

# Near-Total Loss of Caribou on South-Central Canadian Arctic Islands and the Role of Seasonal Migration in their Demise

FRANK L. MILLER,<sup>1,2</sup> SAMUEL J. BARRY<sup>1</sup> and WENDY A. CALVERT<sup>1</sup>

(Received 9 March 2006; accepted in revised form 14 August 2006)

**ABSTRACT.** Caribou (*Rangifer tarandus*) on the south-central Canadian Arctic Islands (Prince of Wales, Somerset, and Russell islands) declined by 98% sometime between 1980 and 1995—a near-total loss of a known genetically distinctive group of Arctic Island caribou. In contrast, caribou on the adjacent Boothia Peninsula seemingly increased by 38% from 1985 to 1995, while experiencing heavy annual hunting pressure. Our evaluation leads us to three primary conclusions. 1) It would have been biologically impossible for the estimated 1985 population on Boothia Peninsula ( $4831 \pm 543$  SE caribou one year old or older) to sustain the estimated annual harvest of 1100 one year old or older animals without continual annual ingress of caribou from beyond Boothia Peninsula. Our analysis of the 540 possible combinations of population parameters indicates that at any size within  $\pm 2$  SE of the 1985 estimate (3745–5917 caribou one year old or older), the Boothia Peninsula caribou population would have gone to “mathematical extirpation”: 99% of the combinations by 1995 and 100% by 1999. 2) The continued unsustainable level of harvest was masked by the annual winter infusion of migrant caribou onto Boothia Peninsula from Prince of Wales, Somerset, and Russell islands. 3) Caribou persisted on Boothia Peninsula, but only because of the simultaneous near elimination of the Arctic Island caribou ecotype in the Prince of Wales, Somerset, and Russell islands geographic population. This caribou resource cannot be properly conserved without adequate monitoring and periodic estimates of population sizes and annual harvest rates throughout the entire Prince of Wales, Somerset, and Russell islands-Boothia Peninsula complex.

**Key words:** Boothia Peninsula, harvest, population decline, caribou, *Rangifer*, seasonal migration, south-central Canadian Arctic Archipelago

**RÉSUMÉ.** Entre 1980 et 1995, le nombre de caribous (*Rangifer tarandus*) du centre-sud de l’archipel Arctique canadien (îles du Prince-de-Galles, Somerset et Russell) a chuté de 98 %, ce qui représente la perte quasi totale d’un groupe génétiquement distinct de caribou de l’archipel Arctique. Par contre, il semblerait qu’entre 1985 et 1995, le caribou de la péninsule de Booth s’est accru de 38 %, malgré l’énorme pression exercée par la chasse tous les ans. Trois conclusions dérivent de notre évaluation. 1) Du point de vue biologique, il aurait été impossible pour la population estimée de la péninsule de Booth en 1985 ( $4\ 831 \pm 543$  (écart type) caribous d’un an ou plus) de soutenir la récolte annuelle estimée de 1 100 bêtes d’un an ou plus sans apport annuel continu de caribous provenant d’ailleurs que la péninsule de Booth. Notre analyse des 540 combinaisons possibles de paramètres de population laisse croire que tout écart de  $\pm 2$  de l’écart-type des estimations de 1985 (3 745–5 917 caribous d’un an ou plus) de la population de caribous de la péninsule de Booth aurait fait l’objet d’une « extirpation mathématique » : 99 % des combinaisons vers 1995 et 100 % vers 1999. 2) Le taux continuellement insoutenable de récolte était masqué par l’infusion hivernale annuelle de caribous en migration sur la péninsule de Booth provenant des îles du Prince-de-Galles, Somerset et Russell. 3) Le caribou a persisté sur la péninsule de Booth, mais seulement en raison de la quasi-élimination simultanée de l’écotype du caribou de l’archipel arctique en ce qui a trait à la population géographique des îles du Prince-de-Galles, Somerset et Russell. Cette ressource en caribou ne peut être bien conservée sans la surveillance adéquate et l’estimation périodique de l’effectif de la population et des taux de récolte annuels à l’échelle de tout le complexe des îles du Prince-de-Galles, Somerset et Russell ainsi que de la péninsule de Booth.

**Mots clés :** péninsule de Booth, récolte, déclin de la population, caribou, *Rangifer*, migration saisonnière, centre-sud de l’archipel Arctique canadien

Traduit pour la revue *Arctic* par Nicole Giguère.

## INTRODUCTION

In summer 1995, Gunn and Dragon (1998) found that the geographic population of caribou (*Rangifer tarandus*) on Prince of Wales, Somerset, and Russell islands in the

south-central Canadian Arctic Archipelago had declined by 98% from its 1980 estimated summer size (Gunn and Decker, 1984). An excessively long interval of 15 years had passed between systematic aerial surveys to estimate population size, and no other quantitative information on

<sup>1</sup> Canadian Wildlife Service, Environment Canada, Prairie & Northern Region, Room 200, 4999 – 98th Avenue, Edmonton, Alberta T6B 2X3, Canada

<sup>2</sup> Corresponding author: frank.miller@ec.gc.ca

population size had been systematically collected in the interim. In contrast, the 1995 aerial survey results on the nearby Boothia Peninsula (Gunn and Dragon, 1998) compared to the 1985 results (Gunn and Ashevak, 1990) suggest a 38% increase over the number of caribou estimated there in 1985—or, as there is no significant difference between the two estimates, that the population size had not changed.

Recently, Gunn et al. (2006) evaluated available information in an attempt to explain the cause of the near-total loss of caribou on Prince of Wales, Somerset, and Russell islands and the conservation implications of that drastic decline. Not knowing the rate of decrease for each year or the variation in that annual rate between 1980 and 1995 hampered their efforts. They examined seven candidate factors that may have contributed to the decline: density-dependent competition for food within the species; competition for food and space with other species, especially muskoxen (*Ovibos moschatus*); emigration, including range shifts, to another island or islands or to the mainland; heavy parasite burdens or widespread contagious disease; exceptionally severe winter and spring weather (snow or ice conditions), resulting in extensive and prolonged relative unavailability of food; high wolf (*Canis lupus*) predation; and high annual harvest by Inuit hunters. They did not find unequivocal evidence that any of these factors had played a direct major role in the near-total loss of caribou on Prince of Wales, Somerset, and Russell islands between 1980 and 1995. Gunn et al. (2006) concluded, however, that the decline was probably the result of long-term reductions in survival rates of breeding females, small calf increments, and low rates of yearling recruitment, accompanied by continued subsistence harvesting of caribou through the 1980s and early 1990s and proportionately increased wolf predation on the dwindling number of caribou on those islands.

Gunn et al. (2006) reviewed the possibility that caribou from Prince of Wales, Somerset, and Russell islands had moved en masse to other locations and concluded that there was no evidence that they had done so. However, they also concluded that if caribou had emigrated undetected, their most likely destination would have been Boothia Peninsula, leaving its possible role in the decline open for further consideration. They did not consider annually occurring seasonal migrations by caribou from summer ranges on Prince of Wales, Somerset, and Russell islands to winter ranges on Boothia Peninsula (Miller et al., 1982, 2005b; Miller, 1990a) as a probable major indirect cause for the decline. Inuit hunters on Boothia Peninsula see caribou from “Kingailik” (Prince of Wales Island) in winter and select them because their meat is preferred to meat from mainland caribou (Gunn et al., 2006). We believe, on the basis of documented seasonal migrations of caribou within the study area, that Kingailik caribou must also include caribou from Somerset and Russell islands (Miller et al., 2005b).

Our investigation is primarily a mathematical evaluation, which we see as a logical extension of the deductive

evaluation made by Gunn et al. (2006). We include Boothia Peninsula in our analyses because its caribou population is fundamental to identifying the direct and indirect causes of the decline of caribou on Prince of Wales, Somerset, and Russell islands. Many caribou from those islands annually made seasonal migrations to and from winter ranges on Boothia Peninsula (Miller et al., 1982, 2005b; Miller, 1990a), and thus would have been available to hunters on the peninsula for much of each year. We hereafter refer to the entire study area north of the Boothia Isthmus (Fig. 1) as the Prince of Wales, Somerset, Russell islands–Boothia Peninsula complex (PSBC).

## BACKGROUND

Eger and Gunn (1999) investigated the evolutionary history of tundra caribou in Canada by using mitochondrial DNA sequence data from the entire control region. They concluded that the Arctic Island caribou on the Canadian Arctic Islands south of 74° N latitude (which includes our study area) evolved from barren-ground caribou (*R. t. groenlandicus*) that spread northward from the mainland after glacial retreat and are most likely the ancestral stock for the Peary caribou (*R. t. pearyi*) found farther north (above 74° N) on the Queen Elizabeth Islands. Røed (2005) recently reached the same conclusions. In addition, both morphometric data (Thomas and Everson, 1982) and microsatellite DNA data (Zittlau, 2004) suggest a relatively high degree of diversity among these caribou, which allows their identification and separation into distinguishable ecotypes.

On the basis of these findings, we refer to the caribou found within the PSBC study area as three different caribou ecotypes. The Arctic Island caribou ecotype is the smallest of the three, having a “short face” and shorter legs and body length than the Boothia Peninsula caribou ecotype and especially the Mainland caribou ecotype (e.g., Thomas and Everson, 1982). The pelage and antler velvet of the Arctic Island ecotype are slate-grey, whereas the Mainland ecotype has brown pelage with a usually pronounced lighter “flank stripe” and dark, chocolate-brown antler velvet. The Boothia Peninsula ecotype falls between the Arctic Island and Mainland ecotypes in size and coloration, but is much closer in appearance to the Arctic Island ecotype. Visual discernment of the Arctic Island and Boothia Peninsula ecotypes from the Mainland ecotype is easy, but distinguishing the Arctic Island ecotype from the Boothia Peninsula ecotype is problematic under some viewing conditions. Inuit hunters believe, however, that they can consistently distinguish individuals of the Arctic Island ecotype from those of the Boothia Peninsula ecotype. Their success in doing so may be due largely to their knowledge of where each ecotype is most often found during various seasons of the year.

Our primary interest is in the estimated numbers obtained by systematic aerial surveys in summer within each

of two geographic areas. We refer to the caribou on Prince of Wales, Somerset, and Russell islands in summer as one geographic population and the caribou occurring on Boothia Peninsula in summer as a second geographic population, even though two different ecotypes occur on the peninsula. Therefore, “population” is synonymous with “geographic population” and is based on all of the caribou found on that area in summertime, with or without reproductive isolation: the “Prince of Wales, Somerset, and Russell islands geographic caribou population” versus the “Boothia Peninsula geographic caribou population.”

The Arctic Island caribou ecotype individuals in the Prince of Wales, Somerset, and Russell islands geographic caribou population use the entire PSBC (Fig. 1: Gunn et al., 2000b; Miller et al., 2005b). To the best of our knowledge, all of these Arctic Island caribou remained within the PSBC year-round. Different segments of this population exhibited different seasonal range–occupancy patterns within the PSBC. Some caribou remained year-round on Prince of Wales, Somerset, or Russell Island; some moved between Prince of Wales and Somerset islands; and apparently most others moved among Prince of Wales, Somerset, and Russell islands and Boothia Peninsula (Fig. 1: Miller et al., 1982, 2005b; Miller, 1990a). Although caribou carried out intricate inter-island and island-peninsula seasonal migrations, they rutted and usually calved only on island areas and apparently did not routinely calve on Boothia Peninsula (Miller and Gunn, 1980). In some years, however, the segment of Arctic Island caribou that wintered on Boothia Peninsula was apparently forced to calve on its northern end because their northward spring migration back to the islands was delayed by deep slush or snow and poor travel conditions on the sea ice (Miller and Gunn, 1980).

The Boothia Peninsula geographic caribou population is composed of both Boothia Peninsula and Mainland caribou ecotypes (e.g., Thomas and Everson, 1982; Miller et al., 2005b). The Boothia Peninsula caribou ecotype calves on the northwestern Boothia Peninsula, and most of its members then spend the summer there and to the southwest on the peninsula. Relatively few of them remain on Boothia Peninsula year-round; the others move southward from the Boothia Isthmus and winter on the mainland at least 300 km farther south (Fig. 1: Gunn et al., 2000a). The Mainland caribou ecotype using Boothia Peninsula has a seasonal range occupancy pattern similar to that of the Boothia Peninsula caribou ecotype. The Mainland caribou ecotype calves on the northeastern Boothia Peninsula, and then most spend the summer there and to the southeast on the peninsula. Relatively few of those caribou remain on the peninsula year-round whereas the others move south of the Boothia Isthmus in early winter to an unknown wintering area but return to Boothia Peninsula in spring (Fig. 1: Gunn et al., 2000a).

In summer, the Arctic Island caribou ecotype is found only on Prince of Wales, Somerset, and Russell islands, and the Boothia Peninsula and Mainland caribou ecotypes

are found only on Boothia Peninsula. In winter, however, many individuals of the Arctic Island caribou ecotype are on Boothia Peninsula, along with fewer individuals of the Boothia Peninsula caribou and Mainland caribou ecotypes. All three ecotypes would therefore have been available to the Taloyoak (Spence Bay) hunters from about November through May and early June of each year. Most caribou hunting occurs during this same period (Jingfors, 1986). But in summer and into autumn, when the least hunting takes place (Gunn et al., 1986; Jingfors, 1986), only the Boothia Peninsula and Mainland ecotypes would have been available on the peninsula.

The caribou on Prince of Wales, Somerset, and Russell islands were first listed as “Threatened” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1979 (e.g., Gunn et al., 1981). After a reassessment in 1991 (based on data from Miller, 1990b), COSEWIC retained this classification, suggesting that the status of these caribou had not deteriorated appreciably; yet, by 1995, their numbers had plummeted by 98%.

A caribou population that is not experiencing an influx of individuals from one or more other populations can grow in size only when recruitment and survival exceed mortality. Initial reproduction does not closely reflect actual yearling recruitment. Therefore, the most important consideration is whether both females and males survive beyond their usual initial breeding age, so that the overall rate of survival exceeds the mortality, allowing the population to grow.

The maximum reproduction rate of caribou is low compared to that of other North American cervids, and it is lowered further by high mortality among caribou calves in their first year of life and among subadults to breeding age (e.g., Kelsall, 1968; Skoog, 1968; Miller, 1974, 2003; Bergerud, 1978, 1980; Bergerud et al., 1983). Although some two-year-olds can produce calves under the most favorable environmental conditions, most female caribou are three years old before they produce their first calf (e.g., Dauphiné, 1976). Virtually all births are singletons, regardless of maternal age, and over several consecutive years or more, only about 50% of the calves live through their first year of life (Bergerud, 1978).

In the following discussion and thereafter, “caribou” always refers to animals one year old or older unless they are specifically identified as calves (less than one year old).

In a typical free-ranging caribou population not subject to exceptionally heavy hunting pressure on adult males, we expect the proportions of caribou to average about 40 males to 60 females (e.g., Skoog, 1968; Parker, 1972; Miller, 1974). On average, 70% of females were pregnant each year from 1966 to 1968 in the Qamanirjuaq caribou population, which had about 42 males to 58 females (Dauphiné, 1976), and 75% were pregnant each year from 1980 to 1986 (Thomas and Kiliaan, 1998) in the Beverly caribou population, which had about 36 males to 64 females in 1981 and 1982 (Gunn, 1984). The theoretical

annual maximum rate of population increase is estimated at about 30% of the postcalving population (cf. 27–30%, Bergerud, 1978; or  $r_m = 0.30$ , the intrinsic rate of increase of a caribou population, Bergerud, 1980). However, this 30% annual production of calves translates into a realized 30% population increase only if all calves born survive to one year of age and no older caribou die in that year—and neither assumption is practical.

To our knowledge, not even half that rate of population increase ( $r = 0.15$ ) has ever been documented over a long series of consecutive years for an established, free-ranging population of caribou in Canada, living year-round with wolves. For example, Messier et al. (1988) estimated that the rate of population increase for the George River woodland caribou (*R. t. caribou*) herd living with wolves in northern Quebec was  $r = 0.11$  between 1970 and 1984. Average annual ratio was 39 males to 61 females, and 67% of those females produced calves. Peary caribou (*R. t. pearyi*) within the Bathurst Island Complex on south-central Queen Elizabeth Islands, Canadian High Arctic Islands, also living with wolves year-round, exhibited highly similar population structure and dynamics: 41 males to 59 females, with 68% of those females producing calves in 1993. Their 20-year growth performance (1974–94) was  $r = 0.12$  (Miller, 1995a; Miller and Gunn, 2003a). For the Avalon Peninsula woodland caribou herd, living without wolves in southeastern Newfoundland, the estimated rate of population increase was still only  $r = 0.12$  between 1967 and 1979 (Bergerud et al., 1983). As in the George River herd, the average annual ratio was 39 males to 61 females, but 73% of the Avalon females produced calves.

## MATERIALS AND METHODS

The study area lies south of the Parry Channel between ca. 69.5° (Boothia Isthmus) and 74.2° N latitude and between 90° and 102° W longitude, with a collective land-mass of about 93 000 km<sup>2</sup> (Fig. 1). The area includes the south-central Arctic Islands of Prince of Wales (33 339 km<sup>2</sup>), Somerset (24 786 km<sup>2</sup>), and Russell (940 km<sup>2</sup>), and their respective satellite islands (ca. 1220 km<sup>2</sup>), as well as Boothia Peninsula (32 715 km<sup>2</sup>). An unknown amount of range south of the Boothia Isthmus to ca. 67° N latitude (Gunn et al., 2000a) is used for wintering by many, if not most, individuals of the Boothia Peninsula caribou population, as described below.

Prince of Wales, Somerset, and Russell islands are locked in sea ice and connected to the nearby Boothia Peninsula for about nine months of each year, allowing caribou to make annual seasonal migrations between and among the islands and the mainland peninsula (Fig. 1; Miller et al., 2005b). Boothia Peninsula is the most northerly extension of the Canadian mainland and the North American Continent. It was an important wintering range for many caribou from the three islands, and its inclusion in our evaluation is critical.

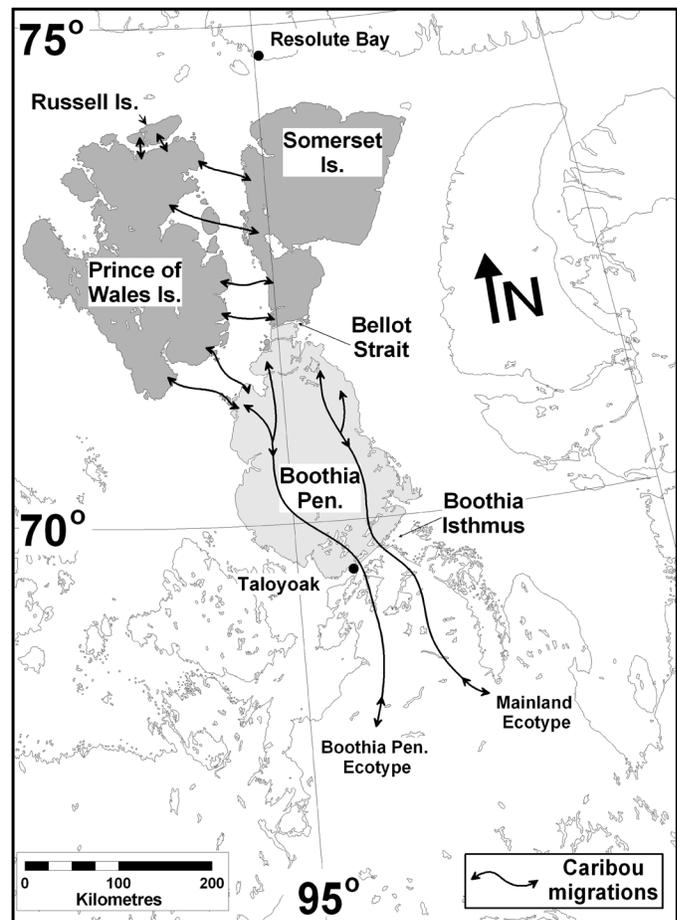


FIG. 1. Shaded area is the Prince of Wales, Somerset, Russell islands-Boothia Peninsula Complex (PSBC) study area, south-central Canadian Arctic Archipelago. Arrows indicate migration routes, as well as southward winter range extensions beyond the PSBC for the Boothia Peninsula and Mainland caribou ecotypes.

Gunn et al. (2006) reviewed all of the aerial surveys and evaluated the reliability of those carried out within the PSBC between 1974 and 1995. This analysis and our evaluation are based on results obtained by systematic aerial survey of caribou on Prince of Wales, Somerset, and Russell islands in 1980 (Gunn and Decker, 1984) and in 1995 (Gunn and Dragon, 1998) and on Boothia Peninsula in 1985 (Gunn and Ashevak, 1990) and 1995 (Gunn and Dragon, 1998). We used these results, together with the limited annual harvest estimates for the early 1980s (Gunn et al., 1986; Jingfors, 1986), to reexamine the population estimates in light of the biological possibility that those caribou on Boothia Peninsula could have supported the reported rate of annual harvest there.

The only relatively detailed estimates for the annual harvest of caribou on Boothia Peninsula are the data that Gunn et al. (1986) and Jingfors (1986) presented from 1983 and 1984. Those authors believed that their estimates were reasonably accurate, and we have no way of reassessing them. Jingfors (1986) used data from Gunn et al. (1986) in addition to his own data; therefore, his treatment is more detailed, and we rely on it for our consideration of the annual harvest on

Boothia Peninsula. Jingfors (1986:172) reported that “the per capita harvesting levels of caribou in the Kitikmeot Region (mean = 3.1 caribou/person/year) were surprisingly consistent between communities and years despite local differences in caribou distribution and availability.” This annual rate of 3.1 caribou per capita was the actual value obtained for Taloyoak in 1983–84.

When we state in our analyses that a caribou population has been “extirpated,” we are only considering the mathematical consequences of the calculations. We do not believe that extirpation would be realized in most cases, mainly because it is most improbable that hunting pressure would remain at such a high level once the population had fallen to below 1000 animals and the return for effort had markedly diminished. However, with a sociable group animal like the caribou, a chance event alone could expose a small remnant population to excessive hunting pressure. From that point onward, the population could be reduced further by wolf predation, extreme snow or ice conditions, additional hunting, or other possible causes, especially if they occur in combination.

#### *Population Structure*

We compensate for not knowing how the 98% decline of the Arctic Island caribou ecotype actually proceeded from 1980 to 1995 by using values from the literature for caribou populations on mainland Canada, Newfoundland, and the Canadian High Arctic Islands (e.g., Kelsall, 1968; Parker, 1972; Miller, 1974, 1995a; Miller and Broughton, 1974; Dauphiné, 1976; Bergerud et al., 1983; Messier et al., 1988; Miller et al., 1988a; Couturier et al., 1990; Thomas and Kiliaan, 1998). We consider these populations typical of caribou in Canada during environmentally favorable times, and because of their similarity in population structure and dynamics, we believe their population parameters are applicable to caribou on Boothia Peninsula. There is no reason to believe that geographic populations of caribou within the study area could increase beyond the average performance levels reported for free-ranging caribou populations elsewhere in Canada.

#### *Population Parameters*

Our assessments use the following assumptions and parameters to approximate the average values most likely to be realized for a maximal growth pattern of a free-ranging tundra population of North American caribou that is subject to light to moderate year-round wolf predation during 10 or more consecutive years.

1. On average, females represent 60% of all caribou one year old or older in the population. We used 60% as well as extreme values of 54% and 66% in our analyses.
2. On average, 72% of these females produce a calf each year. We used 72% as well as extreme values of 66% and 78% in our analyses.

3. On average, the proportion of calves that survive the first year of life (yearling recruitment) is only 50% of the calves born. We used 50% as well as extreme values of 44% and 56% in our analyses.
4. The lowest average annual rate of natural mortality for the entire period is 7% among all caribou. We used 7% as well as extreme values of 5%, 10%, and 13% in our analyses.
5. The estimated annual harvest of caribou during the entire period is assumed to be 1100, based on data from Jingfors (1986) and our recalculations involving the rapidly increasing Inuit population in Taloyoak. This estimate is regarded as conservative because the Inuit population in Taloyoak increased from about 420 in 1984, when Jingfors' data were collected, to about 700 in 1995.

#### *Population Projections and Persistence*

Two of our analyses involved projecting the 1985 population forward: first, we allowed the 1985 population to “seek its own level,” and second, we forced the 1985 population to reach 1995 levels. In the first analysis, we projected the population forward from 1985 ( $N_{1985}$ ), year by year ( $N_t$ ), using a simple population model similar to that used by Davis et al. (1980). Thus,  $N_{t+1} = [N_t - (\% \text{ natural mortality} \times N_t) - \text{harvest}] + [(N_t - (\% \text{ natural mortality} \times N_t) - \text{harvest}) \times \% \text{ females} \times \% \text{ females producing calves} \times \% \text{ calf survival}]$ . This result equals the post-mortality population plus the number of surviving calves. For example, using the average parameter values  $N_{1986} = [4831 - (0.07 \times 4831) - 1100] + [(4831 - (0.07 \times 4831) - 1100) \times 0.60 \times 0.72 \times 0.50] = 4126$ . We applied this procedure iteratively: the population size for successive years became the post-mortality population incremented by yearling recruitment. In our second projection method, we used the same iterative procedure described above, except that we determined the population size for the next iteration. We calculated the fixed annual rate of change as  $(N_{1995} - N_{1985})/10 \text{ yr}$  and predetermined each successive year's population size by adding this fixed rate to the previous year's post-mortality value. This forced the process to achieve the estimated 1995 population size in 10 steps of equal magnitude. In the following analyses we examined the results produced by all combinations of the annual proportions of females (54%, 60%, 66%), females producing calves (66%, 72%, 78%), calf survival (44%, 50%, 56%), and natural mortality (5%, 7%, 10%, 13%). We used the five population values (estimate -2 SE, estimate -1 SE, estimate, estimate +1 SE, and estimate +2 SE) for 1985 only or for 1985 and 1995, depending on the analysis of the population projection: only 1985 values when we let the population seek its own level, and values for both years when we forced the population to achieve the 1995 values.

We then investigated whether, given the estimated annual harvest, the 1985 population (Table 1) could have

TABLE 1. Population information used for caribou one year old or older in this study, obtained by systematic strip-transect aerial survey and presented by population.

Year	Estimate-2 SE	Estimate-1 SE	Estimate	Estimate+1 SE	Estimate+2 SE	Survey Period	Source
Prince of Wales, Somerset, and Russell islands caribou population:							
1980	3677	4387	5097	5807	6517	12-22 July	Gunn and Decker (1984)
1995	(20) <sup>1</sup>	(40) <sup>1</sup>	(60) <sup>1</sup>	(80) <sup>1</sup>	(100) <sup>1</sup>	21 July-3 August	Gunn and Dragon (1998)
Boothia Peninsula caribou population:							
1985	3745	4288	4831	5374	5917	31 May-6 June	Gunn and Ashevak (1990)
1995	3202	4930	6658	8386	10 114	21 July-3 August	Gunn and Dragon (1998)

<sup>1</sup> Arbitrary values used in recognition of the few animals likely missed and to allow comparisons: Gunn and Dragon (1998) made no estimate in 1995, as they saw only seven caribou one year old or older (no calves), and only two of them were on-transect.

even sustained itself, let alone grown 38%, by 1995. We projected the population forward from 1985, as described above, to let it seek its own level. We used all 540 combinations of population performance parameters and population values ( $3 \times 3 \times 3 \times 4 \times 5 = 540$ ). We ran these calculations forward until the population for each combination reached extirpation. At this point, we decided not to consider the 5%, 10%, and 13% rates of natural mortality in subsequent analyses. To be conservative, but biologically accurate in terms of the ongoing demands of wolf predation, we used only 7% average annual natural mortality for caribou. Simplifying our analyses by omitting completely unrealistic values allows a more straightforward interpretation of our subsequent evaluations.

#### *Females Producing Calves and Calves Surviving to Yearlings Needed to Achieve 1995 Population Sizes*

We then forced each of the five 1985 population sizes to achieve the five 1995 population sizes in 10 years by using the same combinations of population performance parameters and harvest, but only the 7% natural mortality rate among all caribou—i.e.,  $3 \times 3 \times 3 \times 1 \times 5 \times 5 = 675$  combinations. We calculated the percent of calf-producing females required in the population if calf survival actually ranged from 40% to 100% at increments of 10%. For each level of calf survival, we back-calculated to obtain the required number of calf-producing females by reversing our first projection method. Instead of using only surviving calves, however, we used the number of surviving calves from each of our forced population projections plus the associated “shortfall” (loss of individuals one year old or older), which we treated as “all calves” in this analysis. This result equals the net number of calves that must have survived after mortality. We inflated this value to obtain the gross number of calves produced before mortality by dividing it by the calf survival rate. This yields the number of females estimated for the 1985 population, plus additional females required to produce calf survival rates that would allow that population to grow to 1995 population values under the estimated annual harvest regime. We express this requirement as a percentage

of existing females. For each combination of parameters, this analysis determined the values for each year of the 10-year population projection; however, we report only the 10-year mean of those values.

#### *Allowable Annual Harvest and Annual Harvest Shortfall*

In the first steps of this analysis, we ignored the estimated annual harvest of 1100 caribou in our forced population projection. Instead we calculated, by iterative, trial-and-error methods, a harvest rate that would have allowed the 1985 population to achieve the estimated 1995 population size.

In the final steps, we determined the “annual harvest shortfall” by subtracting the calculated allowable annual harvest from the assumed annual harvest of 1100 animals. We calculated annual harvest shortfall by this procedure for all 675 combinations of each of the 1985 and 1995 populations (i.e., estimate -2 SE, estimate -1 SE, estimate, estimate +1 SE, and estimate +2 SE), applying each of the population performance parameters (% females in population, % females calving, and % calf survival to one year) and 7% natural mortality. For each combination of parameters, this analysis determined the values for each year of the 10-year population projection; however, we report only the 10-year mean of those values.

#### *Required 1985 Population Size*

In this analysis, we determined the 1985 population size that, given the population parameters stated previously, would arrive at the 1995 population size. We did this without forcing each year’s population size to an annual decrement and without an annual shortfall that would have demanded ingress from beyond the Boothia Peninsula caribou population. To do this, we back-calculated, using the above seek-its-own-level projection procedure one year at a time, beginning with the 1995 population and ending with the 1985 population. We followed this procedure for all 135 combinations of each of the five 1995 population values, applying each of the population performance parameters at an annual harvest of 1100 animals and 7% natural mortality.

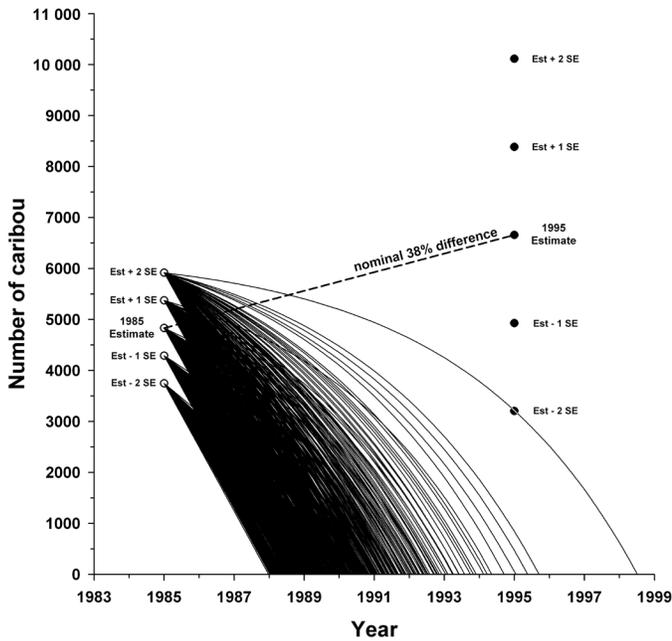


FIG. 2. Boothia Peninsula 1985 caribou population estimate of  $\geq 1$ -yr-old caribou (estimate  $\pm 1$  SE, 2 SE) projected forward until extirpation in 540 combinations at 54%, 60%, and 66%  $\geq 1$ -yr-old females in the population, with 66%, 72%, and 78% of them producing calves; 44%, 50%, and 56% calf survival; 5%, 7%, 10%, and 13% annual natural mortality among all  $\geq 1$ -yr-old caribou; and an annual harvest of 1100  $\geq 1$ -yr-old caribou.

From here on, all references to caribou are synonymous with “estimated caribou.” “Caribou” still means animals one year old or older unless they are specifically identified as calves.

## RESULTS

### *Boothia Peninsula Population Estimates 1985 versus 1995*

The 38% difference between the 1985 and 1995 estimates of caribou on Boothia Peninsula (Table 1) is only nominal (Fig. 2). The two estimates shown in Table 1 are not statistically different ( $t = -1.17$ , 45 df;  $p = 0.25$  from Gunn and Dragon, 1998). The 95% CI for 1995 completely overlaps the 95% CI for 1985. Thus, statistically, there is no support for either an increase or a decrease in the population size between 1985 and 1995. Most importantly, the apparent increase in the size of the caribou population, or even the persistence of that population on Boothia Peninsula suggested by the 1985 versus the 1995 survey results cannot be accepted with biological confidence. The population performance required for the estimated 1985 population to increase to the size estimated for 1995 far exceeds any probable level of population growth under the environmental conditions existing during that time on Boothia Peninsula and adjacent areas.

### *Estimates of Annual Harvests*

By recalculating the data in Tables 2 and 3 of Jingfors (1986), we obtained an estimated mean annual harvest by Taloyoak hunters of  $1286 \pm 43$  SE caribou (including calves). Next we reduced the 1286 caribou by 14% (the estimated percent of calves in the sample, which actually included some yearlings killed in summer at 12–15 months of age) to 1106, which we rounded to 1100 caribou as a conservative value. We then considered the influence of the Inuit population increase at Taloyoak during that time period and the higher demands that this larger population would have placed on the caribou population on Boothia Peninsula. We multiplied the population census for Inuit in Taloyoak in 1986 and 1991 (<http://collections.ic.gc.ca/arctic/inuit/spence.htm>) by 3.1, the estimated harvest rate of caribou  $\cdot$  person<sup>-1</sup>  $\cdot$  yr<sup>-1</sup> (from Jingfors, 1986). The resulting estimates of desired annual caribou harvests were 1500 for 1986 and 1700 for 1991, or an annual mean of about 1600 caribou. To be conservative, we reduced the estimated mean annual harvest of 1600 by 14% to liberally account for calves (cf. Jingfors, 1986). Then we arbitrarily reduced it by a further 20%, to account for a possible shortfall below the desired caribou harvest level for a larger human population, to be in agreement with the 1983–84 estimated annual harvest of 1100 caribou.

### *Population Projections and Persistence*

We documented the incapability of the 1985 Boothia Peninsula caribou population at any size between 3745 and 5917 animals (Table 1; Fig. 2: estimate  $\pm 2$  SE) to sustain a 10-year average annual harvest of 1100 caribou. Our initial analysis examined all combinations of the population performance parameters given in *Population Parameters* above, each at 5%, 7%, 10%, and 13% annual natural mortality throughout the 10-year period, to determine the importance of the average annual level of natural mortality. All 540 possible permutations of the above combinations went to extirpation by 1995, with four exceptions (Fig. 2). Those four exceptions all involved population change at the estimate + 2 SE (5917) level, with an unrealistically low rate of 5% natural mortality. Three of those four became extinct by 1996 and the last one by 1999. None of the 540 combinations of different population sizes and population performance parameters exhibited any period of positive population growth between 1985 and 1995.

The 1985 estimated Boothia Peninsula population of 4831 caribou would have been extirpated by 1991, assuming a 7% natural mortality and an annual harvest of 1100 caribou and the previously stated sex ratios and productivity rates. These are 60% females among all caribou in the population and 72% of those females producing calves each year, yielding the expected annual maximum birth rate of 0.30 for North American caribou, with a long-term average of only 50% of the calves surviving the first year

TABLE 2. Extreme variation in maximum allowable annual harvest of caribou one year old or older on Boothia Peninsula, Nunavut, Canada, 1985–95.<sup>1</sup>

% females in each year	% calf survival in each year	Allowable annual harvests		
		At 66% females producing calves	At 72% females producing calves	At 78% females producing calves
54	44	213	274	334
	50	304	371	437
	56	393	465	535
60	44	288	354	418
	50	386	458	528
	56	481	558	633
66	44	360	431	499
	50	465	542	616
	56	566	648	728

<sup>1</sup> Annual average maximum allowable harvest reported as a 10-yr average of caribou one year old or older obtainable from a 1985 population of 4831 caribou one year old or older that increased to 6658 caribou one year old or older in 1995 while experiencing 7% annual natural mortality, resulting from relatively minor differences in proportion of female caribou one year old or older in the population, proportion of those females producing calves each year, and proportion of calves surviving to yearlings.

of life. Even with a most unlikely high level of performance (i.e., 66% females among all caribou in the population and 78% of those females producing calves each year, with 56% of the calves surviving the first year of life, while experiencing the same level of annual natural mortality and annual harvest), the population would still have been extirpated by 1992.

Assuming that the 4831 caribou on Boothia Peninsula suffered no natural mortality—an impossible condition—but were continually experiencing the same high annual level of harvest from 1985 onward, they would have gone to extirpation by 1991. By 1988, even at a rate of 7% annual natural mortality, they would have been down about 50% to 2426 caribou—and only a continued infusion of “recruits” from beyond Boothia Peninsula could have prevented extirpation within the next three years, assuming a continuation of the reported annual average harvest.

#### *Required Females Producing Calves and Calves Surviving to Yearlings*

All population sizes within the 1985 estimate  $\pm 2$  SE (3745–5915 caribou) had severe annual deficits in the numbers of all caribou, of females producing calves, and of calves surviving to yearling recruitment needed to realize the 1995 estimate  $\pm 2$  SE values (Fig. 2). In all cases, the proportion of all females required to achieve the necessary levels of calf production would exceed 100%. In turn, the necessary levels of annual calf survival can only occur when the proportion of calves surviving each year between 1985 and 1995 approaches 70% for the most favorable cases, 90% for medium-performance cases, and 100% for poor-performance cases—values that are unrealistic to impossible. There is no reason to believe that the Boothia Peninsula or Mainland caribou ecotypes on Boothia Peninsula experienced such exceptionally high performance levels over a decade.

For the 4831 caribou on Boothia Peninsula in 1985 to increase by 38% to 6658 in 1995, given a consistent 30% initial maximum annual birth rate, 7% natural mortality, and annual harvests of 1100 caribou, 135% of all females present would have to produce calves and 187% of the number of all calves produced would have to survive the first year. Even if the average annual rate of calf survival during those 10 years had been 50% higher than the estimated mean annual rate (i.e., 75% of all calves born each year, a long-term high average unknown for any established, free-ranging North American caribou population), the population still would have gone to extirpation in 1993.

#### *Allowable Annual Harvest*

No population of the size estimated in 1985 (between 3745 and 5917 caribou, estimate  $\pm 2$  SE) could even have maintained itself, let alone have grown at a rate suggested by the 1995 population estimate, while being harvested at 1100 caribou each year (Table 2). When we consider only the possible allowable annual harvests from an estimated population of 4831 in 1985 that increases to 6658 animals in 1995, we find that they averaged 19–66% (42% median harvest) of the assumed 1100 animals harvested annually (Table 2).

The largest average allowable harvest—933 animals, or 85% of the assumed annual kill of 1100 caribou—occurred only once in the 675 possible combinations of population change from 1985 to 1995. This one instance required a theoretical 1985 starting population of 5917 caribou that increased by 71% in 10 years, to 10114 caribou (1995 estimate + 2 SE). In total, we found that only 6% of the 675 combinations yielded an allowable average annual harvest of more than two-thirds ( $> 734$ ) of the assumed 1100 annual harvest, and an allowable average annual harvest of 500 or more caribou accounted for only 42% of the combinations. Table 2 shows that the extreme variation possible in

TABLE 3. Extreme variation in annual harvest shortfall of caribou one year old or older, Boothia Peninsula, Nunavut, Canada, 1985–95.<sup>1</sup>

% females in each year	% calf survival in each year	Annual harvest shortfall		
		At 66% females producing calves	At 72% females producing calves	At 78% females producing calves
54	44	887	826	766
	50	796	729	633
	56	707	635	565
60	44	812	746	682
	50	714	642 <sup>2</sup>	572
	56	619	542	467
66	44	740	669	601
	50	635	558	484
	56	534	452	372 <sup>3</sup>

<sup>1</sup> Annual average shortfall reported as a 10-yr average (or additional animals required for an annual harvest of 1100 caribou one year old or older) resulting from relatively minor differences in proportion of female caribou one year old or older in the population, proportion of those females producing calves each year, and proportion of calves surviving to yearlings, obtainable from a 1985 population of 4831 caribou one year old or older increasing to 6658 caribou in 1995, while experiencing 7% annual natural mortality.

<sup>2</sup> Harvest shortfall using average values for all population parameters.

<sup>3</sup> Harvest shortfall using ideal values for all population parameters.

maximum allowable annual harvest during the study period could result from relatively minor differences in the proportion of females in the population, the proportion of those females that produced calves each year, and the proportion of calves surviving to yearlings.

*Annual Harvest Shortfall*

When we assume that an average annual harvest of 1100 caribou was realized between 1985 and 1995, we have a 10-year total shortfall of 6420 animals (Table 3; 642 caribou • yr<sup>-1</sup>: harvest shortfall using average values for all population parameters). This shortfall, 1.3 times the 1980 estimate and essentially equal to the 1980 estimate + 2 SE, would account for all of the caribou lost from the Prince of Wales, Somerset, and Russell islands population between the 1980 and 1995 aerial surveys.

Under the most ideal population performance parameters, the lowest average annual harvest shortfall that must be made up by ingress from beyond the Boothia Peninsula caribou population would be 372 caribou • yr<sup>-1</sup>: that is, 3720 caribou between 1985 and 1995, or 73% of the 1980 population estimate for the Prince of Wales, Somerset, and Russell islands caribou population (Table 3). As was true for the annual harvest, the extreme variation in annual harvest shortfall (Table 3: number of additional caribou needed annually from beyond the Boothia Peninsula population to realize an annual harvest of 1100 caribou) results from relatively minor differences in the proportion of females in the population, the proportion of those females producing calves each year, and the proportion of those calves surviving to yearlings.

*Required Population Size in 1985*

We know from our analysis in Figure 2 that the Boothia Peninsula population of 4831 caribou estimated in 1985

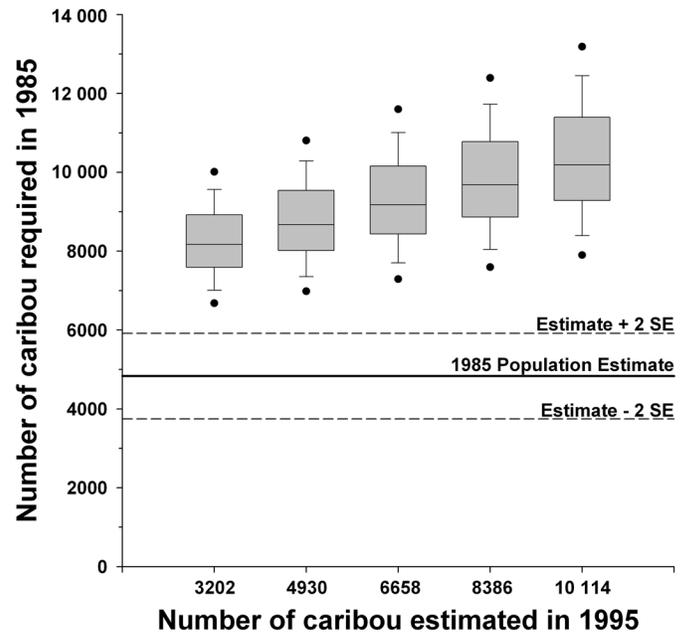


FIG. 3. Number of caribou required in 1985 to realize the 1995 estimate of ≥ 1-yr-old caribou (estimate ± 1 SE, 2 SE) projected forward in 135 combinations at 54%, 60%, and 66% ≥ 1-yr-old females in the population, with 66%, 72%, and 78% of them producing calves; 44%, 50%, and 56% calf survival; 7% annual natural mortality among all ≥ 1-yr-old caribou; and an annual harvest of 1100 ≥ 1-yr-old caribou, Boothia Peninsula, 1985–95.

would be extirpated by 1992 even under ideal conditions. A minimum population of 9179 caribou (nearly twice as large as the 1985 estimate), at 7% natural mortality, is required to reach the estimated 6658 caribou in 1995 and to sustain an annual harvest of 1100 caribou if 60% of all caribou in the population are females, 72% of those females produce calves, and 50% of those calves survive to yearling recruitment each year (Fig. 3).

## DISCUSSION

Gunn et al. (2006) built a qualitative case to explain the 98% decline of caribou on Prince of Wales, Somerset, and Russell islands as the result of long-term reductions in survival of breeding females and of calves during their first year of life. Our reasoning, based mainly on mathematical analyses, supports and expands their explanation by quantitatively examining the mechanics of how caribou on Boothia Peninsula could have or could not possibly have survived a continually high, unsustainable annual harvest from 1985 to 1995. Most importantly, we add the complicating role of seasonal migration to better describe the mechanics of both the severe decline in caribou on Prince of Wales, Somerset, and Russell islands and the concurrent persistence of caribou on Boothia Peninsula.

There appears to be no doubt that the Prince of Wales, Somerset, and Russell islands caribou population declined from several thousand animals in 1980 to only several dozen in 1995 (Table 1). That this major loss is real is further supported by the combination aerial and ground survey of Prince of Wales Island and Somerset Island carried out by the Nunavut Wildlife Service in April–May 2004, during which not a single caribou or any recent sign of caribou was seen (M. Taylor, Government of Nunavut, pers. comm. 2004, cited in Gunn et al., 2006). The failure to find any evidence of caribou on those two major islands about a decade after their near-demise was detected indicates that the recovery of that population to a level that would sustain an annual harvest of any meaningful size is still at least two to three decades away (see Figs. 2 and 3 of Gunn et al., 2006).

We determined that the Boothia Peninsula caribou population at the 1985 estimated size (estimate  $\pm$  2 SE) not only could not have increased 38% by 1995, but could not have grown at all: in fact, it could not even have persisted while experiencing an annual harvest of 1100 caribou in addition to any probable level of natural mortality for those 10 years. Both the number of females producing calves and the resultant number of calves surviving the first year of life would have been too few to sustain the 1985 population, let alone allow it to increase. Given the annual harvest shortfall, the Boothia Peninsula caribou population required ingress of caribou from the outside each year merely to survive.

Kingailik caribou from Prince of Wales Island and from Somerset and Russell islands were occurring on Boothia Peninsula annually in winter and spring, and Inuit hunters were selecting for them, apparently in large numbers (Gunn et al., 2006). In the absence of evidence to the contrary, or of other factors that might have caused the near-total loss of the Prince of Wales, Somerset, and Russell islands caribou population, we believe that the annual seasonal migrations by caribou from those islands to and from Boothia Peninsula explain the near-demise of the caribou on those islands by 1995 while other caribou persisted on Boothia Peninsula despite an excessively high annual harvest. The annual kill of migrants on Boothia

Peninsula brought those caribou remaining on Prince of Wales, Somerset, and Russell islands down to a point where continued harvesting of them on those islands as their numbers diminished, as well as the proportionally greater wolf predation, especially on calves, most likely caused the final phase of the overall decline.

Caribou from Prince of Wales, Somerset, and Russell islands did not have to remain year-round on Boothia Peninsula or join the resident caribou found there to be available to hunters: they only had to occur there annually in winter and spring. In those seasons, the migrant “recruits” made enough caribou available for harvest on the peninsula to allow the Boothia Peninsula population to persist under unsustainable hunting pressure. Also, if the caribou came from any of the other islands to the west or to the north, the Inuit hunters would have recognized them as “new” or “not belonging” on Boothia Peninsula, and no such caribou were reported between 1980 and 1995.

Additional sporadic ingress from elsewhere beyond Boothia Peninsula is a remote possibility and would have added animals in only some years. Of course, we cannot rule out the possibility that the individuals of the Mainland caribou ecotype coming northward onto Boothia Peninsula increased in number, but no Inuit reports or other evidence suggests such an increase between 1980 and 1995. Also, although no complete segregation of ecotypes was made in either the 1985 or the 1995 survey, the observers’ impressions were that caribou on the western half of the peninsula were predominantly individuals of the Boothia Peninsula caribou ecotype and those on the eastern half were predominantly individuals of the Mainland caribou ecotype (A. Gunn, pers. comm. 2004). When we examined the survey maps in Gunn and Ashevak (1990) and Gunn and Dragon (1998), we found a nearly 50:50 west-east split in the number of caribou counted in each survey. This finding suggests nearly equal representation of the Boothia Peninsula caribou ecotype and the Mainland caribou ecotype on Boothia Peninsula at those times. The 50:50 split offers no support for ingress by additional caribou from mainland herds coming onto Boothia Peninsula, which should have resulted in a split that noticeably favored the Mainland ecotype. Most importantly, because most individuals of the Mainland caribou ecotype winter south of the Boothia Isthmus, such ingress would require not just one unusual movement northward onto Boothia Peninsula, but a decade of environmentally forced annual movements beyond their traditional range. Ten consecutive years in which hundreds of barren-ground caribou were annually displaced from their traditional ranges and traveled several hundred kilometres north to Boothia Peninsula are extremely improbable.

We believe that unsustainable harvest pressure was exerted on caribou on Boothia Peninsula during at least the 1980s and early 1990s, but it was masked by the continued annual infusion of the migrant Arctic Island caribou ecotype from Prince of Wales, Somerset, and Russell islands. Now that the “reserve stock” has been exhausted, the decline in

numbers of the Boothia Peninsula caribou ecotype will become apparent if hunting pressure remains high. Unfortunately, this will most likely be recognized only after their number has become critically low. The assumed 20% average annual harvest between 1985 and 1995 far exceeds any sustainable harvest rate for tundra caribou living year-round with wolves. Bergerud (1980) reported that caribou populations with few or no predators (wolves) and more than 5% annual harvest declined in size, and even populations experiencing an annual harvest lower than 5% but living with “normal” levels of predators declined in size.

We judged that 5% annual natural mortality was unrealistically low, given what we know about wolf predation on caribou (e.g., Miller et al., 1985, 1988a; Miller, 1995b, 2003), and 13% was too high, given the level of wolf predation most likely in effect (assumed at ca. 1 wolf • 120 caribou<sup>-1</sup> in 1985). Caribou were the only ungulate prey available to wolves on Boothia Peninsula until after the mid 1990s, and virtually the only ungulate prey source after that, although a few muskoxen began recolonizing the peninsula. We believe that most of the natural mortality of calves was due to wolf predation and that even 40 wolves on the entire Boothia Peninsula (mean = 1.2 wolves • 1000 km<sup>2</sup> or 818 km<sup>2</sup> • wolf<sup>-1</sup>) in 1985 would have removed about 9% of 3745 caribou (estimate -2 SE), 7% of 4831 caribou (estimate), and 6% of 5917 caribou (estimate + 2 SE). At 11.3 caribou • wolf<sup>-1</sup> • yr<sup>-1</sup> times 0.75 to liberally correct for caribou calves in the annual kill, 40 wolves would have killed 339 caribou annually (Miller, 1995b). Those levels of wolf predation, together with an array of minor causes of natural deaths, could easily have resulted in a 7–10% average annual natural mortality among caribou in the Boothia Peninsula caribou population.

In a population not experiencing ingress, any level of annual harvest that removes more animals than the population recruits through reproduction in that year will cause the population size to decline. Although important in itself, the annual harvesting has repercussions on the hunted population beyond the absolute number of animals removed. An important consideration is the proportion of females in the annual harvest and the effect of removing breeding females on future reproduction. We believe the initial annual loss of females in the harvest is only the beginning of the impact on the population. The viable calves that those females and their lost line of female offspring could have produced during 15 years or more constitute a large number of animals lost to the population.

Initially, the importance of this loss of future calf production is not as readily apparent in large populations as in small populations—unless, of course, the absolute number of females killed annually far exceeds the net increase in the population for that year. Under such a scenario, there would have been, as concluded by Gunn et al. (2006), a long-term consequential reduction in survival rates of breeding females and, in turn, smaller calf increments and lower yearling recruitment. Continued

subsistence harvesting of caribou through the 1980s and early 1990s, along with a steady or possibly increased level of wolf predation on the dwindling number of caribou on Prince of Wales, Somerset, and Russell islands after the late 1980s, would have accelerated and deepened the decrease. A proportionately greater selection for newborn calves by wolves when the caribou population was small could have been particularly important in reducing calf survival (e.g., Miller and Broughton, 1974; Miller et al., 1985, 1988a, b) and, in turn, reducing yearling recruitment and thus the population’s potential for growth or even persistence.

## CONSERVATION IMPLICATIONS AND CONCLUSIONS

Wildlife management with harvest as the objective strives to maximize the annual harvest of animals over the longest period of time (cf. Leopold, 1933). The primary concern of the management biologist with the above premise is that annual harvests be carried out at sustainable levels to obtain the longest period of resource use at the maximum rate of harvest. To permit a biologically sound assessment of the population’s capability to sustain annual losses, accurate estimates of population size must be obtained periodically, along with yearly estimates of annual harvest.

Whether a caribou population grows or experiences a marked decline over time is usually governed by a complex web of interacting factors, often acting on different spatial and temporal scales. The quest by some biologists for a single, universal factor that governs the growth performance of a population can seriously detract from a fuller understanding of both population dynamics among free-ranging *R. tarandus* and the complex ecological relationship of those caribou to their environment (cf. Bergerud, 1996). After-the-fact evaluations of changes in population size, particularly declines, are often complicated or confounded by the lack of detailed information or its timely acquisition. Sometimes factors involved in the decline are not discernible at existing levels of monitoring, or subtle cumulative effects occur when several factors act either singly at different times or in combination over a long period. Both situations hamper or prevent accurate assessment. The complexity of interacting factors and the often-associated “ripple effect” created over time usually prevent even a satisfactory understanding of these events, not to mention a complete one.

Factors limiting population growth do not operate in isolation, and any subsequent environmental pressure on these caribou, such as the negative influence of climate change (e.g., Maxwell, 1997; Weller, 2000), could result in further population reduction or even extirpation. We believe caribou will have a negative response to climate change during the predicted transitional phase, in which more frequent severe storms with more precipitation, greater snowfall, and more freezing rain events are expected (e.g., Maxwell, 1997; Miller et al., 2005a). The predicted milder

temperatures would lead to progressively later freeze-up and earlier breakup of the sea ice, which could seriously disrupt or even prevent the caribou's inter-island and especially island-mainland seasonal migrations (Comiso, 2002; Miller and Gunn, 2003a, b; Miller et al., 2005a, b).

Unfortunately, caribou populations in the Canadian Arctic have never been monitored on an ongoing, decadal basis or at a level sufficient for making full evaluations with biological confidence. Adequate monitoring at satisfactory levels is expensive. Limited budgets require agencies to select management activities that, in turn, usually are dictated by an array of socio-political and technical considerations. Agencies are each responsible for many caribou populations and must, at best, spread their efforts among the populations at intervals on a multiyear basis. Many people have lulled themselves into believing that adequate monitoring is not necessary while a population's numbers appear high and hunters are not reporting difficulty in obtaining their desired annual harvests.

Any attempt to develop an adequate monitoring program for caribou populations on the Canadian Arctic Archipelago and Boothia Peninsula would suffer from technical difficulties and high costs due to the vastness, isolation, and remoteness of the region. Periodic monitoring at intervals of three to five years (cf. Miller et al., 2005a) would be hampered by the extreme variability of the weather within and between years. Surveys would require flexibility in timing and rescheduling to maintain satisfactory monitoring. It is hard to justify high-cost, technically difficult monitoring of relatively small caribou populations harvested by a few people in widely scattered small settlements. These conditions often result in unacceptably long intervals between adequate population estimates.

Even though considerable money has been spent collecting caribou harvest data (e.g., Donaldson, 1982), the results have been of limited use. Although some small sets of data and bits of useful information have been obtained, the results for caribou have generally been both fragmentary and lacking in specific details. Few or no data have been routinely obtained on the sex and age of individual caribou killed, or even on the population from which the animals were taken when the same hunters harvested more than one population.

Unfortunately, the importance of the linkage between the number of caribou on Prince of Wales, Somerset, and Russell islands in summer and those on Boothia Peninsula in winter has not been recognized or incorporated as a consideration in management actions or conservation measures. Just as importantly, in terms of what is currently happening to the caribou resource in that region, no effort has been made since 1995 to determine the number of caribou on Boothia Peninsula, or at least none has been reported. Nor, to the best of our knowledge, were any harvest data collected at that time, or from then to now, on the number of caribou being killed on Boothia Peninsula. It will not be possible to manage and conserve these caribou on a biologically sound basis until the PSBC is

treated as a single management unit and an adequate level of monitoring is concurrently carried out in all areas, as is needed to estimate population size and obtain annual harvest data by ecotypes for the entire PSBC.

#### ACKNOWLEDGEMENTS

The aerial surveys and the harvest data used for our evaluation were obtained by the Government of the Northwest Territories, Department of Resources, Wildlife and Economic Development (RWED). The studies of inter-island and island-mainland movements of caribou within the region were carried out by the Canadian Wildlife Service (CWS), Environment Canada. A satellite telemetry study of caribou movements and distribution was carried out on Boothia Peninsula and the adjacent mainland to the south by RWED. Logistical support for all of these studies was provided by the Polar Continental Shelf Project (PCSP), Natural Resources Canada. We acknowledge B. Hrycyk, Director, PCSP, and past PCSP directors for their long-term support of caribou research activities in the Canadian Arctic. We thank E.S. Telfer, CWS, for critically reading and improving the originally submitted manuscript. We thank S.M. Murphy, ABR, Inc.—Environmental Research & Services, Fairbanks, Alaska, U.S.A., and two anonymous reviewers for critical reviews that helped improve the final manuscript.

#### REFERENCES

- 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.
- . 1980. A review of the population dynamics of caribou and wild reindeer in North America. In: Reimers, E., Garre, E., and Skjenneberg, S., eds. *Proceedings of the 2nd Reindeer/Caribou Symposium, Røros, Norway, 1979*. Trondheim: Direktoratet for vilt og ferskvannsfisk. 556–581.
- . 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer*, Special Issue 9: 95–115.
- BERGERUD, A.T., NOLAN, M.J., CURNEW, K., and MERCER, W.E. 1983. Growth of the Avalon Peninsula, Newfoundland caribou herd. *Journal of Wildlife Management* 47:989–998.
- COMISO, J.C. 2002. A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters* 29(20):1956, doi: 10.1029/2002GL015650.
- COUTURIER, S., BRUNELLE, J., VANDAL, D., and ST-MARTIN, G. 1990. Changes in the population dynamics of the George River caribou herd. *Arctic* 43(1):9–20.
- 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. In: Reimers, E., Garre, E., and Skjenneberg, S., eds. *Proceedings of the 2nd Reindeer/Caribou Symposium, Røros, Norway, 1979*. Trondheim: Direktoratet for vilt og ferskvannsfisk. 595–604.

- DONALDSON, J. 1982. Wildlife harvest statistics for the Baffin Region, Northwest Territories. Baffin Region Inuit Association Technical Report 2:1–64. Unpubl. report available from BRIA, Iqaluit, Northwest Territories X0A 0H0.
- EGER, J., and GUNN, A. 1999. Evolutionary history of Peary caribou and Arctic-island caribou on the Canadian high and central Arctic islands. Scientific and Social Programme Abstracts, Poster 82. Rangifer Report No 4:66.
- GUNN, A. 1984. Sex and age composition of the Beverly herd of barren-ground caribou in the fall of 1981 and 1982. File Report 40. Yellowknife: Department of Renewable Resources, Government of the Northwest Territories.
- GUNN, A., and ASHEVAK, J. 1990. Distribution, abundance and history of caribou and muskoxen north and south of the Boothia Isthmus, Northwest Territories, May–June 1985. File Report 90. Yellowknife: Department of Renewable Resources, Government of the Northwest Territories.
- GUNN, A., and DECKER, R. 1984. Numbers and distribution of caribou and muskoxen in July 1980 on Prince of Wales, Russell and Somerset islands, N.W.T. File Report 38. Yellowknife: Department of Renewable Resources, Government of the Northwest Territories.
- GUNN, A., and DRAGON, J. 1998. Status of caribou and muskox populations within the Prince of Wales Island-Somerset Island-Boothia Peninsula complex, NWT, July-August 1995. File Report 122. Yellowknife: Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories.
- 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., JINGFORS, K., and EVALIK, P. 1986. The Kitikmeot harvest study as a successful example for the collection of harvest statistics in the Northwest Territories. In: Native people and renewable resource management. Edmonton, Alberta. Proceedings of the 1986 Symposium of the Alberta Society of Professional Biologists. 249–259.
- GUNN, A., FOURNIER, B., and MORRISON, R. 2000a. Seasonal movements and distribution of satellite collared caribou cows on Boothia and Simpson Peninsula areas, Northwest Territories, 1991–93. File Report 126. Yellowknife: Department of Renewable Resources, Government of the Northwest Territories.
- GUNN, A., MILLER, F.L., and NISHI, J. 2000b. Status of endangered and threatened caribou on Canada's Arctic islands. *Rangifer*, Special Issue 12:39–50.
- GUNN, A., MILLER, F.L., BARRY, S.J., and BUCHAN, A. 2006. A near-total decline in caribou on Prince of Wales, Somerset and Russell islands, Canadian Arctic. *Arctic* 59(1):1–13.
- JINGFORS, K. 1986. Inuit harvesting of caribou in the Kitikmeot Region, Northwest Territories, Canada, 1982–1984. *Rangifer*, Special Issue 1:167–172.
- KELSALL, J.P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monograph No. 3. 339 p.
- LEOPOLD, A. 1933. Game management. New York: Charles Scribner's Sons.
- MAXWELL, B. 1997. Responding to global climate change in Canada's Arctic. Downsview, Ontario: Environment Canada. 82 p.
- MESSIER, F., HOUT, J., LEHENAFF, D., and LUTTICH, S. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. *Arctic* 41(4):279–287.
- MILLER, F.L. 1974. Biology of the Kaminuriak population of barren-ground caribou – Part 2: Dentition as an indicator of age and sex; composition and socialization of the population. Canadian Wildlife Service Report Series 31. 87 p.
- . 1990a. Inter-island movements of Peary caribou: A review and appraisal of their ecological importance. In: Harington, C.R., ed. Canada's missing dimension: Science and history in the Canadian Arctic Islands, Vol. 2. Ottawa, Ontario: Canadian Museum of Nature. 608–632.
- . 1990b. Peary caribou status report. Environment Canada, Canadian Wildlife Service. 64 p.
- . 1995a. Peary caribou studies, Bathurst Island complex, Northwest Territories, July–August 1993. Canadian Wildlife Service Technical Report Series 230. 76 p.
- . 1995b. Status of wolves on the Canadian Arctic Islands. In: Carbyn, L.N., Fritts, S.H., and Seip, D.R., eds. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35. 35–42.
- . 2003. Caribou *Rangifer tarandus*. In: Feldhamer, G.A., Thompson, B.C., and Chapman, J.A., eds. Wild mammals of North America: Biology, management, and conservation. Baltimore, Maryland: John Hopkins University Press. 965–997.
- MILLER, F.L., and BROUGHTON, E. 1974. Calf mortality on the calving ground of Kaminuriak caribou. Canadian Wildlife Service Report Series 26. 26 p.
- MILLER, F.L., and GUNN, A. 1980. Inter-island movements of Peary caribou (*Rangifer tarandus pearyi*) south of Viscount Melville Sound and Barrow Strait, Northwest Territories, Canada. In: Reimers, E., Garre, E., and Skjenneberg, S. eds. Proceedings of the 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 99–114.
- . 2003a. Catastrophic die-off of Peary caribou on the western Queen Elizabeth Islands, Canadian High Arctic. *Arctic* 56(4): 381–390.
- . 2003b. Status, population fluctuations and ecological relationships of Peary caribou on the Queen Elizabeth Islands: Implications for their survival. *Rangifer*, Special Issue 14: 213–226.
- MILLER, F.L., EDMONDS, E.J., and GUNN, A. 1982. Foraging behaviour of Peary caribou in response to springtime snow and ice conditions. Canadian Wildlife Service Occasional Paper 48. 41 p.
- MILLER, F.L., GUNN, A., and BROUGHTON, E. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. *Canadian Journal of Zoology* 63:295–300.
- MILLER, F.L., BROUGHTON, E., and GUNN, A. 1988a. Mortality of migratory barren-ground caribou on the calving grounds of the Beverly herd, Northwest Territories, 1981–83. Canadian Wildlife Service Occasional Paper 66. 24 p.

- MILLER, F.L., GUNN, A., and BROUGHTON, E. 1988b. Utilization of carcasses of newborn caribou killed by wolves. In: Proceedings of North American Caribou Workshop 3:73–87.
- MILLER, F.L., BARRY, S.J., and CALVERT, W.A. 2005a. Conservation of Peary caribou based on a recalculation of the 1961 aerial survey on the Queen Elizabeth Islands, Arctic Canada. *Rangifer*, Special Issue 16:65–75.
- . 2005b. Sea-ice crossings by caribou in the south-central Canadian Arctic Archipelago and their ecological importance. *Rangifer*, Special Issue 16:77–88.
- PARKER, G.R. 1972. Biology of the Kaminuriak population of barren-ground caribou—Part 1: Total numbers, mortality, recruitment, and seasonal distribution. Canadian Wildlife Service Report Series 31. 93 p.
- RØED, K.H. 2005. Refugial origin and postglacial colonization of holarctic reindeer and caribou. *Rangifer* 25:19–30.
- SKOOG, R.O. 1968. Ecology of caribou (*Rangifer tarandus granti*) in Alaska. PhD dissertation, University of California at Berkeley, Berkeley.
- THOMAS, D.C., and EVERSON, P. 1982. Geographic variation in caribou on the Canadian Arctic islands. *Canadian Journal of Zoology* 60:2442–2454.
- THOMAS, D.C., and KILIAAN, H.P.L. 1998. Fire-caribou relationships: (II) Fecundity and physical condition of the Beverly herd. Canadian Wildlife Service Technical Report Series 310. 96 p.
- WELLER, G. 2000. The weather and climate of the Arctic. In: Nuttall, M., and Callaghan, T.V., eds. *The Arctic: Environment, people, policy*. Amsterdam: Harwood Academic Publications. 143–160.
- ZITTLAU, K. 2004. Population genetic analyses of North American caribou (*Rangifer tarandus*). PhD dissertation, Department of Biological Sciences, University of Alberta, Edmonton.