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Status, population fluctuations and ecological relationships of Peary caribou on the Queen Elizabeth Islands: Implications for their survival

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Abstract: The Peary caribou (*Rangifer tarandus pearyi*) was recognized as 'Threatened' by the Committee on the Status of Endangered Wildlife in Canada in 1979 and 'Endangered' in 1991. It is the only member of the deer family (Cervidae) found on the Queen Elizabeth Islands (QEI) of the Canadian High Arctic. The Peary caribou is a significant part of the region's biodiversity and a socially important and economically valuable part of Arctic Canada's natural heritage. Recent microsatellite DNA findings indicate that Peary caribou on the QEI are distinct from caribou on the other Arctic Islands beyond the QEI, including Banks Island. This fact must be kept in mind if any translocation of caribou to the QEI is proposed. The subspecies is too gross a level at which to recognize the considerable diversity that exists between Peary caribou on the QEI and divergent caribou on other Canadian Arctic Islands. The Committee on the Status of Endangered Wildlife in Canada should take this considerable diversity among these caribou at below the subspecies classification to mind when assigning conservation divisions (units) to caribou on the Canadian Arctic Islands. In summer 1961, the first and only nearly range-wide aerial survey of Peary caribou yielded a population estimate on the QEI of 25 845, including about 20% calves. There was a strong preference for range on the western QEI (WEQI), where 94% (24 363) of the estimated caribou occurred on only 24% (ca. 97 000 km^2) of the collective island-landmass. By summer 1973, the overall number of Peary caribou on the QEI had decreased markedly and was estimated at about 7000 animals. The following winter and spring (1973-74), the Peary caribou population declined 49% on the WQEI. The estimated number dropping to <3000, with no calves seen by us in summer 1974. Based on estimates from several aerial surveys conducted on the WQEI from 1985 to 1987, the number of Peary caribou on the QEI as a whole was judged to be 3300-3600 or only about 13-14% of the 1961 estimate. After a partial recovery in the late 1980s and early 1990s, Peary caribou on the WQEI declined drastically between 1994 and 1997 and were estimated at an all-time known low of about 1100 animals by summer 1997. The number of Peary caribou on the QEI in summer 1997 was likely no more than 2000-2400 or only 8-9% of the 1961 estimate. The four known major die-offs of Peary caribou on the WQEI between 1973 and 1997 occurred during winter and spring periods (1 Sep-21 Jun) with significantly greater ($P<0.005$) total snowfall, when compared to the long-term mean obtained from 55 caribou-years (1 Jul-30 Jun), 1947/48-2001/02, of weather records from Resolute Airport on Cornwallis Island. Of ecological significance is that the die-offs occurred when the caribou were at low mean overall densities and involved similar high annual rates of loss among muskoxen (*Ovibos moschatus*). All of the available evidence indicates that Peary caribou (and muskoxen) on the QEI experienced die-offs from prolonged, under-nutrition (starvation) caused by relative unavailability of forage-the forage was there but it was inaccessible to the caribou due to snow and/or ice cover. We cannot control the severe weather that greatly restricts the forage supply but we should try to reduce the losses of Peary caribou from other sources-humans, predators and competitors.

Key words: die-offs, ecology, genetics, population estimates, *Rangifer tarandus pearyi*, taxonomy.

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Introduction

The Peary caribou (*Rangifer tarandus pearyi*) occurs in the Canadian High Arctic. It was listed in 1979 as 'Threatened' and in 1991 as an 'Endangered' form of wildlife in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC: cf. Gunn et al., 1981; Miller, 1990b; COSEWIC, 1991). It is a socially important and economically valuable part of Arctic Canada's natural heritage; the only member of the deer family (Cervidae) found in the Canadian High Arctic-the Queen Elizabeth Islands (QEI).

Peary caribou were listed as 'Threatened' on the basis of the decline in the total number on the western QEI (WQEI) between 1961 and 1974, then as 'Endangered' because of the continued overall decline in the 1980s. Only for Bathurst Island and its associated smaller islands was there evidence for recovery in numbers between, at least, 1985 and 1994, which was most likely initiated in the late 1970s (e.g., Miller, 1998). However, there was no aerial surveys of the other WQEI between 1988 and 1996, therefore, the lack of evidence is not proof that no recovery occurred there. We believe, it is most likely that some recovery was experienced within the Melville-Prince Patrick islands complex from about 1988 to 1994. Then those caribou probably also entered the 1994-97 decline phase, as documented in 1996/97 (Gunn & Dragon, 2002). All of that recovery from the late 1970s to the early 1990s and more was lost during the 3 most severe winters recorded in terms of total snowfall at Resolute Airport (1994-97). By 1997, the number of Peary caribou on the WQEI fell to an all-time estimated low of about 1100 caribou. The long-term overall decline together with the unknown status on the eastern QEI (EQEI) is a concern for Peary caribou conservation. Were those winters part of a human-induced trend consistent with the predictions for global warming or were they within 'normal' climate variability and how does either condition foreshadow future events for Peary caribou?

If the threats to Peary caribou were simply the natural consequences of high variation in weather in an extreme environment, then the need for recovery actions would be less as the caribou numbers would likely recover. However, recent trends in Arctic weather are consistent with the predictions for global climate change (Maxwell, 1997; Tynan & Demaster, 1997; and summarized in Weller, 2000). Some future predictions are ominous (e.g., Bradley, 2000), and we consider that the balance of scientific opinion is that human activity has contributed to global climate change. If the Peary caribou decline is a consequence of human activity, then we have a greater conservation obligation and in addition, the past would not necessarily be an accurate guide to the future. Thus, recovery to population sizes that will sustain meaningful levels of harvest will be slow at best. Most importantly, there is no guarantee of any large-scale recovery if climatic conditions unfavorable to caribou survival become more severe or prevalent (Gunn et al., 2000b).

The following is a summary review of (1) the unique status (taxonomy and genetics) of Peary caribou on the Queen Elizabeth Islands compared to caribou on the southern Canadian Arctic Islands; (2) population sizes and fluctuations that Peary caribou have experienced between 1961 and 1997; and (3) ecological relationships of the Peary caribou. Our aim is to point out the implications of these factors to the long-term survival and thus the conservation of Peary caribou, particularly with respect to an apparently changing climate in the western Canadian High Arctic (e.g., Weller, 2000). That is, to the potential detrimental effects on Peary caribou of climate change and resultant natural and/or anthropogenic warming in arctic regions.

The Queen Elizabeth Islands

The Setting

The Canadian Arctic Archipelago forms the remote and isolated northern apex of the North American continent and the QEI make up the northern point of that apex (Fig. 1). The QEI is collectively all of the islands that lie entirely to the north of about 74°N latitude, spanning about 62° of longitude from 61°W on the east to about 123°W on the west. The QEI include 2126 islands: 2092 are <137 km² in size; 16 are between 137 and 955 km²; 11 are between 1059 and 6995 km²; 6 are between 11 295 and 55 247 km²; and 1 is 196 236 km² (Ellesmere Island, the 10th largest island in the world: data source, Natural Resources Canada, The National Atlas of Canada-Facts about Canada-Sea Islands http://atlas.gc.ca/english/facts/islands.html). The region is known for its extremely harsh climate and low plant growth forms and relative lack of vegetation compared even to mainland tundra ranges (e.g., Edlund & Alt, 1989; Bliss, 1990; Edlund, 1990). In this setting only two forms of large grazing animals have established themselves-the Peary caribou and the muskox (*Ovibos moschatus*).

The climate of the region is unpredictably variable and severe: summers are short, cool and winters are long and cold. Total annual precipitation normally averages <100 mm (Ecoregions Working Group, 1989). Air temperatures average below -17.7 °C from Dec to Mar and mean daily temperatures gen-

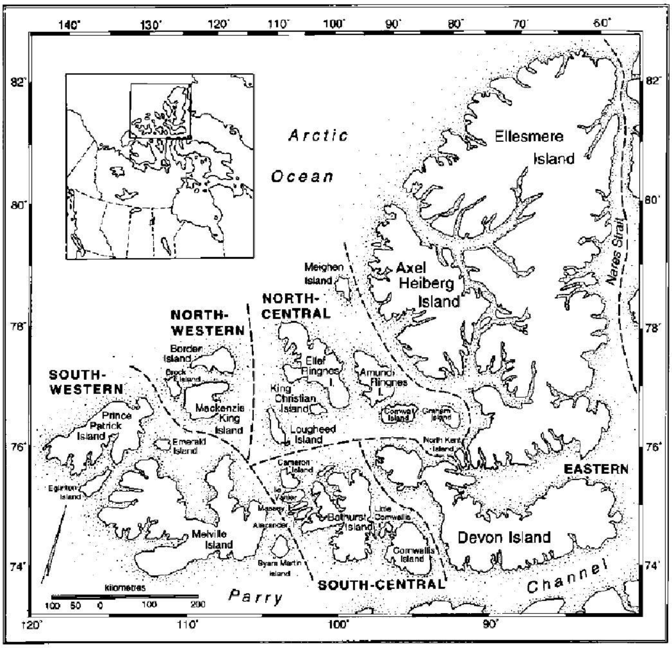

Fig. 1. Current range of Peary caribou (Rangifer tarandus pearyi) in the Canadian High Arctic: Queen Elizabeth Islands shown as five ecoregions (from Miller, 1990b).

erally do not rise above 0 °C until after 1 Jun on the extreme south of the region or 15 Jun on the north of the region (Meteorological Branch, 1970).

Snow cover usually begins melting in early to mid Jun, and often rapidly dissipates to bare ground from mid Jun through late Jun, except for snow banks in sheltered sites (Potter, 1965). In the most unfavorable years, however, considerable areas can remain snow- and/or ice-covered throughout Jun, and even rarely into the first few days of Jul. Summer is the period when the ground is generally essentially snow-free, and lasts from the beginning of Jul into the end of Aug. However, Aug is better thought of as autumn in terms of relative forage quality and supply with the initiation of plant senescence and common occurrence of snowfall. Winter starts when the mean daily temperature falls below 0 °C, usually about or before 15 Sep. The stormiest months are Sep and Oct and much of the annual snowfall may occur in those months. Anticyclones from Dec to Mar dominate the weather causing frequent calms, clear skies, and light snowfall.

Established calendar dates for the seasons of the year do not relate well to the annually prevailing weather in the Canadian High Arctic. Therefore, on a whole calendar-month basis, winter can be considered as being from 1 Sep through 31 May, spring is essentially the month of Jun, summer is Jul; and autumn is Aug. Winter is subdivided into 'early-winter' (Sep-Nov), 'mid-winter' (Dec-Feb), and 'late-winter' (Mar-May) to allow better analyses of the temporal aspects of snow/ice conditions. In reality, most of Jun is wintry and sometimes, if not often, unfavorable to the survival of newborn calves and nutritionally debilitated yearlings and older (1+ yr-old) caribou. Thus, the springtime environmental "bottle-neck" for caribou on the arctic islands is of particular importance in the dynamics of population growth.

The Canadian High Arctic is a collection of island-landmasses with varied topography which contributes to regional climates (Maxwell, 1981). In the context of Peary caribou ecology, the WQEI of Prince Patrick, Melville, Bathurst, and Cornwallis and the north-central islands of Ellef Ringnes and Amund Ringnes fall into Maxwell's (1981) 'Northwestern Climatic Region' and the major EQEI of Ellesmere, Axel Heiberg and Devon are in the 'Eastern Climatic Region.' The above division approximates our major division of WQEI vs. EQEI, based on areas surveyed for Peary caribou, with the exception that we include Ellef Ringnes and Amund Ringnes islands in the eastern group. Weather on the WQEI is caused by cyclones originating from the Beaufort-Mackenzie area while cyclones from the Davis Strait-Baffin Bay-Baffin Island influence the EQEI. Also, in terms of differences in vegetation and relative numbers of animals, the QEI can be subdivided into five 'ecoregions' (Fig. 1: WQEI equals Northwestern, Southwestern and South-central ecoregions, plus Lougheed Island; EQEI equals Eastern and North-central ecoregions (minus Lougheed Island).

The 'Caribou-Year' (1 Jul-30 Jun)

We divide the caribou-year into six seasons on a whole month basis that have ecological significance in terms of range use by Peary caribou.

Summer (1-30 Jul)

All caribou should be in a positive energy balance. This is the annual period of highest quality vegetation, with maximum growth for bulls and high energy demands for maternal cows during early lactation. In general, it is the period of initiation of restoration of body reserves.

Autumn (1-31 Aug)
Caribou remain in a positive energy balance. Restoration of body reserves continues; however, quality of vegetation begins to decline with the initiation of plant senescence.
Early Winter (1 Sep-30 Nov)
Caribou can be in a positive or negative energy balance-depending on the severity of the year, timing of heavy snowfalls and ground-fast ice or icing on or in the snow cover. In some years, forage remains readily available throughout their range. However, in the most unfavorable years, forage becomes greatly restricted and the first stages of malnutrition are initiated among many caribou but they usually do not succumb to extreme undernutrition until mid winter or later.
Mid Winter (1 Dec-28/29 Feb)
Caribou are in a negative energy balance. It is a period of survival, with areas of range occupation depending on then prevailing snow/ice depths and conditions. Snow pack characteristics, depths, hardness and density, are do mainly to wind action but are largely determined by snowfall and icing that took place in early winter. In the worst years, mortality is accelerated by Jan/Feb but often mostly delayed to late winter or even spring.
Late Winter (1 Mar-31 May)
Caribou remain in a negative energy balance. It is usually a period of extreme stress for many caribou and in some years for all caribou. Areas of range occupation depend on then prevailing snow/ice conditions but are mostly tied to snow-free or shallow snow areas. Mortality is markedly elevated in the most environmentally stressful years.
Spring (1-30 Jun)
A period of negative energy balance for parturient or maternal cows. Those cows that were bred the previous year and carried their fetus to full-term likely remain in a negative energy balance throughout the month because the sites that they occupy for calving and early postcalving do not favor early initiation of plant growth. However, in most years bulls initiate body growth by tracking new growth (phenology) of vegetation which appears first on relatively low-lying coastal sites, apparently because they need more time for body growth (e.g., Russell et al., 1993). The condition of subadult females and males can vary among years from negative to positive as the month progresses. In the most severe years, mortality remains high through most of the month and there are major losses in calf crops, sometimes, to the point of near of total failures.

The caribou-year should be considered on a full 12-month basis in terms of range restriction and relative forage availability or relative forage unavailability. That is, adequate ranges (forage and space) are necessary during late winter (1 Mar-31 May) and spring (1-30 Jun) for Peary caribou to get through the most environmentally stressful times of the year. Then, during summer (1-31 Jul) and autumn (1-31 Aug) range conditions have to be adequate for the caribou to not only regain condition to breed but also to survive the following winter. Finally, adequate ranges during early winter (1 Sep-30 Nov) and mid winter (1 Dec-28/29 Feb) will maximize the probability of survival during the subsequent late winter and spring and promote successful initial calf production and early survival of the newborn offspring.

The overall range is only as good as its weakest seasonal link. That is, the protection of the caribou range during the stressful part of the year will be of little value if the caribou cannot subsequently make back their body condition, make new growth and build up their body reserves during the favorable time of the year. Thus, caribou need to have sufficient amounts of forge and space available during all seasons of the year to foster their year-round long-term survival. This is especially true if the population is to remain stable or expand while being harvested at a temporary sustainable level by Inuit hunters. Peary caribou populations are subject to abrupt changes in size. Therefore, sustainable harvesting of Peary caribou at a given level is feasible only on a short-term basis. When a major die-off occurs, the sustainable level decreases markedly, on occasion to zero, and harvesting should be stopped or a new lower rate established until the population has once again recovered sufficiently to support higher levels of annual harvest.

Status of Peary Caribou

Taxonomy and Genetics

The Peary caribou (Rangifer tarandus pearyi) was first described as a distinct species (R. pearyi) in 1902 by J. A. Allen (1902, 1908) from specimens obtained on Ellesmere Island by Lt. R. E. Peary, U.S. Navy (later, Admiral Peary of North Pole fame). The specific rank was later accepted by Jacobi (1931) in his classification of the genus-Rangifer. Subsequently, Flerov (1952) placed all reindeer and caribou in a single Holarctic species (Rangifer tarandus) and reduced Peary caribou to a subspecies-R. t. pearyi. In the late 1950s, Hall & Kelson (1959) followed Lydekker (1898) in arranging all New World forms as subspecies and accepted R. t. pearyi for the Peary caribou. In 1960, however, Manning (1960), still clinging to Richardson's (1829) use of arcticus for all New World forms, identified the Peary caribou as R.

arcticus pearyi. Most recently, Banfield (1961) returned the Peary caribou classification to-R. t. pearyi-in his revision of the genus Rangifer.

Manning (1960) and Banfield (1961) were the first to do or review the taxonomy of caribou on Banks Island and the caribou of the then supposedly extinct Dolphin & Union Herd. Both were classifying at the subspecific level; therefore, they were obligated to place specimens with clear phenotypic diversity below the subspecies into the subspecies that the specimen's taxonomical characters favored. As a result, both authors placed Banks Island caribou (and northwestern Victoria Island without the benefit of any specimens) in the pearyi subspecies and caribou of the Dolphin & Union Herd, from eastern Victoria Island, in the groenlandicus subspecies.

The important point to note for the conservation and especially the preservation of caribou on Banks Island and northwestern Victoria Island is that both Manning (1960) and Banfield (1961) never identified a single specimen from Banks Island as R. t. pearyi. Manning (1960:49) identified all of them as pearyi>groenlandicus, while Banfield (1961:63-64), using mainly the series of specimens from Manning (1960), identified them mostly as pearyi>groenlandicus but also identified a few new ones from southern Banks Island as groenlandicus>pearyi (possibly, from caribou of the Dolphin & Union Herd).

Manning (1960) identified all Dolphin & Union Herd specimens as groenlandicus>pearyi. Banfield (1961) relied on Manning's (1960) findings for the Dolphin & Union herd and discussed them under R. t. groenlandicus as 1 of 5 demes. Banfield (1961:54) noted "Those [5] demes showed no significant differences or clines but rather exhibited a mosaic type of variation. The Dolphin and Union Straits deme was small and pale, indicating some pearyi influence (Manning, 1960)." That is, "small and pale" relative to the other 4 demes of groenlandicus but relatively large and darker compared to pearyi.

Therefore, recognition of those groups as distinct from pearyi on the QEI and keeping them separate is an important consideration in the conservation and preservation of caribou on the Canadian Arctic Islands. Of course, this consideration extends further to include all of the other groups of caribou on the Arctic Islands and the island-type caribou found on Boothia Peninsula (Banfield, 1961; Manning & Macpherson, 1961; Thomas & Everson, 1982; K. Zittlau, pers. comm. 2002). All of these caribou groups can be identified as making a contribution to the biodiversity of caribou in Canada. In the case of these caribou, we believe, a solution relying on genetics and morphology and heavily on ecology should form the best basis for a conservation unit. The most obvious basic unit of conservation for an animal should be a naturally occurring one. Currently, we believe that the most basic and workable caribou conservation unit is the geographic population. We realize that much ecological diversity can and often does exist, however, within a geographic population. This diversity is initiated and most likely retained within an intermingling web of 'subunits': probably akin to 'subpopulations' or in the case of caribou on the Canadian Arctic Islands-'island populations'-with or without reproductive isolation. There could be functional ecological diversity that could greatly enhance the probability of short-term survival of certain groups of individuals and thus long-term persistence of their population.

However, separation of Peary caribou from mainland barren-ground caribou (R. t. groenlandicus or R. t. granti) at the subspecific level is not supported by mitochondrial DNA differences (Eger & Gunn, 1999). That is, Peary caribou do not form a monophyletic group - they have a polyphyletic origin. Therefore, establishing conservation units for caribou on the Canadian Arctic Islands would benefit most from a broad approach as referred to above where genetic classification forms only part of the basis for the conservation unit. The necessity for the use of genetic and phenotypic data along with ecological and behavioral separators will require collaboration and consensus between molecular and ecologically oriented biologists (cf. Crandall et al., 2000).

The classical taxonomy was based mostly on skull measurements and pelage differences (Manning, 1960; Banfield, 1961) and separated caribou on the QEI from caribou on Banks Island, and on northwestern Victoria Island by association, as R. t. pearyi vs. R. t. pearyi x groenlandicus. Microsatellite DNA analysis so far yields a clinal separation for caribou on the QEI from those caribou on the southern Arctic Islands, including Banks Island and northwestern Victoria Island (Zittlau et al., 1999; K. Zittlau & C. Strobeck, pers. comm., 2001).

The DNA findings reveal the diversity of caribou and although caribou on Banks Island are related to the caribou on the QEI, based both on the past classical taxonomy and recent DNA findings, the caribou should not be considered interchangeable between regions. This consideration should be applied to all of the geographic populations of caribou found across the southern Arctic Islands and on Boothia Peninsula. The complexity of the matter appears to be amplified in part by microsatellite DNA findings that indicate that Banks Island caribou are more closely related to an island-type caribou found on Boothia Peninsula than to Peary caribou on the QEI (K. Zittlau, pers comm. 2002). This point is then a major consideration in selecting donor animals in any translocations to boost or rebuild depleted populations. The Peary caribou's morphological and physiological adaptations and its behavioral repertoire mean that Peary caribou have greater fitness for the High Arctic and are distinct from all other forms of caribou.

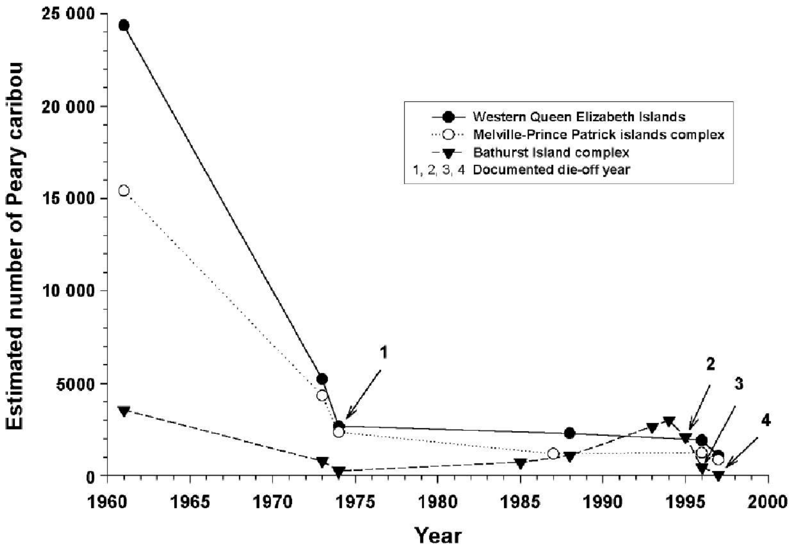

Fig. 2. Trends in the numbers of Peary caribou over 36 years from 1961 to 1997 at three spatial scales: Western Queen Elizabeth Islands; Melville-Prince Patrick islands complex; and Bathurst island complex; Canadian High Arctic.

Fluctuations in Numbers

Peary caribou on the QEI (ca. 411 000 km^2) were estimated at 25 845 when first aerially surveyed in summer 1961 (Tener, 1963: ca. 20% were calves). Most Peary caribou were on the WQEI (ca. 97 000 km^2), where 94% of the estimated caribou occurred on only 24% of the total island-landmass of the QEI (Fig. 2). Since 1961, there has been no comparable aerial survey of the EQEI to that conducted by Tener (1963). However, limited aerial surveys of some sections of Ellesmere Island all revealed few caribou and low mean densities (Riewe, 1973; Case & Ellsworth, 1991; Gauthier, 1996; R. Wissink, pers. comm., 2000).

By the mid 1970s, the overall number of Peary caribou on the WQEI had decreased to about 29% of the 1961 estimate (Fig. 2: Miller et al., 1977a). The following winter and spring (1973-74), the Peary caribou population declined 49% throughout the WQEI. The estimated number was reduced to about 12% of the 1961 estimate, with no calves observed by us in summer 1974. Several aerial surveys from 1985 to 1987 placed the estimated number of Peary caribou on the WQEI at only about 9% of the 1961 estimate (Miller, 1990b). The number of Peary caribou on the QEI as a whole was judged to be 3300-3600 or only about 13-14% of the 1961 estimate. From 1988 to 1996 only Bathurst Island and its neighboring islands were resurveyed and by 1994, the number of Peary caribou there recovered to about 85% of the 1961 estimate. The aerial survey in 1997 revealed that the number of Peary caribou on the WQEI then declined between 1994 and 1997 and in summer 1997 was at an all-time known low of only about 4% of the 1961 estimate (Miller, 1998; Gunn & Dragon, 2002). Currently, there is no reason to believe that more than several hundred to a thousand or so caribou exist on the EQEI. Therefore, at present, an estimate of 2000-2400 Peary caribou (only 8-9% of the 1961 estimate) for the entire QEI seems to be a reasonable 'best guess' (1100 to 1300, WQEI + 900 to 1100, EQEI).

At these low numbers, utilization of island and inter-island populations of Peary caribou by Inuit living on High Arctic Islands creates another important facet to the conservation of Peary caribou. This concern is particularly applicable to those caribou left in remnant populations such as those within the Bathurst Island complex (Figs. 2, 3). In summer 1997, Gunn & Dragon (2002) estimated 78 ± 25 (95% CL ≅ 29-127) Peary caribou left within the Bathurst Island complex. A caribou population within that 29-127 limits would require between 35 and 23 years at an average annual high rate of increase of 13% to reach about 2000 caribou to annually support a harvest of 100 1+ yr-old caribou or more animals (Fig. 3: 13% derived from the estimated finite rate of increase of $\lambda = 1.13$ from 1974 to 1994 for the Bathurst Island complex). Therefore, maintaining the maximum possible number of caribou in a population after a major die-off is all-important in minimizing the time required for that population to recover to a usable size.

Major Die-Offs

We know of four major die-offs and associated subsequent major to near total calf crop losses plus one

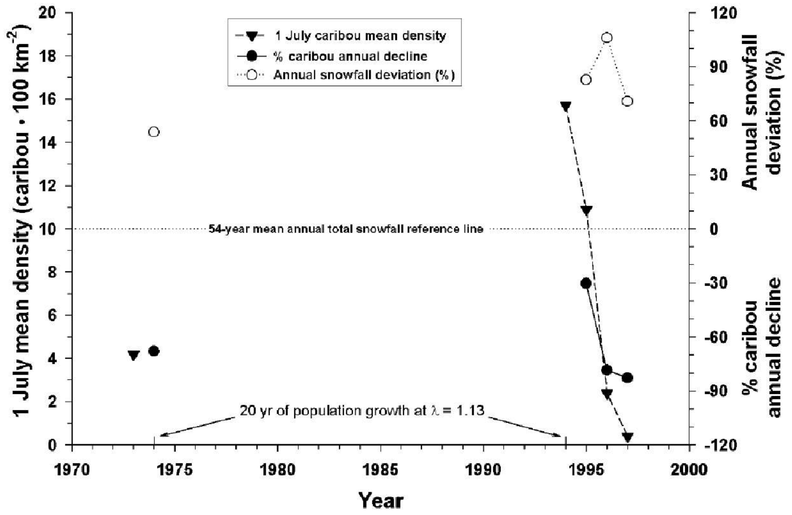

Fig. 3. Four major annual die-offs of Peary caribou, showing low mean density of caribou at start of die-off period, relative severity of total snowfall (1 Sep-21 Jun) expressed as the deviation from the 55-yr mean (in caribou-years, 1 Jul-30 Jun, 1947/48-2001/02) and the resultant percentage decline in the population during each die-off, Bathurst Island complex, western Queen Elizabeth Islands, Canadian High Arctic.

additional major calf crop reduction on, at least, the WQEI: 1973/74, 1989/90, 1994/95, 1995/96, and 1996/97 (Figs. 2-4: Parker et al., 1975; Miller et al., 1977a; Miller, 1992; 1998; Gunn & Dragon, 2002). All 5 of those winters and springs were characterized by significantly greater ($P<0.005$) than average total snowfall between 1 Sep-21 Jun of each year and ranked at the top of 55 caribou-years (1 Jul-30 Jun) for which weather records exist at Resolute Airport, Cornwallis Island (Fig. 4: Miller, 1998-1st, 1995/96; 2nd, 1994/95; 3rd, 1996/97; 4th, 1989/90; and 5th, 1973/74). It is more the extent and characteristics of the snow cover than snow depth per se which result from heavy snowfall and high winds that cause widespread prolonged and extreme relative unavailability of forage. This condition is compounded when associated with extensive icing that will 'lock in' the forage even further and prevent the animals from obtaining an adequate supply of food. However, so far, there has been a direct correlation between total snowfall and die-offs, when significantly heavier snowfall occurs both in early winter and overall throughout the 1 Sep-21 Jun period of that year (Fig. 4). Therefore, total snowfall is the best indicator that we have to date of the potential for an extremely severe 'weather-year' causing die-offs and calf crop failures. The timing, duration, types, and amounts of icing compound the impact of deep snow and tends to cloud the relative importance of the role of deep snow vs. icing in these drastic die-off years. Deep snow alone may severely stress Peary caribou and impact on their subsequent survival and reproduction. It is possible though that extensive and prolonged icing in association with deep snow is necessary or more likely to cause the major die-offs of Peary caribou (and muskoxen) on the QEI. For example, it is likely that relatively few 1+ yr-old caribou died during the deep snow winter of 1989/90 (Fig. 4) because the snow cover remained powdery in many areas throughout the winter until spring (Miller, 1992). Late winter inspection revealed only relatively small areas of hard packed snow cover and in spring many snow-free areas existed before ground fast ice formed on some remaining snow covered areas (Miller, 1992). Snow and ice conditions were still detrimental enough in winter and spring 1989/90 to cause a 40% reduction in potential calf production and/or early calf survival during June-July 1990. It also seems reasonable to predict that widespread and prolonged icing on, in and under the snow beginning in autumn, persisting through winter and being compounded in spring could create lethal conditions for Peary caribou even when in association with relatively shallow snow cover.

Our understanding of the relationship between weather and Peary caribou ecology is limited but has a basis in both on-site empirical observations and after the fact deductive reasoning. However, we need to amplify our understanding of how the various characteristics of snow or ice and particularly the many possible combinations of snow and ice impact Peary caribou. Advancing our understanding of what creates lethal conditions for Peary caribou (and muskoxen) will be through testing predictions about relationships, although this often poses obvious practical difficulties. However, we suggest that monitoring the Resolute weather records and comments by Inuit hunters could alert us to opportunities to test predictions about the effects of weather. This would demand that the responsible parties monitor the caribou when the weather data indicate a possibly lethal situation has taken place during the past autumn, winter and/or spring. For example, we offered a prediction in the preceding paragraph about the effect of icing and shallow snow cover. In Aug and Sep 2001, based on records from the Resolute Airport weather station, there were 26 days with freezing rain, associated with negative mean daily temperatures from 12 Aug through 30 Sep, and measurable snow that fell on 18 days and represented 37% of the total snowfall between 1 Aug 2001 and 21 Jun 2002. Then, in Apr 2002, Canadian Rangers traveling by snowmachine on Bathurst Island reported extensive icing (D. Stern, pers. comm. 2002). However, the total winter and spring snowfall (1 Sep 2001-21 Jun 2002) was below the lower 95% CL for the 55-yr mean at Resolute Airport. We suggest that this would have been a good opportunity to assess any 1+ yr-old caribou mortality at an extremely low mean density, and/or initial calf production and subsequent early calf survival, as well as caribou movements and distribution relative to the geographic extent of the icing. However, the opportunity was lost because no such effective monitoring program was in place.

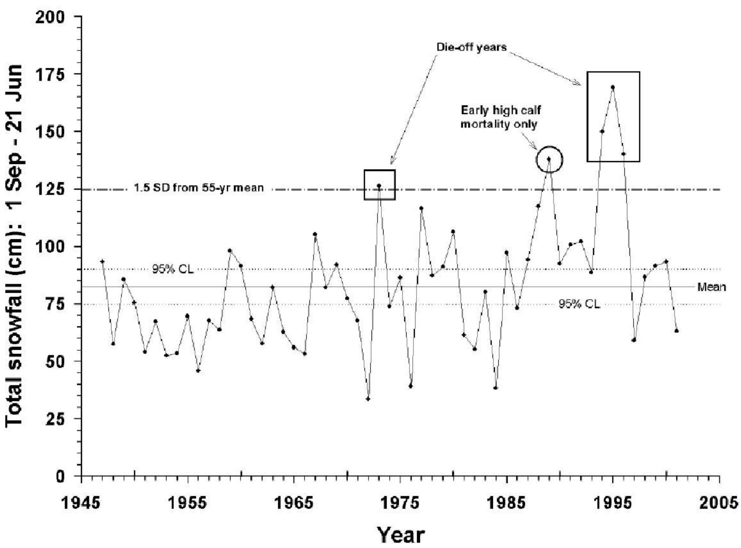

Fig. 4. Long-term (55-yr) trend in total snowfall between 1 Sep and 21 Jun of each caribou-year (1 Jul-30 Jun, 1947/48-2001/02) at Resolute Airport (74°43'N, 94°59'W), Cornwallis Island, Canadian High Arctic: showing highest total snowfalls associated with the four major die-off years (1973/74, 1994/95, 1995/96 and 1996/97) and the one year (1989/90).

The die-offs occurred when the caribou were at low mean overall densities (Fig. 3: Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002). For example, within the Bathurst island complex the four annual major die-offs were initiated at mean densities averaging only 0.08 caribou x km^{-2} (Fig. 3). However, the number of Peary caribou within the Bathurst Island complex plummeted 97% in 3 years between 1994 and 1997 while the number of muskoxen fell precipitously by 89% (Miller, 1998; Gunn & Dragon, 2002). Earlier, two-thirds of the caribou population within the Bathurst Island complex was lost in only one winter and spring during the 1973/74 die-off (Fig. 3). Although we have only two points for major annual die-offs within the Melville-Prince Patrick islands complex, we know that a 46% decline began at only 0.07 caribou x km^{-2} in 1973/74. Then in 1996/97, the second documented major decline in the Melville-Prince Patrick islands complex was about 30% and occurred there at a starting mean density of only about 0.02 caribou x km^{-2}. All four Peary caribou die-off years involved similar high annual rates of deaths among muskoxen. Spatial and temporal synchrony of caribou and muskox die-offs supports snow/ice conditions as the causative factor.

Ecology

To obtain food in winter, caribou dig feeding craters in the snow by pawing down to the vegetation below with their broad hoofs. Wind removes the snow from exposed slopes and redeposits it as shallow but hard compacted cover and drifts in more sheltered and relatively well-vegetated sites. Freezing rain in autumn that results in ground-fast ice before snow cover accumulates, ice layering in the snow cover, crusting of the snow, and the formation of ground-fast ice in spring restrict forage availability (e.g., Miller et al., 1982; Miller, 1992, 1998). Forage restrictions lead to extreme, prolonged malnutrition and markedly reduced survival and low reproductive success (Parker et al., 1975; Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002).

Forage selection by Peary caribou on the QEI is discussed by Parker & Ross (1976), Parker (1978), Thomas & Edmonds (1983, 1984), Miller (1995b, 1998) and Thomas et al. (1999). Lichens are relatively unimportant to those Peary caribou compared to lichen use by mainland caribou. Lichens on the QEI are relatively poorly represented in the plant biomass and they do not occur in extensive lichen mats as they do on the mainland. The general opinion is that the kinds of lichens eaten by caribou were probably never were well-represented or abundant on the QEI (D. C. Thomas, pers comm. 2002). Based on data from Thomas et al. (1999), Peary caribou forage on lichens year-round, but we conclude from the above data sources that their annual utilization of lichens appears to normally be <10% of the annual diet: or several-fold less than for barren-ground caribou (e.g., Thomas, 1998). The Peary caribou's annual use of lichens varies markedly among years on the QEI but is not known to ever, exceed the ca. 18% proportional representation of lichens in the total plant biomass (calculated from Table 12 of Thomas et al., 1999).

In late spring and early summer the caribou feed on vegetated coastal slopes and river valleys dominated in early summer by purple saxifrage (Saxifraga oppositifolia). Then, later in summer they follow the phenology ('greening') as plants flower and leaf-out on the higher elevations and interior sites on upland plains dominated by arctic poppy (Papaver radicatum). The last week or 10 days of Jun (spring) in the most favorable years, Jul (summer) and Aug (autumn) are the only periods of relative abundance and availability of high quality vegetation necessary to build up body reserves. Recovery from the nutritional stress experienced during the previous winter and the initiation of new body growth are particularly important for breeding animals to enter into a favorable reproductive state during the subsequent autumn or early winter rut (e.g., Thomas, 1982; Russell et al., 1993). Peary caribou rut in early winter in terms of their environmental setting.

In winter and spring Peary caribou seek out more exposed areas blown free of snow or with shallow snow cover, such as beach ridges, rock outcrops, and steep slopes along stream drainages (e.g., Parker, 1978; Thomas & Edmonds, 1983; Thomas et al., 1999). Depending on the year, Sep-Nov (early winter) or Dec-Feb (mid Winter), is the period of transition from high quality diet to low quality maintenance diet. In favorable years, animals do relatively well, while in unfavorable years, they fail to remain in good condition because of widespread forage unavailability due to snow/ice cover. In extreme years, the widespread relative forage unavailability often leads to subsequent high levels of winter and spring mortality and poor initial calf production during the next calving period or low levels of early survival of calves at or shortly after calving. Mar-May (late winter), and most of Jun (spring), usually are the periods of greatest range restriction and relative forage unavailability due to snow/ice cover at a time when the caribou are at the lowest ebb in their annual cycle of physical condition. Environmental stress in late winter is most critical when preceded by unfavorable snow/ice conditions in early and mid winter: often making the difference between high mortality among 1+ yr-old animals vs. mainly or only negatively influencing the new calf crop.

We have no evidence that the amount or quality of the absolute forage supply, predation, hunting pressure, competition with other grazers, contagious disease or heavy burdens of parasites, human disturbance, or ecosystem contamination made any significant contribution to the documented declines of Peary caribou on the WQEI in the 1970s or in the 1990s. The past and recent effect of predation by wolves on the size of Peary caribou populations cannot be determined. However, the stage could now be set for wolf predation to have serious impacts on at least some remnant caribou populations, unless the wolves die out quickly or abandon the low-density prey areas to seek new hunting grounds. Although disease and parasites are not known to have been important, warmer and wetter weather could lead to greater exposure to such agents. Other potential threats for the Peary caribou may include human disturbances from resource development and the contamination of arctic ecosystems.

Although Peary caribou are island dwellers, they are not necessarily restricted to a single island. Free movements among the QEI are possible, as those islands are locked in a sea of ice for 9 or 10 months of each year. Movement between or among some islands is possible on a year-round basis either by ice or open water crossings. Seasonal and annual range-use patterns of individual Peary caribou reflects the different alternatives available to them within their traditional range.

Distinct from seasonal and annual movements are irregular movements during periods of environmental stress-most commonly forage unavailability due to snow and ice conditions. Rarely, if ever, do we know the subsequent movements or the fate of environmentally-forced dispersing animals. For example, Peary caribou moved from Bathurst Island to Cornwallis and Little Cornwallis islands in the severe winter of 1995/96 (Miller, 1998). Many of them were killed by hunters (estimated at about 85 deaths). Whether the other migrant caribou on Cornwallis and Little Cornwallis islands died or returned to Bathurst Island is unknown but some likely died and some probably returned. There was no evidence that they stayed on Cornwallis Island or on Little Cornwallis Island.

Seasonal movements or annual migrations by

Peary caribou serve to maximize the use of the best ranges that are available to them on one or more islands (e.g., Miller, 1990a). Such repeated movements allow the animals to become familiar with the different sections of the range that they normally use on an annual basis. Many caribou on the QEI and on the southern tier of islands in the Canadian Arctic Archipelago make both intra- and inter-island seasonal migrations and, thus, function as 'inter-island populations' (Miller et al., 1977a, 1977b; Miller and Gunn, 1978, 1980; Miller et al., 1982; Miller, 1990a, 1990b). We know from aerial surveys and aerial searches, VHF radio telemetry, and satellite telemetry location-data that some Peary caribou live year-round on just one island-sometimes, even on small islands, ca. 20 km^2. Some of them make seasonal intra-island movements to different parts of the island, while others of them remain on relatively small sections of a large island throughout the entire year (e.g., Miller & Barry, this proceedings). Other Peary caribou migrate between summer and winter ranges on two or more islands by traveling over sea ice (Miller et al., 1977b). Some even make open water crossings by swimming between nearby islands (Miller, 1995a). Still others have more complex annual range-use patterns involving more than a dozen back and forth movements among five or six adjacent islands, each island only several kilometers from the next (Miller, 2002; F. L. Miller, unpubl. data).

Conservation Implications

The Canadian Government, as part of the international community concerned with global environmental issues, has accepted the maintenance of biodiversity as an ultimate conservation goal (Biodiversity Science Assessment Team, 1994). We believe, this entails conservation of each of the currently recognized geographical populations of caribou for maintenance of their existing biodiversity. Therefore, consideration must also be given to the need to conserve the caribou within each of the various areas on the Arctic Islands because of their probable different contributions to caribou diversity in Canada and the world and the desire of Inuit people to utilize those caribou populations.

The current state of knowledge supports that on the Canadian Arctic Archipelago there are at least four ecotypes of *Rangifer*. This consideration excludes the Baffin Island region and the islands in Foxe Basin and Hudson Bay where supposedly only the Canadian form of the barren-ground caribou (*R. t. groenlandicus*) is found. Those four ecotypes occur as six regional populations: i.e., populations delineated on a geographical basis by their known seasonal and annual distributions and by their known and perceived genetic and taxonomical relationships and termed 'geographic populations.' Although microsatellite DNA sampling which describes a finer scale of genetic variation than mitochondrial DNA is incomplete, the microsatellite DNA sampled for the western regional populations supports these divisions (Zittlau et al., 1999; K. Zittlau & C. Strobeck, pers. comm., 2001, 2002).

Peary caribou, the first ecotype, appear to occur as two regional groups: one on the WQEI, and the other on the EQEI. The second ecotype which is related to but distinct from Peary caribou are the caribou occurring as another regional group on Banks Island and northwestern Victoria Island. The third ecotype is the larger and distinct caribou of the Dolphin & Union Herd which occurs as a regional population on southern and eastern Victoria Island but winters on the adjacent coastal mainland. And the fourth ecotype, which occurs or occurred as at least two phenotypes, is the caribou occurring as a regional group in the Prince of Wales-Somerset-Russell islands-Boothia Peninsula complex. The ecology of this fourth group appears particularly complex because they use several calving areas on different islands and on Boothia Peninsula with intra- and inter-island seasonal migrations and migrations between islands and Boothia Peninsula. The situation is further complicated by barren-ground caribou (*R. t. groenlandicus*) and island-type caribou (taxonomically identified as *R. t. groenlandicus x pearyi*) on adjacent calving areas on northern Boothia Peninsula and some or all of those island-type caribou moving south of Boothia Isthmus to winter on the mainland (Gunn et al., 2000a). The presence of these island-type caribou on Boothia Peninsula has been documented by microsatellite DNA assay (K. Zittlau, pers. comm. 2002). In addition, at least, until the recent die-off of caribou within the Prince of Wales, Somerset and Russell islands complex (Gunn & Dragon, 1998), many of those caribou migrated to winter range on Boothia Peninsula and returned to the islands in late winter or spring (e.g., Miller & Gunn, 1978, 1980; Miller et al., 1982).

All of the caribou populations on both the WQEI and all of those, except the Dolphin & Union Herd, on the southern tier of Canadian Arctic Islands have experienced major reductions in size during the last part of the 20th century. This fact becomes especially important now as most of those remnant caribou populations are hunted with different Inuit settlements depending on them. Reconciling the needs of people and caribou conservation becomes difficult during caribou declines and periods of low numbers. However, using translocations to boost or quick-start caribou recoveries to help hunting opportunities should not be at the expense of diluting or altering the existing diversity of caribou and not, for example, mixing the regional populations through indiscriminate translocations. All translocation efforts should not proceed before the genetics of both the animals in the area being restocked and the donor animals (those used for the restocking) are worked out and found to be acceptably similar and ideally essentially the same. Caribou populations on the Canadian Arctic Archipelago have probably differentiated so fast from each other due to repeated 'bottlenecks' that finding genetically identical animals might be difficult, if not impossible (K. Zittlau, pers comm. 2002).

The unpredictable occurrence of weather extremes on the QEI limits growth of Peary caribou populations. Peary caribou appear to live in a 'non-equilibrium grazing system' as opposed to an 'equilibrium grazing system' (e.g., Caughley & Gunn, 1993; Behnke, 2000). In the non-equilibrium grazing system the number of caribou, regardless of their density, is driven by a sporadic, unpredictable, abiotic variable-the type, amount, and timing of annual precipitation (e.g., Caughley & Gunn, 1993; Behnke, 2000). In the specific case of Peary caribou-snow and ice-their extent, characteristics, and duration on the ground. The nature of the system means that the safe conservation strategy is to try to retain the maximum number of Peary caribou in the system after major and especially multi-year die-offs such as those in 1973-74 and 1994 to 1997. Inuit have already voluntarily limited their hunting in response to the die-offs of the early 1970s (Freeman, 1975; Ferguson, 1987). From 1989 to 1996, harvesting of caribou on Bathurst Island was allowed, but after the 1994-97 die-off, the Resolute Bay Hunters and Trappers Organization decided that there would be no organized community hunts for Bathurst Island caribou. However, individual hunters can still hunt caribou there. Inuit hunters from Grise Fiord halted caribou hunting on most of southern Ellesmere Island for 10 years, 1986-96 (Ferguson, 1987).

Peary caribou are living at the extreme edge of the species' range and wide population swings can be expected. For example, the caribou population within the Bathurst Island complex, south-central QEI, declined from an estimated 3600 to <300 between 1961 and 1974; then, took 20 years to increase to 3000 animals in 1994, then plummeted to less than <100 animals in just 3 years from 1994/95 to 1996/97 (Figs. 2-4: data sources Tener, 1963; Miller et al., 1977a; Miller, 1995b, 1998; Gunn & Dragon, 2002). If the 1994-97 die-off within the Bathurst Island complex or on the entire WQEI is simply, the pattern typical of range where highly variable weather drives fluctuations in numbers, then the conservation action is to work with Inuit hunters to allow caribou numbers time to recover to support sustainable annual harvests.

If, however, the exceptional winters were part of a longer-term trend with an anthropogenic cause, then the conservation context changes. The weather trends in the western and central Arctic are increasingly warmer temperatures and heavier snowfall, which are consistent with predictions for global warming (Maxwell, 1997; summary in Weller, 2000). Warmer and wetter autumns followed by higher frequency of freezing rain events and heavy winter snowfall (especially in early winter) and frequent or advanced thawing and freezing in late winter and spring will likely cause further reductions in Peary caribou numbers. We can expect brief periods of recovery during the more favorable winters and springs. If a trend toward more severe winters and springs or a greater frequency of recently realized severe winters and springs continues, however, then we can expect less pronounced recoveries and more frequent and deeper future declines. Even the possibility on some islands of island-extirpations of Peary caribou cannot be excluded. While there is uncertainty in predicting the outcome of the weather trends and changes in caribou numbers, there is risk to delaying conservation actions until trends are obvious. It is an asymmetry in the risks attached to decisions that is not that uncommon in conservation. If pessimistic forecasts are not borne out, then scientific credibility is reduced even if the actions resulting from the forecasts themselves do not cause any harm to the wildlife in trouble. On the other hand, actions taken earlier before a crisis in low numbers is further advanced-can be instrumental in averting a greater crisis and minimizing recovery time. It was this logic and extension of the precautionary principle that led in 1997, to the suggestion for captive breeding of Peary caribou but in the absence of local community support, the attempt was canceled. This reinforces the point that Peary caribou conservation has to include those people who share the Peary caribou ranges and conservation planning has to be built on local as well as scientific knowledge: a summary of views can be found in a workshop on Peary caribou conservation in Gunn et al. (1998).

Management and recovery of Peary caribou on the QEI and arctic-island caribou on the southern Canadian Arctic Islands and Boothia Peninsula have been reviewed by Gunn et al. (2000b). They (Gunn et al., 2000b:47) point out that "Management of endangered and threatened caribou populations on Canada's Arctic Islands requires implementation of recovery actions despite gaps in our knowledge and uncertainties in diagnoses of declines." No-one has control over the weather, which in its severest form appears to be the single driving force controlling Peary caribou numbers,. It is not feasible on a wide-spread, let alone range-wide, basis to use emergency or especially ongoing supplemental winter feeding as a tool for Peary caribou conservation (Miller & Reintjes, 1993). Therefore, the first step in a meaningful Peary caribou conservation program is to try to reduce losses from other sources. The obvious first action is to temporarily reduce the number of caribou killed by hunters. To promote this, a guarantee of an alternate source of replacement meat should be made (Gunn et al., 2000b). If the decline continues, the second or parallel step would be wolf control, ideally through non-lethal means and only on islands designated as having a priority for caribou conservation. Justification for taking preemptive actions without detailed knowledge of predation rates is presented in Miller (1998) and Gunn et al. (2000b). Concerned individuals should remember that the ultimate fate of the wolf on the Canadian Arctic Islands is dictated by the long-term success of the combined ungulate prey base-the caribou and the muskox. In turn, if competition with muskoxen causes caribou declines or prevents or seriously impedes recoveries, accelerated harvesting of muskoxen on those islands with a priority for caribou is a feasible option to implement.

The goal of the Canadian Recovery of Nationally Endangered Wildlife Strategy Plan is to prevent extinctions and to maintain and enhance caribou populations. The need for a cooperative approach to Peary caribou conservation is emphasized in national recovery planning. But we collectively also have to be aware that awaiting a more complete understanding of the trends in weather, Peary caribou numbers, and the accuracy of forecasts for global climate change could unnecessarily place the Peary caribou - an 'Endangered Species' - at added risk.

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