

## Changes in the Population Dynamics of the George River Caribou Herd, 1976-87

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**ABSTRACT.** A recent decrease in the George River caribou herd recruitment was caused both by an increasing calf winter mortality since 1977 and an increase in their summer mortality since 1984. A reduction in pregnancy rate could also be partly responsible for a decline in gross recruitment. Evaluation of net recruitment shows that the rate of increase of the herd has been negative since 1984. The probable causes of the decline involve the negative effects and interrelation of various factors: decline of the physical condition of females, habitat deterioration on the current calving grounds (former summer range), increase in energy expenditures related to more extensive movements, delayed birth dates, increase in density within their range and especially on calving grounds, increase in wolf populations and exceptionally high snow accumulation during the 1980-81 winter.

**Key words:** caribou, recruitment, physical condition, forage depletion, George River herd, northern Quebec, population dynamics

**RÉSUMÉ.** Une analyse des diverses facettes de la productivité du troupeau de caribous de la rivière George a permis d'illustrer une diminution du recrutement brut depuis 1977. Cette baisse serait causée par une augmentation de la mortalité des faons en hiver depuis 1977 et par une augmentation, depuis 1984, de leur mortalité estivale. Une baisse soupçonnée du taux de gestation semble également en partie responsable de la diminution du recrutement brut. L'estimation du recrutement net suggère que le taux d'accroissement du troupeau est négatif depuis 1984. Cette baisse du recrutement est probablement causée par les effets négatifs et les inter-relations de divers facteurs: condition physique diminuée des femelles, détérioration de l'habitat sur l'actuel terrain de mise bas (ancien habitat d'été), accroissement des dépenses énergétiques liées aux mouvements plus importants, retard de la date des naissances, augmentation de la densité dans l'ensemble de l'aire de répartition et surtout sur le terrain de mise bas, augmentation de la population de loups, accumulations de neige exceptionnellement élevées de l'hiver 1980-1981.

**Mots clés:** caribou, troupeau de la rivière George, Québec, dynamique de population

### INTRODUCTION

Caribou (*Rangifer tarandus*) herds regularly show population fluctuations more dramatic than those for other ungulates. This tendency has been observed for several herds: Kaminuriak (Gates, 1985; Heard and Calef, 1986), Nelchina (Hemming, 1975; Doerr, 1979), Beverly (Miller, 1983), Western Arctic (Haber and Walters, 1980), St. Matthew's Island (Klein, 1968), Bluenose (Carruthers and Jakimchuk, 1983) and Delta (Davis *et al.*, 1983). However, most of these examples have been documented through only one phase of increase and decline. On the other hand, Meldgaard (1986) described regular fluctuations in caribou numbers in Greenland for the last 250 years.

In North America, some documented cases suggest that two consecutive population peaks can be separated by up to about a hundred years (Hemming, 1975; Haber and Walters, 1980; White *et al.*, 1981). Meldgaard (1986) stated that the length of the caribou population cycles varies from 65 to 115 years for the Greenland caribou population. Numerous intrinsic factors (intraspecific competition, habitat, predation, etc.) or external factors (hunting, weather, etc.) can influence the size and demographic evolution of a herd. The differences between population maxima and minima may be large. A well-documented case is the 1970-80 reduction of the total West Greenland caribou population from a high of 100 000 to a low of 8000 animals (Meldgaard, 1986).

The two leading hypotheses proposed to explain the regulation of caribou populations relate to habitat (Haber and Walters, 1980) and predation (Bergerud, 1980). Haber and Walters (1980) affirm that the George River caribou herd,

with its high density, rapid growth and excellent physical condition, offers the best opportunity to understand the population dynamics of a large herd in the presence of a low wolf population. Messier *et al.* (1988) presented as probable regulatory factors for the George River herd the greater competition for food resources and the greater energy expenditure associated with range expansion.

After a period of abundance at the end of the last century, caribou populations of northern Quebec rapidly declined, causing famine among the native peoples. The fragmentary information available suggests that depleted caribou numbers persisted until the beginning of the 1960s (Elton, 1942; Harper, 1961; Moisan, 1964; Audet, 1979). The George River caribou herd has recently increased in size to become one of the largest in North America. Thus, we think it is important to document the population dynamics of this herd, which is presently changing to a new phase of its cycle. The purpose of this paper is to interpret changes in the population dynamics, particularly changes in recruitment, on the basis of information about physical condition, the importance of wolf populations and the level of habitat utilization, in particular that of the current calving grounds.

### STUDY AREA

The George River caribou herd presently occupies most of the Quebec-Labrador peninsula included between latitudes 53° and 59°N (Fig. 1). Encompassing approximately 675 000 km<sup>2</sup> in 1987 (Vandal *et al.*, 1989), the annual range of the herd extends into three large vegetation biomes (modified according to Payette, 1983). The taiga covers the southern part of the

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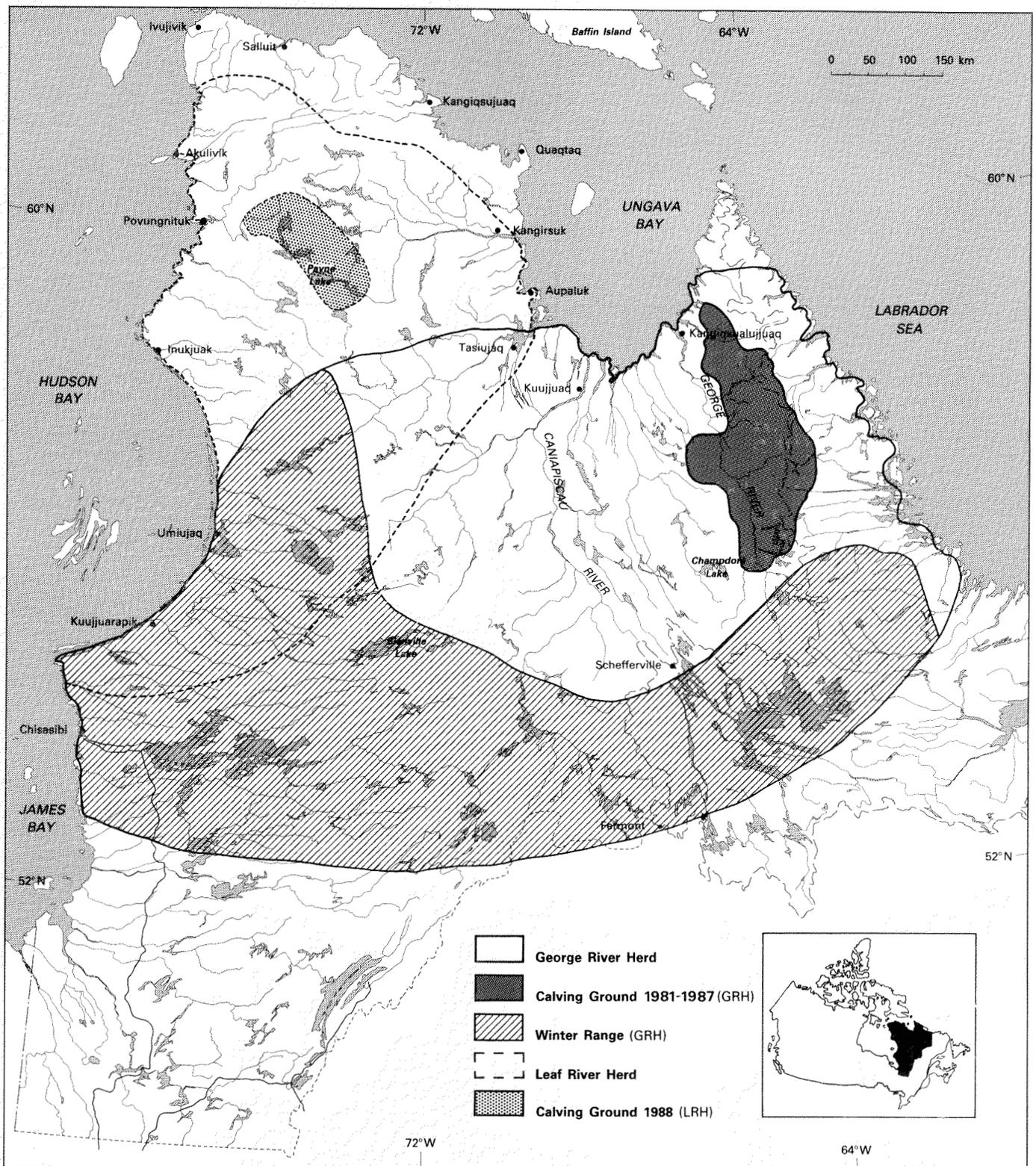


FIG. 1. Distribution and seasonal range of large northern caribou herds in Quebec and Labrador.

range and is characterized by black spruce (*Picea mariana*), Jack pine (*Pinus divaricata*), larch (*Larix laricina*) and terrestrial lichens. Farther north, the forest tundra supports the highest densities of caribou and is distinguished from arctic tundra by the sparse presence of black spruce and, less commonly, of larch. The substantial lichen carpets and stands of ericaceous

plants are potential forage for caribou. Arctic tundra is characterized by the absence of trees and the presence of heath covered with sparse thickets of stunted ericaceous plants on a lichen carpet. The tree line marks the change from forest to arctic tundra and generally stretches from east to west along 58°N. However, due to the altitude (800-1650 m) of the land

east of George River, the tree line turns abruptly to the south so that the area used for calving is tundra.

At this time, it is difficult to describe precisely the seasonal ranges used by the George River caribou herd because of the exceptional dynamism of the migrations observed in the last few years (Vandal *et al.*, 1989). Nevertheless, it is possible to point out some trends in the use of the territory (Fig. 1). For decades, females grouped together on common calving grounds located on upland areas east of the George River. At the beginning of 1980, the summer range was on the same highlands. Caribou remained there until August or September, but now they leave these highlands earlier in July, to migrate westward. Limits of the summer range cannot be delineated with certainty anymore. During the winter, caribou enter the taiga region earlier and penetrate it more extensively. Now during winter, most of the herd occupies the snow-covered black spruce forests from Schefferville and Fermont to the James Bay area. Some caribou aggregations also winter in the southeastern part of the annual range (Fig. 1).

About half of the precipitation in the area falls as snow. The taiga receives about 300 cm of snow (Schefferville, 1951-80 average, 340 cm), while the forest and arctic tundra receive about 200 cm of snow (Kuujuaq, 1951-80 average, 224 cm). The villages of Kuujuaq and Schefferville register average temperatures (1951-80) of  $-23.4$  and  $-22.7^{\circ}\text{C}$  in January. July temperatures average  $11.3$  and  $12.6^{\circ}\text{C}$  in Kuujuaq and Schefferville respectively (unpubl. data). Snow depths average 70 cm in March, 36 cm in April and 5 cm in May in Kuujuaq. In Schefferville, snow depths reached 88, 56 and 5 cm respectively for the same months between 1951 and 1980. The length of the growing season (daily mean temperature  $\geq 5.6^{\circ}\text{C}$ , 1931-60) is about 100 days in Kuujuaq, 110 days in Schefferville and 80 days on the highlands east of the George River (Wilson, 1971).

## METHODS

### *Size and Structure of the Herd*

Results of visual aerial censuses extrapolated to take into account areas not covered were used to estimate the winter populations between 1954 and 1973 (Banfield and Tener, 1958; Desmeules and Brassard, 1963; Bergerud, 1967; Pichette and Beauchemin, 1973; Wetmore, 1973). In June 1976, 1980 and 1982, population size was extrapolated from visual aerial censuses of females present on the calving grounds (Juniper, 1980a, 1982; Goudreault, 1982). Vertical aerial photography was used to estimate the number of females on the calving grounds in June 1984 and 1986 (Goudreault *et al.*, 1985; Crête *et al.*, 1987). The stratified ratio estimate (Cochran, 1977) was used in 1984 and 1986 to calculate the number of caribou in the calving area. After 1980, confidence intervals for the estimates of females on the calving grounds were calculated, but they do not include the variability observed in the fall population composition used to calculate the proportion of females in the herd. This proportion during fall is required to extrapolate the results of the June census to obtain the total size of the herd. Further details about the methods used in aerial censuses and in the later calculations are presented by Goudreault (1985).

The size of the annual range of the herd was estimated from data obtained from radio-collared caribou. This evaluation provides a rough estimate because it includes areas (lakes, mountains, etc.) of little value in terms of caribou foraging. The size of the annual range was used with the fall herd sizes (as extrapolated from the June census) in 1976, 1980, 1984 and 1986 to calculate the density of the herd.

From 1979 to 1987, the Quebec and Newfoundland governments conducted ground counts each autumn between 19 October and 5 November to determine population composition. From 1973 to 1978, the observation period was more variable, between 1 and 31 October. Ground-based composition surveys were also conducted between early April and early May from 1977 to 1987 inclusively. No spring counts were conducted in 1985 and 1986. On 8 and 9 April 1987 in the Kuujuaq region, we surveyed the composition in four sampling areas to estimate mean and standard deviations (s.d.) of the proportion of calves in the population (Cochran, 1977). The adult sex ratio of the following autumn was used to correct the April composition sample (data compiled by Messier and Huot, 1985; unpubl. data, Vandal *et al.*, in prep.) for the absence of adult males, which are segregated from the rest of the herd during most of the year.

### *Pregnancy and Birth Rates*

In March 1986 ( $n=20$ ) and in April 1987 ( $n=98$ ), caribou killed mainly by native and sport hunters were autopsied during a study of the physical condition of George River caribou (Couturier *et al.*, 1988, 1989). Pregnancy status (absence or presence of foetus) were determined for females 21 months and older. The term pregnancy rate refers to the percentage of pregnant females.

The calf-cow ratio was monitored from ground and aerial population composition surveys conducted between 4 and 24 June 1987 to describe the phenology of birth and determine completion of calving. Once calving was completed about 18-19 June, the birth rate (number of newborn calves per 100 females) was estimated in 14 sampling sites randomly selected from telemetry locations of 63 radio-collared female caribou monitored between 11 and 18 June 1987 from a specially equipped DC-3 airplane. Most caribou observed within a 20-minute sampling period were counted in the vicinity of each site during slow-speed helicopter flights. Caribou were classified into five categories: calves, yearlings male and female, adults male and female. The calf-cow ratio was not corrected for early neonatal mortality with the distended udders classification method (Bergerud, 1964), thus underestimating birth rate results.

Independently of these composition surveys, the calving grounds were delimited between 13 to 18 June 1987 by visual surveys flown at low altitude (125-200 m) in a DC-3 (Vandal and Couturier, 1988). Equidistant flight lines were 13 km apart. Relative densities within the 1987 calving range were determined during these flights. Since 1974, the distance between the transect lines (8-25 km) and the type of aircraft used changed slightly (Vandal and Couturier, 1988), but the relative abundance of adult females and cow-calf pairs during the peak of calving always determined the size and location of the annual calving grounds (Gunn and Miller, 1986).

Statistical analyses were conducted with the SPSS/PC+™ package (Norusis, 1986) and the StatView™ package (Feldman and Gagnon, 1985). All probabilities reported refer to one-tailed tests. Confidence intervals (C.I.) at a level of  $p=0.05$  were used throughout the text in the form "mean  $\pm$  C.I." From some other studies, standard deviation (s.d.) or standard error (s.e.) was presented when available.

## RESULTS AND DISCUSSION

### Population Size

Banfield and Tener (1958) undertook the first systematic census of caribou in northern Quebec and probably underestimated the population size, with a result of 4700 caribou in 1954-56. Bergerud (1967) estimated the size of the George River herd at 15 000 caribou in 1958. Subsequently, a few censuses confirmed the continued increase of the herd. Methods were modified, and in spring 1976 herd size was estimated at 176 600 caribou (Juniper, 1982). In June 1980, the pre-calving population was evaluated at  $294\,510 \pm 26\%$  ( $p=0.05$ ) (Juniper, 1980a). Before calving in June 1982, herd size was estimated at  $271\,060 \pm 26\%$  ( $p=0.05$ ) (Goudreault, 1982). In 1984, census techniques were again improved. Vertical aerial photography facilitated the count of females on the calving grounds. Goudreault *et al.* (1985) estimated the George River herd size before calving at  $472\,200 \pm 11.3\%$  ( $p=0.05$ ) caribou in 1984. Crête *et al.* (1987) used vertical aerial photography to estimate the herd at  $254\,750 \pm 29.7\%$  ( $p=0.05$ ) caribou in June 1986 before calving. However, technical problems (incorrect exposure of photographs) and logistic problems (late spring and bad weather conditions) probably adversely affected the results of the June census. Crête *et al.* (1987) concluded that they had underestimated the population because they had no indication of a decline after 1984, especially a decrease of 230 000 caribou in two years.

Messier and Huot (1985) and Québec (1984) indicated that the annual rate of increase was positive and varied between 8 and 14% during the 1960-84 period. This rate is lower than the reproductive potential of caribou ( $r_m=0.29-0.30$ , or about 35% according to Bergerud, 1980, and Bergerud *et al.*, 1983), but it appears high in comparison with other large caribou herds coexisting with wolves (Bergerud, 1980). It has led to the George River herd becoming one of the largest caribou herds in the world (Williams and Heard, 1986).

### Pregnancy and Birth Rates

Pregnancy rates appear to have declined slightly since 1980 (Table 1). However, Messier and Huot (1985) questioned the high pregnancy rates observed in April 1980 by Parker (1981). Parker collected caribou near the calving grounds, which likely biased the calculated pregnancy rates upward. However, the small sample ( $n=22$ ) obtained by Bergerud (1980) in 1976 also suggests high pregnancy rates at that time. The current pregnancy rate is comparable with data published for some other large herds in North America (Table 1).

We weighted the pregnancy rates (Table 1) by the relative abundance of each age class of the population by using the corrected frequencies from the female life table presented by Messier *et al.* (1988). The pregnancy rate value of 67.2% obtained from the pooled data of 1986 and 1987 assumes that the herd's age structure did not vary between September 1984

TABLE 1. Pregnancy rates (%) of the George River caribou herd and comparison with other large herds

Year (source)	Age at the rutting period (years)		
	1.5	2.5	$\geq 3.5$
George River Herd			
1976 (Bergerud, 1980)	100 (1) <sup>1</sup>	100 (6)	100 (15)
1980 (Parker, 1981)	43 (21)	90 (20)	95 (83)
1986-87 (this study)	0 (5)	67 (30)	76 (83)
Kaminuriak Herd			
1966-68 (Dauphiné, 1976)	2 (57)	48 (69)	90 (280)
1981-83 (Gates, 1985)	89 (9)	100 (13)	100 (127)
Beverly Herd (Bergerud, 1980)	33 (3)	50 (16)	78 (69)
Nelchina Herd (Bergerud, 1980)	13 (31)	61 (46)	89 (335)
Western Arctic Herd (Bergerud, 1980)	—	—	78 (130)

<sup>1</sup> Sample size in parentheses.

and 1986-87. For 1987 only, the autopsy results gave a weighted pregnancy rate of 70.3%.

Since 1972, calving composition surveys have shown that the maximum number of calves born per 100 females ( $\geq 2$  years) varied from 73 to 92 (unpubl. data in Quebec Government files). These results and Gagnon and Barrette's (1986) results demonstrate spatial and temporal variability in the ratio of calves per 100 females at birth. For example, calving was prolonged and not completed before 17-19 June in 1987. Thus, any composition survey conducted before this date would provide only an incomplete and biased estimate of reproductive success. Counts to determine calving ground population composition must also consider the variation caused by whether the sample is at the center, on the border or completely outside the calving grounds. The ratio of calves per 100 females ( $\geq 2$  years) ranges from 93.9 to 44.1 (Table 2), according to location in high or low densities of the calving grounds in 1987 (Vandal and Couturier, 1988). Davis *et al.* (1980) observed the same phenomenon in the Western Arctic herd in Alaska.

The 20-minute sampling period was too brief to adequately determine birth rate outside the calving grounds because adult females were too dispersed. In spite of this problem, we believe that our sampling technique provides an acceptable representation of the birth rate of the George River herd. Our result was  $66.1 \pm 5.0$  calves per 100 females ( $\geq 1$  year) for 1987. This is similar to values presented for the Western Arctic herd, whose average ratio in June from 1960 to 1979 was 74.4 (s.d.=5.9; Davis *et al.*, 1980). The birth rate for that herd remained relatively constant during those years. Parker (1972) estimated the birth rate of the Kaminuriak herd at 69 calves per 100 females ( $\geq 1$  year) in June 1967 and 1968. Skoog (1968), for the Nelchina herd, evaluated this ratio at 60 for the period 1955-62.

Our ratio of  $79.6 \pm 4.0$  calves per 100 females ( $\geq 2$  years) from June 1987 is slightly higher than the weighted pregnancy rate calculated for April 1987 (70.3%). We did not adequately account for the females outside of the calving grounds, which are usually less than about 20% of all females and are probably non-breeders. Pregnancy rate determined at the end of winter and birth rate measured at the end of June should be similar because abortions during the last third of gestation are rare (Bergerud, 1980).

TABLE 2. Population structure determined from 22 to 24 June 1987 and evaluation of birth rate

Location <sup>1</sup>	Females (F) (≥2 years)	1 year <sup>3</sup>		Calves (C)	Males (M) (≥2 years)	Ratio	Ratio	Ratio
		Males	Females			1 year:100F <sup>4</sup> (≥2 years)	C:100F (≥1 year)	C:100F (≥2 years)
A(n=8) <sup>2</sup>	962	27	114	903	0	15	83.9±11.4	93.9± 1.2
B(n=4)	390	79	152	172	18	59	31.7±10.7	44.1± 12.5
C(n=2)	4	61	10	4	227	1775	28.5±22.6	100.0
Total	1356	167	276	1079	245	33	66.1± 5.0	79.6± 4.0

<sup>1</sup> A: Calving grounds, high densities.  
<sup>2</sup> B: Calving grounds, low densities.  
<sup>3</sup> C: Outside calving grounds.  
<sup>2</sup> Number of sampling sites.  
<sup>3</sup> Based on sub-sampling to establish the sex ratio of 1-year-olds.  
<sup>4</sup> Serves uniquely to illustrate the incoherence of this ratio when estimated in June.

**Gross Recruitment**

The number of young in the population represents recruitment. The managers of North American caribou herds generally evaluate recruitment from an annual fall and spring count of the proportion of calves or short-yearlings. Throughout this paper, gross recruitment is defined as the proportion of short-yearlings in the spring population.

Fall recruitment has been decreasing since 1984. From 1973 to 1983, the ratio of calves per 100 females in the fall averaged 51.8 and varied between 46 and 57 (data compiled by Messier and Huot, 1985). The ratio decreased to values of 38 in 1984, 39 in 1985 and 41 in 1986 (Fig. 2). In the fall of 1987, the ratio remained at the same level: 39.7 ± 0.9 (n=10 sampling locations; Vandal *et al.*, in prep.). A regression analysis of years 1976-86 for the fall ratio also revealed a decreasing trend (r=-0.654, p=0.011, n=12; Fig. 2).

The values for fall recruitment observed between 1973 and 1983 were high compared to other North American herds. Bergerud (1980) presented values varying between 33 and 39 for the Nelchina, Forty-Mile and Porcupine herds. The Kaminuriak herd, after showing a fall ratio of 26 in 1967 and 1968 (Parker, 1972), underwent a spectacular increase in numbers and recruitment reached about 70 in the fall of 1979 and 1981 (Heard and Calef, 1986). The fall ratio of the Western Arctic herd varied from 41.7 to 48.0 between 1970 and 1978 during a decline in herd size caused mainly by over-harvesting through hunting and predation (Davis *et al.*, 1980). With

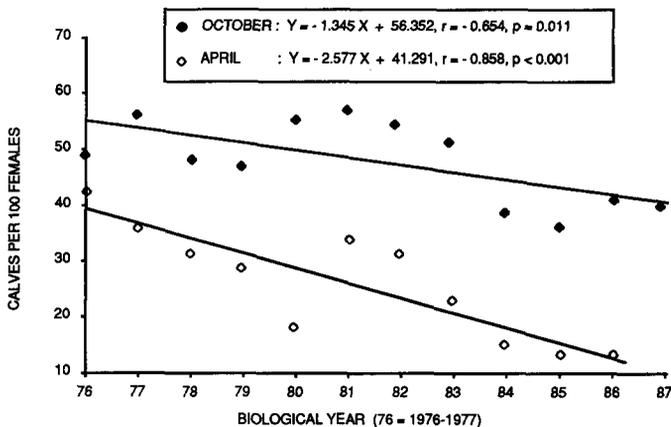


FIG. 2. Ratio of calves per 100 females (≥1 year) in the fall and spring for the George River caribou herd since 1976. The April values for 1985 and 1986 were obtained by regression (see text). The independent variable X is the number of biological years from 1975: 1976=1, 1977=2, etc.

a present ratio close to 40, the George River herd has a fall recruitment close to the average of other herds.

Comparison of gross recruitment is difficult because different procedures and periods (8 April to 15 June) have been used to sample the spring composition since 1974. The late date of some composition counts is the major problem that invalidates comparisons between years. The mother-calf bond is usually broken between April and June. In April, short-yearlings remain with their mother and thus they benefit from maternal experience and social status and reduce their energy expenditure in using the same feeding craters (Vandal and Barrette, 1985, 1987). After mid-May, winter has ended and short-yearlings no longer need to accompany their mother to survive. Accordingly, the short-yearlings linger behind the large female aggregations that are moving toward the calving grounds. In addition, short-yearling males leave their mother earlier than short-yearling females (Bergerud, 1980). Our observations during June 1987 confirm this fact (Table 2).

This aspect of caribou behaviour profoundly influences classification counts conducted after the beginning of May. Near the calving grounds, aggregations are composed mainly of short-yearlings and adult males that sometimes stay away from groups of adult females (Vandal and Couturier, 1988). In June 1987, the ratio of short-yearlings per 100 females (≥2 years) varied from 15 to 59 according to location in high or low densities on the calving grounds (Table 2). This heterogeneous distribution of short-yearlings contributes to the variations observed during some earlier composition surveys. For example, between 26 April and 5 May 1979, the ratio of short-yearlings per 100 females (≥2 years) was 31 (S. Luttich, cited in Calef, 1982). On 7 June 1979, the ratio was 53 (Jean, 1980). In 1974, this ratio was 30 on 31 May (Folinsbee *et al.*, 1975, cited in Messier and Huot, 1985) and increased to 48 between 1 and 3 June (Juniper, 1974). In addition, the classification determined by Ferguson *et al.* (1985) from 11 to 14 May 1982 reveals a seemingly impossible ratio of 189.

Spring classifications have long been a major element of the scientific monitoring of most large North American caribou herds. We disagree with Messier *et al.* (1988) about the validity of spring classifications. Messier *et al.* (1988) recognized that short-yearlings may segregate on the calving grounds in June but did not apparently consider the validity of using samples obtained in April, before segregation occurs.

We believe that the proportion of short-yearlings in the population in April is an adequate estimate of the herd's gross recruitment. To ensure valid comparison and avoid the

TABLE 3. Spring population structures of the George River caribou herd from 1977 to 1987

Date	Number of caribou			N	S-Y <sup>1</sup> :100F ratio	%S-Y (per sample)
	Males	Females	Calves			
1977, 18-26 April <sup>2</sup>	?	4216	1772	5988	42	
1978, 29 April-5 May <sup>2</sup>	?	3664	1320	4984	36	
1979, 29 April-5 May <sup>2</sup>	?	789	243	1032	31	
1980, 18-20 April <sup>2</sup>	?	14 696	4303	18 999	29	
1981, 17-18 April <sup>2</sup>	?	4355	773	5128	18	
1982, 15-27 April <sup>3</sup>	1247	4493	1481	7221	33	20.5
1983, 14-18 April <sup>3</sup>	391	4691	1466	6548	31	22.4
1984, 26-29 April <sup>3</sup>	217	4718	1089	6024	23	18.1
1987, 8-9 April <sup>4</sup>	143	1632	213	1988	13	10.7

<sup>1</sup>S-Y: short-yearlings.

<sup>2</sup>S. Luttich, pers. comm., cited in Calef, 1982.

<sup>3</sup>Ferguson *et al.*, 1985.

<sup>4</sup>This study.

problems previously discussed, we have retained in our analysis population composition sampled as early as possible in the spring, and no later than 5 May (Table 3). No spring count was obtained for 1985 and 1986, and consequently we estimated values for those two years by applying the winter mortality rates of calves from the regression by year (1977-87) to the ratio of the preceding fall. Recruitment obtained from the proportion of short-yearlings in the April population are slightly overestimated because of the mortality occurring among short-yearlings during May and June. In addition, the proportion of caribou surviving 12 months does not strictly represent the real recruitment of the population. Juvenile mortality rate must attain that of adults, that is, toward the age of 18 months (Bergerud, 1980). In practice, the difficulty of identifying 15- to 18-month-old caribou in the fall impedes estimation of their proportion in the population (Parker, 1972; Martell and Russell, 1983).

The gross recruitment, as described by the ratio of short-yearlings per 100 females ( $\geq 1$  year) in April, has progressively declined since 1977 ( $r = -0.858$ ,  $p < 0.001$ ,  $n = 11$ ; Fig. 2). Calef (1982) has already described the decrease in gross recruitment for the period 1977-81, but his analysis has paradoxically remained relatively unknown. Results of the more recent spring classification conducted in April 1987 suggest the lowest gross recruitment in recent years. A ratio of 13 short-yearlings per 100 females was observed, and short-yearlings represented a corrected proportion of  $8.2 \pm 1.0\%$  of the population. The earliest data on gross recruitment for the George River caribou herd were presented by Banfield and Tener (1958). They reported a spring ratio of 34 and 47 short-yearlings per 100 females from small samples in 1954 and 1956 respectively. Bergerud (1967) also described recruitment in March for the period 1957-63, with the percentage of short-yearlings being 11.2% on average.

#### Adult Mortality

Sport hunting of George River caribou has been permitted since 1964 in northern Quebec, and from 1975 (1300) to 1982 (2800) the harvest increased 25% annually. On the assumption that the herd was under-harvested, the quota for sport hunting was set at 2 caribou per hunter in 1983, without respect to sex or age of the animal (Québec, 1987). An annual increase of the sport hunting harvest of 40% was observed between 1984 (4200) and 1986 (8200). It then stabilized in 1987 at 8300 animals. Quebec native peoples (Inuit, Crees, Naska-

pis and Montagnais), who are not restricted by hunting season or quota, apparently increased their harvest of the George River caribou from 1974 (3800) to 1986 (7100) (Québec, 1984, 1987; unpubl. data). It should be noted that Naskapis and Montagnais harvests are rough estimates based only on the knowledge of hunting habits and number of hunters in each community. Similarly, the harvest by Labrador residents has increased from 1974 (1200) to 1986 (5900). Among caribou collected in 1986, approximately 1000 were harvested during the spring commercial hunt. This commercial undertaking has been allowed since 1985 (J. Rowell, pers. comm., 1987).

Adult mortality from sport and subsistence hunting has then been increasing since the mid-1970s. The total harvest of George River caribou, once corrected by an arbitrary factor of 20% to account for wounded and lost animals (e.g., Miller, 1983; Davis *et al.*, 1980), was 7500, 12 500, 15 500 and 25 400 in 1977, 1981, 1983 and 1986 respectively. Harvest rates through hunting from 1977 to 1986 varied from 2.7 to 4.3% for adult caribou. Since 1984, this harvest rate is calculated with the fall herd size extrapolated from the June 1984 census.

The level of exploitation by man can be adequately described, but natural mortality is the most difficult parameter to evaluate in herd dynamics (Thomas, 1969; Bergerud, 1980). Life table analysis is one means to determine adult survival rates. However, Bergerud (1980) states that these tables are not useful for caribou because of annual variations in calf survival that destabilize the age distribution of the population. In addition, the basic assumption that the annual rate of increase during the corresponding period of the life table is constant (i.e., 10-15 years) is rarely respected.

Similarly to Heard and Calef (1986), we used Bergerud's (1980) regression equation ( $Y = 13.8 - 0.386X$ ,  $r = -0.873$ ,  $n = 8$ ) to estimate adult natural mortality. This equation permits the evaluation of adult mortality rate (Y) from the proportion of short-yearlings in the herd at the beginning of spring (X). According to the author, this relationship is based mainly on the negative effects of predation on the two groups. However, this does not exclude factors other than predation (food, weather and winter conditions, etc.) from influencing both adult and calf survival rate. From 1976 to 1986, natural mortality rates varied from 5.3 to 10.8%.

Using radio-collared caribou from the George River herd, Crête *et al.* (1987) estimated total female mortality at 5.1% between June and October 1986. With this figure, we extrapo-

TABLE 4. Net recruitment and size of the George River caribou herd from 1976-77 to 1986-87

Biological year <sup>1</sup>	Number of caribou		(% short-yearlings in the population <sup>2</sup> (April)	Adult mortality (%)		Net recruitment (%)
	June	October (with calves)		Hunting	Natural	
1976-77	176 600	263 100	22.0	3.0	5.3	13.7
1977-78	—	—	16.1	2.8	7.6	5.7
1978-79	—	—	15.7	3.0	7.7	5.0
1979-80	—	—	14.7	3.1	8.1	3.5
1980-81	294 510	390 100	9.7	2.7	10.1	-3.1
1981-82	—	—	16.8	3.1	7.3	6.4
1982-83	271 060	360 450	14.7	3.5	8.1	3.1
1983-84	—	—	12.9	3.2	8.8	0.9
1984-85	472 200	586 600	8.8 <sup>3</sup>	2.7	9.1	-3.0
1985-86	—	—	7.6 <sup>3</sup>	3.4 <sup>4</sup>	9.2	-5.0
1986-87	—	—	8.2±1.0	4.3 <sup>4</sup>	10.8	-6.9

<sup>1</sup> For example, Biological year 1976-77 refers to the 1976 cohort (born in June 1976).

<sup>2</sup> Corrected for the absence of males in the sample, according to the adult sex ratio of the following autumn (ex: 1978-79, 31 / (100 + 31 + 67) = 15.7%).

<sup>3</sup> Estimated from regression; see text for the method of computation.

<sup>4</sup> Harvest rate is calculated from the herd size estimated in October 1984.

lated the natural mortality of both sexes at 10-11%. Our estimate of 10.8% in 1986-87 is thus comparable to the natural mortality rate evaluated by radio-telemetry.

#### Net Recruitment or Rate of Increase

Net recruitment or the rate of increase of the herd is determined by subtracting the adult mortality rate from gross recruitment. Net recruitment of the George River caribou herd apparently decreased from +13.7% in 1976-77 to -6.9% in 1986-87 (Table 4). This decline appears almost linear, with the exception of 1980-81, when there was a larger decrease (-3.1%). Calef (1982) has described the decline in net recruitment between 1977 and 1981. In addition, he noted that the herd size declined in 1980-81 and evaluated the decrease at -3.9%. An 8.0% decrease in population size was observed between the aerial censuses of 1980 and 1982 (Juniper, 1980a; Goudreault, 1982). However, at this time it was believed that the difference was artificial and caused by the large confidence intervals of the estimates (26% for both,  $p < 0.05$ ). Québec (1984) added that there was no indication of any important demographic perturbation between 1980 and 1982. Nevertheless, our net recruitment data and those presented by Calef (1982) illustrate a decline of the herd for the biological year 1980-81 (cohort born in June 1980).

The exponential rate of increase,  $r$  (Caughley, 1977) was 0.128, -0.041 and 0.278 on average for the periods 1976-80, 1980-82 and 1982-84 respectively, as calculated from consecutive aerial surveys using the equation  $r = (\ln N_2 - \ln N_1) / (t_2 - t_1)$  (Bergerud, 1980). Thus, the annual rate of increase was estimated, using the equation  $e^r - 1 \times 100\%$  (Caughley, 1977), at 13.7, -4.0 and 32.1% for the above periods respectively. The net recruitment rates of Table 4 result in annual rates of increase of 7.0, 1.6 and 2.0% for the same periods. The most important deviation in rates of increase calculated by the two methods (aerial survey and our evaluation of net recruitment) occurs for the 1982-84 period. None of the earlier population estimates (1976, 1980, 1982) were corrected for visibility bias, because no such correcting factor has been determined for the George River herd. Thus the large discrepancy between the 1982 and 1984 estimates, which in turn

influence the rate of increase, may reflect differences in techniques used (visual in 1982, photographic in 1984). From work done in the Northwest Territories, photographic surveys yield estimates about 1.6-2.5 times higher than visual estimates (Heard, 1985). However, determining which of these corrections may be appropriate for earlier George River estimates is difficult because of possible differences in methodology, types of aircraft used, calving habitat and other factors.

#### Possible Causes of the Decline in Recruitment

The present analysis suggests that the decline in gross recruitment observed by Calef (1982) has continued until 1986-87. The consequences of this decline on the population dynamics justify an examination of the possible causes by which the growth of this herd could have been stopped. As reported elsewhere in North America, the trend observed in recent years could represent a momentary pause in growth that should resume, or it could be the beginning of a process that would drastically reduce herd size. Thus, certain large continental herds (Western Arctic, Beverly, Kaminuriak, Bluenose and Nelchina) rapidly collapsed, losing 50-86% of their numbers between 3 and 15 years (Parker, 1972; Bos, 1975; Dauphiné, 1976; Bergerud, 1978; Davis *et al.*, 1980, 1983; Miller, 1982, 1983; Carruthers and Jakimchuk, 1983; Gates, 1985). The Porcupine herd may be one of the rare examples of a large caribou herd that has remained elevated and stable at around 125 000 caribou for 20 years (Miller, 1982; Williams and Heard, 1986), which may be its minimum level rather than maximum (Haber and Walters, 1980). This would explain the observed stability, because instability better characterizes the maximum level of a herd. Meldgaard (1986) observed that the population maxima may last from 10 to 25 years and the population minima from 35 to 70 years. More recently the Porcupine herd was estimated at 150 000 caribou, and since the early 1980s it has been increasing (Williams and Heard, 1986).

*Habitat and physical condition.* Habitat studies are just beginning in northern Quebec, but it seems that forage is far from being overly depleted on most of the area used by the herd.

However, forage may be locally reduced because of overgrazing and trampling. Our preliminary observations in June 1986 and 1987 indicate that lichens have partially disappeared on the calving grounds and its surroundings except on the top of big rocks, between rocks and in other natural enclosures inaccessible to caribou. Opinions differ as to whether lichens have always been rare on the calving grounds located on the plateau east of the George River. However, S. Payette (pers. comm. 1988) believes that the climatic and edaphic conditions in this area are favourable for the growth of lichens, as suggested by the abundance of first-stage lichens everywhere on the grounds, indicating the potential for lichen growth in this sector. Willows (*Salix* spp.) or sedges are sparse and mineral soil is exposed in large areas of the calving grounds. Power and Barton (1987) provided further evidence of the locally depleted vegetation, as caused by the abundance of caribou, when discussing the destabilized flow regime of some northern Quebec rivers.

Caribou historically frequented the highlands east of George River during calving at the end of the last century (Turner, 1894, cited in Harper, 1961). More recently, observations documented the use of the highlands during calving and the rest of the summer. Average density of caribou on the calving grounds appears to have increased since 1973 and approximated 33 caribou·km<sup>-2</sup> in 1984 (Fig. 3). The high calving density possibly resulted in a reduction of forage through trampling and overgrazing. In turn, the reduction of forage probably explains the expansion of these calving grounds, which have doubled in size in the last few years (Fig. 3). In addition, the poor quality of the highland habitat explains why caribou no longer spend the summer in these areas, as noted by Juniper (1980b). It is important to clarify that the current calving grounds encompass most of the 1970s summer range (Juniper, 1982). Thus large groups of caribou used this area between June and September in the 1970s and early 1980s, and not only for the calving time.

The increase in size (Fig. 3) and the lower proportion of females on the calving ranges compromise feasibility of censuses based on counts of caribou on the calving grounds; the calving grounds may no longer exist for the George River caribou herd (A.T. Bergerud, pers. comm. 1988). Moreover, in spite of this large increase in size, the proportion of females using calving grounds seems to have been decreasing in recent years and was between 60 and 75% (calculated from radio-collared females; unpubl. data). This proportion ap-

pears low when compared with values of 80-90% (pregnant females) proposed by Gunn and Miller (1986) as criteria for determining herd identity through fidelity to traditional calving grounds.

We believe, on the basis of fragmentary observations, that most of the habitat of the George River herd is moderately used and of good quality. However, some sectors, like the current calving grounds located east of the George River (former summer range), seem locally depleted and of poor quality. The recognized fidelity of females to their calving grounds could thus threaten their survival and that of the calves and short-yearlings accompanying them. This possibility was advanced by Parker (1981), who was also concerned about repeated use of traditional calving grounds. The deterioration of caribou physical condition observed recently could be explained by this local reduction of forage or by an excessive increase in annual migration and energy expenditures. Some data suggest a long-term deterioration. The mandible length decreased by 1.2 cm between 1963 and 1985-86 (Bergerud, 1967; Couturier *et al.*, 1988, 1989). The weight of pregnant females at the end of winter decreased from 101.8 ± 3.3 kg in 1976 (Drolet and Dauphiné, 1976) to 93.4 ± 1.5 kg in 1980 (Parker, 1980) and to 85.6 ± 2.9 kg in 1984-86 (Huot and Goudreault, 1985; Couturier *et al.*, 1988). On a short-term basis or within an annual cycle of fat deposition, other data illustrate a poor fall physical condition of George River caribou. Kidney fat weight (following Riney, 1955) of breeding (lactating or pregnant) females was 36.2 ± 5.6 g (n=25) in late September 1985 and 55.9 ± 14.9 (n=12) in late March 1986 (Couturier *et al.*, 1989). Dauphiné (1976) presented values of 73.9 ± 9.9 g (n=32) and 54.2 ± 5.1 g (n=82) for Kaminuriak female caribou collected in September and April from 1966 to 1968. The fat content of a group of indicator muscles (Huot and Goudreault, 1985) also increased from 1.28 ± 0.13% (n=27) in late September 1985 to 1.78 ± 0.28% (n=12) in late March 1986 (Couturier *et al.*, 1989). Huot and Goudreault (1985) first observed that the females collected in April 1984 were fatter than those in October 1983. This increase in fat reserves between fall and spring represents an uncommon phenomenon for a ruminant living in a northern ecosystem. A slight increase in fat deposits was also observed between December 1985 and March 1986 for barren-ground caribou (*R. t. groenlandicus*) of the Beverly herd (Thomas and Kiliaan, 1986).

These data may indicate that the good quality of the winter range, in spite of its remoteness (up to 1000 km from the calving grounds), can compensate for the poor quality of a portion of the summer range. Some caribou arrive on the calving grounds as early as May and caribou aggregations can be seen until July on the forage-depleted highlands. The nutritional requirements are very high at this period of the year, when females undergo the last part of pregnancy and the first weeks of lactation (Tyler, 1987). The feeding problems at this crucial time, even for a few weeks, probably have a strong negative effect on caribou. In June 1986, a small sample of pregnant females collected on the calving grounds suggested poor physical condition (Couturier *et al.*, 1989). The total body weight (with uterus and its content) was 81.3, 68.0 and 47.0 kg for three pregnant females. For eight adult females, the femur marrow fat was 56.9 ± 15.8%, the kidney fat weight was 10.7 ± 1.7 g and almost no back fat was

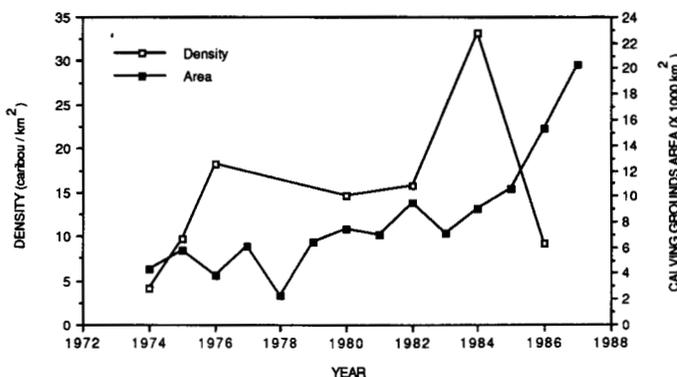


FIG. 3. Area occupied and average density of caribou on the calving grounds since 1974.

measured. Some caribou were observed walking with blood dripping from their noses.

We hypothesize that the poor quality of habitat on the current calving grounds (former summer range) compromises the physical condition of adult females and that of their calves from May to July. The grazing difficulties diminish fall physical condition and delay ovulation and births. From 1972 to 1974, most (i.e.,  $\geq 75$  calves per 100 females) calves were born before 4 June. In 1986, using the same criteria of at least 75 calves per 100 females, this date was delayed to 19 June (Gagnon and Barrette, 1986). The same phenomenon has been described elsewhere (Mitchell and Lincoln, 1973; Clutton-Brock *et al.*, 1982). Delays in birth dates are known to negatively affect the winter survival of short-yearlings by reducing the summer growth period (Clutton-Brock *et al.*, 1982; Reimers *et al.*, 1983; Skogland, 1983). In support of this hypothesis, a linear regression between summer or winter survival and dates of calving since 1976 provided correlation coefficients of  $r=-0.477$  ( $p=0.140$ ,  $n=7$ ) and  $r=-0.670$  ( $p=0.050$ ,  $n=7$ ) for summer and winter calf survival respectively (Fig. 4).

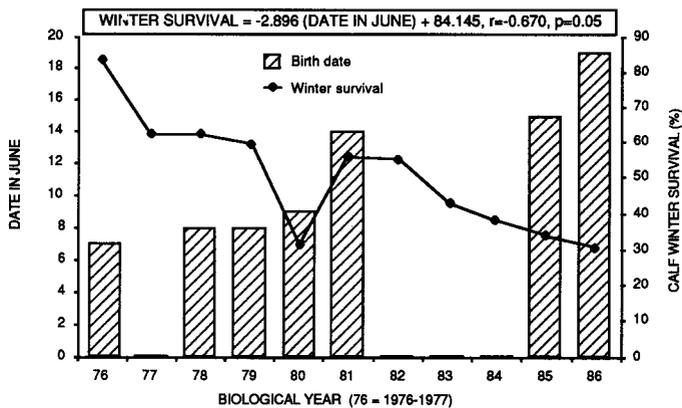


FIG. 4. Delay in calving dates and decline in winter survival of calves since 1976. The date in June was recorded when the ratio of calves per 100 females reached at least 75.

A positive correlation of weight at birth and summer survival has already been described for red deer (*Cervus elaphus*) and reindeer calves (Clutton-Brock *et al.*, 1982; Eloranta and Nieminen, 1986). Calf summer survival for the George River herd was relatively good before 1984, but rapidly declined afterward. In 1987, calf weight at birth was  $6.31 \pm 0.62$  kg ( $n=6$ ) and  $6.89 \pm 0.79$  kg ( $n=8$ ) for female and male respectively. In June 1988, female and male calf weights were  $5.70 \pm 0.59$  kg ( $n=8$ ) and  $6.69 \pm 0.65$  kg ( $n=10$ ) respectively. Verification of the hypothesis for the relationship between calf survival and birth weight will require more data. It is difficult to compare our newborn weight with data published for other herds in North America because of the morphological differences between the barren-ground caribou (*Rangifer tarandus groenlandicus*) and the woodland caribou (*Rangifer tarandus caribou*). Banfield (1961) stated that all caribou in Quebec belong to woodland subspecies. For us, it seems evident that the large migratory herds in northern Quebec (George and Leaf River herds) are similar to the barren-ground subspecies or form a new independent subspecies. A skull morphometric study of a large sample taken

after the drowning of 10 000 caribou in 1984 will help to clarify this point (Couturier *et al.*, in prep.). The newborn of barren-ground caribou are smaller, with 4.7 kg ( $n=19$ ) on average for female calves and 5.2 kg ( $n=24$ ) for male calves (McEwan, 1968). Bergerud (1971) presents for the woodland caribou a newborn weight of 7.6 kg ( $n=332$ ) for both sexes. These large differences in newborn weight probably reflect the higher body size reached by the adult woodland caribou.

**Density and dispersion.** Data suggest that the density of the George River herd changed from 0.6 caribou·km<sup>-2</sup> during 1971-75 to 1.9 during 1976-80, to 1.3 during 1981-84, and to 0.5 during 1985-86. In comparison, for example, from 1963 to 1965, the Nelchina herd in Alaska attained a density of only 1.5-1.9 caribou·km<sup>-2</sup>, when the historical peak of 70 000 animals was surpassed. Ten years later, the same herd reached another historic level, this time the lowest ever recorded, of 10 000 caribou. Changes in the density of the George River herd and the recent decrease in recruitment appear to fit the multiple equilibria model of Haber and Walters (1980). Density was apparently maximal between 1976 and 1984. As predicted by the model, the high density equilibrium was rapidly upset and the herd may have started to decline. The low density equilibrium (< 0.4 caribou·km<sup>-2</sup>), controlled by predation, lasts much longer and effectively describes most North American herds. Haber and Walters (1980) added that dispersion phenomena occurred when herds approached historical peaks. They associated the rapid range expansion of the George River herd with the start of a process leading to the dispersion and emigration of a part of the herd. It is possible that this phenomenon led to the formation and growth of the Leaf River herd. The distinct calving range of the Leaf River herd was first observed in 1975 by Le Hénaff (1976). Winter and fall distribution of caribou from both herds are overlapping (Fig. 1).

The range of the George River herd, as determined from radio-telemetry and field observations, has recently increased from 160 000 km<sup>2</sup> in 1971-75 to about 550 000 km<sup>2</sup> in 1986. In August 1987, the results of radio-telemetry surveys showed that the Leaf River caribou ( $n=31$  radio-collars localized) were mixed with those of George River ( $n=17$  radio-collars localized) in a sector not usually frequented at this period of the year by the George River herd. The radio-telemetry monitoring of the next few years should determine if dispersion movements occur. Recent observations show that the annual range now stretches from Hudson Bay and James Bay to the coast of Labrador, and from 53°N to 59°N (Vandal *et al.*, 1989). Associated with this range expansion, caribou undertake greater movements between seasonal ranges. These increased movements possibly result in greater energy expenditure (Messier *et al.*, 1988).

**Wolf predation.** Wolf populations have apparently increased in northern Quebec and Labrador in the late 1970s (Parker and Lutich, 1986). The study of the Native Harvest Research Committee showed an increase in the number of wolves taken annually between 1976 and 1980 by native hunters of the Inuit communities of Kuujuaq, Tasiujaq and Kangiqsualujuaq (Fig. 1). During these years, the harvest fluctuated between 124 and 276 wolves. This study is the only extensive investigation of the Quebec Inuit wolf harvest. More recently, Vandal *et al.* (1988) analyzed the wolf harvest in 1986-87 of the Kuujuaq residents (the wolf harvest is exclusively restricted

to natives) to re-establish the monitoring of the Inuit harvest in northern Quebec. Kuujuaq hunters alone harvested 113 wolves, while those of the two other communities probably killed at least a hundred, suggesting a relatively high wolf population level. The decrease in caribou recruitment observed since 1976 could have been caused by an increase in wolf population and predation, as suggested by Bergerud (1980) and by Bergerud and Elliot (1986) for other caribou populations, but the data are still too incomplete to support or refute this hypothesis.

*Density independent factors.* Density independent factors, such as severe weather, can also affect herd dynamics in decreasing recruitment (Skogland, 1985; Van Ballenberghe, 1985; Bergerud and Elliot, 1986; Meldgaard, 1986). For example, the pronounced decline in recruitment observed in 1980-81 coincided with an exceptionally high snow accumulation (586 cm, Schefferville weather station) that was 72% more than the average from 1951 to 1980. In addition, in the same winter, precipitation in the form of rain also exceeded the average by 14%. That weather may have reduced access to forage and increased energy expenditure. On Coats Island in Hudson Bay, calf production was low after severe winters (Gates *et al.*, 1986). During more favourable years, however, the herd had the potential of rapid re-establishment, as indicated by the ratio of 76.1 calves per 100 females observed in November 1981. Miller *et al.* (1977) did not observe any calves at all in 1974 following an exceptionally severe winter on Melville Island in the Northwest Territories. However, these last reports concern small, insular populations, and severe winters are unlikely to have significant effects on a large continental migratory herd.

#### CONCLUSION

The possible decline of the George River caribou herd will help reveal the mechanisms regulating the dynamics of large herds. Unfortunately, the lack of certain data prevents us from satisfactorily answering theoretical questions (Skoog, 1968; Bergerud, 1980; Haber and Walters, 1980; Skogland, 1985, 1986). However, it already appears that a combination of factors may explain the recent decrease observed in the herd's net recruitment.

We suggest that the recent decrease in gross recruitment was provoked by an increase in winter calf mortality and by a deterioration of female physical condition caused by poor habitat quality on the current calving grounds. This area encompasses the calving grounds traditionally frequented for decades but also includes the former summer range. Complex relationships exist among summer habitat quality, increase in energy expenditures related to increased movements, female physical condition, calving dates and calf survival. A possible increase in predation may be another factor explaining in part the recent decrease in calf survival. Other factors, like weather conditions and the increase in adult mortality through hunting, may also amplify the demographic trends of the herd. Our evaluation of net recruitment suggests that the rate of increase of the herd has been negative since 1984. The recent decrease of the George River herd density and the increase of the Leaf River herd may support the multiple equilibria model and the dispersion phenomena described by Haber and Walters (1980).

It is presently impossible to determine precisely the maximal level of caribou that could be harvested. This depends on sex and age of the animals harvested (unknown for some users), and also on herd size and annual recruitment. However, it would be a good management strategy to over-harvest the herd temporarily in order to reduce the herd size to a level where the deterioration of the range will not occur. The harvesting strategy will need to be easy to reevaluate if the future monitoring of population dynamics shows some problems.

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#### REFERENCES

- AUDET, R. 1979. Histoire du caribou du Québec-Labrador et évolution des populations. *Recherches amérindiennes au Québec* 9(1-2):17-27.
- BANFIELD, A.W.F. 1961. A revision of the reindeer and caribou, genus *Rangifer*. National Museum of Canada Bulletin 177 (Biological Series 66). 137 p.
- \_\_\_\_\_ and TENER, J.S. 1958. A preliminary study of Ungava caribou. *Journal of Mammalogy* 39:560-573.
- BERGERUD, A.T. 1964. A field method to determine annual parturition rates for Newfoundland caribou. *Journal of Wildlife Management* 28:447-480.
- \_\_\_\_\_. 1967. Management of Labrador caribou. *Journal of Wildlife Management* 31:621-642.
- \_\_\_\_\_. 1971. The population dynamics of Newfoundland caribou. *Wildlife Monographs* No. 25. 55 p.
- \_\_\_\_\_. 1978. Caribou. In: Schmidt, J.L., and Gilbert, D.L., eds. *Big Game of North America, Ecology and Management*. Harrisburg, Pa.: Stackpole Books. 83-101.
- \_\_\_\_\_. 1980. A review of the population dynamics of caribou and wild reindeer in North America. In: Reimers, E., Gaare, E., and Skjenneberg, S., eds. *Proceedings of the 2nd International Reindeer/Caribou Symposium*, Roros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 556-581.
- \_\_\_\_\_ and ELLIOT, J.P. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515-1529.
- BERGERUD, A.J., 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.
- BOS, G.N. 1975. A partial analysis of the current population status of the Nelchina caribou herd. In: Luick, J.R., Lent, P.C., Klein, D.R., and White, R.G., eds. *Proceedings of the First International Reindeer/Caribou Sym-*

- sum. Biological Papers University of Alaska, Special Report 1:170-180.
- CALEF, G. 1982. Report on the George River caribou herd. Nain, Labrador: Labrador Inuit Association. 33 p.
- CARRUTHERS, D.R., and JAKIMCHUK, R.D. 1983. The distribution, numbers and movements of the Bluenose caribou herd, Northwest Territories, Canada. In: Pulliainen, E., ed. Proceedings of the Third International Theriological Congress, Helsinki, 1982. VII. Third International Reindeer/Caribou Symposium, Saariselkä, 1982. Acta Zoologica Fennica 175:141-143.
- CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. London: John Wiley and Sons. 234 p.
- CLUTTON-BROCK, T.H., GUINNESS, F.E., and ALBON, S.D. 1982. Red deer — Behavior and ecology of two sexes. Chicago: University of Chicago Press, Wildlife Behavior and Ecology Series: 378 p.
- COCHRAN, W.G. 1977. Sampling Techniques. 3rd ed. New York: John Wiley and Sons, Inc. 428 p.
- COUTURIER, S., BRUNELLE, J., and LAPOINTE, G. 1988. Decline of physical condition and decrease of recruitment in the George River caribou herd. Proceedings of the Third North American Caribou Workshop. Alaska Department of Fish and Game, Juneau. Wildlife Technical Bulletin No. 8:35-37.
- COUTURIER, S., VANDAL, D., ST-MARTIN, G., and FISET, D. 1989. Suivi de la condition physique des caribous de la rivière George. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. 88 p.
- CRETE, M., LE HÉNAFF, D., NAULT, R., VANDAL, D., and LIZOTTE, N. 1987. Estimation du nombre de caribous associés aux aires de mise bas de la rivière aux Feuilles et de la rivière George en 1986. Unpubl. report. Available from Ministère du Loisir, de la Chasse et de la Pêche, 150, St-Cyrille est, Québec G1A 4Y3. 31 p.
- DAUPHINÉ, T.C., Jr. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. Canadian Wildlife Service Report Series No. 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., Gaare, E., and Skjenneberg, S., eds. Proceedings of the 2nd International Reindeer/Caribou Symposium. Roros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 595-604.
- DAVIS, J.L., VALKENBURG, P., and BOERTJE, R.D. 1983. Demography and limiting factors of Alaska's Delta caribou herd, 1954-1981. In: Pulliainen, E., ed. Proceedings of the Third International Theriological Congress, Helsinki, 1982. VII. Third International Reindeer/Caribou Symposium, Saariselkä, 1982. Acta Zoologica Fennica 175:135-137.
- DESMEULES, P., and BRASSARD, J.M. 1963. Inventaire préliminaire du caribou *Rangifer tarandus caribou* d'un secteur de la Côte-Nord et du secteur centre de l'Ungava. Ministère du Tourisme, de la Chasse et de la Pêche, Service de la faune, Québec. Report No. 3:187-218.
- DOERR, J.G. 1979. Population analysis and modeling of the Western Arctic Caribou Herd with comparisons to other Alaskan Rangifer populations. M.Sc. thesis, University of Alaska, Fairbanks. 341 p.
- DROLET, C.A., and DAUPHINÉ, T.C. 1976. Ungava caribou collections — Preliminary report. Unpubl. report. 9 p. Available at Canadian Wildlife Service, Ottawa, Ontario.
- ELORANTA, E., and NIEMINEN, M. 1986. Calving of the experimental reindeer in Kaamanen during 1970-85. In: Gunn, A., Miller, F.L., and Skjenneberg, S., eds. Proceedings of the Fourth International Reindeer/Caribou Symposium, Whitehorse, Canada, 1985. Rangifer Special Issue No. 1, 1986:115-121.
- ELTON, C. 1942. Caribou herds and modern trade. In: Voles, mice and lemmings: problems in population dynamics. London: Oxford University Press. 362-389.
- FELDMAN, D., and GAGNON, J. 1985. StatView. Calabasas: BrainPower, Inc. 112 p.
- FERGUSON, S.H., LUTTICH, S., and GOUDREAU, F. 1985. Recruitment and overwinter calf survival for the George River caribou herd. Government of Newfoundland and Labrador, Department of Culture, Recreation and Youth, Wildlife Division, Labrador. Field Project Report No. 4009. 25 p. and annexes.
- GAGNON, L., and BARRETTE, C. 1986. Inventaire terrestre des caribous de la rivière George, sur l'aire de mise bas, juin 1986. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction de la faune terrestre. SP 1219-01-87. 79 p.
- GATES, C.C. 1985. The fall and rise of the Kaminuriak caribou population. In: Meredith, T.C., and Martell, A.M., eds. Proceedings of the 2nd North American caribou workshop, Val Morin, Québec, 1984. McGill Subarctic Research Paper No. 40:215-228.
- \_\_\_\_\_, ADAMCZEWSKI, J., and MULDER, R. 1986. Population dynamics, winter ecology and social organization of Coats Island caribou. Arctic 39:216-222.
- GOUDREAU, F. 1982. Dénombrement des caribous sur l'aire de mise bas du troupeau du fleuve George en juin 1982. Unpubl. report. Available at Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec, 1995, Charest ouest, Ste-Foy, Québec G1N 4H9. 18 p.
- \_\_\_\_\_. 1985. Review of caribou census techniques used in Northern Québec. In: Meredith, T.C., and Martell, A.M., eds. Proceedings of the 2nd North American caribou workshop, Val Morin, Québec, 1984. McGill Subarctic Research Paper No. 40:239-253.
- \_\_\_\_\_, LE HÉNAFF, D., CRETE, M., and LUTTICH, S. 1985. The counting of caribou on the George River herd calving ground in June 1984 with the use of vertical aerial photography. Unpubl. report. Available at Ministère du Loisir, de la Chasse et de la Pêche, 1995, Charest ouest, Ste-Foy, Québec G1N 4H9. 19 p. and annexes.
- GUNN, A., and MILLER, F.L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. In: Gunn, A., Miller, F.L., and Skjenneberg, S., eds. Proceedings of the Fourth International Reindeer/Caribou Symposium, Whitehorse, Canada, 1985. Rangifer, Special Issue No. 1, 1986:151-158.
- HABER, G.C., and WALTERS, C.J. 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. In: Reimers, E., Gaare, E., and Skjenneberg, S., eds. Proceedings of the 2nd International Reindeer/Caribou Symposium, Roros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 645-660 and annex.
- HARPER, F. 1961. Land and fresh-water mammals of the Ungava Peninsula. University of Kansas. Miscellaneous Publication No. 27. 178 p.
- HEARD, D.C. 1985. Caribou census methods used in the Northwest Territories. In: Meredith, T.C., and Martell, A.M., eds. Proceedings of the 2nd North American caribou workshop, Val Morin, Québec, 1984. McGill Subarctic Research Paper No. 40:229-238.
- \_\_\_\_\_, and CALEF, G.W. 1986. Population dynamics of the Kaminuriak caribou herd, 1968-1985. In: Gunn, A., Miller, F.L., and Skjenneberg, S., eds. Proceedings of the Fourth International Reindeer/Caribou Symposium, Whitehorse, Canada, 1985. Rangifer, Special Issue No. 1, 1986:159-166.
- HEMMING, J.E. 1975. Population growth and movement patterns of the Nelchina caribou herd. In: Luick, J.R., Lent, P.C., Klein, D.R., and White, R.G., eds. Proceedings of the First International Reindeer/Caribou Symposium. Biological Papers University of Alaska, Special Report 1:162-169.
- HUOT, J., and GOUDREAU, F. 1985. Evaluation of several indices for predicting total body fat of caribou. In: Meredith, T.C., and Martell, A.M., eds. Proceedings of the 2nd North American caribou workshop, Val Morin, Québec, 1984. McGill Subarctic Research Paper No. 40:157-175.
- JEAN, M. 1980. Recensement du caribou sur le terrain de vêlage du lac Champdoré (nord-est de Schefferville), juin 1979, et comparaison avec le recensement de 1974. Ministère du Loisir, de la Chasse et de la Pêche, Direction de la recherche faunique, Québec. RRF No. 54. 9 p. and annexes.
- JUNIPER, I. 1974. Recensement et étude sur le terrain de vêlage du caribou, Nord-est de Schefferville, mai-juin 1974. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Service de la recherche biologique. 22 p.
- \_\_\_\_\_. 1980a. Estimé du niveau de population du troupeau de caribous du fleuve George — 1980. Unpubl. report. Available at Ministère du Loisir, de la Chasse et de la Pêche, 150, St-Cyrille est, Québec G1R 4Y3. 7 p.
- \_\_\_\_\_. 1980b. Problems in managing an irrupting caribou herd. In: Reimers, E., Gaare, E., and Skjenneberg, S., eds. Proceedings of the 2nd International Reindeer/Caribou Symposium, Roros, Norway, 1979. Trondheim: Direktoratet for vilt og ferskvannsfisk. 722-724.
- \_\_\_\_\_. 1982. The George River caribou herd — A preliminary investigation. Québec: Ministère du Loisir, de la Chasse et de la Pêche. 30 p.
- KELSALL, J.P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monograph No. 3. Ottawa: Queen's Printer. 340 p.
- KLEIN, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32:350-367.
- LE HÉNAFF, D. 1976. Inventaire aérien des terrains de vêlage du caribou dans la région nord et au nord du territoire de la municipalité de la Baie James (mai-juin 1975). Québec: Ministère du Tourisme, de la Chasse et de la Pêche, Serv. recherche biologique. 28 p.
- MARTELL, A.M., and RUSSELL, D.E. 1983. Mortality rate in the Porcupine caribou herd. In: Pulliainen, E., ed. Proceedings of the Third International

- Theriological Congress, Helsinki, 1982. VII. Third International Reindeer/Caribou Symposium, Saariselkä, 1982. *Acta Zoologica Fennica* 175:139-140.
- McEWAN, E.H. 1968. Growth and development of the barren-ground caribou. II. Postnatal growth rates. *Canadian Journal of Zoology* 46:1023-1029.
- MELDGAARD, M. 1986. The Greenland caribou — Zoogeography, taxonomy and population dynamics. *Meddelelser Om Gronland, Bioscience* 20:1-88.
- MESSIER, F., and HUOT, J. 1985. Connaissances sur le troupeau de la rivière George. Ministère du Loisir, de la Chasse et de la Pêche, Québec. SP 1025-11-85. 98 p.
- \_\_\_\_\_, LE HÉNAFF, D., and LUTTICH, S. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41:79-87.
- MILLER, F.L. 1982. Caribou (*Rangifer tarandus*). In: Chapman, J.A., and Feldhamer, G.A., eds. *Wild Mammals of North America. Biology, Management, and Economics*. Baltimore: The Johns Hopkins University Press. 923-959.
- \_\_\_\_\_. 1983. Restricted caribou harvest of welfare — northern native's dilemma. In: Pulliainen, E., ed. *Proceedings of the Third International Theriological Congress, Helsinki, 1982*. VII. Third International Reindeer/Caribou Symposium, Saariselkä, 1982. *Acta Zoologica Fennica* 175:171-175.
- \_\_\_\_\_, RUSSELL, R.H., and GUNN, A. 1977. Peary caribou and muskoxen on western Queen Elizabeth Islands, NWT 1972-74. *Canadian Wildlife Service Report Series No. 40*. 55 p.
- MITCHELL, B., and LINCOLN, G.A. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. *Journal of Zoology* 171:141-152.
- MOISAN, G. 1964. Rapport préliminaire sur la situation du caribou au Nouveau-Québec. Unpubl. report. Available at Library, Université Laval, Québec G1K 7P4. 17 p.
- NORUSIS, M.J. 1986. SPSS/PC+™ for the IBM PC/XT/AT. Chicago: SPSS Inc.
- 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 No. 20*. 95 p.
- \_\_\_\_\_. 1980. Physical and reproductive parameters of pre-calving caribou (*Rangifer tarandus caribou*) in northern Labrador. Unpubl. report. Available at Canadian Wildlife Service, Sackville, New Brunswick E0A 3C0. 86 p.
- \_\_\_\_\_. 1981. Physical and reproductive characteristics of an expanding woodland caribou population (*Rangifer tarandus caribou*) in northern Labrador. *Canadian Journal of Zoology* 59:1929-1940.
- \_\_\_\_\_, and LUTTICH, S. 1986. Characteristics of the wolf (*Canis lupus labradorius Goldman*) in Northern Quebec and Labrador. *Arctic* 39:145-149.
- PAYETTE, S. 1983. The forest tundra and present tree-lines of the northern Québec-Labrador Peninsula. *Nordicana* 47:3-23.
- PICHETTE, C., and BEAUCHEMIN, P. 1973. Inventaire aérien du caribou — février 1973. Unpubl. report. Available at Ministère du Loisir, de la Chasse et de la Pêche, 150, Ste-Cyrille est, Québec G1R 4Y3. 12 p.
- POWER, G., and BARTON, D.R. 1987. Some effects of physiographic and biotic factors on the distribution of anadromous Arctic charr (*Salvelinus alpinus*) in Ungava Bay, Canada. *Arctic* 40:198-203.
- QUÉBEC. 1984. Marketing caribou meat in Nouveau-Québec. Feasibility study. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. 210 p.
- \_\_\_\_\_. 1987. Plan de gestion du caribou du Nord québécois, 1987-1992. Version préliminaire 3. Unpubl. report. Available at Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec, 1995, Charest ouest, Ste-Foy, Québec G1N 4H9. 80 p.
- REIMERS, E., KLEIN, D.R., and SORUMGARD, R. 1983. Calving time, growth rate and body size of Norwegian reindeer on different ranges. *Arctic and Alpine Research* 15:107-118.
- RINEY, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. *New Zealand Journal of Science and Technology* 36(5):429-463.
- SKOGLAND, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. *Oecologia (Berlin)* 60:156-168.
- \_\_\_\_\_. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology* 54:359-374.
- \_\_\_\_\_. 1986. Density dependent food limitation and maximal production in wild reindeer herds. *Journal of Wildlife Management* 50:314-319.
- SKOOG, R.O. 1968. Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. thesis, University of California, Berkeley. 699 p.
- THOMAS, D.C. 1969. Population estimates and distribution of barren-ground caribou in Mackenzie District, Northwest Territories, Saskatchewan and Alberta — March to May 1967. *Canadian Wildlife Service Report Series No. 9*. 44 p.
- \_\_\_\_\_, and KILIAAN, H.P.L. 1986. Distribution and physical characteristics of the Beverly herd of caribou in February and March 1986. *Canadian Wildlife Service Report, Edmonton, Alberta*. 35 p.
- TYLER, N.J.C. 1987. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. *Symposium of Zoological Society of London* 57:203-229.
- VAN BALLEMBERGHE, V. 1985. Wolf predation on caribou: the Nelchina herd case history. *Journal of Wildlife management* 49:711-720.
- VANDAL, D., and BARRETTE, C. 1985. Snow depth and feeding interactions at snow craters in woodland caribou. In: Meredith, T.C., and Martell, A.M., eds. *Proceedings of the 2nd North American caribou workshop, Val Morin, Québec, 1984*. McGill Subarctic Research Paper No. 40:199-212.
- \_\_\_\_\_. 1987. Sparring in caribou: Antler use by males and females. *Transactions of the Congress of International Union of Game Biologists* 18:207-208.
- VANDAL, D., and COUTURIER, S. 1988. Délimitation de l'aire de mise bas du troupeau de caribou de la Rivière George en juin 1987. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. 20 p.
- VANDAL, D., ADAMS, J., and COUTURIER, S. 1988. Récolte de caribous et de loups par les Inuit de Kuujuaq en 1986-1987. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. 6 p.
- VANDAL, D., COUTURIER, S., RÉMILLARD, D., and LUTTICH, S. 1989. Distribution saisonnière et migrations des caribous de la rivière George, de 1984 à 1987. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Nouveau-Québec. 93 p.
- WETMORE, S.P. 1973. Three aerial caribou surveys of northern Labrador and northeastern Québec, February, March-April and May-June, 1973. Unpubl. report. Available at Newfoundland-Labrador Wildlife Division, St-John's, Newfoundland A1C 5T7. 20 p.
- WHITE, R.G., BUNNEL, F.L., GAARE, E., SKOGLAND, T., and HUBERT, B. 1981. Ungulates on arctic ranges. In: Bliss, L.C., Heal, O.W., and Moore, J.J., eds. *Tundra ecosystems: a comparative analysis*. Cambridge: Cambridge University Press. 397-482.
- WILLIAMS, I.M., and HEARD, D.C. 1986. World status of wild *Rangifer tarandus* populations. In: Gunn, A., Miller, F.L., and Skjennneberg, S., eds. *Proceedings of the Fourth International Reindeer/Caribou Symposium, Whitehorse, Canada, 1985*. *Rangifer, Special Issue No. 1*, 1986:19-28.
- WILSON, C.V. 1971. The climate of Québec. Part one — Climatic atlas. *Canadian Meteorological Service, Ottawa: Information Canada*. 8 p. and maps.