Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George Caribou Herd

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Abstract: The Rivière George caribou herd (RGCH) was numerically low during the middle part of the century but apparently erupted in the sixties and the seventies. Puberty was early and pregnancy rate was high among RGCH females from 1973 until the mid-eighties when fecundity decreased significantly, in particular among sub-adults; productivity remained low in 1992. Autumn calf female ratios reflected this trend in pregnancy, exceeding 50 calves: 100 cows between 1973 and 1983, but dropping thereafter progressively to a low of 24 in 1992. In 1993, this ratio rebounded back to 42. Annual adult survival rate of radio-collared females was high (0.95) at the beginning of the monitoring in 1984, but exhibited a variable but declining trend until 1992. Simulations were conducted to estimate the demographic trend of the RGCH between 1984 and 1992, using annual survival rates of radio-collared animals and annual autumn calf:female ratios to estimate calf production. Age structure played a minor role in estimating the finite rate of increase (λ). According to the simulations, the RGCH increased in size until 1987, and showed a slight decrease thereafter. The herd should have decreased by 12-15% between 1988 and 1993, according to the simulations. Productivity first caused a decline in λ, but in recent years decreased survival contributed slightly more than productivity to the reduction in λ. Estimation of the herd size by means of aerial censuses in 1976, 1984, 1988 and 1993 suggested a similar pattern in demographic trend, differences being statistically meaningless. We speculated on the future of the RGCH, that could have erupted after many decades of unfavourable weather. The herd will exhibit a rapid descent to low numbers if wolves show a numerical response to current caribou abundance, or if lichen availability on the winter range decreases due to competition with the adjacent and increasing Rivière aux Feuilles herd; otherwise it will exhibit dampened oscillations, whose amplitude will depend on the time-lag of vegetation reaction to decrease grazing pressure on the summer range.

Introduction
Demography of caribou and reindeer (*Rangifer tarandus*) for island populations, as well for continental ones, has often been characterized by huge numerical fluctuations. Changes have occurred on short time frames but also over centuries. The eruption and crash of the introduced reindeer population on St Matthew island in Alaska covered less than 2 decades (Klein, 1968), while the disappearance of a subspecies of small caribou in Greenland and its replacement by a larger one took place over millennia (Meldgaard, 1986). Periodic fluctuations at 65-115-year intervals were also documented during the last centuries in Greenland (Meldgaard, 1986). Large migratory herds of North-American caribou also fluctuated widely in number during the historical period. Most herds declined substantially during the first half of the current century, but have been increasing for the last decade (Williams & Heard, 1986; Klein, 1991).

When attempting to generalize about population dynamics of caribou, one must consider where studied populations are located with respect to the species range. Peripherical populations are generally

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more susceptible to density-independent limiting factors (sensu Messier, 1991). At the southern limit of their distribution, some caribou populations were recently reported to suffer from heavy predation that threatened their existence, e.g., the Quesnel Lake population in British Columbia preyed upon by wolves (*Canis lupus*) (Seip, 1992), and the Gaspésie Park population in Québec, affected by coyote (*Canis latrans*) predation (Crête & Desrosiers, 1995). At the northern limit of their range, Peary caribou on Banks Island have recently been declining dramatically, but the causes remain obscure (Miller, 1991). On the other hand, population dynamics of central Alaskan caribou may be unique due to the richness in large mammal populations encountered.

Population regulation, i.e. feedback mechanisms by which populations tend to come back to the carrying capacity (KCC: MacNab, 1985) when displaced from it (sensu Messier, 1991), should be easier to detect in caribou populations of the core of the species distribution. Caribou reach highest densities at tree-line where they form large migratory herds. They generally gather on the tundra in spring and stay until winter when they commonly move into the forest-tundra and the boreal forest (Williams & Heard, 1986). Strong regulation would result in a quick return to KCC, while weak regulation resulting from a time lag in density-dependance could result in cyclic populations. The model developed by Caughley (1976) to describe the relationships between large ungulate populations and their forage allows for both outcomes.

Some authors proposed that population dynamics of migratory caribou could be cyclic because of their dependence on lichens as winter forage (e.g. Messier *et al.,* 1988). Lichens carry a risk of instability because of their slow growth and their capacity to accumulate the annual production of decades, that can be consumed rapidly by an expanding caribou population (Messier *et al.,* 1988). Caribou expansions could lead to overgrazing of lichens, followed by a crash until lichens recover. After forest fires, lichen species important to caribou feeding in the Québec-Labrador peninsula take ≈30-40 years to recolonize the ground and to become large enough to be edible (Morneau & Payette, 1989). This recovery time is probably longer on the tundra. Messier *et al.* (1988) explored the possible consequences of such time lag in lichen recovery on the demography of RGCH.

It is important to distinguish between cycles and fluctuations in population dynamics because the causes and the mechanisms involved can be different, and can lead to different predictions and management practices. Cycles are characterized by a period (time span between 2 identical states) and an amplitude (difference between maximum and minimum population size); they can be described mathematically by a trigonometric function (sine or cosine). Cycles should normally be driven by endogenous causes to the system (e.g. lichen overgrazing and recovery, predation), but could also result from exogenous causes like cyclic climates (Schlesinger & Ramankutty, 1994). Changes in population level that do not have a regular periodicity, cannot be considered cyclic, although they form a sequence of peaks and troughs when plotted over time. Long term fluctuations in caribou numbers could result from changes in KCC, for instance because of varying snowfalls resulting from climatic changes (Crête & Payette, 1990). If migratory caribou herds are cyclic, the period of cycles certainly cover many decades (Messier *et al.,* 1988). Because it is very difficult to estimate precisely and accurately the size of migratory caribou herds (Crête *et al.,* 1991), and data covering long periods are not available, it is then impossible to determine if some or all migratory herds of caribou in North America exhibit cycles. To further complicate the demography of caribou, Caughley & Gunn (1993) showed that pseudo-cycles with a periodicity of a few decades could be generated from annual random fluctuations in precipitation.

Historical information on the Rivière (River) George Caribou Herd (RGCH) suggests that animals were abundant and followed the same migratory patterns during the second half of the 18th century as they do now (Taylor, 1969). At that time, lichens were probably abundant at the head of the Fraser Canyon since the Inuit used them to cook food and boil water (Taylor, 1969). Animals appeared rare by 1920, a situation that persisted until 1950 (Banfield & Tener, 1958; Bergerud, 1967), but the herd increased rapidly thereafter to peak by the end of the eighties (Couturier *et al.,* 1988, 1989; Messier *et al.,* 1988; Crête *et al.,* 1989; Hearn *et al.,* 1990). Forage availability on the calving and summer range, located on tundra plateaux bordering Rivière George, is apparently responsible for regulation of RGCH (Couturier *et al.,* 1988, 1989; Crête *et al.,* 1990a). Parturient and lactating females have had to compensate for the rarity of lichens before the green-up, and of leaves of deciduous shrubs thereafter, by consuming less preferred forage, in particular graminoids (Crête *et al.,* 1990a). Sub-optimal nutrition has affected body reserves of dams, with females exhausting their fat store during the first month of lactation (Crête & Huot, 1993). Lactation also appears to have been affected as RGCH calves have grown at a slower rate than calves of the adjacent Rivière aux Feuilles

Herd (RFH), or RGCH calves born and raised in captivity (Crête & Huot, 1993; Crête *et al.*, 1993).

The first sign of change in the demographic trend of RGCH showed up in 1984, when the autumn calf female ratio dropped from 52 calves per 100 cows, the average of the previous decade, to 38. This ratio remained around 40 for the next 2 years, but decreased thereafter (Couturier *et al.*, 1990). Annual survival rate of adult females was high at the beginning of telemetry studies in 1983, but also progressively declined until 1987 (Hearn *et al.*, 1990).

The objectives of this paper are to update the information on productivity and survival of the RGCH up to 1993, to evaluate the relative contribution of these factors to changes in the finite rate of increase (λ: Caughley, 1976: 51) during the last decade, to compare aerial censuses versus survival and productivity data, to estimate population trends, i.e. observed rate of increase (r̄) versus the survival-fecundity rate of increase (r_s) (Caughley, 1976: 53-54), and to speculate on the future of the herd.

Study area

Parturient females of the RGCH gather on the tundra plateaux bordering the Rivière George to calve, and spend the first month of lactation in this habitat (Fig. 1). Female density in the most productive tundra habitat, below 600 m asl, slightly exceeded 10 individuals·km^{-2} in June and July, 1988 (Crête & Huot, 1993). Males used to join females along the Rivière George until the beginning of the eighties, and stay with them until September. More recently, males have stayed further west in the forest-tundra during the snow-free period. For the rest of the year, the RGCH migrates south and west and utilizes most of the Québec-Labrador peninsula north of the 52° N latitude; total range of the RGCH expanded in the early eighties and now covers ≈700 000 km² (Messier *et al.*, 1988; Hearn *et al.*, 1990). Lichens prevail in the winter food of the RGCH (Gauthier *et al.*, 1989), being relatively abundant (1223 kg·ha^{-1} over the total range) and seemingly lightly used (<1%: Crête *et al.*, 1990b). During the growing season, leaves of deciduous shrubs and graminoids dominate caribou diet, while lichens become progressively more important during the autumn (Gauthier *et al.*, 1989).
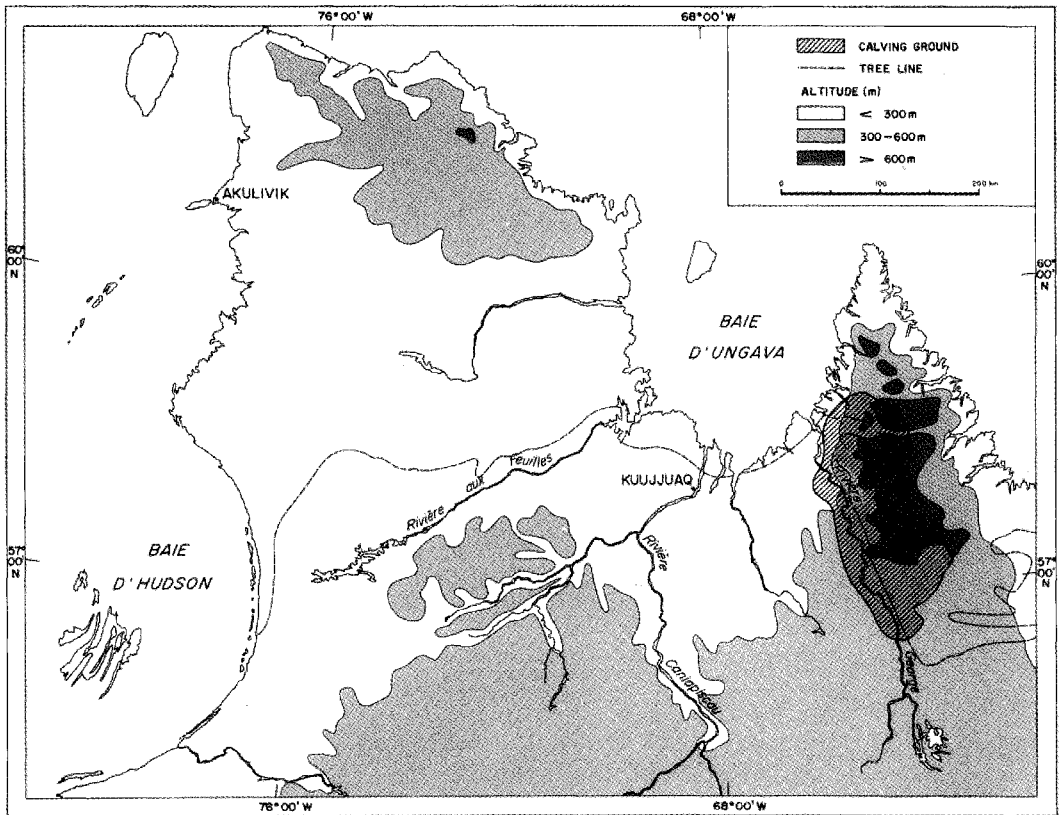

Fig. 1. General location of the calving and summer range of the Rivière George Caribou Herd with respect to the tree line and the altitude in the north of the Québec-Labrador peninsula.

The adjacent RFH is increasing in size, and was estimated at ≈260 000 individuals in 1991 (S. Couturier, unpubl. rep.). During calving and summer, the RGCH and the RFH are separated, but their ranges slightly overlap during the rest of the year (S. Couturier, unpubl. telemetry data). Wolves and, to a lesser extend, black bears (*Ursus americanus*) prey on the RGCH, but predation was a minor limiting factor in the eighties (Hearn *et al.*, 1990). Subsistence, sport and commercial hunting also affect the RGCH, and total kill has approached 30 000 animals in some years during the last decade (Crête *et al.*, 1990c).

Methods

Pregnancy rates were determined in March 1992 from a sample of 70 RGCH females collected near Kuujjuaq by Inuit hunters. Animals were aged as yearling, 2-year old or mature, based on tooth replacement and wearing. Comparisons were made with samples collected in 1976, 1980 and 1986-1987 (Bergerud, 1980; Parker, 1981; Couturier *et al.*, 1990).

Autumn composition counts for the RGCH have been carried out annually in late October and early November since 1973. Sampling techniques varied over time, particularly due to the inaccessibility of the range and to the large area used by caribou in some years. Calf:female ratios were generally estimated by ratio sampling (Cochran, 1977:150), observers counting animals per categories (calf, female, male) for a fixed amount of time per sampling point. Many thousands of caribou have been classified each autumn (see Messier *et al.*, 1988).

Animals from the RGCH have been monitored by telemetry since 1983, but radio-tagging was strongly biased in favour of adult females. At the beginning, only conventional VHF radios were used, but satellite telemetry has been used in conjunction with VHF radios since 1986. Between 30 and 115 female caribou were monitored annually by telemetry. Animals marked with VHF radio-collars were monitored irregularly from fixed-wing aircraft or helicopter. Radios were recovered when in mortality mode, often many months after death, and cause of death was determined whenever possible (Hearn *et al.*, 1990). Here we report only on the annual survival rate of females, estimated with the computer program Micromort (Heisey & Fuller, 1985). Seasonal and cause-specific mortality rates are not analyzed. We assumed that there were equal chances of detecting dead or living animals when transmitter batteries became exhausted, rather than computing also minimum survival rates, assuming that all censored observations resulted from animal death (Hearn *et al.*, 1990).

The size of the RGCH was derived using aerial census by estimating the number of females on the calving ground and by extrapolating to the total herd size with the autumn composition counts. The method used to determine the number of adult females on the calving ground changed over time: visual counts from a helicopter before 1984, black and white vertical air photographs in 1984 and 1988, and vertical colour slides taken from a helicopter in 1993. Visual counts in helicopter were biased in earlier censuses and later corrected (Crête *et al.*, 1989), and the sampling plans were progressively improved (Crête *et al.*, 1991; Couturier *et al.*, 1996).

The finite rate of increase (λ: Caughley, 1977: 51) of the RGCH was estimated in 2 ways: by calculating the survival-fecundity rate of increase (r_s: the rate of growth given current age-specific survival and fecundity (Caughley, 1977: 54)), and by calculating the observed rate of increase ($\bar{r}$) derived from aerial censuses. λ is the natural log (ln) of r or r_s (Eberhardt & Simmons, 1992). Fecundity was not estimated through pregnancy rates but rather with autumn calf:female ratios applied to all females (yearlings and older ones) because gestation rates were available for few years only, because they were based on relatively small sample sizes, and because summer survival rate of calves was not measured adequately. Calves were then assumed to be produced in autumn with balanced sex ratios, after perinatal and summer mortality occurred. In utero sex ratios are balanced in the RGCH (B. Hearn *et al.*,, unpubl.). All calf and adult mortality was assumed to occur in winter and it was estimated using annual survival rates of radio-tagged animals. Adult survival rates, available annually, were used also for calves and yearlings because of their similarity and better precision (Hearn *et al.*, 1990; unpubl.); similar survival for calves, yearlings and older females was reported for the Delta Herd in Alaska (Davis *et al.*, 1988).

λ derived from survival and productivity was computed in 2 ways, to take into account the possible influence of age structure. In both cases, the smoothed age structure computed by Messier *et al.*, (1988) for the RGCH served as the starting age distribution for a population of 1000 yearlings and adult females. We assumed a longevity of 16 years, survival rate being 0 for the last age class. Males were not included in the analysis because of a lack of information on their survival and because the dynamics of cervids rests mostly on females (Nelson & Peek, 1982). We first modelled continuous time from 1984 to 1993, by annually computing birth from the total number of females, then calculating the annual survival rate, and finally increasing each

age class by 1 year. In the second case, we used the deterministic computer model SIMCON (C.E. Walters, Univ. British Columbia, modified by F. Messier, Univ. Saskatchewan and R. Courtois, Min. Environnement et Faune du Québec), assuming no density-dependence. For each year, we ran the program with the corresponding figures on productivity and survival until a stable and stationary age structure was attained, which occurred before 40 generations. Annual λ was computed for both approaches by comparing actual female population (N_t) with N_{t+1}. Population estimates (in autumn, including calves) derived from aerial censuses in 1976 (215 000), 1984 (644 000), 1988 (682 000)(Crête et al., 1989) and 1993 (734 000) (Couturier et al., 1996; Russell et al., 1996) were used to calculate the observed rate of increase (r̄).

The relative contribution of productivity and survival to the decrease of λ from the period of rapid increase (calf:female ratio in autumn = 0.52; winter survival of calves and annual survival of older females = 0.95; λ = 1.18) was estimated with the simulation program SIMCON. Productivity was held constant at 0.52 calf:female (0.26 female calf), while current annual survival, estimated from telemetry between 1984 and 1993, was entered in the simulation. Each run lasted 40 years, to allow stabilization of the age structure. Relative contribution of decreased productivity and survival to annual change in λ was determined by comparison of estimates with constant and observed productivity.

Results

Pregnancy rates decreased for all age groups after 1980, but remained relatively stable between 1986-87 and 1992 (Table 1). In recent years, fecundity of yearlings and 2.5-year olds was very low while the pregnancy rate among older animals (76-79%) was far from being maximal (e.g. Ouellet, 1992). Decreased fecundity, and possibly lower summer survival rate of calves, affected the autumn calf:female ratios (Fig. 2). The latter was relatively stable and high between 1973 and 1983, and
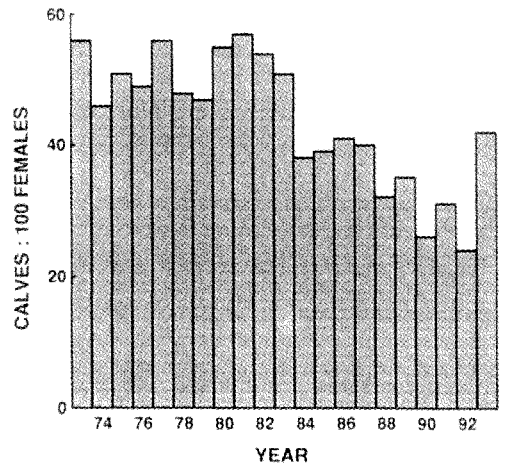

Fig. 2. Autumn (Oct-Nov) calf:female ratios for the Rivière George Caribou Herd, 1973-1993, as estimated with ratio sampling. In general, many thousands of animals were classified each autumn as calves, older females and older males.

diminished progressively afterward. The 1993 composition count showed a reversal in the trend, reaching a value unobserved since 1986-1987.

Annual survival rate of adult females exhibited an irregular but decreasing trend between 1984 and 1992 (Table 2). Data on annual survival of yearlings and calves were scantier than those on adults, and estimates were more variable due to a smaller number of animals being monitored. Annual survival rates of yearlings and winter survival rate of calves showed no tendency to be lower than adult rates.

The 2 approaches used to estimate λ ($\ln(r_s)$)) with productivity and survival rates (simulation with time in continue or until stabilization of the age structure) showed relatively close agreement (Table 3). Age structure had only a minor influence on demographic changes. According to the simulations, the RGCH population growth rate progressively declined to zero by 1987-1989. There was a slight decreasing trend thereafter, and the herd

Table 1. Age-specific pregnancy rate (N̲) for Rivière George caribou, 1976-1992.

| Period | Age (years) during the breeding season | | | Source | |
	1.5	2.5	≥3.5	Overall[a]	
1976	100 (1)	100 (6)	100 (15)	100	Bergerud (1980)
1980	43 (21)	90 (20)	95 (83)	89	Parker (1981)
1986-1987	0 (5)	67 (30)	76 (83)	67	Couturier et al. (1990)
1992	33 (6)	33 (6)	79 (58)	69	This study

[a] weighted according to the smoothed age distribution of Messier et al. (1988).

Table 2. Winter survival rate (November – May) of female calves and annual survival rate of yearling and older female caribou of the RGCH, as estimated from radio-collared animals between 1983 and 1993. Computations made with the computer program MICROMORT (Heisey & Fuller, 1985). Period 1983-1987, after Hearn *et al.* (1990).

Year[a]	≥ 2-year-olds		Yearlings	Calves
1983		---	0.95 (4 078)	---
1984	0.95	(15 190[b])	0.89 (5 773)	---
1985	0.92	(28 091)	---	---
1986	0.91	(28 622)	0.66 (2 508)	---
1987	0.84	(16 281)	---	1.00 (1 065)
1988	0.87	(13 388)	1.00 (1 825)	---
1989	0.93	(20 405)	0.84 (2 123)	---
1990	0.84	(23 779)	---	0.85 (1 317)
1991	0.81	(23 654)	0.83 (1 933)	---
1992	0.83	(25 033)	0.88 2 872)	0.79 (924)

[a] Beginning one June 1 i.e. 1983-1984 etc.
[b] Total radio-transmitter days.

Table 3. Finite annual rate of increase (λ) of RGCH females, as estimated with the annual survival rate of radio-collared animals and the autumn calf female ratio. In one case, λ was estimated with a simulation program until stabilization of the age structure; in the other, the 1984-1992 period was simulated with time in continue.

Year	Stabilization	In continue
1984	1.11	1.13
1985	1.08	1.10
1986	1.08	1.08
1987	0.99	0.96
1988	0.99	1.00
1989	1.07	1.03
1990	0.92	0.95
1991	0.92	0.89
1992	0.99	0.98

Table 4. Relative contribution (%) of productivity and survival in the decrease of λ for the females of the RGCH during the period 1984-1992, in comparison to 1983, when λ = 1.18.

Year	λ	Contribution (%)	
		Productivity	Survival
1984	1.11	100	0
1985	1.08	60	40
1986	1.08	50	50
1987	0.99	28	72
1988	0.99	50	50
1989	1.07	79	21
1990	0.92	48	52
1991	0.92	35	65
1992	0.99	22	78

diminished by 12-15% between 1988 and 1993 according to the simulations. Based on census estimates, λ averaged 1.15, 1.01 and 1.01 for the periods 1976-1984, 1984-1988 and 1988-1993, respectively; comparative figures for the last 2 periods were 1.06 and 0.97 when λ was estimated from survival and productivity data, i.e. r_s.

During the first 2 years λ decreased, productivity was most responsible for the diminishing demographic vigour (Table 4). After 1986, annual survival had a slightly greater influence on reducing λ than productivity.

Discussion
Probable demographic trend in 1993
One might question the validity of simulations using the same annual survival rate for yearlings and adults, and of estimating winter survival of calves with the same value. The comparisons that we could make for the 2 youngest age classes with adults, taking into account sample sizes (Table 2), indicated that survival rates were relatively similar. Moreover, as adults always dominated in the population, overestimation of calf and yearling survival would have resulted in only a slight positive bias in λ. Another positive bias in estimating λ could result from the way we used censored telemetry data, assuming equal chances of detecting living and dead animals at the end of transmitter life.

The 2 independent approaches used to estimate the demographic trend of the RGCH (λ) during the last decade show some disagreement: 1.06 vs 1.01 for the 1984-1988 period, and 0.97 vs 1.01 for 1988-1993 interval. However we cannot conclude that the disagreement between the 2 trend estimates is statistically significant because the confidence interval for the 1988 population estimate was ±36% (α=0.10)(Crête et al., 1991). Therefore it would be impossible to detect a 28% increase for the first period, or a 12-15% decrease for the second one, even if real. The precision of the combined 1993 population estimate improved (±13%; α=0.10: Couturier et al., 1996), so that detection of demographic trends with aerial censuses could be easier in the future. Nevertheless, the use of survival and fecundity rates (r_s) may possess some advantages over aerial censuses in detecting demographic trends. Survival/fecundity rates appear to exhibit less variability than population estimates, although deterministic simulations do not take into account the precision of such rates. In addition, λ could estimated annually with fecundity/survival rates between 1984 and 1992, but only 2 times during the same period from populations estimates. Moreover the 2 estimates of λ derived from aerial censuses were related because they both relied on the 1988 census,

which was imprecise. The disagree-ment between our 2 estimates of demographic trend would be significantly reduced if the 1988 census were an underestimate, a possibility considering the large confidence interval associated with this census.

It is likely that the RGCH decreased slightly between 1987 and 1993 because the trend in autumn calf/female ratios and adult survival rates between 1984 and 1992 was clearly declining (Fig. 2; Table 2). Recruitment improved in 1993, but adult survival would also have to increase for the demographic trend of RGCH to reverse. There must be 52 calves per 100 females in autumn in a caribou population for balancing mortality when annual survival of yearlings and adults reaches 0.80; the autumn ratio must be 39 when annual survival is 0.85. The high calf/female ratio observed in 1993 can be explained by the low 1992 recruitment, which resulted in a high proportion of barren females that were more likely to produce a calf in 1993 due to superior body reserves during the previous breeding season (Crête & Huot, 1993). Moreover the 1993 spring was particularly early, which may have contributed to diminishing perinatal mortality. The poor physical condition of lactating females (Huot, 1989; Crête & Huot, 1993; unpubl.) and the overgrazed summer range (Crête et al., 1990a; M. Manseau & C. Morneau, in prep.) suggest that the RGCH should continue to decline in the near future.

Relative contribution of decreased productivity and survival
Reproduction appears to be the first demographic parameter to have been affected when competition for forage on the summer range became significant at the beginning of the eighties. It continued to decrease afterward but survival also diminished simultaneously. In recent years, the importance of survival slightly exceeded that of reproduction in depressing λ. The first consequence of sub-optimal foraging condition in summer was then decreasing pregnancy and possibly increasing perinatal mortality. With time, deficient nutrition of females in late gestation and during peak lactation resulted in decreasing life expectancy. This could be the result either of cumulative impact of poor physical condition or of selection for a life strategy adapted to high competition for forage (Skogland, 1990).

The future of the RGCH
The biogeography of caribou does not differ much from that of other boreal cervids, highest densities being observed in the core of the species range, with peripheral populations at low density. This pattern suggests that there exists some adjustment between caribou numbers and range quality, and

that the concept of KCC should be applicable to caribou. Oksanen (1988) hypothesized that food chains would be limited to 2 trophic levels in unproductive landscapes like the tundra, and that herbivores would be regulated by forage, imposing much pressure on the vegetation. The diversity of mammals is low in northern Québec, and wolves have almost no alternate preys besides caribou (Crête & Manseau, 1996). The observation that migration is a good life strategy to escape predation (Bergerud & Page, 1987; Fryxell *et al.*, 1988; Heard & Williams, 1992) also suggests that the RGCH should be regulated by forage. Available data indicate that it is the case (Crête & Huot, 1993).

Seip (1992) suggested that population dynamics of RGCH, regulated at high density by forage, contrasted with that of other North American migratory herds, regulated at lower density by the combined impact of wolf predation and forage. However this suggestion is speculative as no regulation mechanisms have been described yet for migratory herds in the Northwest Territories, Yukon or Alaska. Relative stability in size of many herds may have complicated the detection of density-dependance.

Annual variation in summer climate affects forage quality and growth of boreal cervids (e.g. Saether, 1985; Crête, 1988), while snow condition in winter can result in malnutrition and death (e.g. Crête, 1976; Gates *et al.*, 1986). Climate may then influence caribou demography in drastic, but also in very subtle ways. Besides profound climatic changes that occur at a geological scale and that are caused by astronomical, tectonic, cryogenic and oceanic effects (Harrington, 1987), the climate exhibited subtle changes since the last glaciation. The period of warmest temperature (Climatic optimum) happened between 6 000 and 2 500 years B.C. (Lamb, 1977:378) and it was followed by a cooling, culminating with the Little Ice Age, between 1500 and 1650 A.D.(Lamb, 1977:461). For instance, this cooling modified the composition of the mixed forests of the Great Lakes-St. Lawrence region (Campbell & McAndrews, 1993). Afterward, the climate improved, with the first half of the XXth century being particularly warm (Lamb, 1977:478).

Among the factors proposed to explain caribou rarity in the Québec-Labrador peninsula during the first half of the XXth century (predation, hunting, destruction of winter range by fire or by overgrazing of lichens, climate), a high incidence of wet and snowy winters during consecutive decades (Crête & Payette, 1990) appear the most plausible explanation. Archaeological observations suggest that period of warm and wet climate also coincided with rarity of reindeer in Europe (Luoto, 1993).

Conceptually, the first half of the century in the Québec-Labrador peninsula could be viewed as a period with decreased KCC, or a period with prolonged negative demographic balance, when a limiting factor became very important. In the absence of significant grazing, vegetation, in particular lichens, became luxuriant. When the climate became more favourable in the fifties, the RGCH erupted.

The RGCH increased during 3 or 4 decades, peaking by the end of the eighties, and most probably slightly declining since 1987. Two future outcomes which are extreme ends of a continuum, are possible: a rapid descent to low numbers (< 100 000 individuals) or oscillation around KCC (roughly within the bracket 400 000-800 000). In the first case, the demographic model would be that of a cyclic population; in the second, Caughley's (1976) herbivore/vegetation model with dampened oscillations. Assuming constant climate, the RGCH will exhibit cycles if wolves show a numerical response with time lag to caribou. This is possible as the RGCH now spends most of its time in the forest-tundra and the forest, where it could be more vulnerable to predation. Wolves would precipitate a caribou decline, in the same manner as lynx (*Lynx lynx*) does for cyclic snowshoe hare (*Lepus americanus*) populations (Keith *et al.*, 1984). It is much less likely that lichens provoke cycles because they have been overgrazed on the summer range, where animals can compensate by other food sources (Crête & Huot, 1993). The scenario could be different if lichen availability decreased substantially on the winter range, due to intense competition with the increasing RFH. Otherwise, the RGCH will exhibit dampened oscillations, with the amplitude of oscillations dependant on the time of reaction of the vegetation on the summer range to decreasing grazing pressure. First indications suggest the latter is slow on the tundra (M. Manseau & M. Crête, unpubl.), and that adjustment to KCC will not be rapid.

Managers can actually have very limited influences on the RGCH as it has been naturally regulated by forage on the summer range. However their task will be to forecast the future of the herd in order to advise the users in the best possible way. The elements most susceptible to influence drastically the demographic trend of the RGCH in the near future are: recovery rate of the vegetation on the summer range, predation rate by wolves and ease of access to forage in winter. Permanent plots should be established in the most critical summer habitat types, and monitored every 5 years to measure changes in the vegetation. Similarly, cause-specific mortality rates of radio-collared caribou should continue to

be investigated, in order to detect any increase in wolf predation. Finally winter feeding ecology should deserve some research.

Acknowledgements

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