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Catastrophic Die-Off of Peary Caribou on the Western Queen Elizabeth Islands, Canadian High Arctic

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ABSTRACT. The Peary caribou (*Rangifer tarandus pearyi*) is an endangered species in Canada, having been in an overall decline since 1961. Sightings of Peary caribou were compared from two aerial searches, in 1993 and 1998, on Bathurst and its neighbouring islands, western Queen Elizabeth Islands in the Canadian High Arctic. The comparison indicated a near-total (98%) cataclysmic decline in the number of Peary caribou seen per unit of search effort. In summer 1993, 2400 caribou were counted during 33.8 h of low-level helicopter searches. In contrast, in summer 1998, only 43 caribou were seen within the same area during 35.2 h of low-level helicopter searches. The frequency of observation was markedly different: 118.3 caribou/100 min in 1993, but only 2.0 caribou/100 min in 1998. The number of carcasses indicated that the decline resulted from deaths and not from mass emigration. Males died at a disproportionately higher rate than females among all 1+ yr old caribou, and bulls (4+ yr) compared to cows (3+ yr) had died at an even greater rate. Widespread, prolonged, exceptionally severe snow and ice conditions from 1994–95 to 1996–97 caused the die-off. Trends in snowfall are consistent with predictions for global warming in the western Canadian High Arctic. Future climate change may increase the frequency of years with unfavorable snow and ice conditions, which could prevent or at least impede future recovery of Peary caribou populations on the western Queen Elizabeth Islands, particularly to sizes that would support subsistence harvesting.

Key words: Peary caribou, *Rangifer tarandus pearyi*, cataclysmic die-off, western Queen Elizabeth Islands

RÉSUMÉ. Le caribou de Peary (*Rangifer tarandus pearyi*) est une espèce en péril au Canada, vu qu'elle a connu une diminution globale depuis 1961. On a comparé des observations du caribou de Peary faites lors de deux recherches aériennes menées en 1993 et 1998 sur l'île de Bathurst et les îles avoisinantes, celles de la Reine-Élisabeth occidentales dans l'Extrême-Arctique canadien. La comparaison a révélé un déclin cataclysmique quasi-total (98 %) du nombre de caribous de Peary aperçus par unité d'activité de recherche. En été 1993, on a dénombré 2400 caribous durant 33,8 heures de recherches par hélicoptère volant à basse altitude. En revanche, durant l'été 1998, on n'a aperçu que 43 caribous dans la même zone durant 35,2 heures de survol à basse altitude en hélicoptère. La fréquence des observations était nettement différente: 118,3 caribous/100 min en 1993, mais seulement 2,0 caribous/100 min en 1998. Le nombre de carcasses a démontré que le déclin était dû à la mort des animaux et non à une émigration massive. Les mâles mouraient à un taux supérieur à celui des femelles de façon disproportionnée parmi tous les caribous âgés de plus d'un an, et, en comparaison avec les femelles de plus de trois ans, les mâles de plus de quatre ans avaient péri à un taux encore plus élevé. La mortalité massive était due à des conditions d'enneigement et de glace généralisées et persistantes extrêmement rudes. Les tendances dans les chutes de neige rejoignent les prédictions concernant le réchauffement global dans l'ouest de l'Extrême-Arctique canadien. Il se peut que de futurs changements climatiques augmentent la fréquence des années où les conditions d'enneigement et de glace ne sont pas favorables, ce qui pourrait empêcher ou du moins entraver le rétablissement des populations du caribou de Peary dans les îles de la Reine-Élisabeth occidentales, en particulier à des niveaux qui pourraient permettre les prélèvements de subsistance.

Mots clés: caribou de Peary, *Rangifer tarandus pearyi*, mortalité cataclysmique, îles de la Reine-Élisabeth occidentales

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INTRODUCTION

The Peary caribou (*Rangifer tarandus pearyi*) was first listed as 'threatened' in 1979 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) because of a decline between 1961 and 1974 (Gunn et al., 1981). Then, as the decline continued, COSEWIC reclassified Peary caribou on the Queen Elizabeth Islands (QEI; Fig. 1) as 'endangered' in 1991 (Miller, 1990).

The first systematic, range-wide measure of abundance was obtained by aerial survey in summer 1961, when Tener (1963) estimated 24 363 Peary caribou on the western QEI

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(WQEI) and 25 845 on the entire QEI. By summer 1973, the estimated number of Peary caribou on the WQEI was only about a quarter of the 1961 estimate (Miller et al., 1977). However, the precise timing, cause and pattern of that decline were not investigated. The first investigation of winter and spring die-off of Peary caribou on the WQEI was in 1973–74 (Parker et al., 1975; Miller et al., 1977). In that one 'caribou-year' (1 July 1973 to 30 June 1974), the estimated number of Peary caribou on the WQEI declined by 49% and that of muskoxen (*Ovibos moschatus*) by 35% (Miller et al., 1977). Thus, in summer 1974, the estimated number of Peary caribou was down by 89% from the 1961 estimate.

Recovery after the 1973–74 die-off was slow, at least during the first three years, and then varied among islands across the WQEI. However, we are hampered by having relatively little information except for Bathurst Island and the neighboring islands of Vanier, Cameron, Alexander, Massey, and Marc (Fig. 1). On Bathurst Island and those neighboring islands, caribou numbers had recovered to 3000 by summer 1994 (Miller, 1995).

Subsequently, the 20-year recovery in abundance of Peary caribou on Bathurst and its neighboring islands was virtually lost in two years, as aerial surveys revealed a sharp 85% decline from 3000 in summer 1994 to only 452 in summer 1996 (Miller, 1998). The magnitude of that two-year decline led to an aerial survey across the entire WQEI in summer 1997 (Gunn and Dragon, 2002). The results indicated that the caribou on Bathurst and its neighboring islands had plummeted a further 83% from summer 1996 to only 78 caribou in summer 1997—down 98% from the 3565 caribou estimated there in 1961 (Tener, 1963). The 1997 survey recorded an all-time known low of only 1086 Peary caribou throughout the WQEI. This low point represents a 96% decline throughout the WQEI over 36 years, 1961–97 (Tener, 1963; Gunn and Dragon, 2002). Thus, the number of Peary caribou on the WQEI was in an overall decline during the last four decades of the 20th century.

Die-offs are usually uneven in their effects on sex and age classes (e.g., Parker et al., 1975; Gunn et al., 1989). Sex and age composition, as well as the number of survivors of a die-off (effective population size), will determine the initial rates of recovery. As we had data on the sex and age composition of the caribou population before the 1994–97 die-off, we returned to the Bathurst Island complex in 1998 to record the sex and age class of surviving caribou and of carcasses. We recorded these data to document further the extent of the 1994–97 decline, and we used them, along with data from caribou carcasses obtained during that decline, to gain insight into the proportional loss of male vs. female caribou. We report those results in this paper and compare the 1998 sightings to the 1993 results from the same islands. We use these data to illustrate the seriousness of both the recent (1994–97) and the overall decline in the number of Peary caribou on WQEI during the last four decades of the 20th century. We also discuss the conservation implications for those Peary caribou remaining on the WQEI, Canadian High Arctic, Northwest Territories and Nunavut, Canada.

MATERIALS AND METHODS

The QEI lie in the Canadian High Arctic north of about 74˚ N latitude (Fig. 1). We divide them into two major groups (Fig. 1), mainly because the occurrence of Peary caribou is disproportionately higher on the western than on the eastern islands. The WQEI, with only 24% of the collective island landmass of the QEI, held 94% of the Peary caribou estimated in 1961, while the eastern QEI, at 76% of the land area, held the remaining 6%. The eastern QEI have received no range-wide aerial survey since 1961, but there is no evidence that caribou increased markedly on those islands between 1961 and 1997. The 'heartland' for Peary caribou during the last half of the 20th century was on the southwestern and south-central islands (Fig. 1). Bathurst Island (16 042 km^2) and its neighboring islands—Île Vanier (1126 km^2), Cameron Island (1059 km^2), Alexander Island (484 km^2), Massey Island (432 km^2), and Île Marc (56 km^2)—form the major portion of the south-central QEI. Hereafter, we refer to these six islands as the 'Bathurst Island complex' and to the southwestern islands as the 'Melville–Prince Patrick islands complex.' Climate patterns and vegetation vary regionally and locally across the High Arctic QEI (e.g., Courtin and Labine, 1977; Maxwell, 1981, 1997; Edlund, 1983, 1990; Edlund and Alt, 1989; Thomas et al., 1999).

We carried out a nonsystematic aerial search for live caribou and carcasses between 16 and 24 August 1993 and between 23 July and 4 August 1998. We used these data, together with associated data that we obtained during the interim (1994–97) die-off period, to complete our evaluation (Miller, 1995, 1997, 1998; Gunn and Dragon, 2002).

The search crew was two observers and a pilot in 1993 and three observers and a pilot in 1998. A Bell-206 turbo-helicopter (Jet Long Ranger) was flown mainly at 60 to 90 m above ground level and at an air speed of 128 to 180 km/h. The areas searched and the search efforts were virtually the same in 1993 and 1998. Flying conditions were similar in both years, mainly under sunny skies and scattered clouds with some periods of high or low overcast. The exceptions were that in 1993, Île Vanier and Cameron Island received only a cursory coastal search, and in 1998, we had to detour around some of the highest interior parts of Massey and Alexander islands because of heavy fog conditions.

All caribou seen were visually segregated by sex and age class: bulls (mature males, 4+ yr old, i.e., 4 years or older); cows (mature females, 3+ yr old, i.e., 3 years or older); juveniles (males, 2–3 yr old and females, 2 yr old); and yearlings (both sexes, 1 yr olds). Calves were considered to be born in June of the year (e.g., Miller, 1998). We did not attempt to determine the sex of calves in 1993 or 1998. In 1998, we examined the remains of 125 Peary

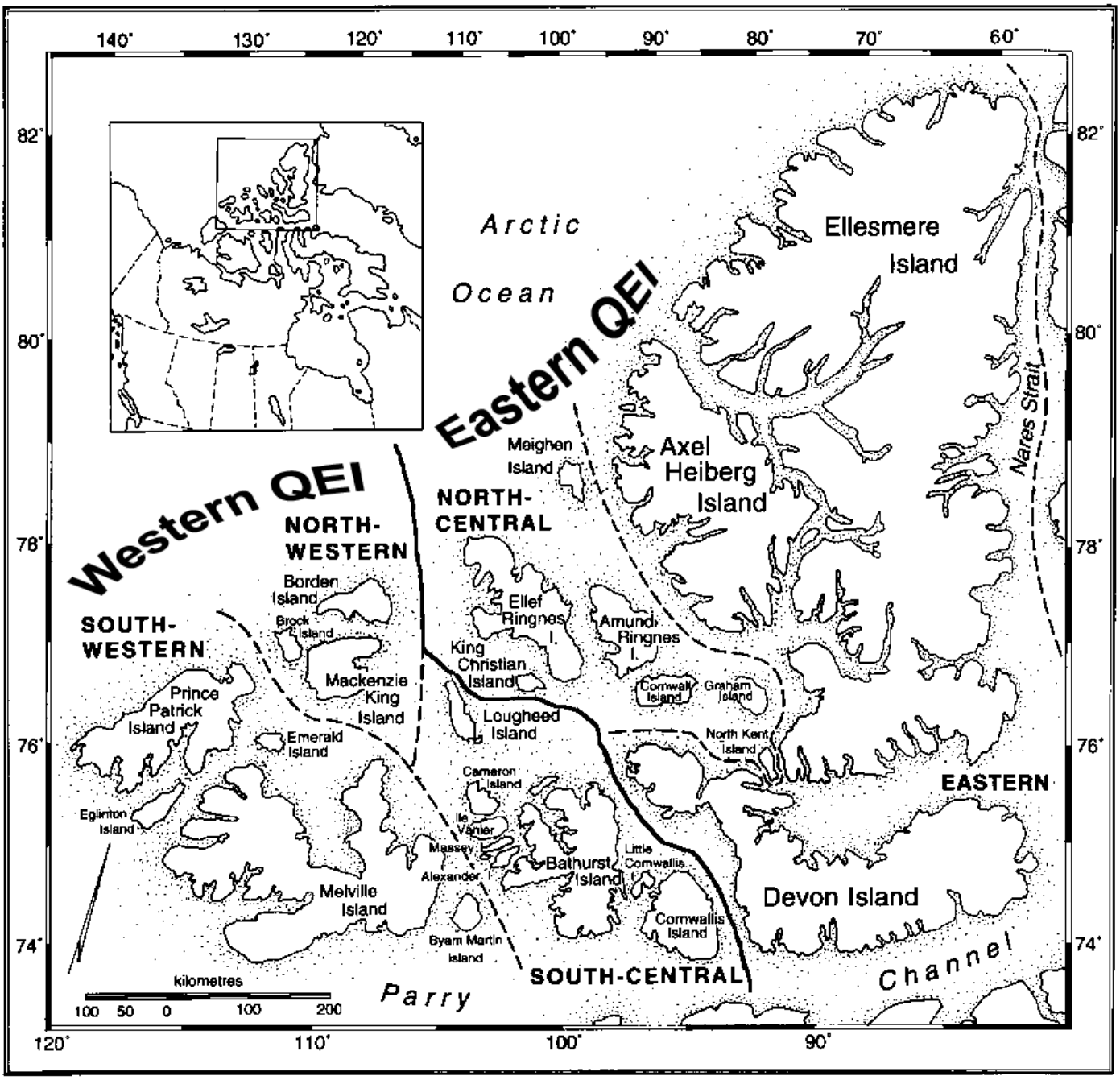

FIG. 1. Current range of the Peary caribou (*Rangifer tarandus pearyi*) on the Queen Elizabeth Islands, Canadian High Arctic, showing Queen Elizabeth Islands as two major divisions and five eco-units.

caribou. Many had been heavily utilized by predators and scavengers and were reduced to patches of skin and hair plus a few bones. Therefore, we could not assign sex and age classes to 22 of them. An additional 12 were calf remains. We were able to place the remaining 91 carcasses from 1+ yr old caribou in sex and age classes as male or female adults vs. male or female juveniles/yearlings.

We calculated a 'Yield/Effort' ratio to assess the differences between the 1993 and 1998 samples. The number of caribou counted (all live caribou seen) was divided by the search effort in minutes × 100, which equals the average frequency of occurrence of caribou per 100 min of search effort. We used the chi-square 'Goodness of Fit' to test for disproportionate abundance of caribou across four major land divisions. We conducted the tests separately for 1993 and 1998. Expected abundances were based on the relative land area and also on the relative number of hours flown. Disproportionate mortality between males and females among all 1+ yr old caribou, and between bulls and cows during the interim three years of die-off, was also tested using chi-square. The level of significance was set at $p < 0.05$.

TABLE 1. Distribution of observations of live Peary caribou obtained by aerial searches in 1993 and 1998, given by sex and age class, south-central Queen Elizabeth Islands, Canadian High Arctic.

	Sex and age class[1] of caribou seen during aerial searches						
Year	Cows	Calves	Juvenile females	Yearling females	Bulls	Juvenile males	Yearling males
1993	691	668	186	141	310	259	145
1998	21	15	1	0	1	4	1

[1] Cows, 3+ yr old; calves, less than 3 months old; Juvenile females, 2 yr old; Yearling females, 1 yr old; Bulls, 4+ yr old; Juvenile males, 2 and 3 yr olds; and yearling males, 1 yr old (see Miller, 1995, for details of sex and age classes).

TABLE 2. Counts of Peary caribou made during low-level helicopter searches in summer 1993 vs. summer 1998 on Bathurst Island and its five major western satellite islands (Vanier, Cameron, Alexander, Massey and Marc), Queen Elizabeth Islands, Canadian High Arctic.

	Major divisions of helicopter search area[1]				
	Bathurst Island				Five western neighboring islands[2]
Year (month)	Northwestern (4068 km^2)	Northeastern[1] (6630 km^2)	Southern (5344 km^2)	Total (16 042 km^2)	(3157 km^2)
1993 (August)					
Caribou counted	315	1790	168	2273	127
Hours flown	8.8	13.4	7.2	29.4	4.4
Yield/Effort ratio[3]	59.5	222.4	39.0	128.8	48.3
1998 (July-August)					
Caribou counted	1	39	3	43	0
Hours flown	4.7	11.3	12.3	28.3	6.9
Yield/Effort ratio[3]	0.4	5.8	0.4	2.5	0.0

[1] The 1993 and 1998 results produced highly significant differences in terms of both the relative abundance of caribou (caribou/100 min; $p < 0.001$) and the relative sizes of the major divisions of land area where the caribou occurred ($p < 0.001$).

[2] Includes the islands of Vanier (1126 km^2), Cameron (1059 km^2), Alexander (484 km^2), Massey (432 km^2), and Marc (56 km^2).

[3] Caribou seen per 100 min.

RESULTS

Caribou Abundance

In summer 1993, we counted 2400 caribou in the Bathurst Island complex during 33.8 h of low-level helicopter searches, yielding 118.3 caribou/100 min of search effort (Tables 1, 2). In summer 1998, we saw only 43 caribou during 35.2 h of low-level helicopter searches, which yielded only 2.0 caribou/100 min of search effort (Tables 1, 2). Thus, with similar aerial search efforts on the same range, we saw about 56 times as many Peary caribou in summer 1993 as we did in summer 1998.

In 1993, 1790 of the 2400 caribou were counted on northeastern Bathurst Island during 13.4 h of low-level helicopter searches, while in 1998, 39 of the 43 caribou were counted on northeastern Bathurst Island during 11.3 h of low-level helicopter searches (Table 2). Thus, the counts for northeastern Bathurst Island yielded 38 times as many caribou per unit of search effort in 1993 as in 1998.

The frequency of occurrence for Peary caribou seen on each of the four survey land divisions was greater than expected by chance alone only on northeastern Bathurst Island in both 1993 (Table 2: $\chi^2 = 1746.91$, df = 3; $p < 0.001$) and 1998 (Table 2: $\chi^2 = 60.48$, df = 3; $p < 0.001$). A similar pattern was found for the four survey land divisions of the Bathurst Island complex. In both 1993 and 1998, Peary caribou were overrepresented relative to land area only on northeastern Bathurst Island (See Table 2, 1993: $\chi^2 = 1231.30$, df = 3; $p < 0.001$); 1998: $\chi^2 = 68.21$, df = 3; $p < 0.001$).

Sex and Age Composition Changes

The sex and age composition of the 1993 sample for 1+ yr old caribou was typical for an increasing population (Tables 1, 3; e.g., Kelsall, 1968; Skoog, 1968; Bergerud, 1978). By August 1995, after the first winter and spring of the die-off, the proportional representation of bulls among all 1+ yr old caribou was already down 23% from summer 1993. By August 1996, after the second winter and spring of the die-off, representation of bulls among all 1+ yr old caribou was down by 47% from the 1993 (pre die-off) level. In August 1998, only one bull was seen. This suggests that by the end of the three-year die-off, bulls had fallen to only 20% of their 1993 level of representation among all 1+ yr old caribou.

After 1997, the ratio of 1+ yr old males to 1+ yr old females was down by 61%, and the proportion of juveniles and yearlings had declined by 48%. Males vs. females among all 1+ yr old caribou died at disproportionately high rates (Table 3: $\chi^2 = 4.61$, df = 1; $p < 0.05$) as did bulls vs.

TABLE 3. Population statistics for a 1993 vs. 1998 comparison of the Peary caribou population on the south-central Queen Elizabeth Islands, Canadian High Arctic.

Population statistics[1]	% representation 1993	1998
Cows among all 1+ yr old caribou	39.9	75.0
Cows among only bulls and cows	69.0	95.5
Calves among all caribou	27.8	34.9
Calves:100 cows	96.7	71.4
1+ yr old females among all 1+ yr old caribou	58.8	78.6
Juvenile/yearlings among all 1+ yr old caribou	42.2	21.4
1+ yr old males among all 1+ yr old caribou	41.2	21.4
1+ yr old males:100 1+ yr old females	70.1	27.3
Bulls among all 1+ yr old caribou	17.9	3.6
Proportion of bulls among only cows and bulls	31.0	4.5

[1] Age classes: Cows, 3+ yr old; Calves, less than 3 months old; Juvenile/yearling females, 1–2 yr old; bulls, 4+ yr old; and Juvenile/yearling males, 1–3 yr old.

cows (Table 3: $\chi^2 = 7.12$, df = 1; $p < 0.01$). Because of the differential mortality among bulls and cows, the proportion of bulls in the population fell by 80% and that of cows increased by 88% from 1993 to 1998.

Calf production of 71 calves per 100 breeding cows in summer 1998 was relatively good for the first year following three years of die-off. It was lower, however, than in the two years before the die-off began: 27% lower than the 1993 rate of 97:100 and 19% lower than the 1994 rate of 88:100. Those favorable conditions in 1993 and 1994 then contrasted sharply with the relatively poor early survival of calves in summer 1995 and the total or near-total absence of calves in summers 1996 and 1997, during the die-off years.

The high percentage of calves among all 1+ yr old caribou in 1998 (Table 3) is misleading, as it reflects the unusually high representation of cows (and lack of bulls) among the die-off survivors. Early survival of calves:100 cows was actually 26% less in 1998 than in 1993. Most importantly, while the 15 calves among the 43 caribou in 1998 were a good sign of initial recovery, such a low number of calves does not assure continuing future recovery.

Evidence from the subsample of 91 carcasses and the 28 live 1+ yr old caribou seen and segregated by sex and age class in summer 1998 indicates that the overall sex and age class ratio for 1+ yr old caribou changed markedly during the die-off (Table 3). The 1998 carcass sample of 1+ yr old caribou yielded a ratio of 112 males:100 females (48 males and 43 females), suggesting that males had died at about 160% of their pre die-off rate (70 males:100 females in 1993). This relatively high rate of deaths among males is further supported by the 1998 sample of 28 live 1+ yr old caribou. Those caribou occurred at a ratio of 27 males:100 females, which indicates that the frequency of males had fallen by 61% after those three die-off years. The ratio of bulls to cows in the 1998 carcass sample (103 bulls:100 cows; 32 bulls and 31 cows), compared to the 1993 ratio of live caribou (Table 3), indicates that between 1993 and 1998, bulls died at 2.3 times their 1993 rate of occurrence. When the 1998 carcass sample is compared to the 1993 sample of live caribou by the four sex and age classes (bulls, cows, juvenile/yearling males, and juvenile/yearling females), only the bulls are overrepresented in the carcass sample. Bulls occurred at nearly twice their expected rate in the carcass sample, while cows and juvenile/yearling males and females were underrepresented ($\chi^2 = 18.75$, df = 3; $p < 0.001$). By contrast, in the 1998 sample of live caribou, cows were overrepresented by nearly twice their expected rate, while bulls and juvenile/yearling males and females were underrepresented ($\chi^2 = 15.76$, df = 3; $p < 0.005$). Thus, the survivors, although relatively few in number, include a higher proportion of potential breeding females than before the major losses occurred.

DISCUSSION

Cause and Effect of the Decline

Three consecutive annual declines in Peary caribou populations occurred on the WQEI between September 1994 and June 1997: all occurred at low mean densities of caribou, and all were associated with extremes in snow and ice conditions (Figs. 2, 3; Miller, 1998; Gunn and Dragon, 2002). Those numerical declines were brought on directly by greatly increased annual mortality. This observation is supported by the many caribou carcasses seen during all aerial searches and the high estimates of caribou dying in those years obtained from our systematic carcass counts during aerial surveys. The carcass numbers were sufficient to rule out mass emigration as anything but a possible minor cause of the changes in numbers.

Estimates from carcass counts obtained by aerial survey in summers 1995, 1996, and 1997 indicate that about 85% of the overall three-year decline between 1994 and 1997 resulted directly from deaths (Miller, 1998; Gunn and Dragon, 2002). Emigration, then, could have accounted for at most 15% of that decline. Also, the extreme weather conditions were regional, so there is no reason to believe that migrants would have fared better than caribou that did not move to new ranges.

The three-year die-off coincided with and was caused by three consecutive exceedingly severe winter and spring periods (Fig. 2: Weather data for 1947–48 to 2001–02, provided by Environment Canada, Climate Archives). The annual die-offs of Peary caribou (and muskoxen) during 1994–97 occurred in three years with exceptionally deep snow (Fig. 2: > 1.5 SD above the 55 yr mean), the deepest recorded between 1 September and 21 June in all years from 1947 to 2002. Perhaps more importantly, most of the snowfall during those die-off years occurred in early winter (1 September to 30 November). It is not the total snowfall per se, but the hardness and density of relatively deep snow packs (caused mainly by wind action) that can result in widespread and prolonged, highly unfavorable

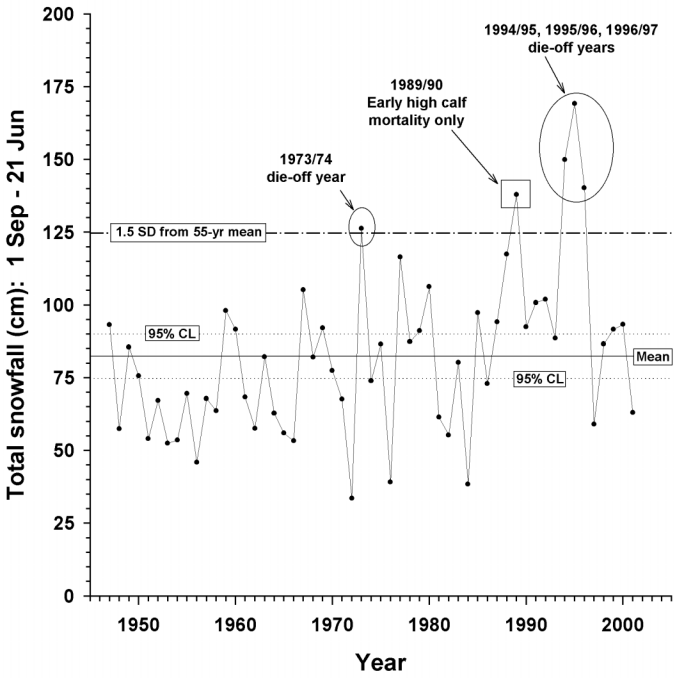

FIG. 2. Long-term (55 yr) total snowfall trend (showing mean ± 95% CL and upper 1.5 SD) between 1 September and 21 June of each caribou-year (1 July–30 June, 1947–48 to 2001–02) at Resolute Airport (74.717˚ N, 94.983˚ W), Cornwallis Island, Canadian High Arctic. The figure shows the highest total snowfalls associated with the four major die-off years and the one year when only a high calf loss was detected (climate data provided by Environment Canada, Climate Archives).

foraging conditions. This is especially true when deep snow cover is coupled with extensive heavy icing on, in, or under the snow cover. Deep snow years result in greater accumulations of snow cover on the relatively low-lying sites where vegetation is most abundant. At such times, the forage plants become unavailable to the caribou when the snow cover becomes compacted, especially when deep snow is associated with widespread icing. However, the forage is still there, and it will be available to the caribou once again when the snow and ice melt off the range.

Not all relatively deep snow years result in major die-offs; 1989–90 ranked fourth out of the 55 years (Fig. 2), and no greater loss of 1+ yr old caribou was detected. However, in 1989–90, the snow remained powdery on large areas all winter, and examination of feeding craters in late winter indicated that the caribou apparently were not experiencing any appreciable difficulties in their foraging. Calving in 1990 was late, however, peaking in the fourth week of June and continuing into the first few days of July (Miller, 1992). Calving among those Peary caribou has peaked during the second or third week of June in relatively favorable years and in the first and second weeks of June during the most favorable years (Miller, 1998; Gunn and Dragon, 2002). Although there is no evidence that deaths among 1+ yr old caribou increased in January–June 1990, subsequent early calf survival was relatively low compared to that of other years between 1988 and 1994. By early July 1990, about half of the estimated maximum production of calves was lost (Miller, 1992). Thus, we suggest that the reduction in forage availability caused by the snow and ice conditions prevailing during winter and spring of 1989–90 was severe enough for pregnant cows to cause the early death of many calves born at nonviable weights in that deep snow year.

The high production and survival of calves immediately before the die-off that began in late 1994 strongly suggests that forage itself did not limit calf production and survival. If caribou densities had reached the threshold at which foraging reduces plant biomass to levels that cause changes in caribou body condition, then calf production and early calf survival would have been among the first demographic parameters to be reduced. The exceptionally high initial production and survival of calves through the first year of life in 1992 and 1993 (and initially in summer 1994) also argue that ecologically meaningful competition with muskoxen was not a factor preceding the three years of die-off (Miller, 1998; Gunn and Dragon, 2002).

There is no evidence that past hunting caused or even contributed significantly to the decline of Peary caribou on Bathurst Island and its neighboring islands or anywhere else in the WQEI (Miller, 1998; Gunn et al., 2000; Gunn and Dragon, 2002). The high productivity immediately preceding the decline and our observation that carcasses had signs consistent with malnutrition argue against disease epidemics. At the time, there were few human activities and certainly no industrial exploration or development activities that could have contributed to changes in caribou condition. The most parsimonious explanation consistent with the timing, geographic spread, and involvement of muskoxen as well as Peary caribou in the die-offs is that extreme weather events (snow and ice) caused a widespread and prolonged reduction in forage availability that led to lethal undernutrition (starvation).

Bull caribou die at higher rates than cows because the males' greater energy demands during early winter rutting activities greatly reduce their body reserves (e.g., Russell et al., 1993). Thus, breeding males commonly face the rigors of the oncoming winter in poor physical condition. Under the most extreme environmental conditions, the smaller-bodied caribou (calves, yearlings, and to a lesser extent, juveniles) also suffer greater proportional losses than do the cows.

Therefore, under favorable environmental winter/spring conditions, the high proportional representation of potential breeding females could advance the recovery at rates greater than those expected among caribou 1 yr and older with an average ratio of about 40 males:60 females (e.g., Bergerud, 1978; Miller, 1995). Although much fewer in number, potential breeding females per 100 1+ yr old caribou in 1998 would be 31% higher than in the 'typical' case above. Therefore, on average, their annual rate of maximum increase due to calf production could be 22% higher among the post die-off survivors, assuming that, on average, 72% of all 1+ yr old females conceive each year (Dauphiné, 1976). Thus, surviving caribou skewed strongly

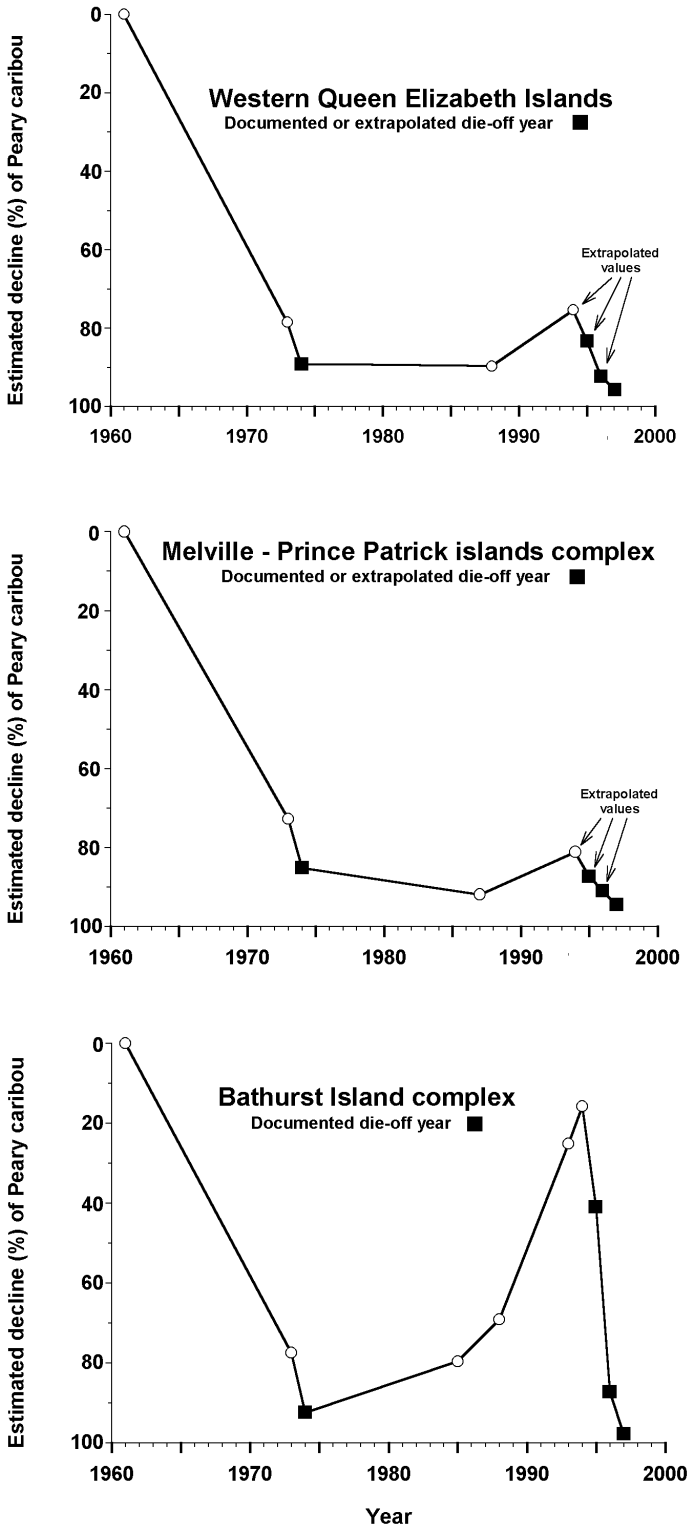

FIG. 3. Approximation of proportional trends in the numbers of Peary caribou over 36 years from 1961 to 1997 in three regions: Western Queen Elizabeth Islands, Melville-Prince Patrick islands complex, and Bathurst Island complex, Canadian High Arctic (data sources: Tener, 1963; Miller et al., 1977; Miller, 1987a, b, 1988, 1989, 1990, 1995, 1998; Gunn and Dragon, 2002).

in favor of females (at about four females for every one male) could encourage recovery, if all other variables remained equal and favorable.

Recovery started immediately after the last year of the 1994–97 die-off, as 15 of the 43 caribou seen in summer 1998 were calves. This first year of recovery in calving in 1998 contrasted with the poor calving success experienced throughout the WQEI during each of the three years following the 1973–74 Peary caribou die-off. Thomas (1982) found that pregnancy rates among Peary caribou females (> 2 yr old) on WQEI remained at only 6–7% in 1974, 1975, and 1976 and then increased to 88% in 1977. Such severe reduction in annual calf production for three to four consecutive years during and/or after major die-off events would markedly slow the recovery of the caribou. A shift in the age structure to older ages with lower reproductive value and a higher level of deaths would further reduce the potential for a rapid increase in numbers (Thomas and Broughton, 1977; Messier et al., 1988; D.C. Thomas, pers. comm. 2002). The absence or low occurrence of several consecutive calf cohorts also would lead to a subsequent depression in annual calf production by markedly reducing the number of females entering the breeding segment.

Potential Impact of Future Hunting

Our results show that the Peary caribou left within the Bathurst Island complex in 1998 were a mere remnant of their former number (Tener, 1963; Miller et al., 1977; Miller 1995, 1998; Gunn and Dragon, 2002). At the low number of only 78 caribou estimated in summer 1997, the population can sustain only very light harvesting of a few males, if any harvest at all. Removal of even a few breeding females would likely be very detrimental to the pace of the recovery within the next several years, as well as to the longer-term well-being of those Peary caribou. Continuance of this restraint in harvesting for another five years would allow the caribou to grow in number by year 2007 to support an annual harvest of perhaps 25 to 50 1+ yr old animals, depending on the sex and age classes of the annually harvested animals. However, that will be true only if those future years experience overall continually favorable winter/spring snow and ice conditions.

We believe, however, on the basis of the caribou literature (e.g., Kelsall, 1968; Skoog, 1968; Bergerud, 1978, and others), that 2500–3000 1+ yr old caribou are needed under favorable environmental conditions to sustain an annual harvest of 200–250 1+ yr old caribou and at the same time buffer against their decline. That would be true only if the population realized a continual 10% or higher annual rate of recruitment over total annual loss. This recruitment rate could be sustained only in the absence of exceptionally severe weather years that cause a widespread and prolonged reduction in forage availability, leading to above-average or major winter and spring die-offs of Peary caribou (and muskoxen).

Recovery could be hindered by any premature annual harvest of other than a few male caribou. The Inuit hunters of Resolute Bay have shown self-restraint in the past: they

voluntarily banned caribou hunting on Bathurst Island in 1975 after the 1973–74 die-off (Freeman, 1975) and subsequently on some of the smaller islands lying between Bathurst and Cornwallis islands (Ferguson, 1987). The ban was honored until about 1990, when recovery of the caribou was well advanced and hunters killed a few caribou within the Bathurst Island complex (Miller, 1998). A similar 15- to 20-year ban or ongoing restriction to a small annual harvest of predominantly (or preferably, solely) male caribou is recommended in order not to impede recovery but especially to foster it.

CONCLUSIONS

On Bathurst Island and its neighboring islands, the 97% decline in caribou abundance from 1994 to summer 1997 led to at least temporary seasonal disuse of ranges on the islands of Vanier, Cameron, Alexander, and Marc. However, it is likely that some survivors will quickly reinitiate seasonal use there. Most probably, they will return first to Cameron Island, which was a primary rutting and wintering area for caribou from Bathurst Island, and then to the other satellite islands when the Bathurst Island complex population once again increases in size.

The majority of Peary caribou on Bathurst Island have usually exhibited seasonal, if not annual, preferences over time for range on northeastern Bathurst (Table 3: Tener, 1963; Fischer and Duncan, 1976; Miller et al., 1977; Ferguson, 1987; Miller, 1987a, 1989, 1991, 1995, 1998; F.L. Miller, unpubl. data). In 1998, 39 of the total 43 caribou seen occurred on northeastern Bathurst Island, representing a larger proportion of total caribou than was found there in 1993. This high use of northeastern Bathurst Island after the 1994–97 losses indicates that the area remains the preferred range for Peary caribou on that island. Therefore, caribou there should receive protection from exploration and developments through biologically sound management and regulation by the Inuit users and responsible wildlife agencies. The establishment of the proposed national park on northern Bathurst Island and at least some of the adjacent western satellite islands would be the best way to afford a high degree of protection from human activities and developments to that preferred range for Peary caribou (cf. Miller, 2001).

Peary caribou have rates of increase and productivity comparable to those of caribou elsewhere (e.g., Davis et al., 1980; Messier et al., 1988; Miller, 1998). However, at unpredictable and irregular intervals, Peary caribou die in relatively large numbers during winters and springs when snow and ice conditions prevent energetically efficient access to forage. The influence of snow and ice conditions on forage availability is extended into the plant-growing season in some years, adding further stresses to the caribou.

Peary caribou are at the edge of the range for herbivores, as the High Arctic is close to the climatic limits for plant growth. It is the variability of weather parameters (such as mean daily temperatures and snowfall) that contributes to the severity of the climate itself. Mean values are close to the limits of plant growth, so even small deviations can have proportionally greater effects. Svoboda (1977) reported only 45 and 80 days from first snowmelt to the return of mean temperatures below freezing in 1970, 1971, and 1972 at Devon Island's Truelove Lowlands. At Resolute, Cornwallis Island, the number of days with mean daily temperatures above 0˚C during the same three years averaged 61 ± 13.5 SD and ranged from 46 to 72 (data from Environment Canada, Climate Archives). Thus, the growing season in the High Arctic is variably short, but the time required for plants to complete their seasonal cycle of growth is fixed and constant (Svoboda, 1977). In years when snow and ice and associated low temperatures persist, the renewal of plant growth can therefore be delayed at least two to three weeks, and the overall quality and abundance of forage can be markedly reduced. Inadequate summertime forage could hinder the early growth of calves and affect the recovery of body reserves, especially in lactating cows and potential breeding males.

Thus, Peary caribou live in a 'non-equilibrium grazing system' where sporadic, unpredictable abiotic variables—i.e., snow and ice—usually govern the fate of the caribou over time (e.g., Caughley and Gunn, 1993; Behinke, 2000). In such a system, the wisest approach to conservation of Peary caribou is to try to maintain the maximum number of caribou in the system. That way, when a major die-off due to exceptionally severe snow and ice conditions occurs, the greatest possible number of animals will still be left in the system after the die-off to advance recovery. This is particularly important, since the fewer the caribou, the greater the random chance of 'island-extirpation' of those caribou and the longer the recovery time during which no appreciable annual harvest can be sustained. Under such environmental conditions, maintaining a broad distribution of Peary caribou across the breadth of their historic range should enhance the probability of their persistence. Unfortunately, however, it would not solve the problem of maintaining populations that could sustain reasonably large (> 50 1+ yr old caribou) annual harvests.

Peary caribou on the WQEI have suffered cataclysmic losses since 1961, with drastic reductions occurring by 1974 (Fig. 3: Tener, 1963; Miller et al., 1977; Miller, 1998; Gunn and Dragon, 2002). The caribou within the Melville–Prince Patrick islands complex (Fig. 1: Southwestern QEI) experienced a relatively weak recovery sometime after 1987 into the early 1990s, but their numbers fell again by 1997 (Fig. 3). The caribou population on the islands of Mackenzie King, Borden, and Brock within the Prime Minister Group (Fig. 1: Northwestern QEI) had declined cataclysmically (98%) from its 1961 size (n = 4012) by 1973, and apparently has remained extremely low ever since the 1970s (Miller et al., 1977; Gunn and Dragon, 2002: down 99% in 1997 from 1961). The caribou within the Bathurst Island complex (Fig. 1: South-central QEI), for which we have the most information, experienced two

population highs and two lows over the 36 years between 1961 and 1997 (Fig. 3: highs, 1961 and 1994; lows, 1974 and 1997).

The available data indicate that the population dynamics of Peary caribou on the QEI are governed primarily by the sporadic occurrence of exceptionally severe (and thus unpredictable) snow and ice conditions in winter and spring. Although the Arctic climate varies annually, decadally, and centennially (Walsh and Chapman, 1990; Appenzeller et al., 1998), global climate change is superimposing recent trends toward warmer temperatures and changes in snowfall (e.g., Maxwell, 1997; Bradley, 2000; Weller, 2000; P. Kyle and J. Ross, pers. comm. 2002). Therefore, we are concerned when we consider predictions for weather changes in Arctic regions.

Should the western Canadian High Arctic continue to warm up, will the intervals between years with extremely unfavorable snow and ice conditions be shortened? Perhaps of equal or greater importance, is it probable that a continuing warming trend will lead to more frequent consecutive multi-year die-off events like the one that occurred in 1994–97 (Figs. 2, 3)? If so, this would prevent or at least seriously impede future recovery of Peary caribou populations to a size that could sustain a meaningfully large yearly harvest of caribou. Populations of Peary caribou throughout the QEI could be limited in the same manner.

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REFERENCES

APPENZELLER, C., SCHWANDER, J., SOMMER, S., and STOCKER, T.F. 1998. The North Atlantic Oscillation and its imprint on precipitation and ice accumulation in Greenland. Geophysical Research Letters 25:1939–1942.

BEHINKE, R.H. 2000. Equilibrium and non-equilibrium models of livestock population dynamics in pastoral Africa: Their relevance to Arctic grazing systems. Rangifer Special Issue 20:141–152.

BERGERUD, A.T. 1978. Caribou. In: Schmidt, J.L., and Gilbert, D.L., eds. Big game of North America: Ecology and management. Harrisburg, Pennsylvania: Stackpole Books. 83–101.

BRADLEY, R. 2000. 1000 years of climate change. Science 288:1353–1355.

CAUGHLEY, G., and GUNN, A. 1993. Dynamics of large herbivores in deserts: Kangaroos and caribou. Oikos 67:47–55.

COURTIN, G.M., and LABINE, C.L. 1977. Microclimatological studies on Truelove Lowland. In: Bliss, L.C., ed. Truelove Lowland, Devon Island, Canada: A High Arctic ecosystem. Edmonton: University of Alberta Press. 73–106.

DAUPHINÉ, T.C. 1976. Biology of the Kaminuriak population of barren-ground caribou – Part 4: Growth, reproduction, and energy reserves. Canadian Wildlife Service Report Series 38. 71 p.

DAVIS, J.L., VALKENBURG, P., and REYNOLDS, H.V. 1980. Population dynamics of Alaska's Western Arctic caribou herd. Proceedings of International Reindeer/Caribou Symposium 2:595–604.

EDLUND, S.A. 1983. Bioclimatic zonation in a High Arctic region: Central Queen Elizabeth Islands. In: Current Research, Part A, Geological Survey of Canada Paper 83-1A. 381–390.

———. 1990. Bioclimatic zones in the Canadian Arctic Archipelago. In: Harington, C.R., ed. Canada's missing dimension: Science and history in the Canadian Arctic Islands. Vol. 1. Ottawa: Canadian Museum of Nature. 421–441.

EDLUND, S.A., and ALT, B.T. 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic 42:3–23.

FERGUSON, M.A.D. 1987. Status of Peary caribou and muskox populations on Bathurst Island, N.W.T., August 1981. Arctic 40:131–137.

FISCHER, C.A., and DUNCAN, E.A. 1976. Ecological studies of caribou and muskoxen in the Arctic Archipelago and northern Keewatin. Edmonton, Alberta: Renewable Resources Consulting Services Ltd. 194 p.

FREEMAN, M.M.R. 1975. Assessing movement in an Arctic caribou population. Journal of Environmental Management 3:251–257.

GUNN, A., and DRAGON, J. 2002. Peary caribou and muskox abundance and distribution on the western Queen Elizabeth Islands, Northwest Territories and Nunavut, June-July 1997. Northwest Territories Department of Resources, Wildlife and Economic Development, File Report 130. 93 p.

GUNN, A., MILLER, F.L., and McLEAN, B. 1989. Evidence for and possible causes of increased mortality of bull muskoxen during severe winters. Canadian Journal of Zoology 67:1106–1111.

GUNN, A., MILLER, F.L., and THOMAS, D.C. 1981. The current status and future of Peary caribou *Rangifer tarandus pearyi* on the Arctic Islands of Canada. Biological Conservation 19 (1980–81):283–296.

GUNN, A., MILLER, F.L., and NISHI, J. 2000. Status of endangered and threatened caribou on Canada's Arctic islands. Rangifer Special Issue 12:39–50.

KELSALL, J.P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monograph 3. 339 p.

MAXWELL, B. 1981. Climatic regions of the Canadian Arctic Islands. Arctic 34:225–240.

———. 1997. Responding to global climate change in Canada's Arctic. Downsview, Ontario: Environment Canada. 82 p.

MESSIER, F., HUOT, J., Le HENAFF, D., and LUTTICH, S. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. Arctic 41:279–287.

MILLER, F.L. 1987a. Peary caribou and muskoxen on Bathurst, Alexander, Marc, Massey, Vanier, Cameron, Helena, Lougheed, and Edmund Walker islands, Northwest Territories, July 1985. Canadian Wildlife Service Technical Report Series 20. 45 p.

———. 1987b. Peary caribou and muskoxen on Prince Patrick Island, Eglinton Island, and Emerald Isle, Northwest Territories, July 1986. Canadian Wildlife Service Technical Report Series 29. 65 p.

———. 1988. Peary caribou and muskoxen on Melville and Byam Martin islands, Northwest Territories, July 1987. Canadian Wildlife Service Technical Report Series 37. 58 p.

———. 1989. Reevaluation of the status of Peary caribou and muskox populations within the Bathurst Island complex, Northwest Territories, July 1988. Canadian Wildlife Service Technical Report Series 78. 86 p.

———. 1990. Peary caribou status report. Environment Canada. Canadian Wildlife Service. 64 p.

———. 1991. Estimating Bathurst Island Peary caribou and muskox populations. Arctic 44:57–62.

———. 1992. Peary caribou calving and postcalving periods, Bathurst Island complex, Northwest Territories, Canada, 1990. Canadian Wildlife Service Technical Report Series 151. 87 p.

———. 1995. Peary caribou studies, Bathurst Island complex, Northwest Territories, July-August 1993. Canadian Wildlife Service Technical Report Series 230. 76 p.

———. 1997. Peary caribou conservation studies, Bathurst Island complex, Northwest Territories, April-August 1994 and June-July 1995. Canadian Wildlife Service Technical Report Series 295. 155 p.

———. 1998. Status of Peary caribou and muskox populations within the Bathurst Island complex, south-central Queen Elizabeth Islands, Northwest Territories, July 1996. Canadian Wildlife Service Technical Report Series 317. 147 p.

———. 2001. Peary caribou – A case for a national park on northern Bathurst Island. Report prepared for the Canadian Nature Federation, Ottawa, Ontario. 40 p. Available from Canadian Nature Federation, 1 Nicholas Street, Suite 606, Ottawa, Ontario K1N 7B7, Canada.

MILLER, F.L., RUSSELL, R.H., and GUNN, A. 1977. Distributions, movements and numbers of Peary caribou and muskoxen on western Queen Elizabeth Islands, Northwest Territories, 1972-74. Canadian Wildlife Service Report Series 40. 55 p.

PARKER, G.R., THOMAS, D.C., BROUGHTON, E., and GRAY, D.R. 1975. Crashes of muskox and Peary caribou populations in 1973–74 on the Parry Islands, Arctic Canada. Canadian Wildlife Service Progress Notes 56:1–10.

RUSSELL, D.E., MARTELL, A.M., and NIXON, W.A.C. 1993. Range ecology of the porcupine caribou herd in Canada. Rangifer Special Issue 8:1–167.

SKOOG, R.O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Dissertation, University of California, Berkeley. 699 p.

SVOBODA, J. 1977. Ecology and primary production of raised beach communities. In: Bliss, L.C., ed. Truelove Lowland, Devon Island, Canada: A High Arctic ecosystem. Edmonton: University of Alberta Press. 185–216.

TENER, J.S. 1963. Queen Elizabeth Islands game survey, 1961. Canadian Wildlife Service Occasional Paper 4:1–50.

THOMAS, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. Canadian Journal of Zoology 60: 597–602.

THOMAS, D.C., and BROUGHTON, E. 1977. Status of three Canadian caribou populations north of 70˚ in winter 1977. Canadian Wildlife Service Progress Notes 85:1–12.

THOMAS, D.C., EDMONDS, E.J., and ARMBRUSTER, H.J. 1999. Range types and their relative use by Peary caribou and muskoxen on Melville Island, NWT. Canadian Wildlife Service Technical Report Series 343. 146 p.

WALSH, J.E., and CHAPMAN, W.L. 1990. Short-term climatic variability of the Arctic. Journal of Climatology 3:237–250.

WELLER, G. 2000. The weather and climate of the Arctic. In: Nuttall, M., and Callaghan, T.V., eds. The Arctic: Environment, people, policy. Amsterdam, The Netherlands: Harwood Academic Publishers. 143–160.