

## Population Ecology of Caribou Populations without Predators: Southampton and Coats Island Herds

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**Abstract:** This paper is a review of the ecology of two caribou populations inhabiting predator-free northern islands, Coats and Southampton Island. Findings are analyzed in light of the hypothesis that in absence of predation or high human harvest, food competition results in delayed puberty, reduced calf production, increased winter starvation of caribou and regulates populations at high densities ( $>2 \text{ km}^{-2}$ ). Caribou were hunted to extinction on Southampton Island (Northwest Territories, Canada) by mid-century. In 1967, 48 caribou were captured on neighbouring Coats Island and released on Southampton Island. Southampton Island is characterized by a high per capita winter food availability in summer and in winter. The population on Southampton Island has been increasing at a rapid rate of growth since re-introduction ( $\lambda=1.27$ ). Fast population growth was possible because females invested early in reproduction and over winter survival rate was high. The population on Coats Island is also characterized by high per capita food availability in summer but low food availability in winter. The population size has undergone some marked fluctuations, abrupt declines followed by relatively rapid recovery and, contrary to predictions, densities were always less than  $1 \text{ km}^{-2}$ . Low population densities on Coats Island result primarily from low food availability. This review suggests that in the absence of predation or high human harvest competition for food regulates caribou population abundance. However, caribou numbers can fluctuate markedly among years because inter-annual variation of weather conditions affects forage accessibility in winter. This review also emphasizes the importance of distinguishing between factors that determine absolute population density and variation in density among years (in our case probably plant production and winter weather conditions which influence forage accessibility) from the regulatory factors, processes that stop population increase (competition for winter food leading primarily to density dependent changes in mortality from starvation) when examining population dynamics.

**Key words:** *Rangifer*, population dynamics, food, snow, density

**Rangifer**, Special Issue No. 9, 17-26

### Introduction

Caribou were hunted to extinction on Southampton Island (Northwest Territories, Canada) by 1955. In 1967, 48 caribou were captured on neighbouring Coats Island and released on Southampton Island, two northern predator-free environments. The dynamics of these two populations differ sharply. The Southampton Island herd has been increasing since its re-introduction, whereas, during the same period of time Coats Island population showed marked fluctuations. In recent years, several aspects of the ecology of these populations have been studied (e.g. Adamczewski *et al.*, 1987a, 1987b, 1988, 1993; Gates *et al.*, 1986a, 1986b;

Heard & Ouellet, 1994; Ouellet, 1992; Ouellet *et al.*, 1994).

In a recent review, Seip (1992) suggested that in absence of major predators or high levels of human harvest, caribou and reindeer (*Rangifer tarandus*) populations generally increase until they become regulated by a density dependent competition for food. Competition for food results in decreased nutrient intake, increased energy costs, reduced pregnancy rates, low calf survival and higher mortality rates. Populations of *Rangifer* regulated by competition for food resources often attain densities over  $2 \text{ km}^{-2}$ . The main objective of this paper is to review the population ecology of two caribou herds

inhabiting northern predator-free islands, Southampton and Coats Islands, in light of the above suggestions. A second objective is to speculate about the future of the re-introduced Southampton Island caribou population.

### Study areas

Coats (5 600 km<sup>2</sup>) and Southampton (43 000 km<sup>2</sup>) Islands are at the north end of Hudson Bay, Northwest Territories, Canada. In winter, open water prevents caribou movements between these two islands and the mainland. The climate is typical of the Arctic (Thompson, 1967 *in* Parker, 1975). Strong winds and a short growing season characterized the climate of these islands. Mean annual temperature is - 11 °C with mean daily temperature above freezing only in July and August. Annual precipitation averaged 300 mm. Snowfall is twice as high as at Baker Lake on the mainland at similar latitude (132 vs 57 cm). Snow cover persist from mid September to mid June. Except for an elevated area of granite and gneiss at the northern end, Coats Island consist of low flat limestone plains. The west half and most of the southeast of Southampton Island is also flat but the remainder of the island is steep to rolling Precambrian shield (Adamczewski *et al.*, 1988; Gates *et al.*, 1986b; Parker, 1975).

### Methods

The paper is primarily a review of all published information regarding the population ecology of Southampton and Coats Islands herds. We incorporated to the paper previously unpublished results of an aerial survey that we conducted on Coats Island during the summer 1991 to estimate caribou numbers. To relate observed changes in caribou numbers to winter harshness we also calculated a winter severity index.

#### Aerial survey

An aerial strip transect survey was conducted on the 23 and 24 of June 1991 to estimate population size on Coats Island. Sample units were the same 31 strip transects that were flown in 1984 (see Gates *et al.* 1986b) where the starting point was selected randomly. Observers counted caribou within 400 m wide strip on each side of the Cessna 337 aircraft which was flown at 122 m of altitude and at an air-speed of 185 km hr<sup>-1</sup>. Transects were systematically spaced 4.3 km apart resulting in 20 % coverage. The census zone was not stratified. The only caribou that could be classified in all cases were neonatal calves. Calculations followed Jolly (1969).

#### Relative winter severity index

A relative winter severity index was calculated according to Gunn *et al.* (1989) based on snow accu-

mulations recorded at the Coral Harbour weather station (Southampton Island). The index is based on percent deviations from the long-term mean (1974-1994) of accumulated snow depth on the last day of the month, for the periods of early winter (September - November), mid winter (December - February), and late winter (March - May).

## Results

### Population dynamics

#### Southampton Island herd

The caribou population on Southampton Island grew from 48 (38 one-year-old or older caribou) in 1967, the re-introduction year, to 13 700 ± 1580 (0.31 km<sup>-2</sup>) one-year-old or older caribou in 1991 (see Fig. 1). The corresponding annual finite rate of growth was 1.27, with no indication of any decline in the rate of growth as population density increased.

Survival rate has not been quantified. However, a population balance model, using known fertility rate, indicated that, assuming 100 % survival of individuals older than calves, calf survival must have been at least 72 % to achieve the observed rate of growth (Heard & Ouellet, 1994). Conversely, if calf survival was 100 % then adult survival must have been at least 92 %. Female (excluding calves) pregnancy rate was near 100 % (all 23 month old females

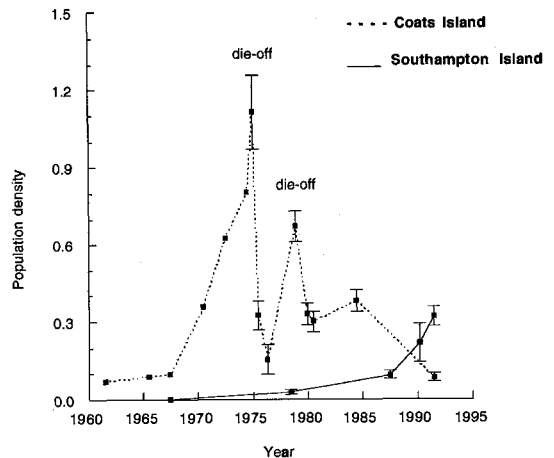


Fig. 1. Trend in caribou population density (number of one-year-old and older animals per km<sup>2</sup>) on Coats Island from 1961 and Southampton Island from 1967 (re-introduction) to 1991. Vertical bars represent one standard error of the estimated density. Data source: Coats Island estimates from 1961 to 1974 (unpub. N.W.T. Government files), 1975 to 1984 (Adamczewski *et al.*, 1986b), and 1991 (this study); Southampton Island estimates (Heard & Ouellet, 1994).

examined over a four year period were pregnant [ $n=21$ ] (Ouellet, 1992).

Hunting did not play an important role into the population dynamics of this herd because quotas were low relative to the population size (i.e. less than 1 %). Hunting quotas increased gradually from 25 males per year beginning in 1977-78 to 300 males and 100 females in 1990-91 (Heard & Ouellet, 1994).

#### *Coats Island herd*

The origin of this population is not known, but caribou have been on the island at least since the early part of the century (Gates *et al.*, 1986b). Over the last three decades the dynamics of this herd was characterized by rapid population increases and occasional substantial winter die-offs (Fig. 1). Substantial winter mortality occurred at least twice between 1961 and 1991. In spring 1975, over two carcasses were observed for every live caribou seen within the transects indicating that over-winter mortality was about 70 %. About 50 % of the caribou apparently died during the winter of 1978-1979 based on a decline in population size from 4200 in November 1978 to 1700 in June 1980. The crash unlikely occurred during the winter 1979-1980 because only about 200 carcasses were estimated in June 1980. Other die-offs could also have occurred during other winters and gone undetected. Except for the fall of 1974, density was always under 1 km<sup>-2</sup>.

Juveniles were particularly affected by over-winter mortalities (Gates *et al.*, 1986b). In June 1975, following the winter die-off, not a single one-year-old caribou was seen. Among older individuals, it appears that adult males were more vulnerable than females. The sex ratio during aerial censuses were strongly female biased (Gates *et al.*, 1986b). For example, during the 1984 survey only 1.6 % of caribou older than one-year-old were obvious mature bulls. There is no doubt that many bulls were not identified during the censuses, nevertheless it suggests a biased sex ratio towards females. Ground surveys (Gates *et al.*, 1986b) also support this claim because males never exceeded 20 % of the adults. Hunting may have also partly contributed to the observed pattern because males apparently predominated in the kill (Gates *et al.*, 1986b). Most mature females (4 years old and older) were pregnant (30 out of 32). Pregnancy rate in younger females was not determined.

Although precise data are not available, it appears that the kill increased in the 1970's to reach a maximum of about 13 % (i.e. about 280 caribou; 177 males and 113 females) of the adult population (i.e. excluding calves) by mid-1980's. Therefore, in the

1980's considering the size of the population, hunting could have been an important limiting factor. Since then, likely because hunting quotas increased on Southampton Island (see above), the kill has decreased gradually in absolute and in relative terms and was possibly no more than 50 individuals by the end of the last decade (i.e. less than 10 % of the population).

#### *Range quality*

In the early 1980's, although the vegetation was low in biomass and diversity, the summer range was considered adequate relative to the population size (Adamczewski *et al.*, 1987b; Adamczewski *et al.*, 1988). Peak ruminal nitrogen in summer was comparable to values found for other caribou populations (Adamczewski *et al.*, 1988). The summer range has also been adequate on Southampton since re-introduction (Parker, 1975; Ouellet, 1992). Summer forage was of high quality and comparable to other arctic sites (Ouellet *et al.*, 1994). The diet of caribou on these two islands during summer was comparable and largely dominated by willows (Ouellet *et al.*, 1994; Adamczewski *et al.*, 1988). Annual production per unit area of sedges, grasses, and willows was high on these islands relative to population size (Table 1). Based on forage annual net primary production and plant consumption, Parker (1975; tables 14 and 15, p.53) suggested that the summer range on Southampton Island can support a density of about 6 km<sup>-2</sup> (i.e. 260 000 caribou). The same model applied to Coats Island suggests that the summer range could support a density of 3.2 km<sup>-2</sup> (i.e. 18 000 caribou). Insect harassment which can reduce foraging time (Klein, 1992) appears to be low, probably because the two islands are characterized by strong winds. All of these reasons support the argument that the summer range, relative to the population size (see Fig. 1), has been adequate on both islands.

However, the winter range is likely of better quality on Southampton Island. Typical feeding sites used in winter (i.e. sites with topographic relief and shallow snow) are overgrazed on Coats Island (Adamczewski *et al.*, 1988), whereas on Southampton Island only a small fraction of these sites are overgrazed (Ouellet *et al.*, 1993). Further, Southampton Island is characterized by a higher lichen standing crop, at least since the late seventies early eighties (Table 1). This difference in lichen standing crop was reflected by a larger proportion of lichens in the diet in the fall and in the winter of caribou on Southampton Island, relative to those on Coats Island (fall: 67 % vs 36 %; winter: 46-49 % vs 2-12 %; Gates *et al.*, 1986a). Based on lichen standing crop Parker (1975) suggested that Southampton Island can support a density of about

1 km<sup>2</sup>. This model applied to Coats Island suggests a population density of 0.3 km<sup>-2</sup> (i.e. 1600 caribou). A better winter range on Southampton Island is also indirectly supported by the observation that body reserves (fat and muscle) in the spring are much lower on females from Coats Island (Adamczewski *et al.*, 1987b; Ouellet, 1992).

## Discussion

The Coats Island herd showed marked fluctuations in abundance over the last three decades in response to a limited supply of winter food and high inter-annual variation in weather conditions affecting its accessibility. However, animals released on Southampton Island in 1967 were clearly not limited by winter food and as a result numbers increased rapidly and steadily throughout the same period. Therefore the comparison between these two genetic related populations is instructive because they represent both ends of a continuum from population growth occurring near the intrinsic rate of growth (i.e. Southampton Island herd) to the relative stability of a population regulated by competition for food (i.e. Coats Island population).

## Fast population growth on Southampton Island

Rapid population growth on Southampton Island resulted from high fecundity and over-winter survival rates, relative to other predator-free populations, and appears to be a consequence of the high overall quality of its range, particularly the winter range. A similar conclusion was reached by Klein (1968) who documented the eruption of the reindeer population on St Matthew.

High fecundity was recorded on Southampton Island because females reproduced early in life. Early investment in reproduction was possible because females grew rapidly (Ouellet, 1992; Leader-Williams, 1988). Physical growth was rapid relative to Coats Island animals probably because the better quality of the winter range on Southampton Island resulted in 1) animals in excellent body condition in the spring thus reducing requirements to replenish their fat and muscle during summer and 2) not needing to accumulate as much fat in preparation to winter (Ouellet, 1992). Because Southampton Island mothers were in excellent body condition in the spring fetal growth during the late pregnancy period and calf growth

Table 1. Lichen standing crop and annual net primary production of sedges, grasses, and willows in the dominant range types found on Coats Island and Southampton Island, Northwest Territories.

| Range types                           | Area (km <sup>2</sup> ) | Lichen standing crop (g DM m <sup>-2</sup> ) | Annual production <sup>3</sup> (g DM m <sup>-2</sup> ) |
|---------------------------------------|-------------------------|--|--|
| <b>Coats Island<sup>1</sup></b>       |                         |  |  |
| Dryas-lichen                          | 590                     | 29.9   | 7.8  |
| Meadows                               | 1 922                   | 9.3  | 26.0   |
| Polygons                              | 133                     | 4.3  | 4.3  |
| Total/weighted means                  | 2645                    | 13.6   | 20.8   |
| <b>Southampton Island<sup>2</sup></b> |                         |  |  |
| Raised-lichen-Dryas sedge             | 5 745                   | 58.0   | 21.0   |
| Lichen-heath felsenmeer plateau       | 7 345                   | 85.7   | b  |
| Lichen-heath felsenmeer lowland       | 3 789                   | 99.7   | b  |
| Polygons                              | 4 840                   | 20.7   | 34.5   |
| Sedge willow meadow                   | 5 957                   | a  | 60.0   |
| Sedge-heath transition                | 5 353                   | a  | 38.0   |
| Total/weighted means                  | 33 029                  | 43.6   | 38.8   |

<sup>1</sup> data from Adamczewski *et al.*, 1988; <sup>2</sup> data from Parker, 1975; <sup>3</sup> annual production of sedges, grasses, and willows; a, lichens are not abundant in these range types; b, not available.

through lactation may have been consistently high. Fetal weight was related to maternal condition on Coats Island (Adamczewski *et al.*, 1987b) and therefore may be related to winter feeding conditions.

#### *Population regulation on Coats Island*

The major die-offs recorded on Coats Island took place at high population density relative to the other estimates and the fraction of animals dying was related to density (Fig. 1). Therefore, even though these die-offs were likely related to adverse snow conditions, mortality was in part density dependent, not solely density independent as suggested by Gates *et al.* (1986b). This conclusion is also supported by the observation that whereas high mortality was recorded on Coats Island, mortality must have been low on the neighbouring Southampton Island considering the rapid and steady rate of growth of the herd since re-introduction (Heard & Ouellet, 1994).

The pregnancy rate of yearlings and the over-winter survival of juveniles and adult males (see above) are likely the demographic features affected most by food shortage in winter as has been shown in other food limited ungulate populations (e.g. Leader-Williams, 1988; Clutton-Brock *et al.*, 1991; Tyler, 1987). Although Coats Island and Southampton Island populations were at two different densities, pregnancy rates of adults (3 years old and older at calving) were similar which confirms the low variability in adult pregnancy rates of caribou (Bergerud, 1983). However, extreme adverse climatic conditions may reduce pregnancy rate substantially (see Thomas, 1982). Unfortunately no data are available on pregnancy rate of yearling females (i.e. 2 years old at calving) from Coats Island. But, relative to other populations (see Leader-Williams, 1988) females on Southampton first reproduce early in life as all yearlings sampled were pregnant (see above). Therefore, age at first reproduction may in part be density dependent (Ouellet, 1992). Coats Island juveniles and adult males were more vulnerable to over-winter mortality and the sex ratio was female biased. Female biased sex ratios are the rule in ungulates (*Rangifer*: Klein, 1968; Skogland, 1985; Leader-Williams, 1988; Roe deer *Capreolus capreolus* L.: Gaillard *et al.*, 1993) but favourable conditions may prevent this situation because on Southampton Island the sex ratio was close to 50:50 (see Heard & Ouellet, 1994).

It was impossible to quantify the impact of weather conditions on the population dynamics of Coats Island herd as there is no weather station on Coats Island. Based on snow data from Southampton Island there was no obvious link between the calculated index of winter severity and the

dynamics of Coats Island herd (Table 2). For example, the 1974-75 winter was not particularly severe based on this index although a major crash took place that year. On the other hand, snow accumulation on the ground began very early that year because there was 10 cm of snow on the ground at the end of September 1974 relative to the long term mean of 3 cm. We need to be cautious when extrapolating climatic conditions from one location to another. Ouellet *et al.* (1993) showed on Southampton Island some variation in snow condition from one site to the another suggesting that the use of climatic data from one site is possibly of little value in depicting the climatic conditions over a large area. Further, such index of winter severity is possibly too simplistic to reflect the real nature of the relationship between winter climatic conditions and caribou population dynamics (Gunn *et al.*, 1989; Tyler, 1987)

Table 2. Relative winter severity index based on snowfall, Coral Harbour, Southampton Island, Northwest Territories.

| Winter  | Total snowfall (cm) | Overall relative severity index |
|---------|---------------------|---------------------------------|
| 1971-72 | 158.1               | 30                              |
| 1972-73 | 118.0               | -38                             |
| 1973-74 | 71.9                | -136                            |
| 1974-75 | 104.4               | -71                             |
| 1975-76 | 128.6               | -8                              |
| 1976-77 | 137.1               | 3                               |
| 1977-78 | 115.9               | -54                             |
| 1978-79 | 80.9                | -122                            |
| 1979-80 | -----               | -15 <sup>a</sup>                |
| 1980-81 | 94.8                | -62                             |
| 1981-82 | 118.9               | -19                             |
| 1982-83 | 149.4               | 33                              |
| 1983-84 | 116.9               | -18                             |
| 1984-85 | 126.2               | -10                             |
| 1985-86 | 142.4               | 30                              |
| 1986-87 | 149.9               | 60                              |
| 1987-88 | 124.3               | -24                             |
| 1988-89 | 145.7               | -4                              |
| 1989-90 | 163.0               | 73                              |
| 1990-91 | 201.9               | 167                             |
| Mean    | 132.1               |                                 |
| C.V.    | 33.2                |                                 |

<sup>a</sup> for the winter 1979-1980 the index was calculated excluding the fall period because snowfall data were missing.

The dramatic declines observed in two reindeer populations, on two islands off the coast of Alaska, were attributed to adverse climatic conditions following overgrazing of the lichens (Klein, 1968; Scheffer, 1951). Important over-winter mortalities were also related to adverse snow conditions on other islands (high Arctic Islands: Gunn *et al.*, 1981, St Matthew: Klein, 1968; Svalbard: Tyler, 1987). In some environments, the impact of weather conditions is so obvious that some authors have argued that adverse snow conditions might contain numbers below KCC (*sensu* McNab, 1985) indefinitely (for review see Tyler, 1987). However, high forage availability may partly act as a buffer against inclement weather (Skogland, 1985). The suggestion that the detrimental effects of snow conditions increased under resource limitation is supported by the observation that while important over-winter mortalities took place on Coats Island no such die-offs occurred on neighbouring Southampton Island. Although, we must recognize the impact of density-independent factors on the dynamics of insular predator-free herds, it is fundamental to specify that these populations are not totally at the mercy of such fluctuating environment because the feedback loop comprising more forage, more individuals, less forage, fewer individuals imposes a centripetality upon the system (Caughley, 1987).

Winter food is influenced not only by snow conditions but also by the summer plant growth response and grazing (*i.e.* plant consumption) throughout the year. The plant growth response is the rate of increase of edible plant biomass per unit area as a function of its standing density and environmental attributes such as temperature and soil moisture (Caughley & Gunn, 1993). Variability in climatic condition in summer could therefore also explain the inter-annual variation in abundance of caribou, but its effect appeared relatively unimportant (but see below) because animals were consistently in excellent body condition in the fall and the adult pregnancy rate was high on both islands.

Fluctuations recorded on Coats Island may also partly reflect the impact of hunting. Hunting mortality was high enough to curtail most increase in good years and possibly precipitate the decline in years with harsh winters. Further, population estimates presented were derived from aerial censuses, that were not corrected for visibility bias which could have been different from one census to another. Nevertheless, the magnitude of the fluctuations documented cannot be accounted solely on the basis of the impact of hunting or variation in sampling bias.

#### Density achieved

Population density on Coats Island, except for one census (*i.e.* 1975) remained under 1 km<sup>-2</sup>, which is

lower than the density (>2 km<sup>-2</sup>) suggested by Bergerud (1980) and Seip (1992); the population density on Southampton Island was under 1 km<sup>-2</sup> but the population is still increasing. This is particularly low relative to other predator-free populations (see Bergerud, 1980; Leader-Williams, 1988). For example, the population on South Georgia reached 23 km<sup>-2</sup>. Why then is density attained on Coats Island so low? Low density on Coats Island is primarily related to the low net primary production. There is a good relationship between the standing crop of vegetation and *Rangifer* biomass-density (Skogland, 1980) (Fig. 2). However, other factors could also influence population density (*e.g.* plant composition, duration and severity of winter, island size and predation) but even if those factors may determine population size, in the case of predatorfree populations it is competition for food that regulates population size.

#### Modelling population dynamics and the future of Southampton Island herd

The eruption model has been used to describe the dynamics of predator-free *Rangifer* populations (*e.g.*

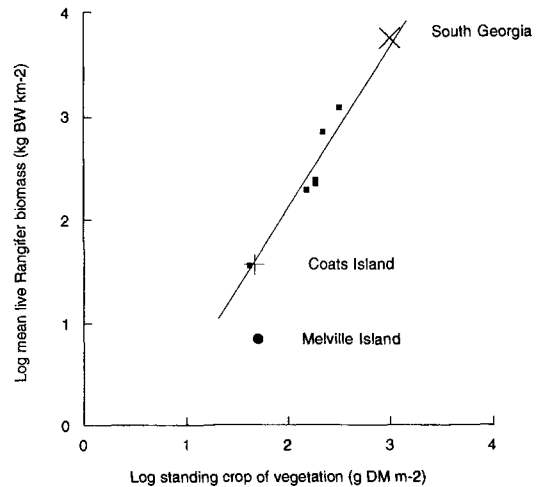


Fig. 2. *Rangifer* biomass in relation to standing crop of the vegetation for various Arctic regions (based on Skogland, 1980), South Georgia (from Leader-Williams, 1988), Coats Island (195 224 800 kg DM of available green biomass over 4152 km<sup>2</sup> [Adamczewski *et al.*, 1988]; 2 000 caribou [see Fig. 1] with a mean body weight of 78 kg which is the mean body weight of adult females [Adamczewski *et al.* 1987b]) and Melville Island (mean above-ground biomass [51.8 g DM m<sup>-2</sup>] of the various range types [Thomas & Edmonds, 1984]; mean of 4 700 caribou [Miller, 1990] over 42 220 km<sup>2</sup> with a mean body weight of 54.3 kg which is the mean body weight of adult females [Thomas *et al.*, 1977]).

Leader-Williams, 1988). Caughley (1970) defined operationally an eruption fluctuation as an increase in numbers over at least two generations, followed by a marked decline. An eruption comprise a sequence of four stages (Caughley, 1970): 1) the initial increase stage covers the period between the population establishment and the attainment of the initial peak which exceed the KCC, 2) initial stabilization stage continues until the population commences a significant decline, 3) decline stage covers the period of this decline, 4) postdecline stage refers to the period thereafter. These four stages imply corresponding changes in reproduction (i.e. age at first reproduction and pregnancy rate) and winter survival in response to competition for food. The initiation of an eruption is a response to a change in conditions of life, favouring positive population growth (e.g. introduction of a population in a new habitat, cessation of heavy hunting), and is terminated by a modification of habitat (i.e. change in standing crop and plant composition) by the animals themselves. This model can apply to established or to newly introduced populations.

The dynamics of the Southampton Island herd do not provide evidence to support or invalidate the eruption model (Caughley, 1970) because the population is still increasing. However, the population could be in the initial stage of the model. It is also difficult to assess whether or not the Coats Island population conformed to the eruptive model (see Fig. 1). Based on previous estimates, the population should have stabilized around 0.5 caribou km<sup>-2</sup>. Therefore, we could reject the model based on the basis on the 1991 population estimate. However, it is possible that external factors such as severe winters (i.e. snow conditions) may have acted to affect the predicted relationships between the caribou and its environment and promote the observed pattern. In other words, frequent impact of density independent factors on the dynamics of such insular predator-free northern populations have the potential to frequently reset the dynamics of a population to the initial stage of the model. On the other hand, differences in reproduction, physical growth, body condition, and survival between the increasing Southampton Island population and food limited populations, including Coats Island, are consistent with the model.

Based on the eruption model and the review conducted by Leader-Williams (1988) summarizing results of introductions of caribou and reindeer populations, we expect that the Southampton Island population will overshoot the KCC. A dramatic population crash may occur following a substantial depletion of lichens. Similar events occurred on other predator-free islands (e.g. St Paul, Scheffer,

1951; St Matthew, Klein, 1968). This situation can be modelled by a simple logistic growth model which incorporates a time delay between food availability and food limitation on the population (Messier *et al.*, 1988). How far the population exceeds the KCC and the importance of the crash that follows is a direct function of the duration of the time delay and the initial rate of growth of the population. The model indicates that populations relying on lichens are more likely to overshoot the KCC and crash because the slow recovery rate of lichens following grazing results in a longer time delay in the model. This conclusion is supported by the dramatic crash observed on St Matthew and St Paul, two populations relying heavily on lichens and growing at a fast rate, and the smooth stabilization of the abundance of the population on Barff Island, a population growing at a slower rate and exploiting graminoids (Leader-Williams, 1988). The model also indicates that the above prediction is valid only if the harvest level remains low relative to population size. Peak density should be influenced by the lichen standing crop and on environmental conditions. Obviously, harsh weather conditions in winter may precipitate the decline by reducing forage accessibility.

So far, we have considered that only winter forage drives the dynamics of insular northern predator-free caribou populations. However, it is possible that forage availability in summer may play a role at the end of the stage 1 of the model (i.e. overshooting of the KCC) when the population density will be unusually high. Observations made on St Matthew by Klein (1968) support this suggestion because before the crash, reindeer were in relatively poor body condition entering winter due to competition to high quality forage in summer (Klein, 1968).

Once the eruption has reached the post-decline stages (see above), the vegetation will be altered irreversibly (Caughley, 1970). At this stage, we suggest that lichens will not remain the key winter forage on Southampton Island. This is supported by the low incidence of lichens in the diet of caribou on Coats island (Adamczewski *et al.*, 1988) and their low abundance on St Matthew following the population crash (Klein, 1968); lichen standing crop remained low even two decades after the crash (Klein, 1987). In that regard, the dynamics of insular predator-free populations may be related to island size. On smaller islands, populations have the potential to reach KCC within a short period of time (e.g. within two decades). Within such a short period of time lichens do not have the ability to grow back (Ouellet *et al.*, 1993; Klein, 1987) because the rate of lichen utilization can exceed their rate

of growth. For populations using a larger range, such as large migratory populations, it will take a much longer period of time to reach KCC following a decline. For example, the George River Herd increased during 40 to 70 years (Crête *et al.*, this issue) which is sufficiently long to allow lichens to grow substantially. Predation can also slow down the rate of increase of large migratory populations allowing more time for lichens recovery. Island size may also influence caribou population dynamics if larger islands have greater topographical and climatic variations. On large islands, like Southampton Island, snow conditions can be variable (Ouellet *et al.*, 1993) so even during harsh snow conditions caribou may be able to find some areas where food is still accessible. On smaller islands, like Coats Island, snow conditions are likely less variable and harsh snow conditions may reduce forage accessibility almost equally over the entire island.

With the predicted marked reduction in lichen abundance on Southampton Island, the abundance of deciduous shrubs, mainly *Salix* spp., and graminoids will play a more important role in the dynamics of caribou on Southampton Island. Because these plant types are more resilient to browsing and grazing (Ouellet *et al.*, 1994), we expect that following the first eruption the duration of the time delay to be shorter, hence a tighter relationships between caribou number and forage abundance. However, due to the impact of frequent density independent factors the population should be loosely regulated by food at low population density (i.e. possibly under 1 km<sup>-2</sup>). The dynamics of Southampton and Coats Island herds will likely be comparable at this stage. Pregnancy rate in yearlings will drop dramatically and population recovery will be slower than the present rate of growth of the Southampton Island herd. Over a longer period of time the influence of larger scale changes in climatic conditions (Meldgaard, 1986) will certainly affect the dynamics of these two populations.

### Conclusion

This review provided an opportunity to examine some basic assumptions relevant to the ecology of ungulates and the general model proposed (Bergerud, 1980; Seip, 1992) to explain the ecology of caribou populations. Our review supports the suggestion that isolated predator-free populations are ultimately regulated by competition for food. However, populations possibly do not attain a stable equilibrium primarily because variation in weather conditions affects forage accessibility in winter. Density achieved by these populations are variable and may be under 2 km<sup>-2</sup>. Low population densities on Coats Island result primarily from low primary

production. This review also emphasizes the importance of distinguishing between limiting factors that determine absolute population density and variation in density among years (in our case probably net primary production and winter weather which influences forage accessibility) from regulatory factors, processes that stop population increase (competition for winter food leading a delay in puberty and increased mortality from starvation) when examining population dynamics (Chitty, 1960; Messier, 1991). Finally, to better understand the ecology of predator-free caribou populations further investigations should be conducted on Southampton Island in the near future. Caribou abundance, fall and spring body condition (including pregnancy rate), and the vegetation should be monitored. Further understanding will also require a quantification of the impact of weather on the plant growth and the numerical and feeding responses of caribou to changes in plant biomass and species composition under various snow conditions.

### Acknowledgements

This research was supported by the Department of Renewable Resources (Government of the Northwest Territories, Canada), the Northern Student Training Grant (Department of Indian and Northern Affairs, Canada), and the Boreal Institute for Northern Studies (Circumpolar Institute). The first author was supported by the Natural Sciences and Engineering Research Council of Canada, the University of Alberta and the Université du Québec à Rimouski. Thanks to Stan Boutin for his support throughout the project. Michel Crête and Jan Adamczewski provided critical comments that improved the manuscript.

### References

- Adamczewski, J. Z., Gates, C. C. & Hudson, R. J. 1987a. Fat distribution and indices of carcass composition in Coats Island caribou (*Rangifer tarandus groenlandicus*). - *Canadian Journal of Zoology* 56: 368-374.
- Adamczewski, J. Z., Gates, C. C., Hudson, R. J. & Price, M. A. 1987b. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an Arctic Island with limited winter resources. - *Canadian Journal of Zoology* 65: 1149-1157.
- Adamczewski, J. Z., Gates, C. C., Soutar B. M. & Hudson, R. J. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. - *Canadian Journal of Zoology* 66: 1986-1996.
- Adamczewski, J. Z., Hudson, R. J. & Gates, C. C. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. - *Canadian Journal of Zoology* 71: 1221-1229.
- Bergerud, A. T. 1980. A review of the population



- dynamics of caribou and wild reindeer in North America. - In: Reimers, E., Gaare, E. & Skjennberg, S. (eds.) *Proceedings of the Second International Reindeer/Caribou Symposium, Norway*. Direktoratet for vilt og ferskvannsfisk, Trondheim. pp. 556-580.
- Bergerud, A. T.** 1983. The natural control of caribou. - In: Bunnell, F. L., Eastman, D. S. & Peek, J. M. (eds.) *Symposium on natural regulation of wildlife populations*. Forest, Wildlife, and Range Experimental Station, University of Idaho, Moscow, ID. pp. 14-61.
- Caughley, G.** 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. - *Ecology* 51: 53-72.
- Caughley, G.** 1987. Ecological relationships. - In: Caughley, G., Sheperd, N. & J. Short (eds.) *Kangaroos: Their ecology and management in the sheep rangeland of Australia*. Cambridge University Press. pp. 159-187.
- Caughley, G. & Gunn, A.** 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. - *Oikos* 67: 47-55.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A.** 1991. Persistent instability and population regulation in Soay sheep. - *Journal of Animal Ecology* 60: 593-608.
- Chitty, D.** 1960. Population processes in the vole and their relevance to general theory. - *Canadian Journal of Zoology* 38: 99-113.
- Gates, C. C., Adamczewski, J. & Mulders, R.** 1986a. Comparison of body composition and growth potential in two related island populations of caribou. - *Rangifer* Special Issue 1: 359.
- Gates, C. C., Adamczewski, J. & Mulders, R.** 1986b. Population dynamics, winter ecology and social organization of Coats Island caribou. - *Arctic* 39: 216-222.
- Gaillard, J. M., Delorme, D., Boutin, J. M., Laere, G. V., Boisaubert, B. & Pradel, R.** 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. - *Journal of Animal Ecology* 62: 778-791.
- Gunn, A., Miller, F. L. & Thomas, D. C.** 1981. The current status and future of Peary caribou *Rangifer tarandus peary* on the Arctic islands of Canada. - *Biological Conservation* 19: 283-296.
- Heard, D. & Ouellet, J.P.** 1994. Population dynamics of an introduced caribou populations in the Arctic. - *Arctic* 47: 88-95.
- Jolly, G. M.** 1969. Sampling methods of aerial census of wildlife populations. - *East African Agricultural and Forestry Journal* 34: 46-49.
- Klein, D. R.** 1968. The introduction, increase and crash of reindeer on St. Matthew Island. - *Journal of Wildlife Management* 32: 350-367.
- Klein, D. R.** 1992. Comparative ecological and behavioral adaptations of *Ovibos moschatus* and *Rangifer tarandus*. - *Rangifer* 12: 47-55.
- Leader-Williams, N.** 1988. *Reindeer on South Georgia*. Cambridge Univ. Press, Cambridge.
- McNab, J.** 1985. Carrying capacity and related slippery shibboleths. - *Wildlife Society Bulletin* 13: 403-410.
- Messier, F.** 1991. On the concepts of population limitation and population regulation as applied to caribou demography. - In: Butler, C. E. & Mahoney, S. P. (eds.) *Proceedings of the Fourth North American Caribou Workshop*. pp 260-277.
- Miller, F. L.** 1990. *Peary caribou status report*. Canadian Wildlife Service. 64 pp.
- Ouellet, J-P.** 1992. *Ecology of an introduced caribou population on Southampton Island, Northwest Territories, Canada*. Ph. D. thesis. University of Alberta, Edmonton.
- Ouellet, J.P., Heard, D. & Boutin, S.** 1993. Range impacts following the Introduction of Caribou on Southampton Island, Northwest Territories, Canada. - *Arctic and Alpine Research* 25: 136-141.
- Ouellet, J.P., Boutin, S. & Heard, D.** 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. - *Canadian Journal of Zoology* 72:1426-1435 .
- Parker, G. R.** 1975. An investigation of caribou range on Southampton Island, NWT. - *Canadian Wildlife Service, Report No 33*.
- Scheffer, V. B.** 1951. The rise and fall of a reindeer herd. - *Sci. Monthly* 73: 356-362.
- Seip, D.R.** 1992. Predation and caribou populations. - In: Heard, D & Williams, M. (eds.) *Proceedings of the Fifth North American Caribou Workshop*. - *Rangifer* Special Issue 7:46-52.
- Skogland, T.** 1980. Comparative summer feeding strategies of arctic and alpine *Rangifer*. - *Journal of Animal Ecology* 49: 81-98.
- Skogland, T.** 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. - *Journal of Animal Ecology* 54: 359-374.
- Thomas, D. C.** 1982. The relationships between fertility and fat reserves of Peary caribou. - *Canadian Journal of Zoology* 60: 597-602.
- Thomas, D. C. & J. Edmonds.** 1984. Competition between caribou and muskoxen, Melville Island, NWT, Canada. *Biological Paper University of Alaska*, Special Report No. 4:93-100.
- Thomas, D. C., Russell, R. H., Broughton, E., Edmonds, J. E. & Gunn, A.** 1977. *Further studies of two populations of Peary caribou in the Canadian arctic*. Canadian Wildlife Service, Progress Notes No. 80.
- Tyler, N. J. C.** 1987. *Natural limitation of the abundance of High Arctic Stalbard reindeer*. Ph.D. thesis, University of Cambridge.