the disruption of antipredator strategies (Bergerud & Elliot, 1986; Bergerud & Page, 1987; Seip, 1991; Edmonds & Smith, 1991; Rettie & Messier, 1998; James *et al.*, 2004).

As industrial pressures on the landscape escalate, concerns over the maintenance of functional habitat and impacts on habitat connectivity increase. High

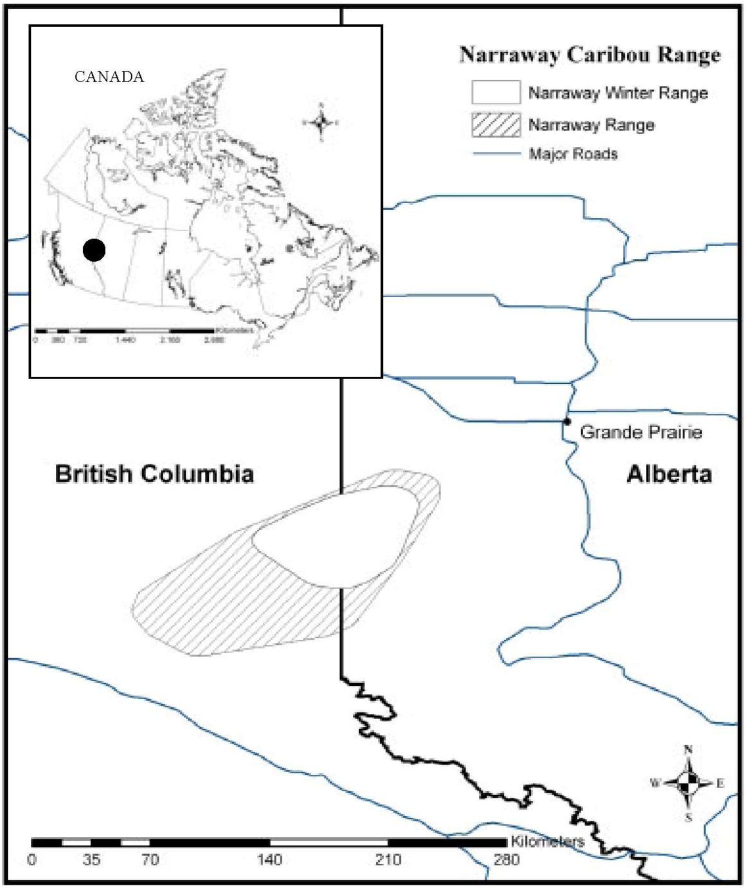

Fig. 1. The Narraway caribou range, located in west-central Alberta and east-central British Columbia, Canada.

habitat connectivity is necessary for caribou persistence on seasonal ranges (Seip, 1991; Rettie & Messier, 1998), and at a larger scale, for travel between summer and winter ranges. Migration can be defined in a number of ways; we adopted the operational definition of Berger (2004), which considers migration to be a "seasonal round-trip movement between discrete areas not used at other times of the year." Migration is typically associated with barren ground caribou (*Rangifer t. groenlandicus*), whose bi-annual migrations range between 800 and 5055 kilometers (Fancy *et al*., 1988; Ferguson & Messier, 2000). However, some woodland caribou herds also migrate, albeit over shorter distances (56–300 kilometers; Fuller & Keith, 1981; Cumming & Beange, 1987; Edmonds, 1988). For both subspecies, migration may serve as an effective predator avoidance strategy, with caribou (prey) distancing themselves from predators (primarily wolves) whose movements are restricted during the denning period (Bergerud 1988; Fryxell & Sinclair, 1988).

Current industrial activities are limited to low elevation areas, potentially effecting caribou only during migration and while on the winter range. Considerable attention has focused on aspects of habitat use during the winter months. While the maintenance of winter range is clearly important, we also recognize the need to maintain connectivity between seasonal ranges. This is central to conservation efforts as woodland caribou display high fidelity to both summer and winter ranges (Schaefer *et al*., 2000), and the availability of functional habitat outside current ranges is questionable, potentially limiting their ability to shift ranges.

Although the general characteristics of many migratory routes have been documented, little is known about caribou habitat use along these routes. We address this by assessing habitat use along migration routes for the Narraway caribou herd in west-central Alberta and east-central British Columbia. The Narraway is unique among caribou ranges in the region, as it has experienced only minor amounts of industrial development. This characteristic allowed us to model migration without the influence of anthropogenic disturbance. Through a combination of non-linear modeling and remote data collection, we developed habitat-based models identifying important coarse-scale attributes of the spring migration routes for the Narraway caribou herd. We validated these models using independent data from additional Narraway caribou. The specific objectives of this project were to 1) quantify the movement patterns of caribou in the Narraway range during the spring migratory period and 2) determine whether these patterns were associated with selection of particular habitat attributes.

Study area

Our efforts focused on woodland caribou using the Narraway range (*ca* 5000 km^2; Fig. 1), which is located approximately 130 kilometers southwest of Grande Prairie, Alberta, Canada, and extends across the Alberta–British Columbia provincial boundary. In British Columbia, this range is referred to as the Belcourt range. From a regional perspective, this range is unique in that it exists in a relatively pristine state. Most animals winter on a large plateau that spans the Alberta–British Columbia border, west of the Narraway River. Much of this area is poorly drained and dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Within this central muskeg area are small patches of upland forest dominated by lodgepole pine (*Pinus contorta*) and black spruce. The winter range is under increasing development pressure from forestry and energy sectors. In the summer, the caribou move southwest into the mountains of British Columbia, near the headwaters of the Narraway and Fraser Rivers. While the summer range is not contained within a protected area, its alpine location currently discourages industrial development.

Methods and materials

Caribou location data

Adult female caribou using the Narraway range were captured using helicopter-based net gunning techniques. All capture and handling methods were approved by the University of Alberta, Faculty of Agriculture, Forestry and Home Economics Animal Care Committee (Protocol 2003-29D) and adhere to guidelines outlined by the Canadian Council on Animal Care. Caribou were outfitted with global positioning system (GPS) collars (Lotek GPS 1000 or Lotek GPS 2200, Lotek Engineering, Inc., Newmarket, Ontario, Canada.). Collars were programmed to acquire a fix on one of two schedules: a standard 2-hour schedule or a variable schedule in which locations were acquired every 30 minutes, two hours, or six hours, depending on the day of the week. While we acknowledge the existence of autocorrelation within the data set, we were interested in selection occurring throughout the entire process of migration and therefore chose not to rarify the data. Use of case-controlled logistic regression (see Selection Analysis) reduced the effect of autocorrelation on resultant relationships. All locations with horizontal dilution of precision (HDOP) values greater than 12, indicating poor location accuracy, were removed prior to analysis. Models were developed using the migration patterns of eight caribou across two years (2002–2003; four different caribou each year). Data were pooled across years and individuals. For two caribou, we had data for multiple spring migration events. Because caribou tended to use the same route in all years, only the first event for which we had data was used in the analysis. All caribou moved independently of one another in time. Data from an additional six caribou were used for model validation.

We defined the start of migration on an individual basis, as three consecutive movements in a southwest direction outside the winter range (100% Minimum Convex Polygon for 1 Dec–30 Apr locations) of an animal. The last cluster of locations acquired prior to 15 June in any migration event was assumed to represent calving and was removed from the analysis.

Identification of scales of movement

Visual inspection of migration pathways indicated that caribou display punctuated movement during migration, whereby a pattern of traveling followed by a period of limited movement was repeated. In order to model what was visually apparent in the data, we used a nonlinear curve fitting procedure to identify scales of movement by individual caribou (Sibly *et al.*, 1990; Johnson *et al.*, 2002). Nonlinear modeling was carried out in SPSS 11.5 (SPSS, Inc.). This method approximates a traditional broken-stick model, allowing behaviors to be objectively split into bouts (Sibly *et al.*, 1990). Resting/foraging movements were assumed to be associated with lower movement rates relative to traveling movements. The nonlinear model takes the form:

$$y = \log_e\left(N_s \lambda_s e^{-\lambda_s r} + N_l \lambda_l e^{-\lambda_l r}\right) \quad [1]$$

where s and l refer to processes that are assumed to generate small (resting/foraging) and large scale (traveling) movements; y is the predicted number of movements that occur during each discrete interval of movement rates. N is the number of small and large scale movements that occur at each rate interval, r is the movement rate and λ represents the probability that an event, either resting/foraging or traveling, occurs in the next movement rate interval.

Following model fit, we used the estimated parameters (N, λ) to identify a scale criterion interval (r_C) that defines the break point between large and small-scale movements (Johnson *et al.*, 2002) and is calculated as follows:

$$r_c = \left(1/\lambda_s - \lambda_l\right)^* \log_e\left(N_s \lambda_s / N_l \lambda_l\right) \quad [2]$$

Movement rates of caribou less than r_C were considered to be associated with resting/foraging and those greater than r_C were assumed to be associated with traveling.

We defined a patch by consecutive locations identified by the nonlinear modeling procedure to be small-scale movements (i.e., clusters of locations classified as resting/foraging). In order to capture the variation within a patch, we randomly selected three locations, separated by a minimum distance of 100 meters, within the patch for analysis. All patches and traveling locations were used in the analysis. If the last large-scale movement prior to the caribou entering a defined patch was a distance of less than the location interval multiplied by the scale criterion interval for that caribou, it was reclassified to a resting/foraging location.

Table 1. GIS predictor variables used to model habitat selection along the spring migratory pathways of woodland caribou using the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002–2003). All response variables were continuous.

Variable code	Name	GIS Data source
elev	Elevation (m)	Digital Elevation Model (DEM)[a]
TRI	Terrain Ruggedness Index	DEM spatial analyst calculation
Distwater[b]	Distance to Water (km)	Spatial Analyst calculation
Distedge[c]	Distance to Edge (km)	Spatial Analyst calculation
age	Stand Age (yr)	Forest cover layer[d]
age^2	Stand Age Quadratic (yr^2)	Calculated from forest cover layer
density	Canopy Cover (%)	Forest cover layer
spruce	% Spruce	Forest cover layer
pine	% Pine	Forest cover layer

[a] The DEM was obtained from the National Topographic Data Base.

[b] Distance to closest permanent water source.

[c] Distance to closest natural or anthropogenic edge. Natural edges included any non-forest classed polygon and forest polygons whose density was <10%, or whose age <30 years, or that had a deciduous component of >70%.

[d] Forest cover layers were provided by Weyerhaeuser Company (Alberta) and the British Columbia Ministry of Forests.

This reduced the risk of misclassification, as locations are classified as either small or large-scale movements based on the previous location.

Habitat attributes

Habitat attributes used in the modeling procedure were obtained from available forest cover and other spatial data (Table 1), within a Geographic Information System (GIS). A grid size of 30 meters was used for all environmental and forest cover data, accounting for the error associated with GPS collar locations (D'eon *et al.*, 2002). These data included distance, terrain, and habitat information. Slope, aspect and distances were calculated in the Spatial Analyst extension in ArcMap 8.3. We used a terrain ruggedness index (TRI) modified from Nellemann & Fry (1995) to account for local topographic variation. This was calculated using a 300-meter circular moving window and the formula: [3]

$$\text{TRI} = \frac{(\text{Aspect Variation} * \text{Mean Slope}) / (\text{Aspect Variation} + \text{Mean Slope})}{100}$$

When calculating distance to edge, we defined an edge as any polygon classified as non-forest (e.g., anthropogenic features, lakes, alpine habitat). If a polygon was classified as forest but had a stand density less than 10%; a stand age of less than 30 years, or had a deciduous component of greater than 70% it was also classed as an edge. We assumed that these forest classes would be recognized as different from the surrounding matrix by caribou.

We tested independent variables for collinearity using Pearson's correlation coefficient. When pairs of variables exhibited correlation values greater than |0.7|, we retained the variable that explained the most variation in the data, determined with a univariate logistic model. We tested all models for multicollinearity (Menard, 1995) using variance inflation factors (VIF). Multicollinearity was a concern if individual parameter VIF values were > 10 or if the mean VIF score for a given model was considerably larger than 1 (Chatterjee *et al.*, 2000). If models exhibited multicollinearity they were removed from the candidate set.

Modeling caribou migration

We conducted a preliminary logistic regression analysis to determine if habitat characteristics differed between resting/foraging sites and traveling sites, and to indicate whether modeling the behaviors independently was warranted.

Resource selection

To adequately describe the detected differences between resting/foraging and traveling sites, we chose to model each behavior separately. We used case-control logistic regression (Compton *et al.*, 2002) to estimate a discriminant function differentiating caribou use sites (either traveling or resting/foraging) from associated random locations. This discriminant function has been shown to be accurate in differentiating use from available locations (Manly *et al.*, 2002) and is equivalent to an RSF of the form exp $(\beta_1 x_1 + \ldots + \beta_p x_p)$ (Manly *et al.*, 2002; Keating & Cherry, 2004). Used locations were compared against randomly generated available locations. Model structure followed the form:

$$w(\boldsymbol{x}) = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \cdots \beta_K x_{ijK}) \qquad [4]$$

where w(x) is the relative probability of use for the *j*th resource unit being selected at the *i*th choice for

Table 2. A priori candidate models used in assessing habitat selection during the migratory period on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada. Models were parameterized using caribou location data from the 2002 and 2003 spring migratory periods.

Model #	Model
1	Age + age^2 + distwater + distedge + pine + TRI
2	Distwater + age + age^2
3	Distwater
4	Pine + age + age^2
5	Spruce + age + age^2
6	TRI + age + age^2
7	Age + age^2
8	Pine + density
9	Spruce + density
10	Pine + distwater + density
11	TRI + density
12	TRI + distedge
13	TRI + distwater
14	TRI + Pine + Age +Age^2

the predictor variables, x_i, and the β_i's are the coefficient estimates for each predictor variable. Models were evaluated in the statistical package STATA 8.2 (Stata Corporation).

Fourteen candidate models were developed a priori, based on biologically relevant habitat attributes (Table 2). Model selection was based on AIC$_c$ (Akaike's Information Criteria, corrected for small sample size bias; Anderson & Burnham, 2002), which balances model fit with model parsimony. Models were ranked based on the difference in the AIC$_c$ values (ΔAIC$_c$), and Akaike weights (w_i) were used to assess the strength of evidence that any particular model was the best model in our set of candidate models (Anderson *et al.*, 2000). The ability of the models to accurately predict resting/foraging or traveling was determined through the validation process.

Selection analysis

We used case-controlled logistic regression to account for the spatial and temporal variation in habitats (Pendergast *et al.*, 1996), by defining availability based on each travel location or resting/foraging patch. Following Arthur *et al.* (1996), random locations were generated within a circle centered on the preceding use location with a radius either equal to the 95th percentile of the distance traveled for that location interval (30 min, 1 hr, 2 hr, 4 hr, 6 hr, 10 hr, 12 hr, and 18 hr) averaged across all animals or the distance between the two locations, whichever was larger. For locations identified as traveling by the non-linear modeling procedure, 20 random points were generated to represent available locations. Locations identified as resting/foraging required additional steps to replicate the clustered nature of the use locations. Twenty random points were generated as per traveling locations. We then buffered these points by the average area of all resting/foraging use areas (276 meter radius). Within this smaller buffer three random points were generated to compare against the three known use locations.

The locations of all random points, and hence available habitat, was limited to elevations less than 2000 meters and habitat classed as either a lake or river was excluded. Consistent with selection of use points within resting/foraging areas, random points were a minimum of 100 meters apart. Random point generation was carried out using Hawth's Analysis Tools extension (Version 2.0) in ArcGIS 8.3.

Spatial interpolation

The best model for each behavior was incorporated into a GIS framework (ArcGIS 8.3), and used to produce maps depicting a relative index of use for traveling and resting/foraging. Maps were area-adjusted, and relative index of use was assigned to 10 quantile bins, containing equal proportions.

Model validation

As our study design was based on used and available locations, model validation through Receiver Operating Characteristic (ROC) curves was inappropriate (Boyce *et al.*, 2002). However, we were able to use independent location data from an additional six caribou for model validation. We classified locations from each of these animals as either traveling or resting/foraging using the same non-linear modeling procedures used for classification of the locations used in model building (Table 5). The behavior-specific relative index maps, derived from the AIC-selected models, were then evaluated for their ability to predict use through a Spearman Rank Correlation, $\alpha = 0.05$. Independent data points classified as traveling were used to assess the relative travel index surface, while those classified as resting/foraging were used to assess the relative index surface for resting/foraging. Strong correlations of the predicted map bins with independent validation data were taken to indicate good model fit and prediction. We use the term "index," rather than "probability" when referring to relative use, in response to recent criticisms from Keating & Cherry (2004) regarding estimation of probability surfaces from use-availability

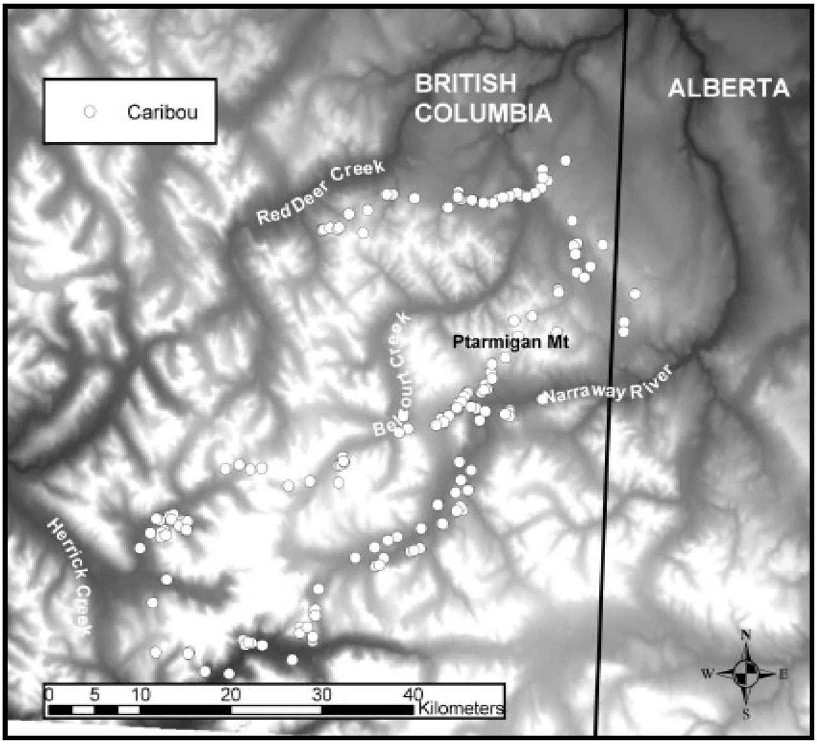

Fig. 2. General pathways taken during the spring migration (2002 & 2003) of collared Narraway caribou in west-central Alberta and east-central British Columbia, Canada.

designs. However, we note that their concerns were particularly acute in situations where higher order polynomials were being modeled, and our most complex models include only a quadratic term.

Results

Caribou relocations

The eight caribou used for model building followed one of two main routes (Fig. 2). While the general route traveled may be the same for multiple caribou included in the analysis, none were traveling together during the migratory period. Therefore, we assumed the decision to rest/forage or continue traveling was independent of the presence of other radiocollared caribou. Two caribou migrated through the northern part of the range using the Red Deer Creek area. A third animal used this area in 2003 but died early in migration and was excluded from the analysis. The remaining six caribou used the Narraway River region (Fig. 2; Table 3). Route selection varied more in this area than in the northern region, with some caribou traversing Ptarmigan Mountain before entering the Narraway Valley, while others went around. Variation was also apparent in the extent of travel in the Narraway River valley. Some caribou remained in this valley until they reached their calving grounds, while others branched off, using the Belcourt Creek drainage (Fig. 2; Table 3). The departure date from the winter range, overall distance traveled, and duration of migration also varied among caribou and year (Table 3).

Identification of scales of movement

Non-linear modeling identified the movement rate above which locations were classified as traveling and below which they were classified as resting/foraging (Table 4). The rate at which behaviors are differentiated is variable among individuals and migration strategies also appeared to vary among caribou with some traveling quickly and spending longer amounts of time at resting/foraging areas and while others traveled at a slower rate and spent less time in resting foraging areas. The migration strategy used and the collar schedule influenced the number of locations each animal contributed to the data set, such that the locations were not balanced across animals. Regardless of the strategy used, we assumed that caribou used similar habitats for each behavior.

Of the 176 caribou locations available for model building, 78 were identified as resting/foraging and 98 as traveling locations. The 78 resting/foraging locations represented 28 patches, thus the sample size for statistical analysis was 28 for resting/foraging models and 98 for traveling models (Table 5).

Modeling caribou migration

Discrimination was possible between habitat associated with resting/foraging and traveling sites, providing justification for modeling the behaviors separately. Resting/foraging locations were further from water and in less dense, older forests than were traveling locations.

Traveling

Of 14 candidate RSF models (Table 2), Model 13 was identified as the best model, indicating that travel loca-

Table 3. General characteristics of the spring migration (2001–2002) for collared woodland caribou using the Narraway range in west central Alberta and east-central British Columbia, Canada. The reported migration distance is the cumulative distance between the first identified migration location and the estimated calving location

Year	Caribou ID	Path	Migration distance (km)	Duration of migration (hr)	Departure date
Model building:					
2002	F709	Narraway	25.3	24	05/25/02
2002	F710	Red Deer Creek	27.5	40	05/27/02
2002	F711	Red Deer Creek	32.5	55	05/28/02
2002	F712	Narraway	73.1	300	06/03/02
2003	F715	Narraway via Ptarmigan	29.4	142	05/29/03
2003	F717	Narraway/Belcourt via Ptarmigan	70.1	116	05/22/03
2003	F722	Narraway/Belcourt via Ptarmigan	73.9	238	05/23/03
2003	F723	Narraway via Ptarmigan	119.1	206	05/16/03
		Mean ± SE	56.4 ± 11.8	140 ± 36	
Model validation:					
2001	F702	Narraway	145.2	360	05/11/01
2001	F704	Belcourt	33.2	75	05/06/01
2001	F705	Narraway/Belcourt	102.8	249	05/15/01
2002	F700	Narraway/Belcourt	76.8	246	05/29/02
2002	F708	Narraway via Ptarmigan	141.5	588	05/11/02
2003	F713	Red Deer Creek	64.9	308	05/11/03
		Mean ± SE	94.1 ± 18.1	304 ± 69	

Table 4. The rates (r_C) identified by non-linear modeling below which caribou locations from the Narraway Range in west-central Alberta and east-central British Columbia, Canada during the spring migratory period (2001 and 2003), were classified as resting/foraging and above which they were classed as traveling.

Model building			Model validation		
Year	Caribou ID	r_C (m/min)	Year	Caribou ID	r_C (m/min)
2002	F709	2.64	2001	F702	6.02
2002	F710	2.99	2001	F704	3.12
2002	F711	3.69	2001	F705	3.71
2002	F712	2.62	2002	F700	4.28
2003	F715	2.61	2002	F708	4.52
2003	F717	5.35	2003	F713	8.94
2003	F722	3.10			
2003	F723	9.81			
	Mean ± SE	4.10 ± 0.88		Mean ± SE	5.10 ± 0.87

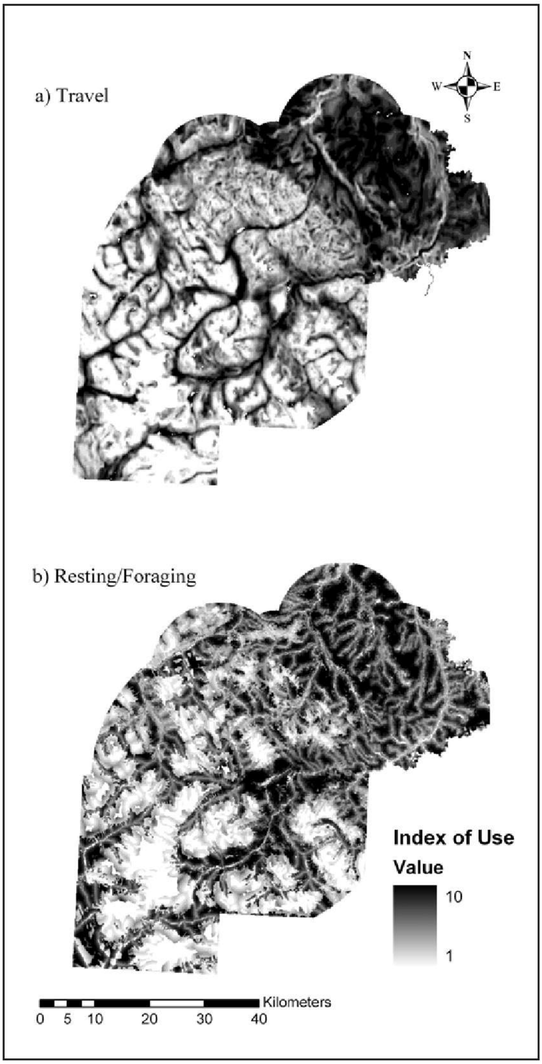

Fig. 3. Interpolated map surface showing the relative index of use during the spring migration on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002 and 2003). The relative index of use for traveling is shown in (a) and that for resting/foraging in (b). Dark colors indicate a relatively high index value and light colors indicate a relatively low index value.

tions were more likely to be associated with less rugged terrain and were closer to water than were random available locations. The model takes the form:

$$\hat{w} = -8.921(TRI) - 0.375(distwater) \qquad [5]$$

The confidence intervals for TRI did not overlap zero, indicating that this variable had a stong influence on selection. The low Akiake weight associated with this model (0.423; Table 6), suggests only weak support that this model is the best predictive model, the second ranked model (Model 12) was also a 2-term model, and contained the TRI covariate, whose coefficient is consistent over both models. In addition, the second variable in Model 12, distedge, is a composite variable containing distwater, although it is not correlated with it. We were thus confident in selecting Model 13 as the top AIC model and incorporated it into a GIS framework identifying suitable traveling habitat for caribou (Fig. 3a).

Resting/foraging

Similarly, of the 14 candidate models evaluated for resting/foraging locations (Table 2), Model 14 was identified as the best model, indicating that resting/foraging locations were more likely to be associated with older, forests that have a greater component of pine, and were further from water than were random available locations. The model takes the form:

$$\hat{w} = 0.015(\boldsymbol{age}) - 0.00003(age^2) + 0.008(\boldsymbol{pine}) + 1.181(\boldsymbol{distwater}) \qquad [6]$$

The confidence intervals for the bolded covariates did not overlap zero, suggesting they had a strong influence on habitat selection. The Akiake weight associated with the global models was 0.633, indicating a moderate level of confidence that this model was the best of those considered, given the data (Table 7). We used this model to generate a GIS map indicating the occurrence of potential resting/foraging habitat for caribou during the spring migration (Fig. 3b).

Model validation

There was a significant positive correlation between the index surfaces and the occurrence of use locations from the independent data set (resting/foraging: $r_{(s)} = 0.697$, $P = 0.025$; traveling $r_{(s)} = 0.636$, $P = 0.048$). We interpreted this as evidence that the models were reasonably robust.

Discussion

In west-central Alberta, all caribou winter ranges fall under Forest Management Agreements, and are subject to timber harvest as well as increasing pressures from the oil and gas sectors. The identification of specific habitat attributes associated with caribou use is critical to the successful integration of caribou conservation strategies and sustainable land use management practices. Most attention has focused on the reduction of industrial effects on caribou winter ranges because these are

Table 5. Caribou locations used in the analysis of habitat selection along the spring migratory path of the Narraway Caribou Herd, west central Alberta and east-central British Columbia, Canada, 2001–2003. Resting/foraging and traveling movements were defined by non-linear modeling procedures.

Year	Caribou ID	# Patches	# Resting/Foraging locations	# Traveling locations	# Areas
Model building:					
2002	709	1	1	3	4
	710	2	6	17	19
	711	1	3	9	10
	712	4	11	7	11
Subtotal	**4**	**8**	**21**	**36**	**44**
2003	715	2	6	2	4
	717	4	10	10	14
	722	7	15	21	28
	723	7	21	29	36
Subtotal	**4**	**20**	**52**	**62**	**82**
Total	**8**	**28**	**73**	**98**	**126**
Model validation:					
2001	702	14	30	18	32
	704	4	10	4	8
	705	7	15	19	26
Subtotal	**3**	**25**	**55**	**41**	**66**
2002	700	8	22	6	14
	708	12	31	15	27
Subtotal	**2**	**20**	**53**	**21**	**41**
2003	713	3	9	3	6
Subtotal	**1**	**3**	**9**	**3**	**6**
Total	**6**	**48**	**117**	**65**	**113**

thought to be most limiting (Bjorge, 1984; Thomas *et al.*, 1996) and subject to the greatest development pressure (Hervieux *et al.*, 1996). However, as industrial activity expands, effects are reaching beyond the winter ranges and potentially influencing the use of traditional migration routes, and therefore affecting connectivity between summer and winter ranges.

Our study is the first attempt we are aware of to link observed movement patterns to habitat selection by woodland caribou during migratory events. We demonstrated that mountain caribou select certain habitat characteristics during migration and that this selection is dependent upon movement behavior, as inferred by the rate at which they are moving. When traveling, caribou select habitat that is closer to water and in less rugged terrain than random locations. This is consistent with least resistance theory (Hedenström, 2003), which hypothesizes animals will choose to travel in areas where they are able to move more quickly and expend less energy, typical of animals traveling between stopover sites. In a mountainous environment, these conditions are met along major drainages. When resting or foraging, caribou moved away from water bodies and into 'old' pine stands. These habitats are also consistent with migration theory, which suggests that stopover areas are used for refueling, resting and shelter (Hedenström, 2003) and occur in areas with relatively less predation risk (Berthold & Terrill, 1991). Although the analyses presented here do not address mechanisms, the general habitat attributes associated with these rates are consistent with those of higher forage (terrestrial lichen and forb) abundance (Pharo & Vitt, 2000). We associate risk of predation with distance to water, as wolves are known to travel along natural (Huggard, 1993) and anthropogenic (James, 1999) features at increased rates, thus increasing the likelihood of a predator–prey encounter (James, 1999; Dzus, 2001).

One of the primary hypotheses for migration by mountain caribou is separation from predators during the vulnerable calving period (Edmonds, 1988; Edmonds & Smith, 1991; Seip, 1991). Increased development on migratory routes connecting caribou summer and winter ranges could have two main effects. First, changes in predator abundance and distribution are likely (Dzus, 2001). As mature forests are replaced with younger forests post harvest, an increase in the abundance of other ungulate species is expected, which in turn will support larger populations of predator species (Seip & Cichowski, 1996;

Table 6. A comparison of habitat use models characterizing traveling locations of Narraway caribou during the spring migration (2002 & 2003). Models are ranked by ΔAIC_c values. Akaike weights (w_i) indicate the likelihood of the model. K indicates the number of parameters in the model.

Model #	K	AIC_c	ΔAIC_c	w_i	Rank
13	2	582.5943	0.000	0.423	1
12	2	583.0963	0.502	0.329	2
11	2	583.8423	1.248	0.227	3
1	6	589.0851	6.491	0.0164	4
3	1	593.1357	10.541	0.002	5
2	3	595.3133	12.719	<0.001	6
14	4	596.6661	14.072	<0.001	7
10	3	596.8473	14.253	<0.001	8
7	2	598.3683	15.774	<0.001	9
4	3	599.5813	16.987	<0.001	10
8	2	600.2523	17.658	<0.001	11
9	2	600.3663	17.772	<0.001	12
5	3	600.4973	17.903	<0.001	13
6	3	602.7233	20.129	<0.001	14

Table 7. A comparison of habitat use models characterizing resting/foraging locations of Narraway caribou during the spring migration (2002 & 2003). Models are ranked by ΔAIC_c values. Akaike weights (w_i) indicate the likelihood of the model. K indicates the number of parameters in the model.

Model #	K	AIC_c	ΔAIC_c	w_i	Rank
14	4	486.673	0.000	0.632989	1
2	3	488.000	1.327	0.326039	2
1	6	492.194	5.521	0.040046	3
4	3	501.284	14.611	0.000425	4
7	2	502.436	15.763	0.000239	5
5	3	503.038	16.365	0.000177	6
6	3	504.974	18.301	6.72E-05	7
13	2	508.356	21.683	1.24E-05	8
10	3	510.088	23.415	5.21E-06	9
3	1	516.158	29.485	2.51E-07	10
12	2	516.766	30.093	1.85E-07	11
9	2	519.402	32.729	4.95E-08	12
11	2	519.814	33.141	4.03E-08	13
8	2	519.954	33.281	3.75E-08	14

Rettie & Messier 1998; James & Stuart-Smith, 2000; Kunkel & Pletscher, 2000). Predator distribution may also be enhanced as they will gain access to previously remote areas through travel on anthropogenic linear features (Dzus, 2001), leading to increased encounter rates with and mortality rates for caribou (Seip, 1992; James, 1999; James & Stuart-Smith, 2000). Secondly, increased habitat alteration and fragmentation associated with industrial activity may lead to increased energetic costs, if caribou attempt to avoid these developments (Nellemann & Cameron, 1998; Dyer *et al.*, 2001; Vistnes & Nellemann, 2001). Migration is characteristically a balance between energetic outputs for locomotion and energetic inputs in the form of fuel intake (Hedenström, 2003). Detours are only possible when alternate areas for foraging exist and can be located without upsetting this balance (Alerstam, 2001; Hedenström, 2003). This has negative implications for long-term caribou persistence, as cows may arrive in the alpine in poor condition, effecting both the survival of the cow and her offspring. Ultimately, the cumulative effect of incremental development may result in the abandonment of migration routes all together (Alerstam *et al.*, 2003). If caribou stop migrating altogether, they may be exposed to higher predation risk year around if they stay on winter ranges, or they may stay in less productive alpine summer ranges.

The limited sample size available necessitated pooling data across years and individuals. We acknowledge that by pooling we may have masked individual variation in selection of habitats by caribou or variation due to changing environmental conditions across years. However, management cannot take place at the level of the individual or even on a yearly basis, in most cases. Global models may thus be most appropriate for management purposes, if they have been validated and shown to predict occurrence. Validation of the models is particularly important when, as in this case, the sampling design is unbalanced. Animals that are more prevalent in the data set, will contribute more information to the models, having a greater influence on the resulting selection coefficients. As our models adequately predicted the occurrence of independent caribou locations on the landscape we do not believe that any one animal from the model building set had undo influence on our models, and that our assumption that habitat selection is consistent across years and individuals was appropriate, at least within the confines of this study. Where sample sizes permit, individual models should be built to substantiate this assumption prior to pooling of data. Data collection over a greater number of years would better represent longer-term environmental variation, and resultant implications for habitat selection.

Migration is an important, and often neglected, component of the life history strategies of mountain caribou, and should be accounted for in conservation planning. The models produced here, while specific to the Narraway range in west-central Alberta, represent an important link between migratory behavior and habitat use. As a visual representation of these models, the maps allow for the identification of habitats selected during migration. These maps provide guidance for land use planners when evaluating management options.

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8000 years of caribou and human seasonal migration in the Canadian Barrenlands

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Abstract: Caribou (*Rangifer tarandus*) are the common thread running through thousands of years of cultural evolution in northern mainland Canada. From the earliest Indian traditions, through the Pre-Dorset and Dene cultural evolution, up to historic times, the vast herds of migratory Barrenland caribou provided food, clothing and shelter. They determined the human cycle -- seasonal migrations, seasonal levels of fitness, and season of procreation. Caribou even permeated Dene mythology and supernatural beliefs. Within the Beverly caribou (*R. t. groenlandicus*) range in the Canadian Barrenlands, investigation of 1002 archaeological sites points to long-term stability of human band and caribou herd interaction. Caribou bone and hunting tools occur in multiple levels, the earliest to 8000 years, based on 131 radiocarbon dates. Through time, specific hunting bands aligned with specific migratory barren-ground caribou herds. This relationship helps to explain observed archaeological and ethnological differences within different caribou ranges for these hunting bands. In general, biological evidence concurs with ethnographic and archaeological evidence. But short-term variations in migration routes between northern boreal forest, taiga and tundra may have followed changes in herd size and environment, e.g., unfavorable snow and ice conditions or forest fires. However, such influences were not discernible archaeologically.

Key words: Barrenlands, Beverly range, Canada, Dene, herd-following, hunters, migratory barren-ground caribou, Pre-Dorset, *Rangifer,* seasonality.

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Introduction and background

As a graduate student in archaeology in the late 1960s, I was asked to investigate stone tools collected by a team from the Calgary Zoo (Calgary, Alberta, Canada) capturing muskox (*Ovibos moschatus*) calves in the Thelon Game Sanctuary, Northwest Territories (Nunavut, as of 1999), Canada. The sanctuary is in the central Barrenlands between Great Slave Lake to the west, Hudson Bay to the east, the two Prairie Provinces (Saskatchewan & Manitoba) to the south, and the Arctic Ocean to the north (Fig. 1). The sanctuary is located roughly in the north-central tundra part of the Beverly caribou (*Rangifer tarandus groenlandicus*) range (e.g., Miller *et al.*, 1988; Hall, 1989).

The stone tools came from sand blowouts beside the Thelon River near its junction with the Hanbury and Clarke Rivers (Gordon, 1996: Fig. 1.6). I examined 68 camps, including two large deeply stratified (300 m^2 × 2 m deep) water crossing camps with almost 5000 artifacts, three smaller shallow downriver sites with several hundred artifacts, and the rest, surface sites (Gordon, 1975: 4). One of the two 2-m deep sites, KjNb-6, had six major levels (*op. cit.*: xvi). One of its lowest levels, Pre-Dorset or ASTt (Arctic Small Tool tradition; *op.cit.*: 125–133), had easily recognizable tools because they had been identified elsewhere. The distinctive, familiar tiny chert ASTt tools, dating from 3450 to 2650 years ago, were compared with similar ones from sites in the Kaminuriak, Bathurst, and Bluenose caribou herd ranges, as defined by the Canadian Wildlife Service (Fig. 2: Kelsall, 1968; Thomas, 1969; Parker, 1972).

Pre-Dorset site locations, like the herd ranges themselves, overlap, mainly from the northern boreal forest along the migration routes through the taiga onto the tundra. The overlap was most prominent where the Beverly and Kaminuriak winter ranges coalesce.

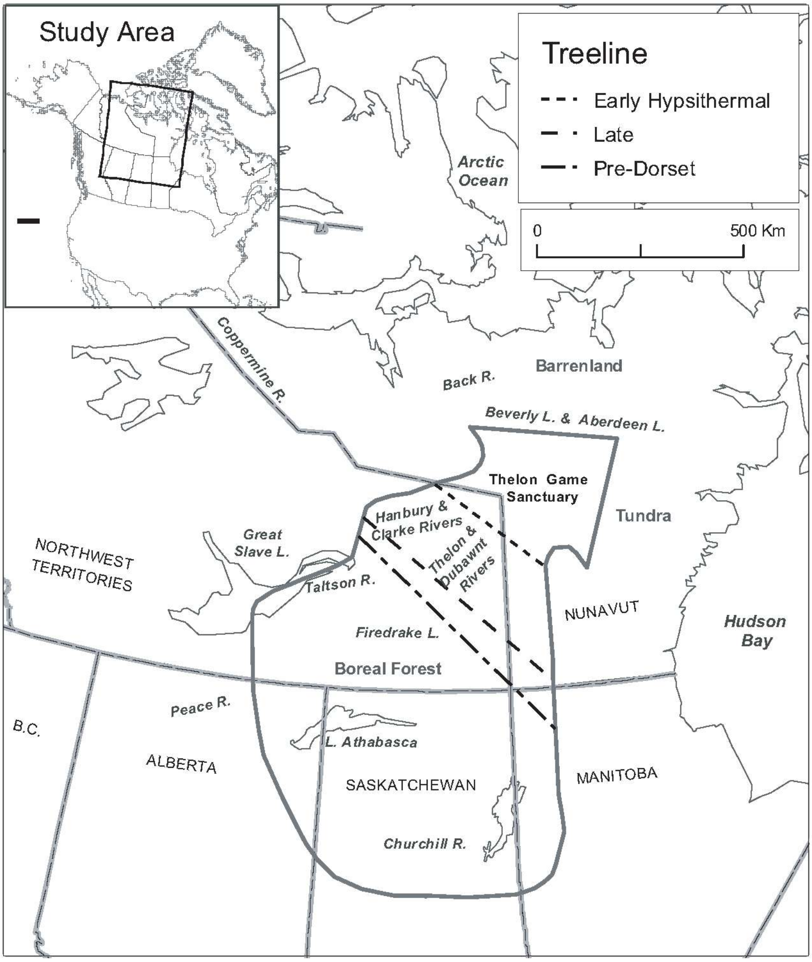

Fig. 1. Study area in northcentral mainland Canada.

And yet the distinctness of artifact traits between ranges could be differentiated. This was consistent with caribou herd data recalculated by Parker (1972) from Miller & Robertson (1967). Six percent of ear-tag returns for Kaminuriak caribou came from range normally occupied by Beverly caribou. Then, using ear-tag returns during the same time period from his study, Parker found that about 5% of Beverly tagged caribou came from range normally used by Kaminuriak caribou. This suggests about 94% herd discreteness between the Beverly and Kaminuriak herds, adding additional support to the belief that the caribou in each population are normally faithful to their respective traditional annual range and offers support for an explanation of why, despite overall similarity, I could separate Beverly and Kaminuriak traits for Pre-Dorset tools. Slight differences between each range probably resulted from limited human contact because hunters focused on the center of the ranges where migrating herds were most predictable. Due to widely separate migration routes and simultaneous migrations, it would have been rare for any migratory Barrenland hunting bands to harvest from several herds. In this paper, band refers to hunters.

Artifact distribution and trait similarities supported my thesis of a band–herd association for the remaining Barrenland cultures. As Pre-Dorset site distribution also coincided with the four historic Dene hunting ranges outlined in 1972 by Smith (1978: Fig. 5), I suggested site distribution of all Barrenland cultures fell within the overlapping Pre-Dorset and Dene hunting ranges and the herd ranges (Fig. 2). Thus, the three disciplines of wildlife studies, ethnology and archaeology meshed, and I postulated a discrete Pre-Dorset band–discrete caribou herd association.

Human occupancy of the Dene or East and West Chipewyan, Yellowknife, and Dogrib hunting ranges coincided with the Kaminuriak, Beverly, Bathurst and Bluenose caribou herd ranges. The names of these Dene tribes have been replaced by the names of smaller local bands; e.g., the Eastern Chipewyan with the Duck Lake, Barrenlands and Hatchet Lake bands; the Western Chipewyan with Caribou-Eater bands at Stoney Rapids and Black Lake; while the Yellowknives were assimilated by the Dogrib (Smith, 1978: 71).

Minor Dene camps may extend beyond each range boundary. By focussing on the center of the herd ranges, hunting bands maximized meat and hide availability. There were no viable alternatives available to hunters over the long term without vacating proven hunting areas for untested ones, something that is absent in the archaeological record. Just as the Beverly and Kaminuriak caribou herds remained 94% discrete in their overlapping winter range, hunting families followed a similar pattern; e.g., the Eastern Chipewyan's Hatchet Lake band range

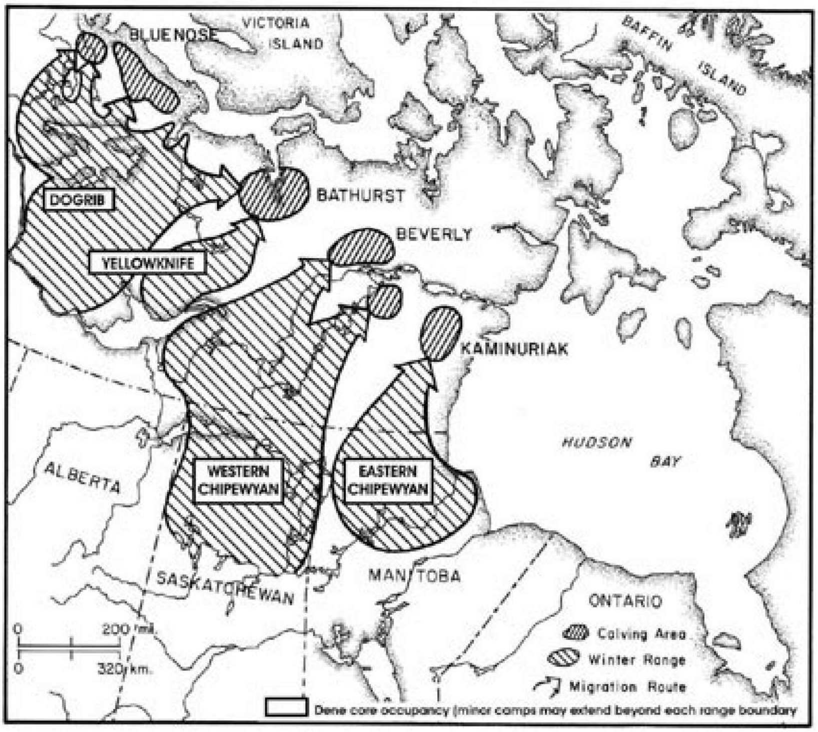

Fig. 2. The ranges of the four major migratory barren-ground caribou herds (late 1900s) and the associated historic Dene occupancy in northcentral mainland Canada.

overlapped that of the Western Chipewyan's Black Lake band. This ensured survival through kinship alliances, as it allowed shared hunting territory in those years when one herd did not appear (Smith, 1978: 83).

The following is a brief account of my investigation to gain insight into how this near total reliance on caribou could have remained functional on an annual basis over several or more millennia.

Criteria for long-term association

Two all-important conditions are linked to the successful long-term association between each archaeological phase of a hunting band and a specific caribou herd.

(1) Hunters virtually were totally dependent on caribou. This did not mean, given the opportunity, other animals and some plant matter were ignored. Other prey included muskox, moose (*Alces alces*), black bear (*Ursus americanus*), grizzly (*U. arctos*), beaver (*Castor canadensis*), hare (*Lepus americanus*), fish, birds and their eggs, and berries. Basically, people could eat everything available and edible, but this array of other potential food items would have contributed relatively little to their total annual diets. At the water crossings, the fast pace of killing and processing meat and skins would have left little time for other activities, including fishing. Most importantly, hunters would not be tempted to forage for other food when 'tasty snacks' of fat and raw meat were readily available in caribou butchering. While butchering and later resting, they likely exchanged stories about the origin and importance of caribou in myths such as Celestial Caribou and Caribou Man (Gordon, 2003: 10–12). Only one non-caribou bone--that of a muskox--was found among thousands of excavated bones. There is no evidence that the absence of other bones was due to decomposition, as tiny caribou bone needles and awls survived. People used bone and antler for tools, sinew for sewing, skins for winter and summer clothing, tents, bags, rope; even fish nets. Thus, such complete dependence on caribou for the necessities of life led annually to seasonal herd-following.

(2) Bands adapted their movement to intercept herds. Essentially, they followed the herds as they moved north to the calving ground and gathered at major water crossings about halfway. Although the people could not keep up with the migrating caribou, they apparently learned to anticipate the return migration in late summer and prepared for mass hunts when the animals returned. During the spring migration hunters must have been able to kill enough caribou to last until late summer migration. They did this by driving groups, sometimes over several months, into pounds where the animals could be dispatched (Hearne, 1958: 50–51). They also drove groups along brush drive-lanes to open lakes or rivers where they were lanced. In the spring, they gathered using 20–40 tents, based on the size and distribution of artifact clusters at these crossings. Over winter in the forest they gathered in even larger numbers of 80–100 tents at pounds (brush or tree enclosures). As each tent averaged two families, each with two children

Table 1. Cultures occupying the Beverly caribou range over the past 8000 years.

Culture	Years ago	Origin. adaptation
Dene Chipewyan	Present–200	From Late Taltheilei. Move to the forest due to fur trade influence for furbearers.
Late Taltheilei	200–1300	From Middle Taltheilei. Seasonal forest and tundra. General deterioration of artifact types.
Middle Taltheilei	1300–1800	From Early Taltheilei. Cultural effluoresence based on site numbers, content and tool quality.
Early Taltheilei	1800–2450	From Earliest Taltheilei. First full alignment with Beverly herd migration corridors.
Earliest Taltheilei	2450–2600	Forest origin in northwest B.C. Mainly forest.
Pre-Dorset ASTt	2650–3450	Palaeo-Inuit from Alaska. Mainly tundra.
Shield Archaic	3500–6500	Northern Plano origin? Mainly forest.
Northern Plano	7000–8000	First Beverly range pioneers. Mainly forest.

> and one grandparent (Hearne, 1958), 800–1000 people could aggregate at one camp. Later, bands divided to hunt more dispersed animals in the forest. Cows and calves winter close to treeline, while bulls venture to the southern limits of their range. During April, pregnant cows begin their northern migration (Smith, 1978: 69–71). Bulls follow later but stop short of the calving grounds. Throughout the year, hunting families located themselves such that kinship ties provided a communications network for reporting on herd movement in given areas, an adaptation for human survival through meat-sharing (Smith, 1978: 75).

One-hundred and thirty-one C14 dates scattered over 1002 archaeological sites show herd-following existed for 8000 years (Gordon, 1976). With caribou the main source of sustenance, archaeological sites are, with few exceptions, caribou hunting camps. They affirm tandem movement of a caribou herd and a hunting band. The general absence of skeletal materials from other species at those crossing sites is not surprising, given that people moved to those locations solely for short intense hunting periods.

In the historical period, hunting patterns changed as Dene began providing meat to Hudson's Bay Company forts. They abandoned mass hunts at water crossings because forts were located for trade, not hunting, and local caribou were soon exterminated. After the Dene adapted to the fur trade, traditional herd-following ceased and most hunters remained in the forest year-round to trap furbearers and trade. They deserted traditional water crossings because these required long walks, waits and boats. Eventually, widespread use of rifles, many equipped with telescopic sites, led to long distance shooting in areas easily reachable by snow machine or charter aircraft (Miller, 1987; Gordon, 1996).

Beverly range past and present

The Beverly range covers about 400 000 km^2, including the northern portions of the two Prairie Provinces (Saskatchewan & Manitoba), east-central mainland Northwest Territories and west-central mainland Nunavut (Fig. 2). The size of the Beverly caribou herd has been estimated from about 100 000 to 420 000 animals at various times in the last half of the 20th century (e.g., Hall, 1989; Thomas, 1998). The herd's range once extended deep into Saskatchewan (Fig. 1), but since the 1970s, its southern migration and range occupancy has shifted north. It now extends from Lake Athabasca and Great Slave Lake northeast to its calving grounds north of Beverly and Aberdeen lakes on the lower Thelon River. Calving to the south of these lakes occurs in years when northward spring migration of parturient cows is delayed by difficult traveling conditions, such as deep or slushy snow. When caribou calve south of Beverly and Aberdeen lakes, cows and calves are close enough to denning wolves that calf mortality increases (Miller *et al.*, 1985; F. L. Miller, pers. comm., 2004).

Three treelines are known: a modern one from the present to 700 BC, which ignores minor Little Ice Age fluctuations; the Pre-Dorset one from 700 to 1500 BC; and the Early Hypsithermal treeline from 2000 to 6000 BC (Fig. 1). The herd crossed each treeline in their respective time period. Despite changes in treeline, location of the calving ground apparently has remained essentially the same for millennia, having served well for calf survival by ensuring relative freedom from predators and humans because of its remoteness and isolation (cf. Miller *et al.*, 1985, 1988).

As archaeological site distribution changed little over the past millennium, despite the Little Ice Age, the Beverly caribou range probably was also quite stable. This relative stability of Dene hunting camps contrasts with great changes in human distribution farther north during a very cold period (Nichols,

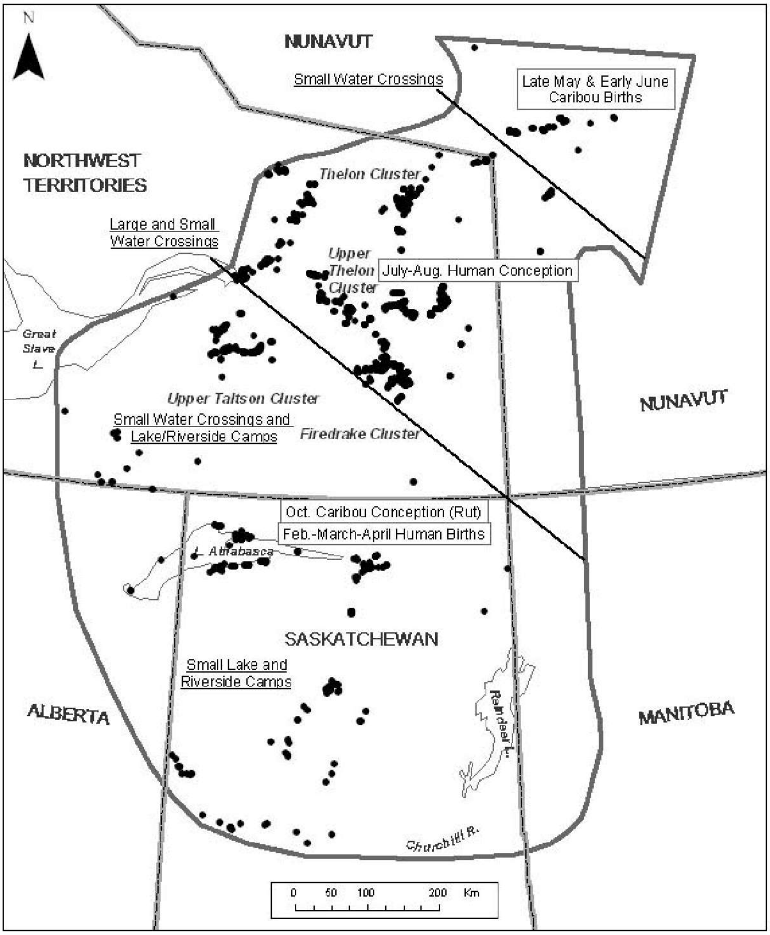

Fig. 3. One thousand and two archaeological sites showing 8000 years of caribou and human conception and birthing in northcentral mainland Canada.

1967: 176), when earlier Inuit-like Pre-Dorset hunters abandoned coastal seal hunting under thickening ice and began following caribou herds (Gordon, 1975: 52).

North–south changes in the treeline and associated climatic factors apparently did not influence the overall location of the Beverly calving grounds (cf. Gunn & Miller, 1986). However, the size of the herd over time and year-to-year variations in weather, travel conditions, availability of vegetation and changes in the absolute food supply, etc., can and do influence what sections of the overall calving grounds are used in any given year. These short-term changes in caribou movements were undoubtedly devastating for the hunting bands depending upon caribou, but are not reflected in the archaeological evidence to date.

To test for long-term herd-following in the Beverly caribou range, I examined artifacts from 1002 archaeological camps involving eight cultures (Table 1). Range use by hunters varied from incipient in the pioneering Northern Plano period to full coverage in the Middle Taltheilei period. Climate change caused northern advance of the treeline in the Post-Glacial Northern Plano period, when Plano and Shield Archaic were mostly forest-adapted cultures. When the extremely cold Pre-Dorset period followed, the treeline retreated 200 km and this culture was mainly tundra-adapted. Warming began with the return of Indian Taltheilei cultures, beginning about 2600 years ago. Since that time, climate has undergone minor cycles, save for the colder Little Ice Age in Late Taltheilei.

Historic Chipewyan (Dene) camps

My sample consists of 181 Chipewyan or Etthen-Eldeli Dene (Caribou Eater) camps that represent the most recent Dene bands, descendants of prehistoric Late Taltheilei hunters, and occupying the range from Samuel Hearne's time (1769–72) to the present (Fig. 3). These camps represent hunters of late summer–autumn herds migrating southwest along the Thelon and Dubawnt Rivers. Forest and tundra camps along these caribou migration routes contain trade goods of steel fish hooks and cartridge-reloading tools, lead shot, copper rivets, brass kettles, glass beads and bottles, clothing, tents and thread, birchbark baskets, wooden fur stretchers, fish-drying racks and tent poles (some still standing!) and bone awls and beamers (lengthwise split caribou leg bones with both internal edges sharpened for removing fur from skin) (Gordon, 1996: Figs. 3.1, 3.4, 3.10, 3.12, 3.15). As far as discernible, the historic range of the caribou was identical to the modern range, extending northeast from Saskatchewan to the Beverly calving grounds. Despite poor traveling conditions and the great distance involved, some Chipewyan were apparently able to follow the herd to the calving grounds (Burch, 1976).

Examination of post-1846 Roman Catholic baptismal records shows the influence of caribou upon human health and procreation. Chipewyan records indicate four of five babies were born in February, March, and April, with a pronounced birth peak in April. This is nine months after the major southern caribou migration, when bands aggregated to hunt at water crossings. At the largest northern sites (Fig. 3, Thelon cluster), the herd crosses the river in early to mid-July, crossing the Upper Thelon cluster several weeks later. At this time, caribou were abundant. Hence, humans were healthy and most likely to conceive.

Late Taltheilei camps

The latest Dene prehistoric phase (Late Taltheilei), descendants of Middle Taltheilei, has 218 forest and tundra sites. These contain mostly stone tools but some bone and wood tools persist, as does some natural copper (for lanceheads) that was traded from the Coppermine River area.. Culturally diagnostic tools are crude asymmetric, unground, side-notched arrowheads characteristic of the introduction of the bow (Gordon, 1996: Fig. 4.4). Evidence of trade goods in advance of European exploration include Hudson's Bay Company brass kettle fragments (Gordon, 1996: Fig. 4.14).

Middle Taltheilei camps

Middle Taltheilei was the effluorescence of Dene culture and the descendants of Early Taltheilei. Its 327 camps were larger and artifacts denser in occurrence than any other period. Based on the number and extent of hunting camps, climate must have been ideal for herd and hunter growth (Table 1; Gordon, 1996: 85). Extensive camps along the Thelon and Dubawnt Rivers depict parallel migrations. Distinct diamond-shaped lanceheads with ground bases (Gordon, 1996: Figs. 5.2–4) and many scrapers and oval knives (Figs. 5.7–9) permit easy tracing of herd-following in this period.

Early Taltheilei camps

A less dense concentration of 170 archaeological sites represents Early Taltheilei; the first Taltheilei hunters to fully align throughout both Beverly herd migration corridors. Fewer Dubawnt sites suggest smaller caribou migrations than on the Thelon. Diagnostic tools are fine symmetric shouldered points with ground tapered or square bases (Gordon, 1996: Figs. 6.3-4). An earlier subphase (Earliest - Gordon, 1996: Fig. 6.7) has few sites because it represents the first Dene pioneers who arrived from northwest British Columbia via the Peace River and Lake Athabasca. They began herd-following when the preceding Pre-Dorset hunters returned to the Arctic Coast with climatic warming (Gordon, 1995).

Pre-Dorset Taltheilei camps

The 222 Pre-Dorset or Arctic Small Tool tradition sites represent Palaeo-Arctic newcomers arriving in an extremely cold period, when sea-hunting was interrupted due to ice thickening (Nichols, 1967: 176,177; Gordon, 1995: 325–340). Treeline was at its southernmost, so sites that were in forest for other phases were on the tundra during the Pre-Dorset period, a comfortable situation for a coastal tundra culture (Irving, 1970: 340–42). These people also adapted to the winter forest to the south around Lake Athabasca and Black Lake (Minni, 1976). There is, however, no evidence from site locations that this cold period caused any major alterations in the overall location of the Beverly calving grounds. The tiny Pre-Dorset banded chert tools, distinct even in surface finds, include harpoon points and sideblades, spurred endscrapers, burins, microblades and cores, gravers and skin flexers (Gordon, 1996: Figs. 8.2, 8.6-7, 8.21-22). Pre-Dorset hunters probably returned to the coast about 700 BC when climate ameliorated (Gordon, 1975: 95).

Shield Archaic camps

Before climate cooled with the arrival of the Pre-Dorset, the Beverly range was occupied by Shield Archaic Indian bands enjoying the last of the Post-Glacial warming. Indeed, most of their 111 sites would have been in the forest because the treeline was at its northernmost position (Gordon, 1985). Nonetheless, the calving ground location seems to have remained stable. Site clusters are larger than they were with earlier Northern Plano camps, although sampling methods were the same, reflecting a growing population. Tools include diagnostic finely ground, asymmetric rocker-based lanceheads (Gordon, 1996: Fig. 9.2). Absence of sites on the Churchill River is likely due to difficulties in archaeological survey in the heavy forest. Distribution elsewhere of Shield Archaic sites resembles that of other cultures.

Northern Plano camps

The 33 scattered Northern Plano sites represent the range's first inhabitants, descendants of Great Plains Plano hunters who followed the melting Keewatin Ice Sheet northeast to become the first herd-followers. The northern extension of the treeline placed almost all sites in forest, where hunters on the Thelon and Dubawnt rivers intercepted the autumn migration, just as they did later, when these valleys became tundra. Diagnostic tools include finely made Agate Basin lanceheads with ground bases (Gordon, 1996:

Fig. 10.4), virtually identical to those on the Great Plains. Site absence on the Churchill River probably again relates to survey logistics. Of necessity, Southern Plano hunters must have crossed this area when they switched from hunting prairie bison (*Bison bison*) to barren-ground caribou, but the exact time and place remains unknown and they may have done this earlier and further south (Wright, 1976: 95).

Summary discussion and conclusions

Caribou are the common thread running through thousands of years of cultural evolution in northern mainland Canada. The people living there must have relied on the vast herds of migratory barren-ground caribou. The Beverly Herd's range has been used by caribou and hunters for 8000 years. Most sites are at water crossings on rivers or on the shores of large lakes (Gordon, 2003: Figs. 6–7), where hunters used mass hunts to profit from herd concentration. Herds were forced into brush enclosures (pounds) and canyons in the winter when frozen bodies of water were no impediment to movement and no help to hunters. South to north, heavy site clusters are on migration corridors on the Churchill River, Black Lake, Lake Athabasca, upper Taltson River, Firedrake Lake, and the upper Thelon–Dubawnt drainage divide. Camps are few at the calving grounds because few herd-followers could make the long trip there before summer, due to deep slushy snow, distance, water barriers and calf skins that were of less value to hunters before August (F. L. Miller, pers. comm., 2004).

Evidence from archaeological sites demonstrates long-term relative stability of human and caribou herd interactions on the Beverly caribou range. Archaeological and ethnographic evidence, together with biological data, confirm long-term range stability. Although short-term variation in migration patterns most likely occurred after marked changes in herd size, their influence on fidelity to Beverly core range was small or at least indiscernible. Caribou, the major source of food, clothing and shelter, permeated mythology and supernatural belief. The long-term continual bond found in this study between different Dene cultural groups and individual caribou herds helps to explain ethnological differences between these cultures in northcentral Canada.

The temporal interlocking of human and caribou conception and birthing in Chipeywan or Dene birth records indicate most babies were born in April – nine months after the major migration in early July a few hundred kilometers north, when herd and human nutrition, especially fat in human diet, was highest (Fig. 3; Gordon, 2003: 13, Fig. 11). A woman needs about 18% body fat to bring a fetus to full-term (e.g., Frisch, 1988; Rosetta, 1992), which could be difficult to achieve during much of the year due to seasonal restrictions in herd-follower diet.

Hunters for many generations shared meat and skins among band members at water-crossing camps (Smith, 1978; Sharp, 1984). An example of the continual bounty annually available to herd-followers comes from the 6857 caribou captured and ear-tagged by Canadian Wildlife Service field parties on Thelon River water crossing sites during two-week periods in each year between 1960 and 1967. In those years, biologists were able to hand capture and ear tag an average of 1143 caribou annually at just a few sites (Parker, 1972).

The phenomenon of herd-following of large migratory herds of caribou by hunters to avail themselves of a usually dependable staff of life has persisted for millennia. In all likelihood, this time-tested strategy was employed in other parts of the world throughout prehistory, wherever food animals migrated in large aggregations - waterfowl, anadromous fish, and migratory reindeer, antelope, deer, horse, and mammoth.

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Wright, J. V. 1976. The Grant Lake site, Keewatin District, N.W.T. –*Archaeological Survey of Canada, Mercury Series 47*, Canadian Museum of Civilization.Table 1. Cultures occupying the Beverly caribou range over the past 8000 years.

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Rebuilding the Fortymile caribou herd: A model of cooperative management planning

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Abstract: We examined the public process used to develop the 1996–2001 Fortymile Caribou (*Rangifer tarandus*) Herd Management Plan adopted by state and federal management boards. The process differed from most government-supported planning processes because it was initiated by residents of Alaska and Yukon, and not by an agency. State, federal, and territorial agencies were asked to participate in and support development of a management plan that would include a broad range of interest groups. We describe the planning effort, issues addressed by the planning team that posed significant challenges during both the planning and implementation phases, and then identify unforeseen costs and benefits derived from the process. Critical decision points in plan development and implementation are discussed.

Key words: Alaska, consensus, fertility control, herd recovery, management plan, management team, nonlethal wolf control, predator management, sterilization, translocation.

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Introduction

Development of the Fortymile Caribou (*Rangifer tarandus*) Herd Management Plan (Plan), which incorporated predator management to help recovery of the Fortymile caribou herd, has been held up as a model for grassroots public participation in brainstorming solutions to challenging wildlife management issues. The Plan has been cited as "novel" in its unique holistic approach to wildlife management, making possible bold approaches to solving management issues (Boertje & Gardner, 1998; 2000).

Predator–prey management in Alaska has been and continues to be controversial and has created mistrust among groups interested in wildlife issues. The last predator control program that was completed as planned ended in 1982. From 1982 until 1997, no programs were designed that were publicly or politically acceptable and although a few programs were initiated, none were completed.

The first concerted effort to resolve this management and public dilemma was the creation of the Alaska Wolf (*Canis lupus*) Management Planning Team in 1990 (National Research Council, 1997). Team members represented a variety of interests from both rural and urban Alaska. All members shared the goal of maintaining viable wolf populations throughout the state and agreed to work together to find suitable solutions for wolf–prey management issues. The team produced by consensus a draft plan that was reviewed and revised by the Alaska Department of Fish and Game (ADF&G) and the Alaska Board of Game (Board). ADF&G and the Board used the revised plan to develop 3 implementation plans for areas where wolf control would occur, including one to benefit the Fortymile caribou herd. Many viewed the decision by the Board to initiate 3 wolf control programs simultaneously as excessive and not within the scope of the wolf management plan. The resulting social opposition prompted Governor Walter Hickel to rescind the programs and to initiate the Alaskan Wolf Summit to further explore steps necessary to resolve this controversy. The consensus point developed by groups attending the summit was that a public planning process that broadly represented the diverse interests in Alaska was neces-

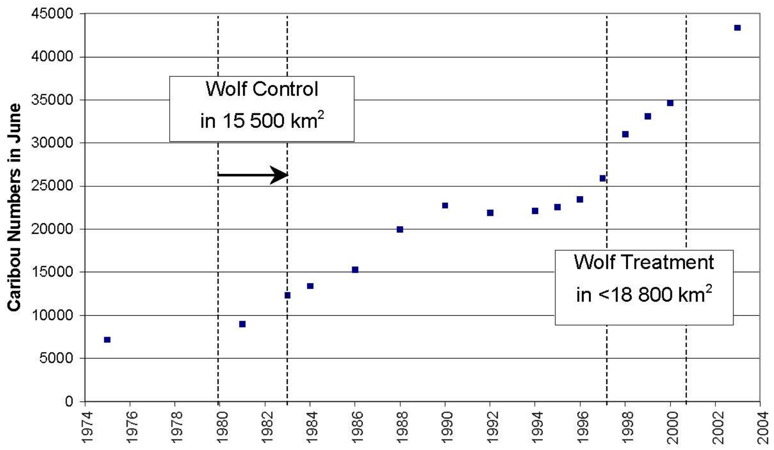

Fig. 1. Estimated abundance of caribou in the Fortymile Herd and periods of wolf control efforts, 1974–2004.

sary. This recommendation and the growing feeling that agencies had become ineffective in managing the Fortymile caribou herd prompted residents of Alaska and Yukon to initiate a public process that would develop management options that agencies could use to promote the recovery of the Fortymile caribou herd.

Background

In the early 1920s, the Fortymile caribou herd was estimated at 568 000 animals and considered to be the largest caribou herd in Alaska (Murie, 1935; Valkenburg *et al.*, 1994). Murie (1935) described the herd's range during the 1920s as being 220 000 km^2, extending from the White Mountains in eastcentral Alaska to Whitehorse, Yukon. The herd fluctuated in size from the 1930s through the 1950s, but continued to use most of its range in Alaska and Yukon. The Fortymile Herd was the most economically important wildlife resource in Interior Alaska and Canada throughout this period.

Between the mid-1960s and 1973, the herd declined precipitously, probably due to a combination of high harvests, severe winters, and high numbers of wolves (Davis *et al.*, 1978; Valkenburg & Davis, 1989). During 1973 through 1975, new photocensus techniques were developed and the population was estimated at an all time low of 5700 to 8600 caribou (Fig. 1; Valkenburg *et al.*, 1994).

Caribou herds typically reduce their range size as the population declines (Boertje & Gardner, 2000). Due to decreased herd size between 1966 and 1975, the Fortymile caribou herd reduced its range size and changed its seasonal migration patterns. The herd stopped crossing the Steese Highway in Alaska in 1967, and by 1973 few animals moved into Yukon each year. From the early 1970s to 1998, the herd's range size was about 50 000 km^2, less than 25% of the historic size (Valkenburg *et al.*, 1994).

The Fortymile caribou herd began increasing in 1976 in response to favorable weather conditions, reduced harvests, and a natural decline in wolf numbers (Fig. 1; Valkenburg *et al.*, 1994). In 1990 the herd was estimated at 22 800 caribou. The annual rate of increase during 1976–1990 was 5–10%. During 1990 through 1995, the herd remained relatively stable at between 21 900 and 22 600 caribou. During this period, except immediately after the severe winter of 1992–1993, indicators of herd nutritional status showed moderate to high condition, yet the Fortymile Herd was stable or possibly declining. In the early 1990s, Boertje & Gardner (2000) found that predation on calves by wolves and brown bears (*Ursus arctos*) was the major factor limiting growth of the herd. They also concluded that range condition was excellent and could support a much larger herd.

Following the Fortymile Herd decline in the early 1970s, few Alaska and Yukon residents saw Fortymile caribou because the herd's range size was markedly reduced. Many people within the herd's range supported management programs designed to increase herd size. Optimism and support for herd recovery increased following annual growth of 7–10% during the 1980s.

In 1990, ADF&G reviewed statewide caribou management policies as a step toward developing specific caribou management plans (Whitten, 1990). Biologists from the Yukon Department of Renewable Resources, the Canadian Wildlife Service and the ADF&G met later in 1990 to determine a future management direction for the Fortymile Herd. A common goal included restoring the herd to its historic range in Alaska and Canada, to be accomplished by limiting harvest to bulls only and establishing an annual quota based on herd size and growth. The herd size objective was 50 000 caribou by year 2000. Predator management would only be considered if the herd failed to respond to reduced harvest and predators were determined to be the primary limiting factor.

Also in 1990, the federal government assumed responsibility for regulating the subsistence harvest of wildlife on federal public lands in Alaska, in order to fulfill the mandates of Title VIII of the Alaska National Interest Lands Conservation Act of 1980. The resulting "dual management" system created conflicting objectives and complicated efforts to manage harvest of the herd. This conflict resulted in more complex harvest regulations and increased the potential for overharvest of Fortymile caribou.

During the early 1990s, the Fortymile Herd was no longer increasing and in an attempt to meet the population goal set by ADF&G, the Board adopted a wolf control program to be implemented in 1993. Bowing to public pressure, primarily from individuals and organizations outside of the herd's range, Governor Walter Hickel rescinded the program. It was apparent that greater input from the public and federal agencies was necessary before management that would benefit herd recovery could be implemented. During this time, no land or wildlife management agencies had a good plan for developing management direction to benefit the Fortymile Herd.

Public dissatisfaction with state and federal management of the Fortymile Herd increased after 1993. The Fortymile Herd continued to be essentially absent from Yukon and along the Steese Highway in Alaska and harvest allocations were very low in Alaska and Yukon. Much of the habitat available to the herd was not being utilized. What was once the most economically important herd in Yukon and Alaska had become essentially unavailable over much of its former range.

In 1993, the chief of the Dawson First Nation in Yukon contacted the chair of the Upper Tanana–Fortymile Fish and Game Advisory Committee in Tok, Alaska, suggesting a grassroots coalition be formed to work toward rebuilding the herd. By February 1994, these visionaries assembled representatives from Yukon and Alaska federal, state, and territorial agencies, First Nations, Alaska Native organizations, and other interest groups and individuals "to discuss present and future management of the Fortymile caribou herd" (Entsminger, 1994). At that meeting, agencies were asked and agreed to help develop a grassroots management plan involving all interests. Direction from the meeting was clear. A full management plan, not just a harvest plan, involving all interests would be developed. During this meeting, groups were identified that needed to be on a planning team, including a representative from each of the state advisory committees within the herd's range, and representatives from various environmental groups, hunting groups, and state, federal, and territorial agencies.

Among the challenges that had to be addressed to benefit herd recovery were the complex harvest regulatory structure in Alaska and developing acceptable methods for managing predation and habitat. In Alaska, subsistence hunting was managed by both the state and federal governments under different mandates. In the early 1990s, state regulations applied primarily to hunting on state and private lands and were designed to provide harvest opportunity while promoting growth of the Fortymile Herd. Federal regulations, on the other hand, governed subsistence hunting by local rural residents on federal public lands and had the potential to allow an increase in harvest levels unfavorable to herd growth. To meet the goal of promoting the return of caribou to the herd's traditional range in Yukon and Alaska, steps had to be taken to increase herd size. These steps had to be both biologically and socially acceptable. Habitat protection measures would have to meet mandates and objectives of private, state, and federal landowners. A public awareness campaign to keep Alaska and Yukon residents involved in the herd's recovery was recognized as an essential component early in the process.

This 1994 meeting initiated the Fortymile caribou herd planning process. This paper examines the 6-year history and evolution of this planning effort and evaluates the strengths and weaknesses of the process.

Planning process

Forming the planning team

In 1994, ADF&G conducted public scoping meetings in the local communities of Eagle, Tok, Fairbanks, and Delta Junction, Alaska and Dawson, Yukon. These meetings helped to identify issues and further identified interests that needed to be represented on a planning team. In late 1994, representatives of state fish and game advisory committees within the herd's range, Native organizations, First Nations, subsistence advisory councils, environmental groups, and state, federal, and territorial agencies met to form the Fortymile Caribou Herd Planning Team (FCHPT or Team). During the first 2 meetings participants identified other groups, including environmental, tourism, and animal welfare interests, which they believed should be involved to assure success of the planning effort. The Team recognized that as group size increased, achieving consensus would become more difficult, but knowing that the Plan would involve contentious issues, they needed a balance that ensured broad representation on the Team. Many organizations were invited to participate and 20 accepted. Those that declined largely supported the management planning effort, provided input, and asked to be kept informed via the Team mailing list and publications.

All meetings were open to the public. The Team further agreed to invite representatives of groups that did not have formal members on the Team to attend meetings and be part of the discussion when input from their interest was needed for development of plan alternatives. In most cases this worked, but became a point of contention within some groups that did not have formal membership (see chapter Challenges in the process).

The primary benefit of such a public process is drawing from a wide range of experiences, wisdom, and interest in the problem to be solved. Many minds of varied viewpoints, but shared vision, developed the unique solutions in this planning effort and were able to support the recommendations.

The Team consisted of 20 members representing the local state fish and game advisory committees (advisory committees) from Eagle, Upper Tanana–Fortymile (Tok), Delta, and Fairbanks; the federal subsistence Eastern Interior Regional Advisory Council (advisory council); Tanana Chiefs Conference; Tanacross Village Council; Tr'ondëk Hwëch'in First Nation, Yukon (formerly Dawson First Nation); the Northern Alaska Environmental Center; Alaska Outdoor Council; Tanana Valley Sportsmen's Association; Alaska Wildlife Conservation Association; Alaska Wilderness Recreation and Tourism Association; Alaska Wildlife Alliance; a public member at large; Yukon Department of Renewable Resources (now called Yukon Department of the Environment); ADF&G; Bureau of Land Management (BLM); National Park Service; and U.S. Fish and Wildlife Service (FWS) (FCHPT, 1995). Previous state agency management efforts had not included federal land managers, and it was recognized that their participation was critical to assure that they would be able to support recommendations for managing the herd. The Team set as its initial goal the development of a plan that would benefit the Fortymile caribou herd without being subject to subsequent changes in state political administrations (Gardner *et al.*, 1994). In order to ensure participation by nonagency members, ADF&G, BLM and FWS provided travel and per diem support as needed.

Team building and goals

During the first meetings, the Team made 4 important decisions that contributed to the ultimate success of the plan: 1) It identified a rounded and inclusive list of participants, 2) established a common vision which was and continues to be the recovery of the Fortymile caribou herd in its historic range, 3) hired an independent facilitator, and 4) agreed on a consensus process and developed ground rules for that process. Establishing a common vision and doing so early in the process was paramount to success of the planning effort and implementation of the plan. The common vision the Team developed for the Fortymile caribou herd and its ecosystem was:

> "To restore the abundance and diversity of wildlife in this ecosystem, of which the Fortymile Herd is the most important indicator species, and
> To promote healthy wildlife populations for their intrinsic value, as well as consumptive and nonconsumptive uses" (FCHPT, 1995).

A major factor contributing to the success of the planning process and support for the resulting recommendations was the hiring of an independent facilitator. An ADF&G planner served as facilitator for the first few meetings. It soon became clear, however, that a facilitator affiliated with a resource management agency might be perceived as lacking objectivity. ADF&G, FWS, and BLM pooled funds to hire an independent facilitator, who guided the Team through the formative stages of the management plan. This facilitator proposed ground rules governing the conduct of Team members at planning meetings and recommended that decisions be made by consensus. She began working with the Team to develop issues and options for solutions. The assemblage of those options eventually became the 3 plan alternatives. The facilitator placed high demands on the Team and spent many hours reviewing and compiling information that served as the building blocks for the plan.

Under the ground rules, decisions were made by consensus, and a process was developed to use when consensus was not reached. "Consensus" as used by the Team was a package of compromises that all can live with and meets members' most important concerns. All Team members agreed to abide by these procedures, under which they could present viewpoints and experience but also convey the interests they represented.

Impartial facilitation and the development of ground rules helped create a foundation for an effective process and outcome. Both helped to develop a strong feeling of trust among Team members and contributed to their ability to work by consensus. A member who could not work under a consensus process was asked to resign from the Team. Minority opinions were included in the draft Plan. Even with minority opinions from members who were unable to work within this framework, the Team was able to address tough issues and go forward with implementation of the Plan with little criticism. The diversity of the Team, the public process, and the common vision to restore the herd to the landscape helped to maintain public and government support for and endorsement of the Plan.

Plan development

Prior to scheduling any formal Team meetings, ADF&G was directed by the process founders to hold a series of public meetings to identify issues for the Team to address. Meetings were conducted from July and November 1994. A comprehensive search of public and agency issues enabled the Team to establish the necessary Team membership and carefully craft management actions and justifications for those actions that could withstand public and political scrutiny.

The Team held preliminary planning meetings in November 1994. Active planning began in May 1995, when the independent facilitator was hired, and by August 1995 the Team had produced a Draft Fortymile Caribou Herd Management Plan. The draft plan, which included potential impacts of alternatives, was published in newspaper format for public review and comment (FCHPT, 1995). The draft plan described the Team's vision and presented 3 alternatives: 1) no change from existing management, 2) moderate population growth (5–10%), and 3) more aggressive population growth. Each alternative recommended different approaches to achieving plan goals over the 5-year period of July 1996–June 2001. These goals were to:

Benefit the Fortymile caribou herd and the people who value the herd and its ecosystem;
Provide an opportunity for the caribou population to increase and expand into its historic range;
Promote similar goals between the agencies involved in management of the Fortymile caribou herd;
Resolve conflicts among interest groups; and
Encourage sound wildlife management decisions that consider diverse values.

Within each alternative, recommendations were developed on each issue. The Team's preferred alternative to restore the herd recommended the following actions: maintain habitat quality, reduce harvest of Fortymile caribou, decrease predation on calves by wolves using nonlethal control, possibly decrease predation on calves by grizzly bears, and increase public involvement and awareness through outreach. The preferred alternative, which became the draft plan, was supported by all Team members except the Alaska Wildlife Alliance and the member at large, neither of whom could come to consensus on the use of nonlethal wolf control to reduce predation on calves.

Plan recommendations

Maintain habitat quality

Research from the early 1990s had shown that Fortymile caribou winter range condition was excellent and nutrition was not considered to be a strong limiting factor to herd growth (Boertje & Gardner, 1998). The recommendation therefore emphasized maintaining habitat quality. A habitat management needs assessment was published, primarily for land managers, mining interests, the air service industry, the military, and other land users and developers, and provided a strong means for public awareness and involvement during implementation (FCHPT, 2000). The assessment identified critical use areas and also established outreach to increase awareness of the importance of these habitats. ADF&G developed a website for use by exploration companies, miners and the military to help prevent their activities from disturbing caribou on any given day, especially during critical times, such as calving and postcalving.

Reduce harvest of caribou

Reducing the harvest of Fortymile caribou in Alaska became a cornerstone for further consensus within the planning process. The annual harvest quota was reduced from 450 to 150 bulls for the 5-year life of the plan, motorized access to some popular hunting areas was prohibited, and hunting permits were issued only in hunt area communities. Hunters recommended the harvest reduction because they were willing to forego harvest opportunity in the short-term for future returns.

Harvest was not considered to be a limiting factor in herd growth but the Team agreed that a reduction in harvest was necessary for Team and public support of any proposed actions to reduce predation. Reducing harvest would also help isolate the effects of other management actions being proposed. This recommendation became pivotal in the acceptance of the Plan by Team members representing Yukon, animal welfare, and tourism interests.

The impacts of a substantial reduction in the harvest quota from regulatory years 1995–1996 through 1999–2000 were fortuitously offset in part by the increased availability of Nelchina caribou in the Upper Tanana region during the winter months. The presence of Nelchina caribou allowed both state and federal subsistence laws to be met and helped ensure that subsistence users had alternatives to Fortymile caribou for meeting their subsistence needs, making possible the reduction in the Fortymile harvest. Although the Team believed local subsistence uses would be accommodated with the reduced quota, members acknowledged that other hunters and local businesses that supported nonlocal hunters were impacted in the short term by this recommendation.

Decrease wolf predation on calves

Predation on calves and the resulting low calf survival were found to be the primary constraints on herd growth in the 1990s (Boertje & Gardner, 1995). Of the estimated 8260 Fortymile caribou calves born in 1994, about 5000 were killed by predators within their first year. Wolves were the primary predator, killing 27% of the annual calf production. Reducing predation by wolves therefore emerged as a necessary and predictably controversial element of the plan.

Lethal predator control was and remains a divisive issue in Alaska. The Team agreed that recommending its use would be socially or politically unacceptable and therefore was not an option toward achieving herd growth. Additionally, difficult access to the calving and summer ranges limited the effectiveness of efforts by local trappers, although increased trapping activity was successful in reducing wolves within other portions of the Fortymile range, primarily the herd's winter range. Trappers independently organized the Fortymile Caribou Calf Protection Association program during 1996, which offered financial incentives ($400 per wolf) to trappers to take wolves within the herd's range. This program substantially reduced wolf numbers in the herd's wintering range, but had limited success in the calving and summer ranges and calf mortality from wolf predation was not significantly reduced (Boertje & Gardner, 1999).

The Team realized that if the goal of herd recovery was to be met, a new direction in predator management had to be found, one that was more socially acceptable even if it might be less successful than lethal control. During the 1993 Alaskan Wolf Summit and from comments received during the public scoping meetings for this process, there appeared to be support for nonlethal wolf control. Since most of the calf mortality occurred on the herd's calving and summer ranges, the Team proposed experimental fertility control on alpha pairs within the calving and summer range, in combination with translocation of subordinate pack members and public trapping. This option, combined with reduced caribou harvest, was supported by most Team members.

Experts on fertility control in wild canids, wolf biology, and predator–prey relationships assisted the Team in developing this option and the rigorous study design to implement and monitor its effects. The recommendation to translocate wolves also expanded the planning effort to include people throughout northern and western Alaska to find suitable release sites. Decisions on where wolves would be moved were made using public processes and required permission from the local advisory committees or council(s) representing the area.

The Team limited the number of possible packs to receive treatment to 15 that resided within the herd's calving and summer ranges but outside of Yukon–Charley Rivers National Preserve. National Park Service policies prohibit predator control unless it is part of an endangered species management plan. All the subordinate wolves (>9 months of age) in these packs were captured and moved at least 150 miles from the territory to areas that supported ungulate densities as high as or higher than the Fortymile area. The adult breeding pairs were also captured but were sterilized and released back into their territory. The desired outcome was that the 2 sterilized pairs would continue to defend their territory and maintain a pack size of 2. Using wolf relocation and fertility control to significantly reduce wolf numbers (≥70% reduction) and maintain reduced wolf numbers over a large area (15 pack territories) for at least 4 years was a new and largely untested technique (Mech *et al.*, 1996; Spence, 1996), but the team agreed on the need to find predator management tools that were both socially acceptable and biologically sound. Ten independent North American and Australian scientists experienced in fertility control in canids either helped to develop or reviewed the study design.

The Team included in the Plan the importance of monitoring the impacts of additional trapping and nonlethal wolf control on wolves, caribou, moose (*Alces alces*), and Dall sheep (*Ovis dalli*). In response, the state and federal agencies funded and conducted a research experiment evaluating effects and results (Boertje & Gardner, 2000).

Decrease predation on calves by grizzly bears

Caribou calves are most vulnerable to grizzly bear predation during the first 2 weeks of life, after which they are able to evade these predators in most situations. The Team recommended that the Plan include provisions for relocating bears from calving areas during the fourth year of implementation, if bear predation limited calf recruitment after wolf predation had been reduced. Based on past experience, biologists believed that bears moved from the calving area to locations north of the Yukon River or at least 150 miles away, would not return to home areas until at least 2 weeks after the peak calving period (Miller & Ballard, 1982). Relocation of 30–45 bears was proposed for the final year of the Plan if needed, with the assumption that most of the bears would return to the calving area later in the summer. Yukon and Native representatives were reluctant to move bears, but agreed to this provision as part of the package. The compromise was that this step would only be taken if bear predation was found to be compensatory and became the primary limiting factor to herd growth. Consideration of bear translocation, and a decision that it was not necessary, would be considered implementation of this step. Grizzly bear predation did not increase after wolf predation had been reduced and no bears were moved during the last year of Plan implementation.

Public involvement and awareness

The Team realized that the Plan and the recovery effort would not gain or maintain public support without an active outreach program. The primary tool used was *"The Comeback Trail,"* a newsletter published and circulated once or twice a year to over 4500 people, primarily Alaska and Yukon residents. Publication began in June 1994, and 13 issues have been published to date. Periodic news releases also were issued throughout the planning and implementation phases. These 2 outreach programs continue to be used. Additionally, roadside information exhibits are being constructed along the Taylor, Top of the World, and Steese highways. Art and other contests increased public understanding of the issues and created opportunities for people to experience the herd firsthand during the development and implementation of the plan.

Implementing the recommendations

All 5 management actions in the Plan were important to the success of Fortymile Herd recovery. Developing each recommendation required substantial compromises by all Team members, and the Team agreed that no one section was more important than another. Timing of implementation differed for each of the recommended actions. To ensure that actions were not implemented independently, the Team developed and presented the Plan as a package, so that if any one section was not implemented by either the state or federal regulatory boards or management agencies, the Plan would be terminated.

Plan approval

Habitat protection, reduced caribou harvest, and nonlethal wolf control were the primary recommendations contained in the plan. The draft gained consensus by all but 2 Team members. These members could not accept the recommendation for nonlethal wolf control. During September 1995, the facilitator and Team took the Plan to the public through a published draft and 6 public meetings held in Dawson, Yukon, and Delta Junction, Fairbanks, Anchorage, Eagle and Tok, Alaska. Written comments were also accepted. All comments received were considered and used to produce the final Fortymile Caribou Herd Management Plan (FCHPT, 1995).

Team approval

As noted above, consensus was reached on the draft by all but 2 team members. One member (public at large) could not accept nonlethal wolf control and voluntarily left the Team after the draft plan was completed. She supported the process but decided she could not support the final Plan. Instead of eroding the process or delaying implementation, she decided to resign her membership. The other member that did not reach consensus, representing the Alaska Wildlife Alliance, did not support the process or the agreement that each recommendation was dependent on the others. This person and the group he represented operated outside of the established ground rules and the Team asked him to resign.

The final Plan was approved by the Eagle, Upper Tanana–Fortymile, Delta, Fairbanks, and Central advisory committees, the Eastern Interior Regional Advisory Council, the Tr'ondëk Hwëch'in First Nation, and was endorsed by Alaska's 3 largest newspapers (Anchorage Daily News, Fairbanks Daily News-Miner, and Juneau Empire).

The Plan was presented to the Board of Game and the Federal Subsistence Board as a package. Both regulatory bodies endorsed the plan, concluding that the appropriate interest groups had been involved in the process and that the Team had built a consensus-based plan with broad public participation and support. The boards recognized the importance of accepting the Plan as a package and made strong statements on record that, even though the management actions recommended in the Plan had different implementation times, all steps were to be implemented over the 5-year life of the Plan.

The Plan was implemented in stages with reduced harvest (beginning in fall 1996) occurring before fertility control and translocation of subordinate wolves was initiated (fall 1997). The Board adopted the wolf predation reduction recommendations into regulation in 1996. Before the recommendations could be implemented, the Plan had to meet predator control criteria established by then Governor Tony Knowles: it was to be 1) based on solid science; 2) make economic sense for Alaskans; and 3) have broad public support. The governor had commissioned the National Academy of Sciences to summarize what was known about the impacts of predator control on both predator and prey populations, and to assess the economic value of and public support for predator control (National Research Council, 1997). The governor used these findings to make his decision and approved the Fortymile nonlethal wolf control program to begin in November 1997. This was the first time in more than 2 decades that a predator control program in Alaska had been endorsed by both the state and federal management agencies, and state government.

Implementation and monitoring

ADF&G developed a study design for implementing and evaluating the recommendations of the Plan (Boertje & Gardner, 1996). ADF&G, with funding from BLM and FWS, monitored the effects of the management actions not only on the Fortymile caribou herd, but also on wolves, moose and Dall sheep. The Team remained active during implementation, and using these data in combination with public comments, continued to evaluate the effects of the actions. Management actions were reopened for discussion but continued to weather criticism, demonstrating the effectiveness of the planning process (Todd, 2001). The Team assessed each new issue or comment by asking whether, during the Plan development phase, that particular issue had been discussed and included in the decision making process, and if that particular suggestion would improve the chances of Fortymile caribou recovery into traditional range. It was important for the Team to continue in this capacity so that the many interests who helped to develop the Plan understood that their concerns were still being treated fairly and not diluted.

Further increasing the Plan's stability were the several contingencies, or "safety valves," that had been incorporated into the final Plan. For example, the Plan was a package of recommendations to be taken as a whole, and it incorporated criteria for early termination if caribou survival and population size failed to improve after 3 winters of implementation. The research design also included criteria for terminating nonlethal wolf control if sterilized pairs did not maintain territories (Boertje & Gardner, 1996).

Additionally, a harvest plan was developed by a coalition of 5 advisory committees (Eagle, Upper Tanana–Fortymile, Delta, Fairbanks and Central) and the Eastern Interior Advisory Council, and endorsed by the regulatory boards (Fish and Game Advisory Committees, 1999). The advisory committees worked closely with the public and the Team to produce a 5-year plan that allowed a moderate increase in harvest opportunity beginning in fall 2001 but ensured continued herd growth and recovery to traditional ranges.

The Team became more active in habitat conservation issues, developed the "Fortymile Caribou Herd Habitat Management Needs Assessment," and worked actively with industry and others to assure maintenance of Fortymile caribou habitat (FCHPT, 2000). One of the most effective tools became a website developed by the Team and maintained by ADF&G, which documented the location of caribou during calving and postcalving. Exploration companies, miners, and the military used the information to help prevent their activities from disturbing caribou at these critical times. The response from these user groups was favorable, with many contacts indicating that they were taking pride in their efforts to protect recovery of the Fortymile Herd.

Evaluation of the plan

This Plan can be evaluated on both its success in facilitating growth of the Fortymile caribou herd and as a model for other complicated or controversial wildlife planning efforts in Alaska. In terms of public process, the Team was able to design a management program including predator and harvest management that was endorsed both politically and socially. Many factors worked in concert allowing the Fortymile process to succeed where other predator management plans had failed.

The Fortymile process included a broad representation of interests on the Team and worked within a consensus framework. These factors alone are not responsible for the success of this planning effort. ADF&G's previous statewide Wolf Management Team was also diverse and worked by consensus. However, 3 differences were very apparent between the 2 teams. First, the public started the Fortymile process and had a large role in selecting the Team members, while ADF&G initiated the Wolf Management Team and designated its members. Second, the Fortymile Team worked on only 1 issue—recovery of the Fortymile Herd—while the Wolf Management Team was trying to find compromises for the entire state. Third, and most important in the case of the Fortymile Plan, all the agencies involved in the process made, and honored, a commitment to support and implement the consensus reached by the group. ADF&G and the Board selectively adopted the recommendations of the Wolf Management Team, which undermined support for the consensus package.

The commitment to a clear and shared focus on rebuilding the Fortymile Herd opened the doors for development of a package of compromises that most members could accept, one in which members could give on some issues in order to gain on issues of greater importance to them. It also lent power to maintaining the entire plan, thereby preventing any single management agency or regulatory board from dissecting any recommendations from the package.

These elements helped the Plan to gain endorsement and weather criticism.

Largely due to the skill of the facilitator and careful selection of team members during the planning phase, a functioning Team developed, whose members had mutual respect for and trust in one another. Additionally, the facilitator maintained contact with Team members between meetings and made sure everyone completed their assigned tasks. No decisions were made between meetings, and trust was maintained by ensuring that any new information collected between meetings was distributed to the entire Team. Another measure of the effectiveness of using a facilitated, consensus process was the shifting of these management issues from being contentious, front-page news to being reported more often as innovative management.

The Team requested that agency representatives participate fully as team members. Although agency personnel were cautious about being full members, this ultimately increased agency buy-in and strengthened managers support for the Plan package. Agency representatives were experienced enough in their respective agencies to take and maintain firm positions on recommendations. This was important because, as established in the ground rules, decisions were to be made following debate by the Team, rather than after members had conferred with their agency heads or constituents. This ground rule ensured that public and agency Team members decided direction based on information debated by the Team and not by political agendas.

The team actively sought and included input from the public. Meetings were open to the public and during the planning phase were held in Fortymile communities. This resulted in increased public and political awareness of concerns for the herd and its management. This awareness has made it possible to justify and defend regulatory actions and the need to maintain habitat. Communication through newsletters and websites also helped to develop informed consent from the public.

Extensive research results were used to develop and support Plan options. Experts on canid fertility control and predator–prey ecology participated in meetings. Independent expert peers reviewed the research design for reducing predation. "Safety valves" were inserted into the Plan to provide for uncertainties, such as compensatory predation on calves or failure of sterilized pairs to maintain territories.

Industry, the military, planners, and developers have shown support for rebuilding the herd by voluntarily incorporating new approaches to minimize impacts to the habitat and herd. The goals of Fortymile Herd recovery were also an important consideration in establishing land designations in the state's Upper Yukon Land Use Plan (Alaska Department of Natural Resources, 2003).

To ensure continued herd recovery, the Team recognized the need to develop a plan for managing harvest after completion of the implementation phase. The local advisory committees and regional council agreed to develop the harvest plan. This was a better division of duties, because to many Alaskans the Team would appear to be usurping the regulatory function of the advisory committees, advisory councils, and regulatory boards if the Team developed the harvest plan. The Fortymile Caribou Herd Harvest Plan became the first publicly created harvest plan developed in Alaska. The harvest plan allowed a moderate increase in harvest opportunity and ensured that harvest did not cause annual herd growth to decline below 10%. The authors equitably allocated harvest across the herd's range in Alaska and Yukon. This harvest plan also met both federal and state subsistence requirements, allowing a joint quota and permit that has further reduced the complexities of dual management and benefited both the herd and the hunters. The advisory committees are beginning to work on the next 5-year plan and the Board and Federal Subsistence Board are expected to continue their support.

The Team remained together through Plan implementation, largely with the same membership, which allowed for monitoring of the Plan and responding as issues developed. The Team was "sunsetted" in December 2000. Implementation of the Plan continued through June 2001. ADF&G, with additional funding support from BLM and FWS, continues to monitor the effectiveness of the implemented management actions (Boertje & Gardner, 2003).

Challenges in the process

One aspect of including a wide range of viewpoints in the planning process is that management actions will most likely not utilize the most aggressive (and potentially the most effective) management options. In the case of the Fortymile planning effort, the total number of wolf packs treated and the timing of treatment were less than optimal to ensure herd growth, as only packs on a portion of the calving and postcalving range were treated. Several important packs on territories that overlapped state lands and the national preserve were not treated. Additionally, the Fortymile Herd ranges across the territories of about 40 wolf packs. Even though the reduction of wolf numbers on the calving range was most important, these other wolves compensated and took more calves during the winter, thereby reducing the effectiveness of wolf control. Also, the Team limited control activities to 7 packs per year, requiring 2-1/2 years to reach complete treatment. All these compromises were made to balance public acceptance with program success. This approach worked both politically and socially, as the Fortymile wolf control program was the first predator management program to be carried to completion in Alaska in more than 20 years. Biologically, however, the compromises slowed herd recovery and may have demonstrated, at least for large herds with large ranges, that controlling wolves only on a portion of the calving grounds may not be adequate.

During the initial scoping meetings, many issues were identified that merited representation by some group or individual. The Team decided that some of these issues could be represented by individuals on the Team because they were members of a formal group or were very knowledgeable on the issue. This decision meant that all of the public members on the Team potentially represented more than one interest group. This worked well throughout the process except with decisions that dealt with trapping. Although members of the Team who were active trappers represented trapper's views, the Alaska Trapper's Association (ATA) was not formally on the Team. ATA did not support nonlethal wolf control and lobbied against the plan. ATA believed that a trapping program would be sufficient to allow the herd to recover. The Team asked ATA to help write the language managing trapping once wolves were sterilized. ATA did help craft the language, but never supported it because of their disagreement with the method used to achieve reduced predation. ATA, the Tanana Valley Sportsmen's Association, and the Caribou Calf Protection Association petitioned the Board to halt fertility control in 1997. However, the strengths of Team diversity, including the presence of several respected trappers, the consensus approach, and broad public support were the basis for the Board denying the petition after carefully considering ATA's arguments.

ATA was asked to be a member of the Team during the implementation phase but declined because of its continued opposition to nonlethal wolf control. ATA remained a vocal opponent of the Plan throughout the Plan's life. Since trapping was an important issue for both the success and acceptance of the Plan, formal representation by ATA would have been desirable.

The Alaska Wildlife Alliance (an animal welfare group) agreed with the vision of Fortymile Herd recovery but eventually "took a seat in the audience" because its leadership did not agree with the recommendation of using nonlethal wolf control as one of the tools. Without animal welfare involvement on the Team, the Plan could have lost strength. However, an animal welfare advocate who had followed development of the Plan came forward to represent that interest. In a press conference in November 1997, she stated that this process diverted from "management by decibel" to focus on the big picture of what actions would benefit the herd and its ecosystem.

Native representatives approached fertility control with caution, viewing it as disrespectful to the animals. Many came to support fertility control because they could see the connection to traditional practices, such as "pupping" (the traditional practice of killing wolf pups in dens). Others agreed with fertility control because as one member expressed it, "When our main source of food (moose and caribou) is in jeopardy, you try to solve the problem in any way necessary to put dinner on the table."

Another aspect of the Team process that was not clearly foreseen, which caused delays and membership changes, was the effects of constituent pressure on Team members. The ground rules stated that, following discussion, decisions were to be made at the meetings so that all the Team members had the same information and that these decisions would not be changed unless it was recognized that pertinent information had been overlooked. This was an important ground rule because it instilled trust in the Team that important compromises were not going to be changed. What was not fully anticipated, however, was the intense pressure some Team members encountered outside the process from their constituents who did not agree with Team decisions that appeared to conflict with their ideals. These conflicts threatened friendships and caused some Team members to be dropped from groups in which they were formerly very active. Some Team members could not face those pressures, and decided either to renege on previous decisions or to stop participating in the process.

The Habitat Management Needs Assessment became and continues to be a valuable habitat management tool, but it has no authority, and no habitat protection was designated in Alaska. The authors of the state's Upper Yukon Land Management Plan (Alaska Department of Natural Resources, 2003) used the needs assessment as a planning tool and incorporated protection from future development within the calving and summer ranges of the herd. Debate is ongoing in Yukon on how to protect the Fortymile range in Canada.

Recovery of the herd

The Fortymile Herd increased by 78% during the life of the Plan (Table 1) and began expanding its

Table 1. Fortymile caribou population estimates, harvest allocations and reported harvest, 1995–2003.

Year	Population estimate	Harvest allocation	Estimated harvest[a]	
			M	F[b]
1995	22 558	450	203	22
1996	23 458	150	138	7
1997	25 910	150	143	8
1998	31 029	150	151	3
1999	33 110	150	142	5
2000	34 640	150	142	3
2001	40 204	850	493	200
2002	No estimate	950	667	197
2003	43 375	950	613	181

[a] From 1 July to 30 June of the next year.

[b] Bag limit was bulls only regulatory years 1995–1996 through 2000–2001.

range eastward into Yukon and westward to the Steese Highway in Alaska. These biological successes were not just the product of the Plan's management actions. The Caribou Calf Protection Association trapping effort, promoted and financed by a Fairbanks group, contributed to reducing wolf numbers in the winter range and near the periphery of the range for the Fortymile Herd early in the planning process. The availability of Nelchina Herd caribou to local hunters lessened the impacts of the Fortymile caribou harvest allocation reductions and helped to avoid conflicts with state and federal subsistence laws. Moist summers and mild winters in Fortymile country during the planning and implementation phases also probably increased productivity and facilitated herd growth.

During the late 1990s the recovery of the Fortymile Herd was becoming apparent to residents of eastern Alaska and western Yukon. By 2002–2003, Fortymile caribou were regularly crossing the Steese Highway in Alaska into the Preacher Creek drainage for the first time since 1967. Thousands of Fortymile caribou wintered in Yukon in 2002–2003, crossing the Yukon River for the first time in over 30 years. The herd's arrival made national news and drew many people to the area to view the herd. The Tr'ondëk Hwëch'in First Nation could have hunted the herd but instead chose not to, allowing the herd to once again establish its traditional migration patterns. A quota of 300 animals had been established for Yukon residents, yet hunting remained closed throughout Yukon, further allocating those animals to herd growth.

Wolf numbers have been increasing in the control area and as of 2004 are at about 60% of pretreatment levels. Research has shown that wolf relocation combined with public trapping can be effective in reducing wolf numbers >75% and that sterilization can maintain reduced wolf numbers for a period of years (Boertje & Gardner, 2003). Sterilized pairs continued to hold territories for periods ranging from 1 to 6 years. As long as the sterilized wolves held their territories, the positive effects of the program continued.

Conclusions

Prior to the creation of the Team, many attempts had been made to rebuild the Fortymile caribou herd. None of them was fully implemented or accepted by all interest groups or resource managers. A large measure of the success of this process was its conceptual origin with Yukon and Alaska local residents. Perhaps most importantly, the diverse group of Team members was willing to work together, try new approaches, and take some criticism from their constituents, because they believed in the vision and the process.

This effort has shown that when resource management issues are controversial, as is predator reduction, a process involving diverse public interests, identifying the common vision, and working within a consensus framework can yield management recommendations that are endorsable by decision makers and they can be implemented successfully. In this case, involving environmental, animal welfare, and outdoor recreation and ecotourism groups in the planning process, along with the harvesters and managers, diffused contentiousness and minimized controversy. The Team included many "safety valves" in the Plan that also prevented critical recommendations from being sabotaged during the implementation phases.

The following factors were keys to success:

Team composition: The Team assembled a diverse group of strong-minded people who all had an intense interest in wildlife. Team members were willing to work together, make compromises, and recognize compromises made by others.

Strong facilitators: Facilitators were experienced in natural resource issues and were not afraid to stir the pot while maintaining strict ground rules. Facilitators pushed the Team to think outside the box, while remaining focused on the primary goals and objectives.

Agency support: The Team had adequate financial support and sufficient data to develop informed recommendations. The agency representatives were careful to explain to the Team what mandates and financial realities agencies had to meet. Because agency representatives were members of the Team, agencies had buy-in during the planning phase. The agencies stood by the Team's decisions because they were both biologically and financially feasible, even when actions were politically uncomfortable.

Public awareness: The public was continually informed and updated on management direction and outcomes, and asked to provide comments and ideas. These steps helped create and maintain public support for the Plan recommendations.

A little bit of luck: The combination of the right mix of players, a political climate in Alaska and Yukon receptive to such a planning effort, availability of Nelchina caribou as an alternative source of subsistence harvest, and favorable weather for the herd to grow all helped with the success of the process and implementation of the plan.

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4-6 May, 2004.

Harvest estimates of the Western Arctic caribou herd, Alaska

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Abstract: A generalized least squares regression model was developed to estimate local harvest of the Western Arctic caribou (*Rangifer tarandus granti*) herd. This model provides herd and community level harvest based on community size, proximity of the herd to the village. The model utilizes community harvest survey information from the Alaska Department of Fish and Game, Subsistence Division and cooperation from the nonprofit organizations Maniliq and Kawerak. The model will assist in an annual selection of communities to survey. The predicted local resident harvest of the Western Arctic caribou herd is 14 700 with 95% lower and upper confidence limits of 10 100 and 19 700 respectively.

Key words: generalized least squares, *Rangifer tarandus granti*, regression modeling.

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Introduction

Caribou (*Rangifer tarandus granti*) are important sources of food and material for families in northwest Alaska. Information on the local consumption of caribou is important for effective managing of the Western Arctic caribou herd (WAH). Harvest of the WAH in northwestern Alaska, until now, has been unknown. In 1999 the Alaska Department of Fish and Game (ADF&G) began community surveys to gather harvest information in Game Management Units (GMU) 22 (Seward Peninsula) and 23 (Kotzebue Sound). Combining this survey information with GMU 26A (Western North Slope) survey information available from the North Slope Borough and ADF&G, a generalized least squares model has been developed.

This model's prediction of harvest is a function of village population, the availability of the herd to the village, and GMU the village is within. Village population represents the idea the larger the village the higher the harvest. The availability measure is a set of 3 indicator variables (high, medium, and low) representing the availability of caribou to the village for harvest. High availability would indicate larger harvest and low availability would mean less harvest. The 3 GMUs are ADF&G geographic units containing villages sharing common interests and having a common heritage within each GMU. A map showing WAH seasonal ranges, villages, and GMUs is in Fig. 1.

A generalized least squares (GLS) (Pinheiro & Bates, 2000) modeling is necessary because of issues with spatial and temporal dependence of observations. GLS is a model for correlated observations or which have differing variances (Rencher, 2000; Waller & Gotway, 2004). Ordinary least squares regression requires independent observations for the proper estimation of the variance-covariance matrix. A correct variance-covariance matrix is essential for proper model selection, inference of equation coefficients, and confidence intervals of predictions.

The sets of GLS equations are used to estimate harvest for each community in GMUs 22, 23, and 26A, and provide GMU and herd-wide local harvest estimates with 95% confidence intervals.

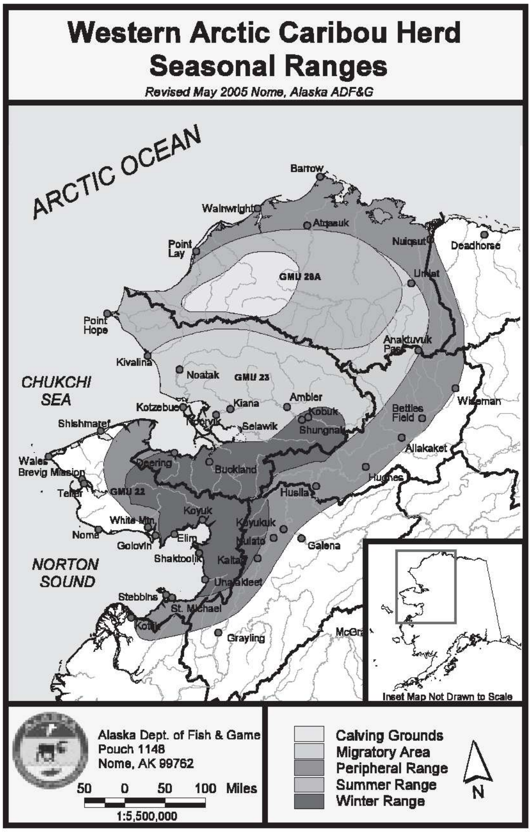

Fig. 1. Western Arctic Herd seasonal ranges.

Material and methods

Harvest data for the model are gathered from community harvest surveys gathered from households. The exception being Nome where harvest information will be gathered by a registration hunt. Initial approval for survey work from village tribal councils is obtained before the project begins. For GMUs 22 and 23, local residents are trained by ADF&G Subsistence Division staff in partnership with the regional nonprofit staff from their respective corporation (Kawerak or Maniliq). In Unit 26A, community harvest surveys were completed by the North Slope Borough Department of Wildlife Management, ADF&G/Subsistence Division, or S. R. Braund & Associates, Inc. Barrow was surveyed by S. R. Braund and Associates, Inc., in conjunction with the Institute of Social and Economic Research, University of Alaska. For modeling purposes, Anaktuvuk Pass was included in the GMU 26A village grouping because of their cultural, economic and political ties with the North Slope villages.

The household survey is used to gather information on caribou hunting for a 12-month period May through April. Survey data are expanded through the use of weights for the nonresponding households. At most 8% of the households did not respond for any village survey making many efforts at acquiring community harvest data a census rather than a sample. The Kotzebue and Barrow community surveys were stratified random samples of households. Table 1 lists the communities sampled by year.

Village population is obtained from State of Alaska Department of Community and Economic Development community database online.

The availability component represents the accessibility of the herd for harvest due to seasonal migrations, shifts in herd ranges, and the ability of villagers to approach the herd to hunt. The ability of villagers to hunt the herd could depend on several items, primarily adequate conditions to access the herd like adequate snow cover for snowmachine use or open water to operate boats. But it also could depend on other necessities like gas prices and having the right gear. Availability is a qualitative variable because of the difficulties measuring each of its components and is also a confounded variable.

ADF&G area management biologists select which of the availability states applies to each village. This information is based on examination of VHF and satellite collars locations, herd flyovers by biologists, reports from villagers, and an assessment of terrestrial conditions for allowing travel to hunt caribou.

Game management units provide a geographical means to separate villages. Each GMU usefully matches to a separate Alaskan Native for-profit regional corporation. GMU 22 corresponds with the Bering Strait Native Corporation; GMU 23 corresponds to the NANA Regional Corporation; and GMU 26A to the western portion of the Arctic Slope Regional Corporation. These regional corporations are composed of a relatively culturally homogeneous Native people formed under the Alaska Native Claims Settlement Act (PL 92-203, Sec. 7a). Within a GMU, villagers display similar subsistence traditions that are different between game management units (Georgette, pers. comm., 2000). Villages nearest each other are expected to exhibit similar harvest since they share caribou harvest, family members in separate villages often hunt together and they display common subsistence customs (Georgette, pers. comm., 2000).

Model construction relied on residual diagnostics to determine if violations of assumptions were made. Residuals were examined with partial regression plots, studentized residual plots, leverage, influential cases (Cook's distance, dffits, dfbetas) and spatial and autocorrelation (variogram analysis, inspection of residuals against time and the Durbin-Watson test).

Table 1. Villages, harvest survey dates and availability groupings.

Survey year	Community	GMU	Availability grouping			Village population	Village harvest
			High	Med	Low		
1987	Point Lay	26		1		121	157
1989	Golovin	22	1			169	40
	Shishmaref	22		1		472	197
	Barrow	26			1	3379	1656
	Wainwright	26	1			468	711
1990	Anaktuvuk[a]	26 (24)	1			314	592
1991	Kotzebue	23	1			2751	3782
	Anaktuvuk[a]	26 (24)	1			272	545
1992	Point Hope	23			1	699	225
	Kivalina	23		1		344	351
	Barrow	26			1	3908	1993
	Wainwright	26	1			584	748
	Atqasuk	26		1		237	262
	Nuiqsut	26			1	361	672
	Anaktuvuk[a]	26 (24)	1			270	566
1993	Wales	22			1	152	4
	Nuiqsut	26	1			361	672
	Anaktuvuk[a]	26 (24)	1			318	574
1994	Noatak	23	1			379	615
	Deering	23		1		147	142
	Nuiqsut	26			1	418	258
	Anaktuvuk[a]	26 (24)		1		318	322
1995	Shishmaref	22		1		560	342
1998	Koyuk	22	1			277	263
	Shaktoolik	22	1			235	167
	Shungnak	23	1			245	561
1999	Elim	22	1			306	227
	Stebbins	22			1	543	16
	St Michael	22			1	368	11
	Unalakleet	22		1		757	439
	Shaktoolik	22	1			216	125
	White Mtn	22	1			197	93
	Noatak	23		1		423	683
	Kiana	23		1		398	488
	Selawik	23	1			767	1289
	Nuiqsut	26		1		468	413
2000	Brevig	22		1		291	74
	Shishmaref	22		1		547	286
	Teller	22			1	281	21

[a] Anaktuvuk Pass is located in GMU 24, but because of its cultural and political ties to villages in GMU 26A, is used in GMU 26A modeling efforts.

Most often violations were outliers resulting from misplacement of a village in a availability grouping, influential cases due to Barrow and Kotzebue, and nonconstant variances. To gauge the effect of the possible influential cases of Barrow and Kotzebue, equations were fit with the two villages left out and reported harvest was perturbed by 5, 10, and 20 percent. Variance functions were used to model the variance structure of the within group errors. Akaike information criterion (AIC) was used as a guide to choose the best model when there were several candidates.

Community harvest levels are predicted for each community based on the GLS regression equations. Confidence intervals were calculated using the prediction of a new response.

Caribou harvested in GMU 26A can be harvested from three different herds, the WAH, the Teshepuk Herd and the Central Arctic Herd. The percentage of total harvest comprised of WAH caribou is estimated based on the distribution of collared caribou in each herd. Although there is uncertainty associated with assigning harvest levels to individual caribou herds where they mix, we felt this approach was better than ignoring mixing of herds altogether. (Dau, 2003; G. Carroll, ADF&G, pers. comm., 2001) The variances and the upper and lower limits of the confidence intervals are also proportionally reduced for each community.

Total local harvest of the WAH is the sum of the predictions for each community. Confidence limits for individual communities were summed to produce an interval around total harvest.

The availability groupings were randomly altered for each of the three GLS regression models as a simple way to study what effect the change in availability grouping would have on harvest for each GMU. However, for Kobuk, Ambler and Shungnak the high availability grouping was not permuted because of their proximity to the WAH migrations through Onion Portage. The GMU 23 villages located outside any WAH range (Wales, Brevig Mission, Teller, Shishmaref, and Nome) were limited to permutations of low and medium availability.

The availability groupings were randomly permuted 1000 times for each of the three GMUs. The total local harvest was calculated for each of the permuted groupings and summary statistics are produced.

Results

The GLS regression equation for GMU 22 contains both an intercept and slope for each availability group. This is commonly known as an interaction model of Analysis of Covariance. Modeling the variance–covariance matrix is needed. A model was specified in which the variance increases linearly with the fitted values.

Table 2. Predicted local harvest of Western Arctic Herd caribou by game management unit (GMU).

GMU	Estimated harvest	95% Confidence interval	
		Lower	Upper
22	2300	1600	3000
23	10800	8100	13400
26A	1600	400	3300

A data plot and regression lines for GMU 22 are in Fig. 2. Regression equations, AIC, and ANOVA table are in Table 3. Predicted harvest and 95% confidence intervals for each village in the GMU is presented in Fig. 3.

The low availability group slope and intercept coefficients are not significantly different from 0. This implies a model could be built without the low availability grouping, however, without it residual diagnostics show an unequal variance problem. Inclusion of this group of villages in the model makes sense because those villages are part of the herd harvest.

The GMU 22 model predicts 2300 caribou will be harvested annually by local residents, with 95% lower and upper confidence interval limits of 1600 and 3000 caribou harvested respectively.

The GLS regression equation for GMU 23 is a classic analysis of covariance model with one slope for all availability levels and a separate intercept for each availability state. Modeling the variance–covariance matrix is needed. A model was specified in which the variance increases linearly with the fitted values.

A data plot and regression lines for GMU 23 are in Fig. 4. Regression equations, AIC, and ANOVA table are in Table 4. All terms are significant and should be included in the model. Predicted harvest levels and 95% confidence intervals for each village in the GMU is presented in Fig. 5. Kotzebue is not shown in the figure because it would render it unreadable. Kotzebue predicted harvest is 4200 caribou with a confidence interval of between 3800 and 4600 caribou.

The GMU 23 model predicts 10 800 caribou will be harvested annually by local residents, with 95% lower and upper confidence limits of 8100 and 13 400 respectively.

The GLS regression equation for GMU 26A is a classic analysis of covariance model with one slope for all availability levels and a separate intercept for each availability state. Modeling the variance–covariance matrix is needed. A model was specified in which the variance increases linearly with the fitted values.

Table 3. Game Management Unit 22 regression equations and ANOVA table.

Low availability: (village) harvest = 3.097 + 0.029 (village) population
Medium availability: harvest = -167.361 + 0.828 population
High availability: harvest = -240.007 + 1.682 population

AIC	logLik
131.0473	-58.523671

Coefficients:

	Value	Std. Error	*t*-value	*P*-value
Slope Low	0.02947	0.02579	1.142949	0.2826
Slope Med	0.82787	0.08308	9.964230	<0.0001
Slope High	1.68217	0.20823	8.078300	<0.0001
Inter Low	3.09701	8.24228	0.375747	0.7158
Inter Med	-167.36064	37.41956	-4.472544	0.0015
Inter High	-240.00730	43.80178	-5.479396	0.0004

Residual standard error: 2.048057
Degrees of freedom: 15 total; 9 residual

A data plot and regression lines for GMU 26A are in Fig. 6. Regression equations, AIC, and ANOVA table are in Table 5. All terms are significant and should be included in the model. Predicted harvest levels and 95% confidence intervals for each village in the GMU is presented in Fig. 7. Barrow is not shown in the figure because it would render it unreadable. Barrow predicted caribou harvest is 2300 with a confidence interval of between 800 and 3700 caribou.

The percent of caribou harvested, by GMU 26A communities, made up of WAH caribou:

Village	Percent
Anaktuvuk Pass	80
Atqasuk	40
Barrow	30
Nuiqsut	10
Point Lay	80
Wainwright	40

The GMU 26A model predicts 4700 caribou will be harvested annually by local residents, with 95% lower and upper confidence interval limits of 1100 and 9600 respectively. The local harvest of WAH caribou is predicted to total 1600 by GMU 26A residents, with 95% lower and upper confidence interval limits of 400 and 3300 respectively.

Total local harvest of the WAH is 14 700 caribou with a 95% confidence interval of between 10 100 and 19 700 caribou. Examination of Table 2 shows almost 11 000 of the nearly 15 000 caribou harvested annually have been by GMU 23 residents.

Random permutations of availability groupings produced a mean harvest of WAH caribou of 15 700 with a minimum harvest of 10 900 caribou and a maximum harvest of 20 700 caribou. The GMU 22 random permutations of availability groupings produced local harvest counts from 400 to 3900 with a mean of 2000 and a standard deviation of 649. For GMU 23, random permutations of availability

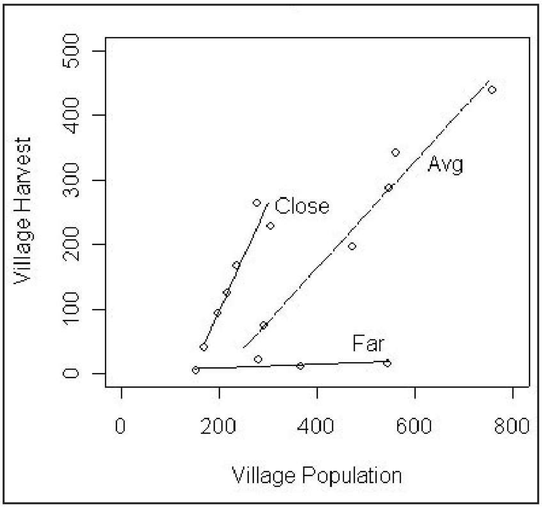

Fig. 2. GMU 22 regression model.

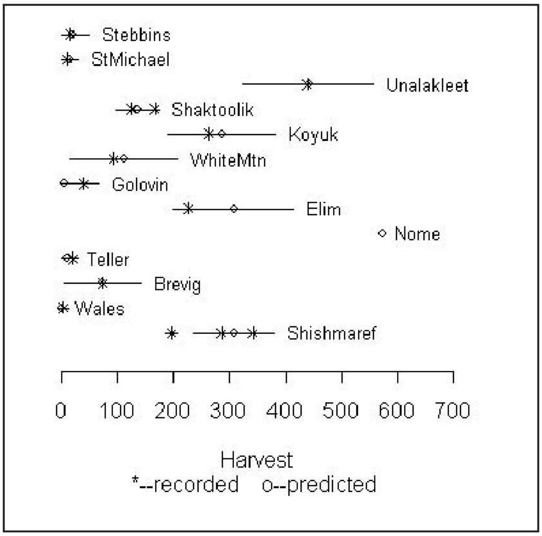

Fig. 3. GMU 22 WAH harvest and CI by village.

Table 4. Game Management Unit 23 regression equations and ANOVA table.

Low availability: harvest = -747.692 + 1.392 population
Medium availability: harvest = -75.587 + 1.392 population
High availability: harvest = 155.962 + 1.392 population

AIC	logLik
83.2502	-36.6251

Coefficients:

	Value	Std. Error	*t*-value	*P*-value
Slope Pop	1.3915	0.05729	24.290566	<.0001
Inter Low	-672.1048	50.30333	-13.361039	<.0001
Inter Med	-75.5868	27.81702	-2.717288	0.0419
Inter High	231.5488	41.21232	5.618437	0.0025

Residual standard error: 2.538328
Degrees of freedom: 9 total; 5 residual

groupings produced local harvest counts ranging from 6600 to 11 700 with a mean of 9200 and standard deviation of 973. For GMU 26A, random permutations of availability groupings produced harvest counts ranging from 3900 to 5100 with a mean of 4500 and a standard deviation of 333.

Discussion

A generalized least squares regression model has been presented relating village caribou harvest to village population size and herd availability for a village within each of 3 game management units.

Regression equations for the GMUs 23 and 26A are similar and represent analogous harvest patterns. Caribou historically have been available for these villages since many of them lie in WAH summer or migratory ranges. Caribou are considered a staple in their diet (Georgette, pers. comm., 2000). The regression equations reflect this with a common slope (for population) but separate intercepts for the 3 availability groups, indicating each could be thought of as a level or degree of harvest.

The regression model for GMU 22 is an interaction model for which each availability state is represented by a distinct equation with an individual slope and intercept for each state. The model for GMU 22 indicates each availability state has a different harvest regimen.

The villages in the low availability state are outside or near the fringe of the range of the herd. Harvest from this group is negligible as noted by the near zero statistically nonsignificant slope coefficient for population. The medium availability state is composed of villages nearby or within the outer or winter ranges but villages close enough to harvest WAH caribou when accessible. The importance of the harvest from this group is suggested by the statistical significance of the slope coefficient for population. The villages in the high availability state are within the winter range. The slope coefficient for population is double the same coefficient of the medium availability grouping suggestive of increased dependence on caribou by the high availability group.

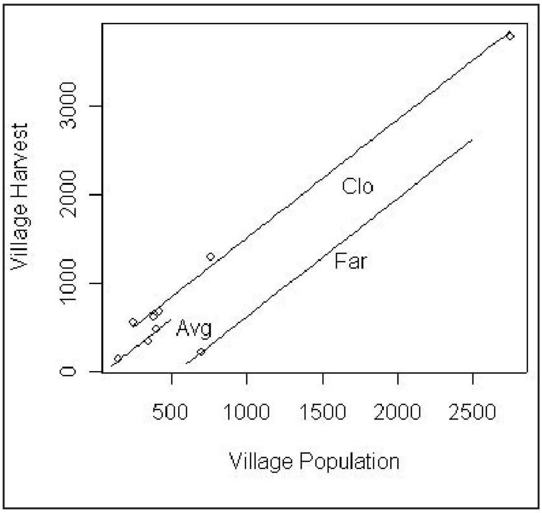

Fig. 4. GMU 23 regression model.

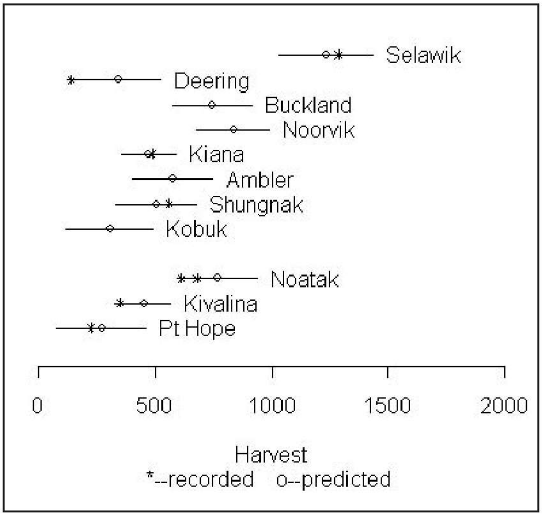

Fig. 5. GMU 23 WAH harvest and CI by village.

Table 5. Game Management Unit 26A regression equations and ANOVA table.

Low availability: harvest = 59.151 + 0.491 population
Medium availability: harvest = 140.975 + 0.491 population
High availability: harvest = 446.91 + 0.491 population

AIC	logLik
141.5113	-65.75564

Coefficients:

	Value	Std. Error	*t*-value	*P*-value
Slope Pop	0.49081	0.016158	30.376120	0.0000
Inter Low	-81.82445	23.850279	-3.430754	0.0056
Inter Med	140.97545	13.989387	10.077314	0.0000
Inter High	305.93522	20.460161	14.952728	0.0000

Residual standard error: 1.632186
Degrees of freedom: 15 total; 11 residual

Population has varied little in WAH-area villages through time. The effect of increasing village population size will increase WAH harvest. Since population sizes have not changed appreciably, WAH local harvest is expected not to change much either.

The random permutation of availability groupings shows harvest changes depending on accessibility of caribou. This is most striking in GMU 22 where, for the worst-case scenario, harvest could be less than a quarter of what it is now. This could be a situation where the herd shrinks and/or winters out of GMU 22. In the situation where the herd becomes highly available to all villages, harvest will double.

Random permutation of availability groupings for GMUs 23 and 26A produces less notable changes in village harvest. This exercise indicates local village harvest is not as dependent on herd availability.

The existing village sampling has been subjective. A scheme is needed to select villages for harvest surveys to ensure we obtain information from each element in our model space. This directs a village should be sampled from within each of the 3 availability states in a GMU for a total of 9 villages surveyed per year. Villages surveyed should be randomly chosen from within each availability grouping in the GMU. Funding is improbable for a complete yearly selection of 9 villages. A reduced village sample selection effort should be examined for its effects on harvest estimates.

WAH herd size is not incorporated into this model but may affect harvest. A larger herd may allow increased opportunity for harvest for all villages. It may also visit areas not usually frequented by the WAH allowing for harvest near or outside its periphery range. Addition of a herd size component to the models deserves investigation.

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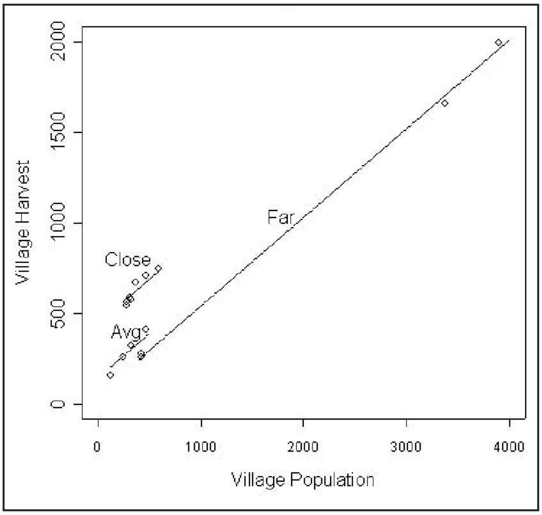

Fig. 6. GMU 26A regression model.

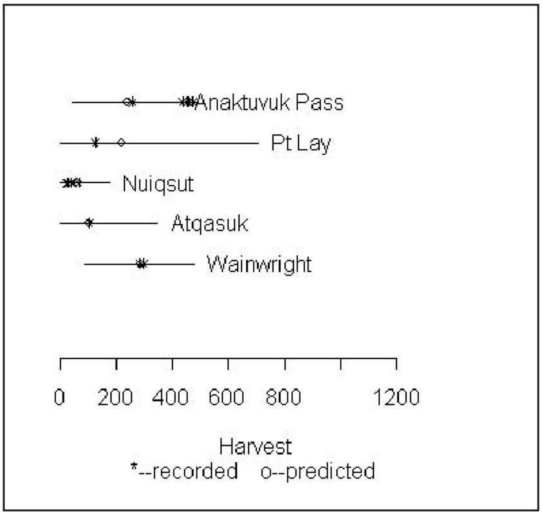

Fig. 7. GMU 26A WAH harvest and CI by village.

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St. Matthew Island reindeer crash revisited: Their demise was not nigh—but then, why did they die?

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Abstract: Twenty-nine yearling reindeer (*Rangifer tarandus*) were released on St. Matthew Island in the Bering Sea Wildlife Refuge in 1944: 24 females and five males. They were reported to have increased to 1350 reindeer by summer 1957 and to 6000 by summer 1963. The 6000 reindeer on St. Matthew Island in summer 1963 were then reduced by 99% to 42 by summer 1966. The evidence suggests that after growing at a high average annual rate of $\lambda = 1.32$ for 19 years, the entire die-off occurred in winter 1963–64, making it the largest single-year crash ever recorded in any *R. tarandus* population. Although a supposedly meaningful decline in successful reproduction and early survival of calves was originally reported for the population between 1957 and 1963, our reevaluation indicates this is an error resulting from the wrong sample being used in the between-year comparison. The quantitative data indicate no meaningful change occurred, and the calf:cow ratio was about 60 calves:100 cows in both 1957 and 1963. Calf production and survival were high up to the crash, and in the die-off population the age distribution (72%, 1–3 years old) and the sex ratio (69 males:100 females) reflected a still fast-growing *R. tarandus* population. All of these parameters do not support the hypothesis that the limited abundance of the absolute food supply was at a lethal level between 1957 and 1963 or in winter 1963–64. We now know from other studies that a high density of *R. tarandus* is not a prerequisite for a major single-year winter die-off. Existing population dynamics data do not support lack of lichens as a major causative factor in this single-year crash. If a decline had been caused by the limitation of the absolute food supply, it would have followed a multi-year pattern—it would not have been a single-year event. There was no evidence of a sudden, massive, island-wide loss of the absolute food supply, or that its nutritional value was inadequate for sustaining the reindeer. Mean weights of reindeer by sex and age class declined between 1957 and 1963, but only to levels similar to those of mainland reindeer. The reindeer population on St. Matthew Island undoubtedly was or soon would have been seriously influenced by heavy use of the lichens and the future did not bode well for continued population growth. Although the food supply through interaction with climatic factors was proposed as the dominant population-regulating mechanism, a general acceptance that only density-dependent food-limitation was necessary to cause the crash remains strong in some quarters. We challenge this; we believe that the winter weather was the all-important factor that led to the premature, extreme, and exceptionally rapid, near total single-year loss of 99% of the reindeer on St. Matthew Island in winter 1963–64.

Key words: climate, forage, growth rates, introduced population, *Rangifer tarandus*, single-year die-off, weather.

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Introduction

Growth of populations of reindeer and caribou (*Rangifer tarandus*) and other large ungulates can be regulated by limitation of the absolute food supply, especially in the absence of exceptionally severe weather years and heavy predation or hunting pressure (e.g., Riney, 1964; Caughley, 1970; Leader-Williams, 1980; Skogland, 1986; Fowler, 1987). Our intent here is not to challenge regulation of a population through density-dependent limitation of its absolute food supply per se, but to suggest that such regulation of *R. tarandus* populations is often overemphasized and accepted uncritically without adequate proof. In fact, both biotic and abiotic limiting factors, in the absence of density-dependent limitation of the absolute food supply, can and do play a dominant sporadic or periodic functional role in population setbacks.

Twenty-nine yearling reindeer were released on St. Matthew Island in 1944. Klein (1959, 1968) estimated that they increased about 46-fold by 1957 and 207-fold by 1963. The reindeer population then crashed, leaving only 42 reindeer alive when he returned to St. Matthew Island in summer 1966 (Klein, 1968). He believed that the entire 99% die-off of 6000 reindeer occurred in winter 1963–64, making it the largest single-year crash known for any *R. tarandus* population. Klein (1968: 366) concluded that the "Food supply then, through interaction with climatic factors, was the dominant population-regulating mechanism for reindeer on St. Matthew Island." However, this statement does not unambiguously identify which factor specifically caused the crash of reindeer on St. Matthew Island. We believe the St. Matthew Island crash has been commonly referenced (e.g., Haber & Walters, 1980; Reimers, 1982; Gates *et al.*, 1986; Adamczewski *et al.*, 1988; Leader-Williams, 1988; Ouellet *et al.*, 1996) and widely used in discussion as an example of density-dependent population regulation that can often be expected to occur in *R. tarandus* populations. This inference has created a serious shortcoming in understanding the true relationship between *R. tarandus* and its environment.

Unfortunately, many biologists have focused on the high density of reindeer at the time of the St. Matthew crash as a supposed prerequisite for the crash and have accepted Klein's (1968: 366) statement that "… the relatively poor condition of the reindeer going into the winter [1963–64] as a result of competition for high quality summer forage during summer 1963 …." as factual—when in fact there are no quantitative measures to support this supposition. Leader-Williams (1988) subsequently made a detailed comparison between reindeer introduced to South Georgia and those introduced to islands around the world, especially to Alaskan islands, and particularly to St. Matthew and St. Paul islands. In doing so, he perpetuated the same points that we challenge herein, as he did no reanalysis of the data for those points. The inference that reindeer on St. Matthew Island would not have crashed if population density had not been high and food had not been depleted remains strong.

We argue that neither the state of the absolute food supply nor the condition of the reindeer going into the winter of 1963–64 played a major role in either the single-year precipitous decline or in the magnitude of that crash. There are examples of caribou populations with low mean densities and some with relatively high mean densities before the initiation of a single-year crash where the absolute food supply was adequate but made relatively unavailable due to extremely unfavorable snow or ice conditions. This paper is not meant to be a general review of population dynamics of *R. tarandus* populations on islands; rather, our sole aim is to address what really caused the St. Matthew Island reindeer crash in winter 1963–64 and what in fact dictated the number of animals that survived it. We are not expanding this consideration to multi-year declines of reindeer or caribou populations and, especially, not to large mainland *R. tarandus* populations. We consider only this one isolated event and compare it to other isolated events in island environments, to explain the St. Matthew Island reindeer crash.

In reevaluating the reindeer crash on St. Matthew Island in winter 1963–64, we have the benefit of hindsight and good documentation from a number of new studies of different reindeer and caribou herds over the past 36 years. Our intent is to clarify and expand the ecological considerations associated with Klein's (1959, 1968) findings, not to criticize the original interpretation. We review the evidence from Klein (1959, 1968) and come to the conclusion that only the winter weather was the all-important factor that caused the crash. We hope that this paper will stimulate others to further evaluate limiting factors influencing *R. tarandus* population growth with adequate consideration given to the many factors that influence population size (e.g., Valkenburg *et al.*, 1996; Whitten, 1996; Boertje & Gardner, 2000).

Materials and methods

The subarctic oceanic island of St. Matthew is 332 km^2 (128 mi^2), lying in the north-central Bering Sea at 60°30'N, 172°30'W. Although multi-year weather records are available only from St. Paul and Nunivak islands about 400 km away, the St. Matthew Island climate is similar to those islands, being subarctic maritime characterized by cool and humid summers but with a relatively long plant growing season compared to interior mainland and arctic island ranges. Winter snowfall is relatively heavy, and strong winds and above-freezing temperatures are common. Klein (1968: 360) describes the island as arctic tundra low-lying vegetation—only a few grasses and forbs annually exceed 30 cm in height. The only common shrubs are decumbent willows (*Salix* spp.). He also noted that the vole (*Microtus abbreviatus*) and the arctic fox (*Alopex lagopus*) were the only native land mammals found there before the introduction of reindeer.

On 20 August 1944, 29 yearling reindeer, 24

Table 1. Total quantitative data available from Klein (1959, 1968) for determining the size and sex and age composition of the St. Matthew Island reindeer population in 1957 and 1963.

Year	Parameters	Sample	N	Calves	Yearlings	Cows	Bulls
1957	Total count	A	1226	?[a]	?	?	300
	Calf sample	B	910	267	?	?	none
	Yearling sample	C	(218)[b]	75	45	99	none
	Population estimate	D	1350	280	190	470	410
1963	Calf:cow ratio	E	1652[c]	60 calves:100 cows			
	Yearling:cow ratio	F	705[c]	26 yearlings:100 cows			
	Population count	G	6000	?	?	?	?
1966	Skeletal sample[d]	H	241	48	56	86	51

[a] "?" values not reported in Klein (1959, 1968).

[b] Reported by Klein (1959) as "218" but 75 + 45 + 99 = 219.

[c] No numbers were reported for calves, yearlings, cows, or bulls in the two 1963 samples or in the 1963 total population count.

[d] Skeletal sample was collected by Klein (1968) in summer 1966: he assumed it was representative of the 1963–64 die-off population.

female and five male, were released on the island. Only 105 reindeer are known to have been harvested on St. Matthew Island between 1944 and 1964, all during the 1957–63 period.

Klein (1959, 1968) recognized five sex and age classes: calves, female yearlings, male yearlings, cows, and bulls. We report the quantitative values obtained in 1957, 1963, and 1966 by Klein (1959, 1968) and our calculations of sample compositions, calf:cow and yearling:cow ratios, percent calves, percent yearlings, and also our corrections to some values used by Klein (1968).

The main focus of Klein's (1959, 1968) studies was the investigation of the vegetation on St. Matthew Island and its changes from 1957 to 1963, with some follow-up in 1966. Information on population dynamics was secondary to the above studies. However, those population data are what allows a reader to interpret and evaluate the 1968 report—and it is impossible to do so without also reading the 1959 report in detail and comparing the two. Therefore, we have carried out a detailed comparative review of both papers to provide a fuller assessment along with a reasonable alternative evaluation for what in fact caused the crash event.

Counts of reindeer made in summers 1957 and 1963 do not lend themselves directly to a complete evaluation of the sex and age composition of the entire population (Tables 1 and 2). The population data obtained by direct count for the reindeer in 1957 and 1963 were fragmentary and require calculations and estimation to attain a fuller set of values. Even then, little sex and age information can be extracted for reindeer in summer 1963, so the skeletal sample obtained by Klein (1968) in summer 1966 representing the 1963–64 die-off population must be relied upon.

Klein (1959) made three counts in 1957: the first is termed a 'total count' (Table 1: A-see sample column in table) and the other two are referred to as the 'calf sample' (Table 1: B) and the 'yearling sample' (Table 1: C). Klein (1968) then produced the 'population estimate' (Table 1: D) by inflating the total count by 10% and rounding to the nearest multiple of 10. The only count of any sex or age class in the total count was of bulls, so the number of non-bulls in the total count is 926 (1226 - 300). Therefore, to reproduce the values for the total population estimate in Klein (1959), we calculated the numbers of calves, yearlings, and cows as follows: calves equal the number of calves in the calf sample times the total count minus the number of bulls divided by the size of the calf sample (272 = 267 × 926/910); yearlings equal the number of yearlings in the yearling sample times the total count minus the number of bulls divided by the size of the yearling sample (190 = 45 × 926/219); and the number of cows equal the total count minus the number of bulls minus the summation of the number of calves and yearlings (464 = 926 - 272 - 190). The number of calves, yearlings, cows, and bulls in the population estimate is then obtained by inflating the number of calves and cows calculated for the total count to the next multiple of 10 (Table 1: D), holding the yearlings at their calculated value for the total count and inflating the number of bulls in the total count by 37% (0.367 = (410 - 300)/300). Klein (1959) believed that most of the missing animals were bulls: he counted 300 in the total count and estimated 410 in the population estimate; therefore, he extrapolated an additional 110 bulls. The remaining 14 animals among the 124 extrapolated were calculated to be eight calves and six cows. There were no bulls in the calf and the yearling samples in 1957 and bulls in the total count are underrepresented by

Table 2. Comparisons made for evaluating the 1957 and 1963 St. Matthew Island reindeer population parameters: see Table 1 for raw data from Klein (1959, 1968).

Studies	Parameter	1957 Sample sourcea	1957 versus 1963		1963 Sample source[a]
			1957	1963	
Klein	% Calves	C	(34%)[b]	20%	H
	% Calves	B	29%[b]		
	% Calves	D	21%		
	Calves:100 cows	C	75:100[b]	60:100.	E
	Yearlings:100 cows	C	45:100[c]	26:100[d]	F
This study	% Calves	D	21%	20%	H
	Calves:100 cows	D	60:100	56:100	H
	Yearlings:100 cows	D	40:100	65:100[e]	H

[a] See Table 1 for raw data from sample source.

[b] Biased high for calves.

[c] Biased slightly high for yearlings.

[d] Questionable value: most likely biased low for yearlings.

[e] Questionable value: most likely biased high for yearlings.

37% compared to the population estimate; so, we assume that the most accurate calf:cow and yearling: cow ratios come from the population estimate in 1957 (280/1350 and 190/1350, respectively).

The calf:cow ratio was obtained from the larger of the two samples in 1963 and the yearling:cow ratio from the smaller sample (Table 1: E and F). The 1963 total population count was obtained directly from the aerial survey results (Table 1: G). Klein (1968) did not report the numbers of calves, yearlings, cows, and bulls in the 1963 total population count or the two samples that the calf:cow and yearling:cow ratios come from in 1963. Both ratios can be derived from the 1966 skeletal sample of the 1963–64 die-off population (Table 1: H). Proportional representation of calves, yearlings, cows, and bulls can only be calculated from the skeletal sample (Klein, 1968).

Defining crash

The term 'crash' has been used loosely over the years to equate to virtually all marked downturns in population size. This use is common, regardless of the number of years involved in the downturn. Perhaps, most importantly, no due notice is given to the annual magnitudes of changes in population size during these "crash" events. This is true, even if annual changes vary from losses to temporary annual gains, as long as the end result is a major reduction in the size of the population. This seriously detracts from any ecologically or biologically accurate evaluation of the differences in a rapid population crash versus a prolonged population decline often lasting more than a decade, following an extended period of moderate to high population growth (*cf.* Caughley, 1970).

Merriam Webster's Collegiate Dictionary (10th ed.) defines a 'crash' as "a sudden decline (as of a population), marked by a concerted effort and effected in the shortest possible time." We define a 'population crash' as a single-year event where 30% or more of a population is lost in that year. We argue that the term crash should be restricted to describe only annual events that exceed the 30% level of decline. We would define an 'extreme population crash' as a single-year event where ≥ 50% of the animals die. Annual crashes occurring over three consecutive years are known (Miller, 1998; Gunn & Dragon, 2002; Miller & Gunn, 2003a, b). To refer to a major loss of animals that takes place over a decade or more as a crash is misleading. This is true even if the end result is essentially the same. More than anything else, it is the rapidity, sporadic infrequency, and unpredictability of a crash event that sets it apart from a protracted downturn and marked decline that takes place over a series of years after and as a consequence of an extended continual period of appreciable overall population growth.

There are a number of density-dependent relationships that could cause a major protracted population decline; however, we know of no possible density-dependent mechanism that could or would cause an extreme single-year crash in the first year of a decline. On the other hand, some density-independent abiotic factors could have and have caused exceptionally large annual winter die-offs and crashes among island populations of reindeer and caribou (e.g., Reimers, 1977, 1982, 1983; Gates *et al.*, 1986; Adamczewski *et al.*, 1988; Stimmelmayr, 1994; Ouellet *et al.*, 1996; Miller & Gunn, 2003a, b). Biotic factors (predation, disease, and parasites) could act to dampen or reverse population growth in a density-independent or density-dependent fashion, but most likely would not affect a rapid near-total single-year decline in a population.

Defining starvation

We use the term 'starvation' to mean death by extreme and prolonged undernutrition. Some ruminal contents may be present but not of adequate quality to sustain life.

Reevaluation of population status in relation to density-dependent food limitation

Calf to cow and yearling to cow ratios

Klein (1968: 352) states "In the 1957 counts, the ratio of fawns to adult females was obtained from a sample of 910 animals and the ratio of yearlings to adult females from a sample of 218 [actually 219] reindeer. In these samples there were 75 fawns and 45 yearlings per 100 adult females." The stated value of "75 fawns ... per 100 adult females" cannot be reproduced from the 1957 sample of 910 reindeer (Table 1: B). The only explanation based on existing data is that the 75 fawns per 100 adult females reported by Klein (1968: 352) was inadvertently taken from the smaller 1957 sample of 219 reindeer with 75 calves and 99 cows (see Table 1: C). This error creates a false impression that there was a documented major decline—when there was not.

Of particular importance in determining which sample must have been used is the fact that no measure of cows is provided in the 1957 sample of 910 reindeer; as a result, no ratio of calves:100 cows can be calculated directly from that sample (Table 1: B). It can be extrapolated indirectly from other information provided in the 1959 report. When the extrapolation is made, the calf:cow ratio is only 60 calves:100 cows (Table 2). Notably, Klein (1959: 7) rejected and did not use the small sample of 219 to calculate a calf:cow ratio because he believed it was biased. Calves were markedly overrepresented, as there were no bulls present in the sample (Table 1: C) and the total population estimate yielded a ratio of only 60 calves:100 cows.

The three measures of the number of yearlings:100 cows that can be obtained from the 1957 data are all similar: there were 40 yearlings:100 cows from the values for the total herd of 1350 animals (Klein, 1959: Table 2); 41 yearlings:100 cows from the extrapolated sex and age composition of the total count of 1226 reindeer; and 45 yearlings:100 cows from the sample of 219 reindeer. We believe the 40 yearlings:100 cows is the best measure in 1957, as it is drawn from the total population estimate (Table 1: D; Table 2).

In 1963, Klein (1968: 352) reports 60 calves:100 cows from a sample of 1652 reindeer and 26 yearlings:100 cows from a sample of 705 reindeer (Table 1: E and F). In the 1966 skeletal sample, which Klein (1968) said was representative of the 1963 population, there were 56 calves:100 cows. When the calves in the skeletal sample are arbitrarily adjusted by 10%, in accordance with Klein's (1968) suggestion of underrepresentation for calves, this ratio rises to about 61 calves:100 cows in the 1963 population.

The 1957 yearling sample indicates that the number of yearlings to cows ranged between 40 and 45 yearlings:100 cows. In the 1966 skeletal sample, there were about 65 yearlings:100 cows (Klein, 1968). This certainly suggests a greater representation of yearlings than the 40–45 yearlings:100 cows obtained in 1957. Most importantly, it is also 2.5 times greater than the value obtained by Klein (1968: 352) from his sample of 705 reindeer in 1963. This puts both the yearling:cow counts obtained in summer 1963 and the 1963 yearling:cow count obtained from the 1966 skeletal sample into serious question. Even the average of 26 yearlings and 65 yearlings would still provide a value of 46 yearlings:100 cows; therefore, the number of yearlings to cows in 1963 most likely was similar to those values from 1957.

There is an unexplained contradiction in the acceptance of the 1966 skeletal sample as representative of the sex and age composition of the 1+yr-old segment of the 1963 population (Klein, 1968). We do not understand why the low 1963 yearling:cow ratio from the sample of 705 animals was used instead of the much larger yearling:cow ratio obtainable from the 1966 skeletal sample that Klein (1968) said was supposedly representative of the 1963–64 die-off population. Given the lack of evidence for a significant reduction in proportional representation of calves and yearlings from 1957 to 1963, the low value obtained for yearlings in the 1963 sample of 705 reindeer and the high value obtained from the skeletal sample are enigmas. It seems highly questionable that either the low contribution of yearlings in the sample of 705 or the high contribution from the skeletal sample was truly representative of the relative occurrence of yearlings in the entire herd of 6000 reindeer in 1963. It is more reasonable to believe the true value fell somewhere in between. Thus, there is no quantitative evidence to support meaningful breeding depression or reduced early survival between 1957 and 1963 or even in 1963 only, particularly in terms of the pending crash of the population and the required 28% average annual rate of population increase from 1957 to 1963.

Observed rates of population growth and required annual rates of increase

The observed rate of growth during the 13 years from 1944 to 1957 required an average annual rate

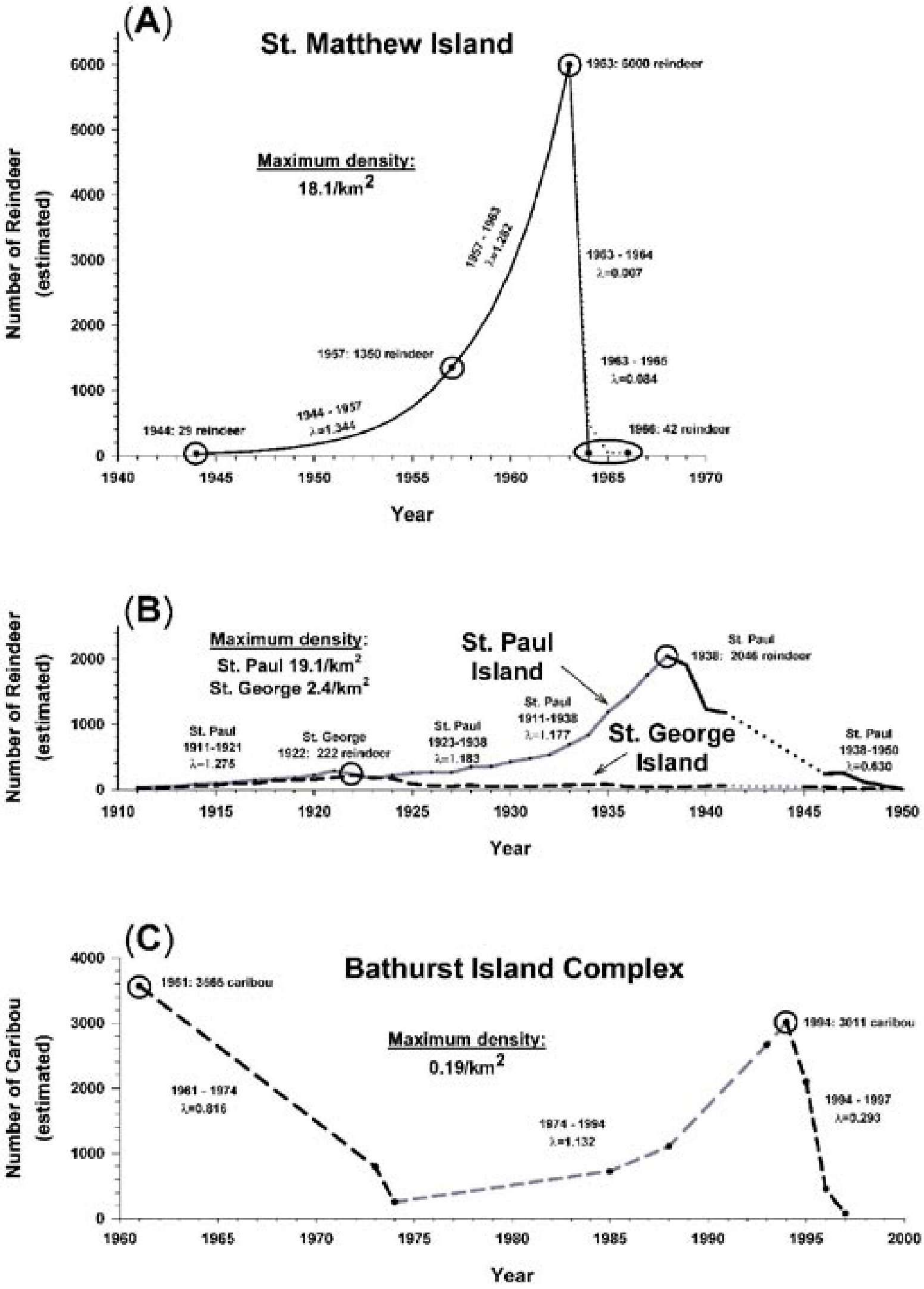

Fig. 1. (A) Assumed population growth of St. Matthew Island reindeer herd: a high-density introduced reindeer population experiencing a single-year crash (after Klein, 1968: Fig. 2; data sources Klein, 1959, 1968); (B) Assumed population growth of St. Paul Island and St. George Island reindeer herds: St. Paul—a multi-year decline of a high-density introduced reindeer population with continued decline at low densities; and St. George—an introduced reindeer population 'locked in' at relatively low densities (data from Scheffer, 1951: Table 1; Fig 1); and (C) Assumed population growth of Bathurst Island complex indigenous Peary caribou population: the fall, rise, and consecutive 3 years of single-year crashes of an extremely low-density Peary caribou population (data from Tener, 1963; Miller *et al.*, 1977; Miller, 1987, 1989, 1995, 1998; Gunn & Dragon, 2002).

of increase of $\lambda = 1.34$ (Fig. 1A). This is considerably greater than population growth rates in established, free-ranging, indigenous caribou populations (e.g., Davis *et al.*, 1980, Western Arctic Herd, 14%, 1976–79; Messier *et al.*, 1988, George River Herd, 14%, 1955–84, and 11%, 1970–84), although Valkenburg *et al.* (2000) did record similar high mean rates of increase for shorter periods of time among four of seven herds of *R. t. granti* translocated in Alaska.

As reported by Leader-Williams (1980), reproduction and survival at the theoretical maximum annual rate of increase could have meaningfully altered the realized average annual growth rate. Klein (1968: 352) suggested that "Under the assumed ideal range conditions on St. Matthew Island at the time of the release, the introduced nucleus herd probably increased at a rate approaching the theoretical maximum during the years immediately following." If so, and the theoretical maximum was realized with no mortality among calves and the 1+ yr olds in the first two years of pristine range conditions, the introduced herd would have grown at 83% from 1944 to 1945 and at 68% from 1945 into 1946. The sex ratio was highly skewed in favor of females at 24 to five in summer 1944. By summer 1946 under this scenario there would have been 89 reindeer and the sex ratio would have become balanced at about 60 females:40 males, assuming no mortality and a 50:50 sex ratio among calves. For the following 11 years, an average annual rate of increase of 28% would be all that would be necessary to get to the population estimate of 1350 in 1957. This is the growth rate documented by Klein (1968: $\lambda = 1.28$) for the 6 years from 1957 to 1963. This would suggest that after an initial two-year increase at the maximum rate of population growth, it would be necessary for the reindeer population to average only 28% per year—not 34%— to reach 1350 by 1957 and 6000 by 1963. Under this scenario, there could be no meaningful change in the reindeer's capability to sustain themselves on the absolute food supply, in the relative availability of that food supply for the reindeer up until the crash, or in annual rates of reproduction, survival, or mortality during those last 17 years. If so, there is no support for advanced limitation of the absolute food supply being in place.

Changes in body weight between 1957–63 and 1963 range conditions

There was a general reduction in body weight by sex and age class after 1957 (Klein, 1968: Table 2), but this may not equate to reduced biological performance. It does not follow that the reduced weights were critical to future reproductive success or survival of those reindeer: statistical significance is not in itself a measure of biological meaningfulness, especially when the statistical differences are based on such small samples (e.g., Yoccoz, 1991; Steidl *et al.*, 2000; Anderson *et al.*, 2001; Guthery *et al.*, 2001). It is the nutritional state and physical condition of the individual that matters, not total body mass. The reported decline in body weight is in itself unconvincing; given the small sample sizes for all reindeer and especially for the young animals, and given that only the mean values are presented with no measures of variation. Although individual body weights dropped to a level similar to those of reindeer on the mainland of Alaska (Klein, 1968), we contend that the sex and age composition argues more strongly for no large change in production and survival from 1957 to 1963 or 1963–64. Two 1963 calves were pregnant (Klein, 1968), suggesting no reduction in forage sufficient to markedly reduce reproductive rates.

Even though the lichen mat component of the food supply had been seriously reduced on St. Matthew Island by summer 1963, Klein (1968: Tables 8 and 9) reported 16–21% protein in summertime rumen samples. These protein values are high compared to other published values (e.g., Nieminen & Heiskari, 1989) and are adequate for nutrition, breeding, and reproduction. The overall average annual rates of population growth from 1944–63, the reported percentages of 1963 calves still alive in winter 1963–64, and the sex and age composition of 1+ yr-old animals estimated in the die-off population do not indicate any major slowdown in population growth before the crash. All of these population parameters actually suggest the potential for continued high rates of population growth.

Alternative explanation and associated ecological implications

Extreme weather restricting forage availability in winter 1963–64

Klein (1968: 354) reported "The winter of 1963–64 on the islands of the Bering Sea was one of the most severe on record from the standpoint of the amount and duration of snow on the ground and extreme cold." The magnitude of a single-year crash is virtually independent of any density-dependent relationship between the reindeer and their absolute food supply before the weather event took place. That is, it is the severity, extent, and duration of the unavailability of the forage caused by exceptionally severe snow conditions that dictated the number of animals that would survive – not the starting density or nutritional condition of the animals in this particular situation.

Our position does not completely rule out the possibility that the state of the absolute forage supply at the time of the extreme weather contributed somewhat to at least the initial acceleration of deaths during the crash. However, the important point is that the single-year crash would have occurred regardless of the abundance of the absolute food supply. This is true because the absolute food supply had to be rendered unavailable island-wide for a long enough time to create lethal conditions of this magnitude (i.e., 99% loss), regardless of the abundance of the absolute food supply, the initial density of the reindeer, or the condition of those reindeer.

Reindeer in relatively poor nutritional condition entering such an exceptionally stressful time might die sooner than 'healthy' reindeer, but when the extremely severe condition persists long enough, the end result is the same and most animals will die. An important question is whether the St. Matthew Island reindeer population would have necessarily crashed in 1963–64, especially to the same degree, if it had not experienced exceptionally prolonged, unfavorable snow conditions. We believe the answer is—no! The lichen mat component of the forage had received heavy reindeer use on some wintering areas on St. Matthew Island as early as 1957, but sedges and grasses actually had increased (Klein, 1959, 1968).

Another important question is whether the reindeer would have crashed in 1963–64 under the same weather extremes but with the lichen mat component still abundant? We believe the answer is—yes! The lichen loss over the several years before the crash did not greatly reduce calf births, survival of calves to yearlings, or winter survival of reindeer of either sex and all ages. We believe that the estimated decline in growth from 34% (1944–57) to 28% (1957–63) per year does not reflect a population suffering extreme nutritional stress, nor a meaningfully dangerous depression in population growth. If it did, then virtually every *R. tarandus* population in the world would have to be considered in a continual state of extreme nutritional stress! Also, if the theoretical maximum annual rate of population increase was realized in 1944–46, as previously discussed, there would have been no depression in the average annual rate of population growth for the 17 years from 1946 to 1963. The 28% per year population growth rate, occurring after serious reduction of the lichens, still approaches the suggested realized maximum rate of $r \approx 0.30$ for North American caribou (Bergerud, 1978).

Similar to the reindeer on St. Matthew Island, the reindeer introduced on St. Paul Island increased rapidly over nearly 3 decades (27 yr) at about one-half the annual rate of increase of reindeer on St. Matthew Island: i.e., $\lambda = 1.18$ *versus* $\lambda = 1.32$, respectively. After the peak in 1938, their temporal patterns of decline differed markedly from the St. Matthew Island population, but the end result was essentially the same (Fig. 1B). The St. Paul reindeer herd declined during a 12-year period nearly to extirpation in 1950 (Scheffer, 1951). They then experienced a population recovery over the next 12 years and suffered a crash of about 40% in winter 1962–63 at only about one-third of the overall density they were at in the first year of decline in 1938–39 (Swanson & Barker, 1992: Fig. 6). When the reindeer were at their highest mean density of $19.1 \bullet \mathrm{km}^{-2}$ in 1938, they declined < 7% in one year. Then in 1939, when at $17.8 \bullet \mathrm{km}^{-2}$, they declined 36% in 1 year. Yet, 7 years later, in 1947, three consecutive years occurred with major crashes, with the reindeer population falling at 68% per year from a mean density of only $2.2 \bullet \mathrm{km}^{-2}$ to $< 0.1 \bullet \mathrm{km}^{-2}$.

The reindeer decline on St. Paul Island, unlike the one on St. Matthew Island, appears to have followed the pattern of decline that was hypothesized by Caughley (1970) for irrupting ungulate populations. However, we believe, as did Gunn *et al.* (2003), that the last 3 years of the first overall decline (1938–50) do not appear to be a solely density-dependent relationship—the 68% average annual rate of decrease suggests that unfavorable weather was driving the decline at that time. Most likely the decline was accelerated and deepened by compaction of the snow cover by strong winds and the presence of different mechanisms of widespread or even range-wide icing on, in, or under the snow pack caused by winter rain events and thaw-freeze periods. These have been reported previously for St. Paul Island and other islands in the region (e.g., Scheffer, 1951; Bos, 1967; Lent, 1999); also for Svalbard reindeer, *R. t. platyrhynchus* (e.g., Reimers, 1977, 1982, 1983); and for Peary caribou, *R. t. pearyi* (e.g., Parker *et al.*, 1975; Miller *et al.*, 1977; Miller & Gunn, 2003a, b) and elsewhere.

Although winter 1963–64 was reported as one of "extreme cold" for St. Matthew Island (Klein, 1968) and reiterated by Leader-Williams (1988), what is considered "extreme cold" is relative to the geographical location under consideration. Weather records from St. Paul Island indicate considerable fluctuations in temperature above and below 0 °C during the 1963–64 winter. The coldest month on St. Paul Island was February 1964 with a monthly average minimum of -12.7 °C and a monthly average maximum of -5.7 °C. By contrast, the monthly average minimum and maximum temperatures for February 1964 in the central Canadian Arctic Archipelago (Resolute Airport: Climate Archives of Canada) were -38.1 °C and -31.3 °C or about 25 °C colder than on St. Paul Island. Only three monthly average maximum temperatures fell below the freezing point on St. Paul Island in winter 1963–64 (Jan, -0.6 °C; Feb, -5.7 °C; and Mar, -2.8 °C) (http://www.wrcc.dri.edu/summary/lcdak.html). No one knows whether there was extensive icing compounding the severity of the snow pack on St. Matthew Island in winter 1963–64—and no one ever will. Freezing rain events could have occurred under the temperature regime recorded in any month of the 1963–64 winter on St. Paul Island, and by inference on St. Matthew Island. Thus, the probable role of icing cannot be ruled out and should not be ignored, as it can be an important factor in the life equation of any *R. tarandus* population living on islands with low-growth tundra forms of forage plants (e.g., Miller *et al.*, 1977, 1982).

Comparison to Canadian High Arctic Islands

The reindeer situation on St. Matthew Island is not directly comparable to the Peary caribou situation on the Canadian High Arctic Islands because the High Arctic has a more unpredictably severe climate and the islands are linked by sea ice for 9–10 months of the year. Peary caribou can disperse in response to environmental conditions or migrate seasonally between or among islands (e.g., Miller, 1990; Miller *et al.*, this proceedings). Also of importance, Peary caribou live with a larger grazer, the muskox (*Ovibos moschatus*) and their major predator, the wolf (*Canis lupus*).

However, the most detailed examples of a low-density Peary caribou population experiencing winter–spring crashes come from the Bathurst Island complex (Fig. 1C). The single-year crashes that occurred in 4 out of 24 years between 1973 and 1997 among Peary caribou on the western Queen Elizabeth Islands of the Canadian High Arctic conclusively show that a high animal density is not mandatory for population crashes (Parker *et al.*, 1975; Miller *et al.*, 1977; Miller, 1998; Gunn & Dragon, 2002; Gunn *et al.*, 2003; Miller & Gunn, 2003a, b). Such major crashes could occur even at exceptionally low caribou densities. Bathurst Island at 16 042 km^2 and Melville Island at 42 149 km^2 are 48 and 127 times as large as St. Matthew Island (332 km^2). On Bathurst Island, Peary caribou crashed by 68% in 1973–74 from 0.04 caribou • km^{-2}; by 30% in 1994–95 from 0.18 caribou • km^{-2}; by 78% in 1995–96 from 0.11 caribou • km^{-2}; and by 83% in 1996–97 from an exceptionally low 0.03 caribou • km^{-2}. On Melville Island, Peary caribou crashed by 51% in 1973–74 from 0.81 caribou • km^{-2} and crashed by 30% in 1996–97 from an exceptionally low 0.02 caribou • km^{-2} (Miller *et al.*, 1977; Miller, 1998; Gunn & Dragon, 2002).

Thus, prolonged extremely unfavorable snow and ice conditions caused crash events in low-density populations of Peary caribou that were capable of travel on the sea ice to escape from individual islands in a region of 100 000 km^2 or beyond. It is noteworthy that muskoxen at low densities and on different diets from Peary caribou also experienced crashes in similar proportions during the same years on the same ranges (Miller *et al.*, 1977; Miller, 1998; Thomas *et al.*, 1999; Gunn & Dragon, 2002). Also, like other stochastic events, crashes can occur in consecutive years, with three consecutive years of crashes documented on the south-central Queen Elizabeth Islands (Fig. 1C: see also Fig. 3 of Miller & Gunn, 2003a). As a result, the Peary caribou population in the Bathurst Island complex plummeted an estimated 97% between winter 1994–95 and summer 1997. In each year, the apparent single cause of each crash was snow and ice conditions that were exceptionally severe and prolonged.

Ecological implications of cause versus effect (response)

In order to advance our ecological understanding of a crash event, it is necessary that we comprehend why the crash occurred. Thus, it is all-important to first clearly identify the fundamental cause of the crash. In the absence of a sudden island-wide massive loss of vegetation and in the absence of predators, competitors, contagious disease or heavy parasite burdens, only weather in the form of deep snow, densely compacted snow, snow compounded by extensive icing, or thick island-wide icing can cause such a single-year cataclysmic crash event. Total snowfall on St. Paul Island in 1963–64 was 2.6 m. If a similar, or even a considerably lesser, amount fell on St. Matthew Island and persisted throughout the winter, the depth of the snow cover alone would have caused the island-wide starvation and the death of 99% of the St. Matthew Island reindeer population in winter 1963–64.

Although the high density of reindeer on St. Matthew Island in summer 1963 meant that there were many reindeer present, density-dependent effects cannot necessarily be inferred. It is our contention that the reindeer crash on St. Matthew Island would have happened even if the reindeer were at a much lower density. The magnitude of the crash is mostly related to the duration of exposure to severe abiotic factor(s) and not to the density of animals present per se (e.g., Behnke, 2000). In a parallel situation, Stimmelmayr (1994) reported a reindeer die-off on Hagemeister Island (east of St. Matthew Island) in 1991–92 during a winter with deep snow and concluded that, despite a poor winter lichen range, there was no conclusive evidence that the herd had experienced effects of density-dependent food limitation. Scheffer (1951) had previously commented on the importance of icing during wintertime on St. Paul Island, as had Palmer for subarctic Alaskan islands in general (*in* Scheffer, 1951; Palmer, 1929).

The lichen mat component of the forage supply available to the reindeer on St. Matthew Island was reduced to a mere remnant of its pristine abundance by summer 1963. Although the loss of lichens did not bode well for the future growth of the reindeer population, there was no evidence that it seriously influenced the population's performance, which was still exceptionally high. Klein (1968: 361) reported that the removal of lichens allowed sedges, grasses, and some forbs to increase in abundance and although willows were being used heavily by 1963, they had decreased only 4% from their 1957 level. He noted from Palmer (1929) that reindeer on ranges where lichens are depleted graze heavily on grasses and sedges during winter. Scheffer (1951) noted that on St. Paul Island, after a marked reduction in lichens, reindeer fed heavily in winter on the abundant sea grass (*Elymus*). Scheffer (1951: 359) reported "The availability of this grass, rather than the amount, is the critical factor." Also, L. J. Palmer (*in* Scheffer, 1951: 359) "cautioned that 'because of winter rains... herds may suffer great losses through starvation, since the animals cannot paw through hard crust to get food'."

It is possible that the reindeer entered the 1963–64 winter in "relatively poor condition" as a result of competition for high quality forage in summer 1963, but that is only supposition. Importantly, a 'relatively poor condition' does not necessarily equate with a potentially lethal condition, and the proportions of calves and yearlings in the 1963–64 die-off population were both high. Not only were initial calf production and early survival of calves in 1962 and 1963 favorable, the overwinter survival of 1962 calves to yearlings in 1963 also must have been at least average, if not higher, based on the 1966 skeletal sample of the 1963–64 die-off population.

We believe that the extreme crash experienced by the St. Matthew Island reindeer in 1963–64 was weather-related and not an inevitable consequence of high population density. Regulation of a population through the limitation of its absolute food supply should be measurable by reductions in successful reproduction and rearing of calves and serious reduction in yearling recruitment, and elevated mortality in general (*cf.* Caughley, 1970). There are no quantified population data from Klein (1959, 1968) that support any serious depression in reproduction and survival between 1957 and 1963. Rather, the data clearly show no meaningful change occurred between 1957 and 1963 or even between 1944 and 1963.

With regards to Riney's (1964) and Caughley's (1970) four hypothetical stages of population change following liberation of herbivores on new ranges, the St. Matthew Island reindeer population had not even reached stage 2 of 'initial stabilization' where the rate of increase would be zero. If the reindeer population on St. Matthew Island had followed the Riney–Caughley model, they would have increased throughout stage 1 and reached a peak density at stage 2, with rates of increase tending to zero; then, becoming negative at stage 3, and subsequently returned to and fluctuating around zero in stage 4. Leader-Williams (1980, 1988) interpreted the St. Matthew Island situation as follows: the reindeer went through stage 1, completely skipped stage 2, bottomed out in an exaggerated stage 3, and then were nearly extirpated and never made it into stage 4. Such extreme variation on the concept of a 4-stage model greatly detracts from the usefulness of its general application. Caughley (1970) apparently recognized this when he concluded that "While the generality of the [4-stage] pattern should not be accepted uncritically, it may be useful as a hypothesis to be tested further." We believe that his emphasis on 'further testing' has been overlooked or at least not actively pursued and examined critically. Most importantly, neither Riney (1964) nor Caughley (1970) ever stated or implied that an irrupting population will inevitably crash (*cf.* Gunn *et al.*, 2003). It appears the boundary separating theory from fact remains blurred in the quest for understanding the population dynamics of *R. tarandus* and the relationship between *R. tarandus* and its environment.

Conclusions

We do not believe density-dependent food-limitation was the primary factor or even a necessary essential factor in the 1963–64 St. Matthew Island reindeer crash. The population parameters do not substantiate lethal or even advanced severe food limitation prior to the crash. The reindeer population grew at an exceptionally high average annual rate of 32% for all 19 years after introduction and up to the year of the crash. We do not question Klein's (1968) conclusion that the rapidly expanding reindeer population reduced the lichen abundance and we believe that there would have been a future density-dependent response if the severe winter weather of 1963–64 had not prematurely caused the crash. However, there was no evidence in 1963 that such a correction would have occurred soon and especially not in the winter of

1963–64. Even when such a correction happened, it would have taken years of overall decline—not just a matter of months. In addition, the magnitude of any long-term decline would not necessarily approach the size of the 99% single-year crash.

There are no conclusive facts to indicate that the abundance and quality of the absolute food supply, other than lichens, was critically depleted in 1963. Given what we now know about the relationship of reindeer and caribou to their environment, the high density of the reindeer and the serious deterioration of the lichen component of the range in itself is only evidence that the population was already locked into an initial phase of increasing density-dependent forage-limitation with future consequences to come in subsequent years. It does not support the inference that it was in a well-advanced phase and surely not that it was in an imminently lethal and final state. Single-year crashes have to be the result of rapid extremely severe changes in the animals' environment that occur in a matter of weeks or a few months on a regional or an area basis. Perhaps, even only one extremely severe snowstorm, especially one associated with extensive icing, or even a single heavy freezing rain event in early winter could be enough to set up conditions that would reduce the relative availability of the food supply to a point where a late winter–spring die-off or crash would occur as a result.

Our intent is not to universally reject density-dependence effects. We are dealing only with the St. Matthew Island reindeer crash in 1963–64 and our thesis is that density-dependency was not a necessary part of the crash and, in fact, could not have caused such a rapid near-total single-year crash. We believe the more important query is not what dictates the number of animals that will die, but what dictates the number of animals that can possibly survive a crash event. That is, in a situation where a viable escape by dispersal and subsequent return is not possible (or is not freely employed), it is the severity, extent, and duration of the abiotic factors that will dictate how many individuals can survive. Under extreme conditions, it does not matter that the absolute food supply is abundant, when it is nearly all unavailable until snowmelt. When foraging is not energy-efficient or the animal cannot get to the food for an extended period of time, the end result is death by starvation, regardless of the animal's initial nutritional status.

It was the island-wide, prolonged unavailability of forage that the reindeer experienced in winter 1963–64 that dictated the maximum number of animals that could possibly survive the weather event. The all-important point is that it was neither the number nor density of the animals, nor their nutritional state at the beginning of the die-off period that caused the crash and determined the number of survivors. In winter 1963–64, the record-setting, extremely severe weather created a rare and near total relative unavailability of the food supply across St. Matthew Island. Those lethal conditions persisted and only about 50 reindeer survived. We need to look no further than the record-setting exceptionally severe winter conditions of 1963–64 for the cause of this spectacular single-year population crash.

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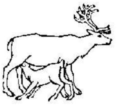
Information from the Nordic Council for Reindeer Husbandry Research (NOR)



Second Announcement

14th Nordic Conference on Reindeer and Reindeer Husbandry Research

NOR's 14th conference will be held in Vantaa near Helsinki, Finland 21-22 March 2006 with reception the preceding evening 20 March.

National organizers are the Finnish Game and Fisheries Research Institute (RKTL), Helsinki University and the National Veterinary and Food Research Institute of Finland (EELA).

The conference is arranged in conjunction with the Annual Meeting of the national delegations of NOR and will also be the 25th anniversary celebration for NOR.

Venue will probably be at SOKOS hotel VANTAA near Helsinki international airport.

In due time (about 1 December 2005) you will find invitation, programme and information about the registration in NOR's web pages www.rangifer.no

Participants are invited to give oral or poster presentations on all relevant topics concerning reindeer and reindeer husbandry. The main lectures will reflect scientific development and today's situation in different research fields.

Contact persons are: for the national organizers senior research scientist Mauri Nieminen (mauri.nieminen@rktl.fi) and for NOR, secretary Rolf Egil Haugerud (nor.rangifer@sami.uit.no).

Grants 2006

Grants are allocated to researchers and students who study reindeer or reindeer husbandry. Applicants should belong to Nordic institutions or they should be students abroad having direct co-operation with Nordic institutions.

The NOR grants for 2006 will primarily be allocated for participation and presentation at the 14th NOR-conference (Nordic Conference on Reindeer and Reindeer Husbandry Research) in Helsinki, Finland, 21-22 March, 2006.
The applications will also be considered for:

- participation in other congresses, symposia, other scientific meetings about reindeer and reindeer husbandry or topics of relevance for the studies of reindeer and reindeer husbandry.
- contact meetings for planning Nordic projects.

NORs working committee will decide upon further priorities as required.

The closing date for applications has been extended to 1st February, 2006.

See full announcement in web pages http://www.rangifer.no/eng/grants.html

1st Call for Papers for The 11th North American Caribou Workshop

April 23 – 26th, 2006

The Sawridge Inn, Jasper, Alberta, Canada

Workshop Theme:

Managing Caribou Populations That Are At Risk

You are invited to submit titles and abstracts for presentations at this Caribou Workshop in Jasper, Alberta. Presentations on the Workshop theme and other topics of caribou biology and management are welcome. Presentations will be 20 minutes in length, including introduction of the presenter and time for questions. You are also invited to submit abstracts for poster presentations.

We would like to develop a draft of the program ASAP. Consequently, we will accept Titles for presentations until February 28, 2006. Abstracts must be received by March 31, 2006 in order for them to be included in the final program.

Contact

asykes@ualberta.ca
Ainsly Sykes, CW405 Biological Sciences Building, University of Alberta, Edmonton, AB, Canada T6G 2E9

Venue

The conference will be held at the Sawridge Inn, Jasper, Alberta, Canada. A block of rooms will be held until March 8, 2006. Room rates are $90.00 Single/$100.00 Double and this includes a buffet breakfast. Triple and quadruple occupancy available at an additional cost of $20.00 per person. Conference rates will be available 2 days prior and 2 days after the conference. Reservations can be made by calling 1-800-661-6427 or 1-780-852-5111. Indicate that you will be attending the North American Caribou Conference and quote reservation number 300679.

The 6th International Deer Biology Congress

The 6th International Deer Biology Congress will be held in Prague, Czech Republic, 7-11 August 2006.

Information on the congress will be appearing on this website: http://www.af.czu.cz/idbc/

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Rangifer

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