Long-Term Control of Peary Caribou Numbers by Unpredictable, Exceptionally Severe Snow or Ice Conditions in a Non-equilibrium Grazing System

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ABSTRACT. The number of Peary caribou (*Rangifer tarandus pearyi*) on the Queen Elizabeth Islands, Canadian High Arctic, is at an all-time known low. Yet some populations are still hunted, and there is no adequate monitoring program in place to determine the consequences. We evaluate information from the Peary caribou population on the south-central Queen Elizabeth Islands as a standard for an accurate and realistic assessment of what controls Peary caribou population dynamics. Between 1973 and 1997, major population crashes related to severe winter or spring weather are known to have occurred on the south-central Queen Elizabeth Islands in four caribou-years (i.e., 1 July–30 June). Population losses were 67% in 1973–74, 33% in 1994–95, 78% in 1995–96, and 83% in 1996–97. There is no evidence for direct density-dependent responses during either the favorable weather years of population growth or during any one of the years with a disastrous die-off. It appears that Peary caribou on the Queen Elizabeth Islands are living in a non-equilibrium grazing system driven mainly by abiotic factors (emergent properties), particularly by exceptionally unfavorable snow or ice conditions. Changing levels of predation by the High Arctic gray wolf (*Canis lupus arctos*) compound the uncertainty. In this High Arctic ecosystem, non-equilibrium–governed population dynamics plus wolf predation represents an appropriate conceptual model for Peary caribou populations on the Canadian High Arctic islands. The application of our findings to decision making, together with an adequate monitoring program by the responsible agencies, would promote the biological management and ecological conservation of Peary caribou on the Queen Elizabeth Islands.

Key words: Arctic Canada, population dynamics, *Rangifer tarandus pearyi*, weather-related density-independent population crashes

RÉSUMÉ. Le nombre de caribous de Peary (*Rangifer tarandus pearyi*) répertoriés dans les îles de la Reine-Élisabeth, Extrême-Arctique canadien, se trouve au niveau le plus bas à n'avoir jamais été enregistré. Pourtant, certaines populations font toujours l'objet de la chasse et il n'existe aucun programme de surveillance adéquat pour en déterminer les conséquences. Nous évaluons ici des données relatives à la population de caribous de Peary des îles centre-sud de la Reine-Élisabeth afin d'aboutir à une norme d'évaluation précise et réaliste pour déterminer ce qui influence la dynamique de population des caribous de Peary. Entre 1973 et 1997, d'importants déclins de population attribuables aux hivers ou aux printemps rigoureux ont été enregistrés dans le centre-sud des îles de la Reine-Élisabeth sur une période de quatre années-caribous (c'est-à-dire du 1er juillet au 30 juin). Les déclins de population se sont élevés à 67 % en 1973–1974, 33 % en 1994–1995, 78 % en 1995–1996 et 83 % en 1996–1997. Il n'existe aucune preuve de résultats directs dépendant de la densité pendant les années de croissance de la population au cours desquelles les conditions météorologiques étaient favorables ou pendant l'une ou l'autre des années de désastreux déclins. Il semble que le caribou de Peary des îles de la Reine-Élisabeth vive dans un système de pâturage hors équilibre répondant principalement à des facteurs abiotiques (propriétés émergentes), surtout lorsque les conditions d'enneigement ou de glaciation sont exceptionnellement défavorables. L'incertitude est aggravée par les taux de prédation changeants chez le loup arctique (*Canis lupus arctos*). Dans cet écosystème de l'Extrême-Arctique, les dynamiques de population hors équilibre, alliées à la prédation par le loup, représentent un modèle conceptuel adéquat pour les populations de caribous de Peary des îles de l'Extrême-Arctique canadien. La gestion biologique et la conservation écologique du caribou de Peary dans les îles de la Reine-Élisabeth auraient avantage à tenir compte des constatations émanant de notre étude dans la prise de décisions de même que d'un programme de surveillance convenable de la part des organismes responsables.

Mots clés : Arctique canadien, dynamique de population, *Rangifer tarandus pearyi*, déclins de population indépendants de la densité attribuables aux conditions météorologiques

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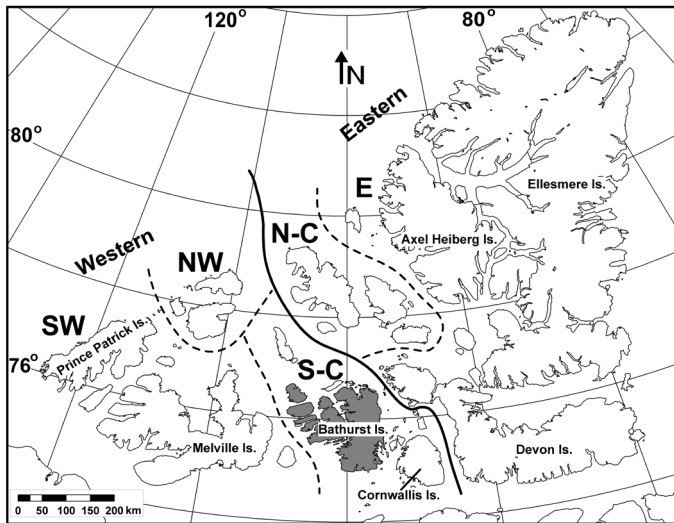[2] 1223 – 85 Street NW, Edmonton, Alberta T6K 1X7, Canada

FIG. 1. Map of the Queen Elizabeth Islands, Canadian High Arctic, showing the division of the archipelago into two major zones (Western and Eastern) and five eco-units: southwest (SW), south-central (S-C), northwest (NW), north-central (N-C), and eastern (E). The five shaded islands in the S-C eco-unit comprise the area of our case study.

INTRODUCTION

Aboriginal peoples of northern Canada view the use of caribou (*Rangifer tarandus*) as central to their cultures; therefore, the conservation of those caribou is complicated. Most of those caribou populations are subjected to year-round hunting by aboriginal people, either without kill limits or, if regulations exist, without enforcement of those limits. It is not practical in this situation to attempt to conserve these caribou populations at small sizes, as the preservation of unharvestable caribou populations will not be seen by the aboriginal users as a satisfactory long-term solution. Thus, an accurate and realistic assessment of what controls Peary caribou (*R. t. pearyi*) population dynamics must be a first step in both their biologically sound management for human consumption and their ecologically sound conservation for preservation.

Peary caribou on the Queen Elizabeth Islands (QEI: Fig. 1) live at the edge of the species' range (Miller and Gunn, 2003b) and, perhaps more importantly, on range that approaches the limits of plant growth (Edlund and Alt, 1989; Edlund, 1990) and experiences extreme weather perturbations (Maxwell, 1981). Such peripheral populations are usually more susceptible to density-independent limiting factors (Crête et al., 1996), and we suggest this is the case for these Peary caribou. The number of Peary caribou on the QEI is now at an all-time known low (Miller and Gunn, 2003b). The overall decline of population numbers on the QEI accelerated and deepened as a result of several major to cataclysmic weather-related die-offs (crashes) between 1973 and 1997. In all four of the die-off years, the crashes occurred in association with prolonged and exceptionally severe snow or ice conditions in winter or spring (Parker et al., 1975; Miller et al., 1977a; Miller, 1998; Gunn and Dragon, 2002; Miller and Gunn, 2003a, b).

Those remaining Peary caribou now potentially face additional future uncertainties from climate change and pervasive negative changes in their environment (Maxwell, 1997; Weller, 2000; Comiso, 2002; Miller and Gunn, 2003b; Miller et al., 2005b). If those changes proceed as predicted, Peary caribou might not be able to cope with the new conditions and still reach population sizes that will support desired levels of annual harvest by aboriginal hunters (Gunn et al., 2000, 2003; Miller and Gunn, 2003b). For these reasons, and because the data support the primary importance of weather in the prosperity—and at times, the very persistence—of Peary caribou populations, our objective here is to detail what really controls Peary caribou population dynamics on the QEI. We focus on the Peary caribou population found on the south-central QEI, which has the best documentation, as a case study. We believe the findings will be applicable to most, if not all, Peary caribou on the QEI.

MATERIALS AND METHODS

Background

Peary caribou and muskoxen (*Ovibos moschatus*) are the only two ungulates that have established themselves on the QEI. The High Arctic gray wolf (*Canis lupus arctos*) is also found throughout the QEI in association with its major prey base—Peary caribou and muskoxen (Miller, 1995c; Miller and Reintjes, 1995). Miller et al. (2005a) identified five eco-units in the QEI: southwest (SW), south-central (S-C), northwest (NW), north-central (N-C), and eastern (E). Of these, the SW and S-C eco-units have served as the "heartland" for Peary caribou, at least during the last half of the 20th century (Fig. 1). Peary caribou were abundant in the NW eco-unit in 1961, but rare and probably absent at times thereafter. Caribou have been uncommon to rare from at least 1961 onward in the N-C and E eco-units.

Data Sources

We used data from Tener (1963), Slaney (1975), Fischer and Duncan (1976), Miller et al. (1977a), Ferguson (1987), Miller (1987, 1989, 1991, 1992, 1993, 1994, 1995b, 1997, 1998), Gunn and Dragon (2002), and Miller and Gunn (2003a) to determine the size, trend, and reproductive performance of the five-island Peary caribou population on the south-central QEI between 1961 and 1998 (Figs. 1, 2). We adjusted Tener's (1963) 1961 caribou estimate of 3565 for the five-island complex to 3509 to correct for differences in island sizes used by Tener (1963) and those currently reported in *The Atlas of Canada* (http://atlas.nrcan.gc.ca, under Facts about Canada, Sea Islands).

Because published estimates for 1993 and 1994 were based on slightly different land areas (Miller, 1998:35) and to maintain a constant survey area among all years, we made the following changes. To obtain a 1993 estimate, we
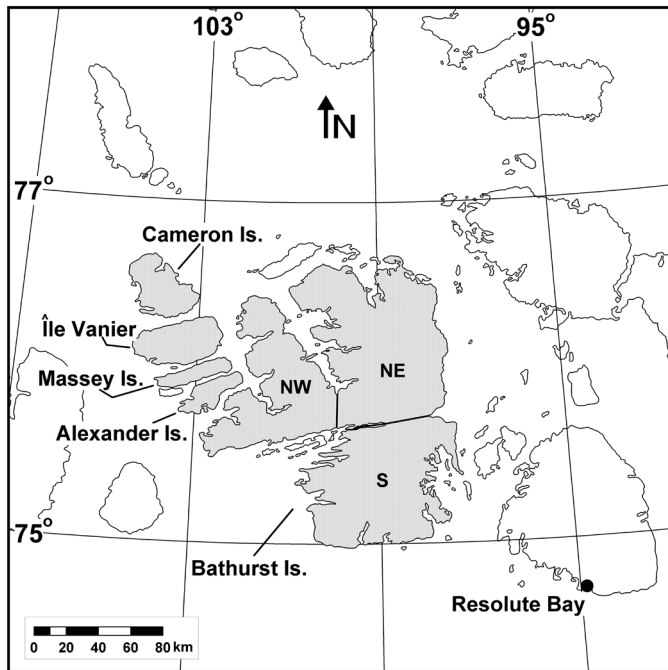
FIG. 2. Map of the south-central Queen Elizabeth Islands, Canadian High Arctic, showing the five-island study area (shading) and the division of Bathurst Island into NW, NE, and S survey strata.

conservatively expanded the 2387 caribou counted in the 1993 non-systematic aerial survey by taking the number of caribou counted on Bathurst, Alexander, and Massey islands in 1993 and multiplying it by the average annual growth rate from 1985 to 1988 (i.e., the last two surveys prior to 1993). Since fog had prevented a survey on Île Vanier and Cameron Island in 1993, we added to the estimate 106 animals, extrapolated from the average of 1985 and 1988 values for those two islands (Table 1: i.e., $(2387 \times 1.123) + 106 = 2787$). We then conservatively obtained a 1994 estimate by multiplying our 1993 estimate by the average annual growth rate between 1974 and 1993 (Table 1: i.e., $2787 \times 1.132 = 3155$) as a reasonable expansion from 1993. These calculations resulted in a 120-animal (4%) increase (from 2667 to 2787) in the 1993 estimate and a 144-animal (5%) increase (from 3011 to 3155) in the 1994 estimate over previously reported values.

As a measure of calving success, we used the percentage of calves observed among all caribou seen during a single post-calving count made between the end of June and late August each year to determine sex and age composition. We based this measure on the assumptions that most calf mortality occurs at birth or within the first week of life (Miller et al., 1988) and that maximum representation of newborn calves would be 30% among all caribou seen (i.e., $r_m = 0.30$; Bergerud, 1980), assuming minimal mortality around calving time among animals one year old or older. We also evaluated the performance of breeding cows using two ratios obtained from each annual count: the number of calves per 100 breeding cows and the number of calves per 100 females age one year or older (1+-year-old females).

W.A. Gould (pers. comm. 2008) provided us with the tabulated data (derived from GIS polygons of vegetation classes) that were used to produce the vegetation maps in Gould et al. (2003: Figs. 3, 4, and 5). We grouped those data for our five-island study area into two vegetation types, "High Arctic semidesert" and "polar desert." We then obtained estimates of the area represented by each vegetation type by island and adjusted them to conform to the sizes reported in *The Atlas of Canada* for Bathurst, Vanier, Cameron, Alexander, and Massey islands (http://atlas. nrcan.gc.ca, under Facts about Canada, Sea Islands). Then we estimated the oven-dried weight for the total annual aboveground net primary production ($kg \cdot km^{-2} \cdot y^{-1}$) of each vegetation type by island, using those rates from Bliss and Matveyeva (1992: Table III). High Arctic semidesert vegetation was calculated at $25\,000 \ kg \cdot km^{-2}$ and polar desert vegetation at $700 \ kg \cdot km^{-2}$ times their respective area of coverage (km^2) on each island.

Working Definitions

We use the term "crash" to identify all major die-offs that occur within a population in a single caribou-year (1 July – 30 June; Miller and Gunn, 2003b:215 – 216) that meet the criteria of Miller et al. (2005c:188). That is, a population crash must be (a) unpredictable, (b) rapid within a single caribou-year, and (c) result in a population decline of 30% or more in that year. Crashes occurring in consecutive years should be considered multiples of single-year events. For example, the consecutive three-year disastrous 98% decline in the Peary caribou population on the south-central QEI resulted from three annual crashes: 1994 – 95, 33% decline; 1995 – 96, 78%; and 1996 – 97, 83%.

We define the negative aspect of a "density-dependent factor" as one that affects the ability of a caribou population to continue to grow as a direct result of that population's density. A density-dependent factor would retard population growth, as the density increases beyond a hypothetical equilibrium point (K) by decreasing births and increasing deaths.

We define a "density-independent factor," such as exceptionally unfavorable snow or ice conditions, as one that negatively influences a caribou population, but that is independent of the existing population's density and its absolute forage supply. Thus, a density-independent factor (i.e., the chance occurrence of abiotic weather factors) is free of any fixed hypothetical equilibrium point.

We define "High Arctic semidesert" as those sections of the five-island study area having a 5 – 50% vegetation cover, based on a horizontal structure canopy; 100–500 $g \cdot m^{-2}$ aboveground plant biomass; and 20–50 $g \cdot m^{-2} \cdot y^{-1}$ annual above and belowground net primary productivity (from Gould et al., 2003: Figs. 3, 4, and 5).

We define "polar desert" as those sections of the five-island study area with less than 5% horizontal structure as vegetation cover; less than 100 $g \cdot m^{-2}$ aboveground plant biomass; and 0–20 $g \cdot m^{-2} \cdot y^{-1}$ annual above and belowground

TABLE 1. Population dynamics exhibited by the Peary caribou (*Rangifer tarandus pearyi*) on Bathurst, Vanier, Cameron, Alexander, and Massey islands within a 19 143 km^2 survey area, south-central Queen Elizabeth Islands, Canadian High Arctic, 1961–97.

Survey Year[1]	Total Caribou	Density (caribou • 100 km^{-2})	Mean Annual Growth Rate (λ)	Source
1961	3509	18.3	–	Tener (1963)
1973	797	4.2	0.884	Miller et al. (1977a)
1974	**266**	**1.4**	**0.334**	Miller et al. (1977a)
1975	361	1.9	1.357	Fischer and Duncan (1976)
1981[2]	345	1.8	0.993	Ferguson (1987)
1985	727	3.8	1.205	Miller (1987)
1988	1030	5.4	1.123	Miller (1989)
1993[3]	2787	14.6	1.220	Miller (1995b, 1998)
1994[4]	3155	16.5	1.132	Miller (1997, 1998)
1995	**2100**	**11.0**	**0.666**	Miller (1997, 1998)
1996	**452**	**2.4**	**0.215**	Miller (1998)
1997	**78**	**0.4**	**0.173**	Gunn and Dragon (2002)

[1] Bold indicates weather-related crash years.

[2] Ferguson (1987) estimated 289 caribou on Bathurst Island only in August 1981; we adjusted his estimate to 345 caribou for the total five-island area, basing the calculation on the proportionate land area of Bathurst Island.

[3] The 1993 estimate equals the number of caribou counted on Bathurst, Alexander, and Massey islands times the mean annual growth rate (λ) for 1985 to 1988, plus 106 animals extrapolated from the average of 1985 and 1988 values for Île Vanier and Cameron Island, to maintain the 19 143 km^2 survey area in all years, i.e., (2387 × 1.123) + 106 = 2787.

[4] The 1994 estimate equals the 1993 estimate times the mean annual growth rate (λ) for 1974–93, i.e., 2787 × 1.132 = 3155.

net primary productivity (from Gould et al., 2003: Figs. 3, 4, and 5).

RESULTS AND DISCUSSION

Population History

As an example, we use the Peary caribou population for which we have the most available information. It is found on five islands—Bathurst (16 042 km^2), Vanier (1126 km^2), Cameron (1059 km^2), Alexander (484 km^2) and Massey (432 km^2)—covering a total 19 143 km^2 of range within the south-central QEI (Table 1, Fig. 2). The highs and lows of the Peary caribou and muskox populations within the south-central QEI paralleled each other through at least 1973–97 (Fig. 3).

The first systematic aerial survey of Peary caribou and muskoxen on the QEI to cover nearly their entire range was carried out in summer 1961 (Tener, 1963). That survey has served as the benchmark for determining trends in numbers and distribution of Peary caribou (and muskoxen) on the QEI (Miller et al., 2005a). Little information about the numbers and distributions of Peary caribou and muskoxen on the QEI was available before 1961. Local knowledge was limited, as only two small and isolated Inuit settlements existed on the QEI, having just been established there in the mid 1950s. These were Resolute Bay (74.72° N, 94.98° W) on the southwestern coast of Cornwallis Island and Grise Fiord (76.42° N, 82.91° W) on the south coast of Ellesmere Island).

In 1961, the Peary caribou population size was at an all-time known high (Table 1). Unfortunately, no one will ever know whether the population was at a peak, still coming up, or already going down. Nor are there any data on the pattern
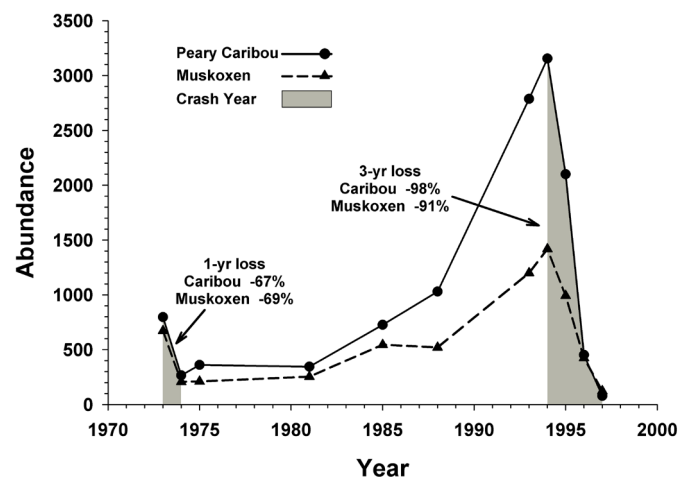

FIG. 3. The 20-year growth curves for the Peary caribou population and the associated muskox population on the five-island, 19 143 km^2 survey area, south-central Queen Elizabeth Islands, Canadian High Arctic. The graph starts with the 1973–74 crash year and ends with the three consecutive crash years in 1994–97.

or causes of the decline that occurred during the next 12-year period (1961–62 to 1972–73), when the population fell by 77%. Then, in 1973–74, the population crashed a further 67% in just one year (Fig. 3). Recovery was slow. The caribou population increased by ca. 4% • y^{-1}, on average, over the first seven years after the crash (1974–75 to 1980–81). Over the next 13 years (1981–82 to 1993–94), the population increased to 9.1 times its estimated 1981 size. The 20-year growth phase then ended abruptly. In three years (1994–95 to 1996–97), three single-year winter or spring weather-related crashes reduced the population to only a remnant, ca. 2–3% of its 1961 or 1994 size (Table 1, Fig. 3: Miller et al., 1977a; Miller, 1998; Gunn and Dragon, 2002).

TABLE 2. Area representation and annual aboveground net primary productivity, by island, of the two major vegetation types on the five-island study area, south-central Queen Elizabeth Islands.

| Vegetation Type[1] | Vegetation Type by Island (Island Size) | | | | |
	Bathurst (16 042 km²)	Vanier (1126 km²)	Cameron (1059 km²)	Alexander (484 km²)	Massey (432 km²)
Area (km²) representation of vegetation type by island[2]					
High Arctic semidesert	10 995	1126	714	484	432
Polar desert	5047	0	345	0	0
Annual aboveground net primary productivity (kg•km⁻²•y⁻¹) of each vegetation type by island[3]					
High Arctic semidesert	274 875 000	28 150 000	17 850 000	12 100 000	10 800 000
Polar desert	3 532 900	0	241 500	0	0

[1] See MATERIALS AND METHODS for working definitions of High Arctic semidesert and polar desert, based on Figures 3, 4, and 5 of Gould et al. (2003).

[2] Obtained from tabular data used to produce Figures 3, 4, and 5 of Gould et al. (2003), which W.A. Gould (Dec 2008) provided directly to us. We adjusted the five island sizes slightly to conform exactly with those island sizes reported in *The Atlas of Canada* (http://atlas.nrcan.gc.ca, under Facts about Canada, Sea Islands).

[3] Total annual dry weight values for aboveground net primary productivity (kg•km⁻²•y⁻¹) of vegetation were calculated by island from Bliss and Matveyeva (1992), at 25 000 kg•km⁻² for High Arctic semidesert and 700 kg•km⁻² for polar desert, then multiplied by the respective area (km²) of representation on each island.

Satellite and conventional VHF radio telemetry studies of Peary caribou on the south-central QEI indicate that various patterns of seasonal range occupancy are carried out annually (Miller, 1995a, 1997, 1998, 2002; Miller and Barry, 2003). Some caribou move annually on a seasonal basis among all five islands; others restrict their annual seasonal movements to only two, three, or four of those islands; and still others remain year-round on a single island. On Bathurst Island, some caribou remain year-round on the NE survey stratum, while others remain on the NW or S of the island (Fig. 2). Peary caribou on the south-central QEI seem to be exercising nearly every alternative pattern of seasonal and annual range occupancy available to them. The size of their seasonal range was smallest in winter and largest in summer, and their greatest displacements occurred during the pre-calving and pre-rut periods (Miller, 2002; Miller and Barry, 2003).

Forage Availability

The vegetation on the QEI has been described by Edlund and Alt (1989), Bliss (1990), Edlund (1990), and Gould et al. (2003), among others. Vegetation on the south-central QEI is limited compared to vegetation on the mainland tundra, but much of the caribou range is relatively productive for the QEI (Table 2; Gould et al., 2003: Figs. 3, 4, 5). About 72% of the 19 143 km² study area is High Arctic semidesert, and the remainder is polar desert (Table 2).

We estimate that on average, the 13 751 km² of High Arctic semidesert yields 25 000 kg•km⁻² of aboveground vegetation per year, whereas the 5392 km² of polar desert yields an average of only 700 kg•km⁻². That is, annual production per km² of the High Arctic semidesert is 36 times that of the polar desert. The 72% of the study area in High

Arctic semidesert could thus produce about 91 times as much aboveground new plant growth each year as the 28% of the study area in polar desert. Although 99% of the estimated new aboveground plant growth occurs annually on the High Arctic semidesert areas, the more exposed polar desert areas are most likely important to Peary caribou for short periods (several days or a few weeks) when accessibility of the forage supply has been temporarily and critically restricted nearly range-wide by extreme snow or ice conditions.

The total estimated annual production of aboveground vegetation in both High Arctic semidesert and polar desert is 347 549 400 kg (Table 2). The annual dry weight forage requirement of Peary caribou has been estimated at 730 kg • caribou⁻¹ (Miller, 1998). Therefore, it appears that even the two largest numbers of Peary caribou ever estimated on the five-island study area, 3509 in 1961 and 3155 in 1994 (Table 1), would have required only about 1% of that total annual production for all to have survived. If the Peary caribou within the 19 143 km² study area could obtain even 2% of the estimated total aboveground vegetation production each year, those five islands could collectively support 10 000 Peary caribou.

Thus, there is no evidence to suggest that wintertime forage accessibility in the study area was always inadequate to maintain the annual numbers of caribou that were estimated between 1961 and 1998. To the contrary, the annual rates of reproduction and early calf survival were high, and the study population was in an overall growth phase from 1974–75 though 1993–94 (Tables 3, 4, 5, Fig. 3). The level of population performance was high even compared to the levels of large, established mainland caribou populations. Also, in those 20 years, mortality among 1+-yr-old caribou was so low that it was nearly undetectable: we observed at most three carcasses per year, and none in some years,

during 60–100 h of low-level helicopter search efforts in each year from 1988 to 1994, when the population was estimated to have increased 3.1 times (Table 1).

Population Dynamics

No data or empirical observations suggest that snow cover reduces Peary caribou access to forage to a small fraction of the total vegetated area in all years: it is only in those few years with exceptionally severe snow or ice conditions that such extreme restriction occurs. In fact, the snow cover is relatively shallow compared to mainland caribou winter ranges, and in many years, snowpack conditions (i.e., hardness, density, and icing on, in, or under the snowpack) are highly favorable throughout the period of snow cover, with icing alone in those years not being a problem (Miller, 1992, 1993, 1994). When the snow remains powdery with some granular ("sugar") snow on the bottom, the caribou can feed everywhere, except in some relatively small areas of deep depression or in snowdrift areas at the bases of steep slopes or cliffs. In years of favorable snow conditions, the caribou do not even have to crater—they simply push the snow cover aside with their noses (Miller, 1995b).

In some years, subtle environmental pressures can act on the caribou, with only relatively small reductions in population performance; in other years, the impact from unfavorable snow or ice conditions can lead to poor calf production and markedly reduced early calf survival, and in a few years, to near-total failure of the calf crop. Only a few unpredictable years with exceptionally extreme and prolonged snow or ice conditions are known to have caused single-year crashes (Figs. 3, 4).

Most importantly, no one has ever documented even small-scale local overgrazing, let alone an extensive area of severely deteriorated or destroyed range, caused by caribou grazing on the south-central QEI or anywhere else in the QEI. In the summer of 1998, which was the first summer after the three consecutive annual crashes that caused a 98% loss of the Peary caribou study population, Greg Henry, an experienced Arctic range ecologist, did a visual assessment, on foot and by low-level helicopter flights, of the vegetation on Bathurst Island. He concluded that the post-die-off range on Bathurst Island could support at least several thousand caribou without their having any serious impact on the vegetation (G.H.R. Henry, pers. comm. 1998).

Gunn and Dragon (2002) argue that it was not the caribou's absolute forage supply that caused the major crashes, for the following reasons:

1. During the weather-related crashes, population reductions occurred at high and similar mortalities among both Peary caribou and muskoxen—two species with important differences in diets and temporal and spatial selection of feeding sites—over a vast geographic region throughout the western QEI (ca. 100 000 km²) (Miller et al., 1977a; Miller, 1998). (Fig. 3 shows the crashes for the south-central QEI only.)

2. The QEI have different regional climatic and vegetation patterns, constituting distinctive "bioclimatic zones" (Maxwell, 1981; Edlund and Alt, 1989; Edlund, 1990).

3. There is no evidence of changes in range occupation, or in daily, seasonal, or annual movement patterns, prior to the severe winters and springs. Such alterations would be expected in response to a seriously reduced forage supply that could no longer support the animals using it.

4. It appears that only extreme environmental episodes could cause deaths among Peary caribou and muskoxen that are correlated both spatially and temporally to such a degree.

The 20-year period (1974–75 to 1993–94) is the only period of continual population growth for a Peary caribou population on the QEI that is known and relatively well-documented (Table 1, Fig. 3). In the first 11 years (1974–75 to 1984–85), when densities were only 1.4 to 3.8 caribou • 100 km⁻² , the mean annual growth rate (λ) was 1.096. Over the next nine years (1985–86 to 1993–94), as caribou more than quadrupled, the densities increased from 3.8 to 16.5 caribou • 100 km⁻² , and the mean annual growth rate (λ) was 1.177, or 1.8 times that of the earlier period of low caribou densities. Mean calving success, measured as all calves among all caribou, was 25.3% ± 3.7% SD (range = 18.6–28.6%), where 30% calves would be the expected maximum. These high annual levels of reproduction and early calf survival could not have persisted throughout 1988–94 if the population's breeding cows had not been healthy, with high body fat reserves (Thomas, 1982). Thus, annual reproduction did not decrease with increasing population density, and the mean annual growth of the caribou population accelerated as density increased rather than decelerating, as in a density-dependent response (Table 1, Fig. 3). This pattern of better performance at higher densities offers no evidence for an inadequate absolute forage supply and the presence of population control by density-dependent factors.

After the 20-year growth phase, the 98% Peary caribou population decline and the 91% muskox population decline both followed immediately in 1994–95 to 1996–97. Those three crash events, which involved starvation deaths as forage became inaccessible nearly range-wide, were disastrous for those populations (Miller et al., 1977a; Miller, 1998; Gunn and Dragon, 2002). There was no indication that the south-central QEI caribou population (or the associated muskox population) had reached or passed through some biologically or ecologically meaningful threshold where a density-dependent response would have had to come into play with subsequent dire results.

Effect of Uneven Caribou Distribution on Bathurst Island

The use of range-wide mean density to evaluate environmental stress on caribou populations characterized by persistent, uneven spatial distribution can be misleading, because it averages the high and low densities that occur on

TABLE 3. Numbers of Peary caribou (*Rangifer tarandus pearyi*) estimated by survey stratum on the survey area, south-central Queen Elizabeth Islands, Canadian High Arctic, 1961–97.

Year[1]	Bathurst Island (survey stratum size)			Northwestern Satellite Islands (survey stratum size)			
	NE ($6630 km^2$)	NW ($4068 km^2$)	S ($5344 km^2$)	Vanier ($1126 km^2$)	Cameron ($1059 km^2$)	Alexander ($484 km^2$)	Massey ($432 km^2$)
1961[2]	1467	1177	12	389	265	187	12
1973	127	160	425	24	9	0	52
1974	**187**	**44**	**0**	**15**	**20**	**0**	**0**
1981[3]	160	70	59	–	–	–	–
1985	178	201	116	67	51	38	76
1988	460	231	130	85	9	31	84
1993	2032	357	191	(76)[4]	(30)[4]	70	31
1996	**300**	**131**	**12**	**9**	**0**	**0**	**0**
1997	**44**	**20**	**10**	**0**	**0**	**0**	**4**

[1] Years in bold are known weather-related die-off years. Population estimates were made in 1975, 1994, and 1995, but not at the stratum level.

[2] Values of Tener's (1963) 1961 caribou estimates for the five-island complex were adjusted to correct for the difference in island sizes used by Tener (1963) and those currently reported in *The Atlas of Canada*.

[3] The August 1981 survey by Ferguson (1987) covered Bathurst Island only.

[4] Approximated from the mean number of caribou seen in 1985 and 1988 for each island to retain the 19 143 km^2 survey area in all survey years.

major land areas in different parts of their range. In 1961, Tener (1963), using estimates calculated by survey stratum (Table 3), found that 67% of the land area on Bathurst Island held 99.5% of the estimated caribou and calves represented 20% of all caribou. The observed skewed distribution was 22.1 caribou • 100 km^{-2} on NE Bathurst, 28.9 caribou • 100 km^{-2} on NW Bathurst, and only 0.2 caribou • 100 km^{-2} on S Bathurst (Fig. 2). In 1993, when 2273 caribou were actually seen on Bathurst Island alone and 2580 were estimated there, 79% of them were on the NE section, 41% of the island's land area, and calves represented 28% of all caribou. Thus, in 1993 there were 30.6 caribou • 100 km^{-2} on NE Bathurst, but only 8.8 caribou • 100 km^{-2} on NW Bathurst, and 3.6 caribou • 100 km^{-2} on S Bathurst (Table 3). Caribou demands on the forage supply during summer 1993 thus varied by stratum, being 3.5 times greater in the NE than in the NW and 8.5 times greater in the NE than in the S. This highly uneven distribution means that the use of range-wide mean density values to evaluate caribou pressure on the range is questionable, as this method could mask important differences and produce misleading results regarding the actual pressure on forage plants.

Caribou performance parameters were high on all three sections of Bathurst Island in 1993, but were highest in the NE, where the density of caribou was also the highest (30.6 caribou • 100 km^{-2}), almost double the mean density for the island as a whole (16.1 caribou • 100 km^{-2}). High population growth throughout the early 1990s, high calf survival, and high representation of yearlings and juveniles all indicate a healthy, fast-growing population, with excellent potential for continued growth in the absence of extremely severe weather years (Tables 4, 5). Thus, there is no evidence to even suggest that whatever kept the population from realizing its full potential directly involved the abundance of

its absolute food supply or that it occurred in a density-dependent manner. Had the population responded in a density-dependent manner, it would have experienced a detectable and serious reduction in reproduction and early calf survival, and under especially severe conditions, markedly reduced survival among the 1+-yr-old caribou as the population grew larger. Instead, however, the caribou population grew at a mean annual rate of 13%, a high rate of population growth over two decades, even when compared to that of established large populations of North American caribou on much more productive mainland ranges (Messier et al., 1988; Davis and Valkenburg, 1991) and on the island of Newfoundland (Bergerud, 1983).

Density-Dependence Is Not an A Priori Fact of Life

An important question is, why should all observed limitations in reproduction and survival necessarily be interpreted as density-dependent responses? In all likelihood, population productivity could be controlled by a combination of annual and cumulative weather events, either singly or in combination with other factors that are subtle but moderately severe in nature. For example, it is most likely that the effect of reduced forage accessibility would be compounded by different annual rates of wolf predation, which could be quite independent of caribou densities (Valkenburg et al., 1996; Whitten, 1996).

Because of the extreme low growth of vegetation and the patchy appearance of High Arctic caribou ranges, some observers may seriously underestimate forage abundance, leading to speculation that all reductions in population dynamics during the relatively favorable weather years had to be caused by mechanisms operating in a density-dependent manner in response to food limitation. We believe the

TABLE 4. Values describing the population status and performance for Peary caribou (*Rangifer tarandus pearyi*) on Bathurst Island and in its three major survey divisions, south-central Queen Elizabeth Islands, Canadian High Arctic, in August 1993 (based on 2273 caribou observed).

Statistic	Bathurst Island (16 042 km^2)	NE Bathurst (6630 km^2)	NW Bathurst (4068 km^2)	S Bathurst (5344 km^2)
1+-yr-old males per 100 1+-yr-old females	69.2	64.4	91.4	80.0
Juveniles[1] and yearlings per 100 bulls[2] and breeding cows[3]	73.1	71.8	87.0	62.6
Bulls per 100 breeding cows	43.6	32.9	81.9	130.6
Calves per 100 1+-yr-old females	65.9	69.9	54.7	44.0
Calves per 100 breeding cows	96.8	97.1	97.2	91.7
% calves among all caribou	28.0	29.8	22.2	19.6
% yearlings among all caribou	12.1	12.6	10.5	10.1

[1] Juveniles are 2-yr-old and some older nonparous females and 2- and 3-yr-old males.

[2] Bulls are considered 4+-yr-old males.

[3] Breeding cows are 3+-yr-old females, but might include some few primiparous 2-yr-old and even a few yearling females, which would vary proportionally with the favorableness of the year.

evidence in this case argues to the contrary. Not all reductions in population size or performance are necessarily triggered by the status of the absolute forage supply or even its accessibility.

In theory, it is possible that density-dependence could occasionally be important in regulating population growth of Peary caribou on the QEI. However, there are no on-site data from anywhere in the QEI at any time in the past to support this possibility. Also, it is probable that other crash events occurred between 1962 and 1971, a period when the status of the population was unknown. In some years, in the absence of deep snow cover, freezing rain events in early winter (Sep-Oct), late winter (May), or spring (Jun), together with freeze-thaw events and lingering snowmelts, could produce widespread ground-fast ice, ice layering in the snow, or heavy crusting of snow. When widespread or nearly range-wide, these conditions, either singly or in combination, will restrict access to the vegetation for prolonged periods—and many caribou will die (Parker et al., 1975; Miller et al., 1977a; Miller, 1998; Gunn and Dragon, 2002). Thus, it is possible that exceptionally severe widespread icing occurred during some or many of the years from 1961–62 to 1972–73, and that icing alone created lethal conditions for many caribou, even when snow depth was relatively low. Such icing on, in, or under the snowpack would have gone undetected: it was not reported in Arctic weather station records, and no caribou biologists were on site at that time.

The influence of crash years on caribou populations is compounded by those intervening years when calf increments and thus yearling recruitments are lower than average. This is especially true when a near-total loss of the calf crop is accompanied by an increase in deaths among 1+-yr-olds. These unpredictable poor calf crop years would also cause serious reduction in the size of the breeding female segment several years later. Therefore, we suggest that if a density-dependent response to the absolute forage supply ever does become the paramount condition for the control of Peary caribou, it would occur—because of the vagaries of the weather and wolf predation—about once a century at most, rather than every few decades. It is only the absence of extremely severe snow or ice conditions, along with wolf populations being below or in balance with their prey base, that allows these Peary caribou populations to experience high growth rates occasionally over a long series of years.

Berryman et al. (2002) concluded that population regulation is merely one of the many behaviors possible in populations of organisms that may or may not occur as *a posteriori* emergent properties of particular ecological structures, depending on the circumstances. However, White (2001:148) noted that after 60 years of controversy over population regulation, there is still no widespread evidence for it and much evidence against it. He declared a predetermined equilibrium point is a mean, which is "a human construct that does not exist or have any meaning in nature. So how can mortality factors be density-dependent, restoring numbers to something that does not exist?" (White, 2001:150). Krebs (1991:6) concluded that "the density-dependent paradigm is bankrupt because it is descriptive and *a posteriori*. It does not lead to understanding because no mechanisms are specified. It is an equilibrium-based concept that sheds no light on a non-equilibrium world." Biologists and ecologists, he later added, should "seek mechanisms by which population effects are achieved. Density is not a mechanism" (Krebs, 1995:9).

Density-Independent Factors Operate in a Non-equilibrium Grazing System

Although the Peary caribou population on the south-central QEI experienced an average annual rate of increase of 13.2% for 20 years from 1974 to 1994, 17.7% for the last nine years from 1985 to 1994, and 20.5% for the last six years from 1988 to 1994 (Table 1), there were no reports of range deterioration. When the first year (1994–95) of the three years of annual winter and spring crashes began, and in each of the next two years (1995–96 and 1996–97), the loss of most of the forage supply through inaccessibility

TABLE 5. Values describing population status and performance for Peary caribou (*Rangifer tarandus pearyi*) on Bathurst, Vanier, Cameron, Alexander, and Massey islands, within a 19 143 km^2 survey area, south-central Queen Elizabeth Islands, Canadian High Arctic, summers 1990 to 1993, prior to the three consecutive annual crashes in winter and spring 1994–97.

Statistic	Mean	± SD	Range
All caribou observed	1462.8	707.4	87 – 2387
1+-yr-old caribou observed	1085.3	473.6	709 – 1720
Calves observed	377.5	235.6	162 – 667
1+-yr-old males per 100 1+-yr-old females	59.5	6.7	54.5 – 69.1
Juveniles[1] and yearlings per 100 bulls[2] and breeding cows[3]	83.1	16.6	65.6 – 101.6
Bulls per 100 breeding cows	51.9	11.4	41.2 – 65.5
Calves per 100 1+-yr-old females	51.9	14.0	35.4 – 65.6
Calves per 100 breeding cows	88.4	10.8	72.6 – 96.7
% calves among all caribou	24.3	4.8	18.6 – 28.6
% yearlings among all caribou	15.2	2.4	13.0 – 18.3

[1] Juveniles are 2-yr-old and some older nonparous females and 2- and 3-yr-old males.

[2] Bulls are considered 4+-yr-old males.

[3] Breeding cows are 3+-yr-old females, but might include some few primiparous 2-yr-old and even a few yearling females, which would vary proportionally with the favorableness of the year.

was sudden (i.e., within the crash season each year, while the snow or ice cover was still present). The 20 years with relatively favorable weather apparently were too few to allow the Peary caribou, and especially both the Peary caribou and the muskoxen, opportunity to overshoot some unknown, conjecturally critical threshold population size at which the range would have afterwards suffered even serious deterioration, let alone destruction.

There was no indication of any marked reduction in the annual calf crops from 1991 to 1994, when the population was at its highest densities, but just the opposite: the annual rates of reproduction and calf survival remained high (i.e., in 1991–94, mean percent calves was 26.5% ± 3.0% SD, range 22.2–28.6%). Also, the minor reliance of Peary caribou on lichens in their seasonal and year-round diets makes it most unlikely that they would experience such a density-dependent condition caused directly by the state of the absolute food supply. Vascular plants—particularly sedges, rushes, and grasses—recover quickly from grazing; some are even stimulated to produce more growth after grazing.

The importance of predation and other limiting factors should not be ignored, nor should a constant state of importance in all things controlling caribou numbers be assumed. There is a suite of controlling factors, and the relative importance of each to the reduction of a caribou population can vary from year to year. However, the extreme weather-related crash experienced by the study population in 1996–97 was so severe that it caused the estimated population of 452 caribou (only 2.4 caribou • 100 km^{-2} of range) to decline by 83% to only 78 animals (0.4 caribou • 100 km^{-2}). Therefore, we believe this extreme level of weather-induced severity occurring at such a low starting mean density within the 19 143 km^2 five-island area, puts weather—extremely severe snow or ice conditions, abiotic density-independent factors—in the primary position of importance for Peary caribou on the QEI. The post-crash range in summer 1998, the first plant-growing season after the three

annual crashes from 1994–95 to 1996–97, appeared adequate to support several thousand caribou (G.H.R. Henry, pers. comm. 1998), a conclusion that is strongly supported by the magnitude of the estimated annual aboveground production of vegetation (Table 2).

We remain confident that the dominant factor controlling the population dynamics of Peary caribou on the south-central QEI and elsewhere on the QEI has been unfavorable winter or spring weather. In those relatively few years when extremely severe and prolonged snow or ice conditions persisted, the Peary caribou population experienced nearly complete loss of its calf crops and suffered all known major crash events (Parker et al., 1975; Miller et al., 1977a; Miller, 1998; Gunn et al., 2000, 2003; Gunn and Dragon, 2002; Miller and Gunn, 2003a, b). The magnitudes of the 1973–74 single-year crash and the three consecutive winter and spring annual crashes between 1994 and 1997 for both the Peary caribou and the muskox populations appear to be independent of animal or plant density.

SPECIAL CONCERNS AND GENERAL PROBLEMS

Emergent Properties of Forage and Weather

We believe that Peary caribou live in a non-equilibrium grazing system on the QEI where they experience extremely unfavorable stochastic weather events (Gunn et al., 2003; Miller and Gunn, 2003a, b) leading to reduced or failed reproduction, poor early calf survival, and high mortality among 1+-yr-old animals. These responses occur at rates that will depend mostly on the frequency, duration, and severity of their exposure to the stressful weather events. The response of the caribou is to a remarkable degree independent of their density (Caughley and Gunn, 1993; Valkenburg et al., 1996; Whitten, 1996; Behnke, 2000). Forage accessibility, rather than animal density, drives changes in Peary caribou populations in an unpredictable manner,
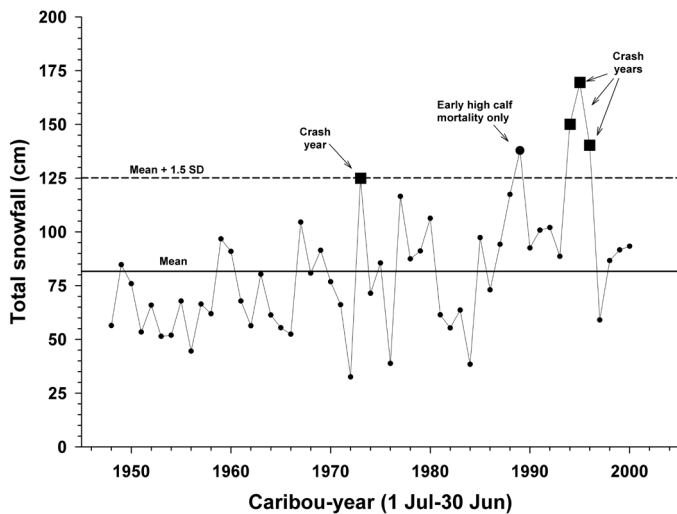
FIG. 4. Total snowfall trend between 1 September and 21 June of each caribou-year (1948–49 to 2000–01) at Resolute Airport (74.72° N, 94.98° W), Cornwallis Island, south-central Queen Elizabeth Islands, Canadian High Arctic. A "crash year" (■) is a year with an estimated decline in population size of 30% or more.

and it does so rapidly, causing the extreme severity of the weather-related winter and spring crash events.

These high levels of environmental stochasticity that exist in the High Arctic prevent the vegetation-herbivore feedback loop from becoming a dominant regulating factor for Peary caribou on the QEI. Therefore, long-term fluctuations in these populations are "essentially a mathematical artifact of among year variation in weather, even when the weather exhibits no trend over time" (Caughley and Gunn, 1993:54; see also Behnke, 2000:147). That is, the size of a population at a given time is primarily a function of the size to which the population was last reduced and the number of years with favorable weather that have passed since the last die-off (Valkenburg et al., 1996). Thus, these changes in size of a population caused by environmental fluctuations are largely independent of population size (Figs. 3, 4; Gunn et al., 2003; Miller and Gunn, 2003a, b) and will lead to nearly the same proportionate decrease in numbers whether the population is large or small (Figs. 3, 4; Caughley and Gunn, 1996:170; Behnke, 2000:146). In addition, in the case of Peary caribou on the QEI, this outcome could be altered from time to time by the increasing pressure of wolf predation, especially when the ungulate prey base dwindles from one or more other causes (Gunn et al., 2000).

The exceptionally low growth forms of most of the vegetation on the QEI make it susceptible to being locked down by freezing rain or hard-packed, windblown snow. Such events can occur at snow depths of only 30 cm, or as little as 10 cm, depending on the snow density (compaction) or the coarseness (infiltration qualities) of the substrate. Woo et al. (1982) have shown that because of the hydrological processes involved, ground-fast ice can form under any depth of snow—and even on snow-free sites under certain conditions. The strong correlation between known caribou crashes (Fig. 3) and years with the heaviest total snowfall

(Fig. 4) is misleading when accepted intrinsically, as it is only one of several lethal scenarios. We believe that relatively deep snow per se is not necessary to create lethal conditions, but that heavy snowfall does have a greater potential for leading to unfavorable snowpack conditions that are life-threatening. Snow is redistributed by wind action across the range. This redistribution allows widespread or range-wide development of extremely severe snow characteristics (i.e., hardness and density) that lead to extreme relative unavailability of the forage for both Peary caribou and muskoxen—and in the worst years, to death by starvation. Also, widespread icing alone, in shallow snow cover or even in the absence of snow cover, can create lethal conditions. Fortunately, in all but the most extreme years, there were either enough areas with favorable snow conditions without the presence of extensive ice, or enough snow-free patches and shallow snow areas free of icing, to allow the caribou to forage without having to dig feeding craters in the hard-packed snow or attempt to do so in the iced-over areas (Miller, 1992, 1993, 1994, 1995b).

The finding by Thomas et al. (1999) that caribou made intensive use of shallow snow or snow-free areas on sparsely vegetated upland ridges where the rush *Luzula* spp. and lichens were relatively abundant could be misconstrued to mean that lichens constitute the major or a major component of the Peary caribou's diet, which is not the case. Although Peary caribou seek out such sites with shallow or no snow cover, there is no evidence that they consistently use lichens in their diet at much beyond the rate of lichen occurrence on their range. It is therein that the problem lies—lichen growth is slow, and abundance is low in the High Arctic (Klein, 1980; and see the references to this fact given in Miller, 1998:48). Also of great importance, lichens on the QEI virtually do not occur in extensive dense mats like those that foster grazing by caribou on the mainland. Additionally, any food selection on those sites may have been for *Luzula*, which is an important year-round food item (Thomas et al., 1999).

Lichens are reported as contributing ca. 8% collectively to the plant biomass on Bathurst, Melville, and Prince Patrick islands, and the proportions of lichens in caribou rumen samples from those three islands (10%, 11%, and 2%) were roughly comparable to or well below that level (Thomas and Edmonds, 1983). Lichen cover is sparse on these islands because of the calcareous sedimentary substrates in association with harsh weather (Thomas and Edmonds, 1983). From those findings, it appears that the possible selection for lichens is of minor consequence in terms of the Peary caribou's seasonal and year-round diets. It would be impossible for Peary caribou to have the same strong dependence on lichens that mainland barren-ground caribou (*R. t. groenlandicus*) have and still live on the QEI.

Bergerud (1996:105) stated that "weather is density independent hence not regulatory" and "weather can only cause death as an interaction since animals don't die directly from exposure, if in good nutrition (and or in the absence of predation)." However, we believe, on the basis of evidence from

the QEI, that exceptionally severe weather causes extreme single-year crashes in caribou (and muskox) populations, and that those crashes result from starvation (Gunn et al., 2003; Miller et al., 2005c) and possibly in part from accelerated predation by wolves because killing calves and debilitated prey is quicker and easier (Miller and Broughton, 1974; Miller et al., 1985, 1988). Therefore, we agree with Skoog (1968) that if caribou deaths result from starvation (or predation) caused indirectly by weather conditions, then the controlling factor is the existing weather, and not the wolves or the size or relative accessibility of the absolute food supply (see also Miller, 2003:980). Skoog (1968) concluded that no other factor affects caribou more than the climate, and that weather can hold populations at levels where density-dependent factors are not important. We concur.

Peary Caribou Behavior

Caribou in general are known for their mobility. The caribou of the *R. t. pearyi* ecotype on the Canadian Arctic Islands exhibit a highly mobile feeding strategy, usually feeding while almost continually on the move (i.e., 2.5– 4 km•h^{-1} while foraging, Miller et al., 1982). They often take only one or, less often, two or three bites of forage from any one position. They seldom spend more that a few minutes on an area, even on large (> 100 m^2) snow-free patches, and their time spent at a site is not related to forage richness (Miller et al., 1982; Miller, 1995b). Even caribou coming off the sea ice after making inter-island migrations of 30– 84 km (minimum straight-line horizontal distances) and being deprived of food for several hours or more exhibit the same feeding strategy (Miller et al., 1982, 2005b). In contrast, the extensive dense lichen mats and, in general, the more abundant vegetation on mainland ranges allow individual caribou there to feed longer in place or stay on much smaller areas for longer periods of time.

Inter-island populations of caribou have been documented throughout most of the Canadian Arctic Archipelago (Miller, 1990; Miller et al., 2005b). Peary caribou specifically have been documented in the SW eco-unit (Fig. 1; Miller et al., 1977a, b) and in the S-C eco-unit (Fig. 1; Miller, 1995a, 1997, 1998, 2002). Intra-island and inter-island seasonal migrations and in some cases more frequent back-and-forth movements of Peary caribou (Miller, 1995a, 2002; Miller and Barry, 2003) appear to maximize the seasonal use of the best sections of their range and minimize caribou grazing pressure on their winter range (Miller, 1990). Annually switching from winter and spring ranges used during the period of snow cover to different areas of summer range during the snow-free period then back to winter range the next year allows a greater amount of new growth of forage plants on winter ranges during the intervening growing season. Some Peary caribou achieve this same result by seasonal displacements of just a few kilometers or by selecting different micro-sites for foraging on a seasonal basis (Miller and Barry, 2003). Ranges used during the snow-free period of the year are larger than ranges used during the period of snow cover, and the availability, abundance, and quality of the forage supply reach their peak in the middle of the snow-free period.

Is K a Useful Concept for High Arctic Caribou?

On the basis of the four weather-related crashes, we do not believe that the concept of an ecological carrying capacity (K) is applicable to Peary caribou on the QEI. Carrying capacity cannot be defined or measured with biological confidence only by the highest density ever estimated for a caribou population (MacNab, 1985; Gunn et al., 2000, 2003). An adequate definition would also require measuring the abundance of the absolute food supply. On the QEI, however, this measurement would be sporadically confounded by widespread inaccessible forage. That is, density of the absolute food supply does not matter when sporadic widespread or range-wide extreme snow or ice cover makes the forage inaccessible. Therefore, we suggest that the idea of long-term sustainable harvest of Peary caribou at some satisfactory level is wishful thinking at most, and harvesting these endangered Peary caribou populations, without continually updating their status, is courting disaster. The level of monitoring on the QEI has never been satisfactory for carrying out the biologically sound management and ecologically sound conservation of Peary caribou populations (see Miller et al., 2005a:72–73, for the minimum requirements). It is paramount that responsible parties realize and agree that none of these populations of endangered Peary caribou on the QEI be hunted without first updating their status. The status must be determined by aerial survey each time and the actual number of animals seen—not the number extrapolated—should be used to determine whether the desired harvest is sustainable. The hunters must then restrict their kill to the agreed-upon number or fewer caribou.

Caribou field biologists usually detect reduced population performance and even a marked reduction in population size only well after the fact. Therefore, they often do not have enough details to identify the exact cause and effect (response) that led to poor reproduction, low calf survival, and high mortality among 1+-yr-old animals. They often work with the obtainable approximate mean density value for caribou on the total range, so that they can "tell a story" that may or may not be an accurate account of population dynamics or ecological relationships at a given time or over a period of time. It is common knowledge among caribou field biologists, however, that distributions of caribou are never uniformly even, whether on mainland or on island ranges.

No matter what brought down the Peary caribou population on the south-central QEI to a mere remnant in 1998, it will take at least 30 years at its previous high average annual growth rate of λ = 1.13 under continually favorable weather conditions, and 59 years at half that growth rate (λ = 1.065), to recover to its 1994 size. This vividly illustrates that while population declines can be rapid because

mortality has no biological restraints, recovery must be relatively slow because calves can be born and recruited only so fast (Caughley and Gunn, 1993; Whitten, 1996).

A population that persistently approaches or realizes its potential annual maximum level of performance would, in reality, suffer greater setbacks sooner and deeper than a population growing at slow or moderate rates and continually under moderate-to-strong environmental pressure. Caribou biologists need to understand that while shortfalls in reproduction and small-to-moderate increases in mortality among all caribou appear undesirable, such losses caused by ongoing exposure to environmental pressure are actually highly beneficial to the population's well-being over the long run—that is, as long as the population remains in a stable or positive growth phase under existing and future hunting pressure.

For example, a starting population of 10 000 animals on a range that would hypothetically support 100 000 animals, when experiencing a mean annual growth rate (λ) of 1.05, would reach 100 000 animals in ca. 47 years, in the absence of any exceptionally severe weather years. The same population at a high mean annual growth rate (λ = 1.15) would reach 100 000 animals in just ca. 16 years, and at a higher annual growth rate (λ = 1.20), in only ca. 13 years. Even the largest of these growth rates is still well below the intrinsic annual maximum rate of increase (r_m = 0.30, Bergerud, 1980), at which rate it would take only nine years to exceed 100 000 caribou! Thus the number of years required to reach the maximum 100 000 or more caribou is highly variable, depending on the annual rate of growth; it is much less favorable to the population over the long run when this growth happens in only 13–16 years than when it takes nearly half a century. This is particularly true for Peary caribou on the QEI, as the frequency of extreme weather events would most likely double the time necessary (i.e., from 50 to 100 years) to reach a density at which the range could no longer support all of the caribou without a serious impact on the forage plants.

The vagaries of weather in the Canadian High Arctic are such that the number of Peary caribou that the range can support is constantly in a state of flux—by week, month, season, or year. In fact, a range's capacity to support Peary caribou can change drastically within days as a result of one or several severe storms. Extremely unfavorable snow or ice conditions can reduce the number of caribou a range can support from several thousand to several hundred animals or less. However, the capacity to support caribou on this same range will rebound once the snow and ice have melted away.

Thus, we share the frustration in the probable folly of the "cavalier use of the constant K as if it had a precise ecological meaning rather than being simply a mathematical convenience" (Caughley and Gunn, 1996:172). Pimm (1991:136) concluded, while examining models for time to extinction, that "quite what K has to do with real populations is far from obvious" and that he had "no idea whether it [K] exists or how to calculate it." We accept the observation

that mathematical models are at best simplistic approximations of the complex real world and that the unrelenting quest for an underlying equilibrium ignores the probability that there might be no equilibrium (Gleick, 1988:59–64). Unfortunately, models also are flexible, and although past data can be fitted to them, these data do not guarantee that the model's predictive power will be accurate or even real. This negative condition could be strongly influenced by the existence of incomputable emergent phenomena (Orrell, 2007:114, 118, 205), which would most likely be common in a non-equilibrium grazing system that is controlled primarily by abiotic weather factors. An important consideration (and probably a major shortcoming in general) is that researchers are not even working with the right factor. To evaluate correctly the capability of a range to support a population of herbivores, the density of the vegetation (forage plants)—not the density of the animals—should be used (Caughley and Gunn, 1993; Whitten, 1996). Even then, such an evaluation of the vegetation would be applicable only when the absolute forage supply was not largely inaccessible.

CONCLUSIONS

The Peary caribou study population exhibited high levels of annual reproduction, early calf survival, and low mortality among 1+-yr-old animals from 1988 to 1994, when the population estimate tripled from 1030 to 3155 during years of relatively favorable weather. The high levels of population performance and growth of these caribou rival those of much larger established mainland caribou populations with much better forage supplies on ranges with more hospitable environments. It appears that at present, the primary requirement for the well-being of Peary caribou, in the absence of further human interference, is the absence of years with prolonged and extremely severe snow or ice conditions.

We assert that the effects of infrequent, isolated single years or a short series of years with exceptionally severe snow or ice conditions have been the primary control of the study population and, thus, by extension, of Peary caribou populations on the QEI. It is most probable that these abiotic controlling factors were compounded annually by differing levels of wolf predation—a biotic factor. Collectively, the impact of these controlling factors has been too great to allow Peary caribou populations to even reach, let alone exceed, any conjectural equilibrium. There is no evidence, either on site or from anywhere within the QEI, that proves—or even suggests—otherwise.

We remain confident that the four single-year winter and spring crashes were all caused by exceptionally severe and prolonged snow and ice conditions. The pattern of favorable weather years erratically intertwined with less favorable years (with poor reproduction and survival of calves) and a few extremely unfavorable crash years (with nearly no reproduction and disastrous mortality levels) has been

in place for centuries and possibly for millennia. Therefore, it is most likely that Peary caribou populations on the QEI would seldom, if ever, reach the sizes (densities) at which density-dependent regulation through negative feedback loops with the absolute forage supply would be the sole or even the primary controlling force. The estimated absolute abundance of aboveground annual plant production relative to the number of caribou estimated on the study area gives credence to our position. We believe this applies in general to Peary caribou populations throughout the QEI, which all occur at relatively low mean densities.

We conclude that large random fluctuations in the environment that occur in the High Arctic prevent the vegetation-herbivore feedback loop from becoming a dominant regulating factor for Peary caribou on the QEI. Those caribou are living in a non-equilibrium grazing system where they are controlled mainly by infrequent, nearly range-wide extremely severe abiotic weather elements—independent of either the caribou density or the abundance of their food supply. Therefore, we propose that the dynamics of a non-equilibrium grazing system with a compounding effect from wolf predation would represent an appropriate conceptual model for Peary caribou populations on the QEI in the Canadian High Arctic.

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