

Demography of the George River Caribou Herd: Evidence of Population Regulation by Forage Exploitation and Range Expansion

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ABSTRACT. The George River caribou herd in northern Quebec/Labrador increased from about 5000 animals in 1954 to 472 200 (or 1.1 caribou·km⁻²) prior to the 1984 calving season. The range used by the herd expanded from 160 000 to 442 000 km² for the period 1971-84. The exponential rate of increase (r) was estimated at 0.11 in the 1970s. Calf:female ratio in autumn was relatively constant ($x = 0.52$) from 1973 to 1983, but decreased to about 0.39 in 1984-86. The harvest rate was relatively low in the 1970s (about 3%·yr⁻¹), but seemingly increased in the mid-1980s to 5-7% as a result of more liberal regulations and a greater impetus to exploit caribou for subsistence. The cumulative impact of lower calf recruitment and more intensive hunting may have appreciably depressed the growth rate of the herd in 1984-86. A greater year-round competition for food resources and a greater energy expenditure associated with range expansion are presented as probable regulatory factors for the George River herd. It is argued that the nature of caribou-habitat interactions in continental regions generate long-term fluctuations in caribou numbers if human exploitation remains low. At present, wolf predation does not appear to be an important mortality factor capable of regulating the George River herd.

Key words: caribou, population regulation, food limitation, northern Quebec, Labrador, wolf predation

RÉSUMÉ. Le troupeau de caribous de la rivière George dans le nord du Québec et au Labrador a augmenté de 5000 têtes en 1954, à 472 200 (soit 1,1 caribou·km⁻²) avant la saison de vélage de 1984. Le territoire utilisé par le troupeau s'est agrandi de 160 000 à 442 000 km² pendant la période allant de 1971 à 1984. On a estimé le taux de croissance exponentielle (r) à 0,11 dans les années 70. Le rapport veau:femelle à l'automne était relativement constant ($x = 0,52$) de 1973 à 1983, mais il est descendu à environ 0,39 en 1984-86. Le taux de chasse était relativement faible dans les années 70 (environ 3%·an⁻¹), mais il semble avoir augmenté jusqu'à 5-7% dans le milieu des années 80, à la suite d'une plus grande libéralisation des règlements et d'une augmentation de l'intérêt dans la chasse au caribou pour la subsistance. L'effet cumulatif d'un taux de reproduction plus faible et d'une chasse plus intense pourrait avoir ralenti de façon appréciable le taux de croissance du troupeau en 1984-86. On montre que l'augmentation de la concurrence pour les sources de nourriture tout au long de l'année, ainsi que l'accroissement des dépenses énergétiques associé à l'agrandissement du territoire, sont des facteurs probables de régulation pour le troupeau de la rivière George. On soutient que la nature des interactions du caribou et de son habitat dans les régions continentales créent des fluctuations à long terme dans le nombre de caribous si ceux-ci restent peu chassés par l'homme. À l'heure actuelle, la prédation des loups ne semble pas être un facteur de mortalité important qui puisse réguler le troupeau de la rivière George.

Mots clés: caribou, régulation de la population, limitation de la nourriture, nord du Québec, Labrador, prédation des loups

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INTRODUCTION

Much effort has been devoted to determining the factors limiting caribou (*Rangifer tarandus*) numbers. Recent studies conducted in South Georgia (Leader-Williams, 1980) and Norway (Skogland, 1985, 1986) illustrated the direct effects of intraspecific food competition in the regulation of reindeer (*Rangifer tarandus tarandus*). This relationship, however, was documented in predator-free areas, and food limitation may not apply to most caribou herds in North America. Bergerud (1980, 1983) has suggested that caribou populations in North America are limited largely by hunting and predation by gray wolves (*Canis lupus*) and grizzly bear (*Ursus arctos*). Much of the information collated by Bergerud pertains to caribou populations cohabiting to some extent with moose (*Alces alces*). Because the presence of an alternative ungulate species may exacerbate wolf predation on caribou (Bergerud and Elliot, 1986; Edmonds, 1988), Bergerud's view (1980, 1983) may incorrectly depict the demography of large migratory caribou herds in tundra and forest-tundra ecosystems that lack an alternative ungulate species. At present, only limited data are available for understanding the dynamics of caribou and wolves in such ecosystems (Kuyt, 1972; Parker, 1973; Stephenson and James, 1982; Miller *et al.*, 1985; Parker and Luttich, 1986).

This paper summarizes the demography of the George River caribou herd, northern Quebec and Labrador, from 1955 to 1986. The George River herd has been expanding since the

1950s (Messier and Huot, 1985) in the absence of any active predator control. This herd offers a unique opportunity to test the wolf predation hypothesis proposed by Bergerud (1980, 1983). In addition, the expansion of the George River herd provides further insights on caribou-habitat interactions in continental regions.

STUDY AREA

The current range of the George River herd encompasses most of northern Quebec and Labrador between 55° and 60°N latitude from the Labrador Sea to Hudson Bay. The relief consists mostly of rolling hills, with the exception of the coastal plain along Ungava Bay, the highly dissected Labrador plateau, and the rugged peaks of the Torngat Mountains in northern Labrador. Tundra covers an extensive area in northern Labrador, as well as in Quebec north of 58°N latitude (Fig. 1). Elsewhere, the forest-tundra and the boreal forest, both with a highly disjunct distribution, prevail (Payette, 1983).

The dominant tree species are *Picea mariana*, *P. glauca*, *Larix laricina*, *Populus balsamifera*, *Betula glandulosa*, *Alnus* spp., and *Salix* spp. Shrubs are common in swamps (in association with various species of mosses) and in the tundra: mainly, *Empetrum nigrum*, *Vaccinium* spp., and *Ledum* spp. Lichens grow in abundance in the forest-tundra and boreal forest ecoregions, whereas mosses and graminoids dominate in the tundra of the Labrador plateau.

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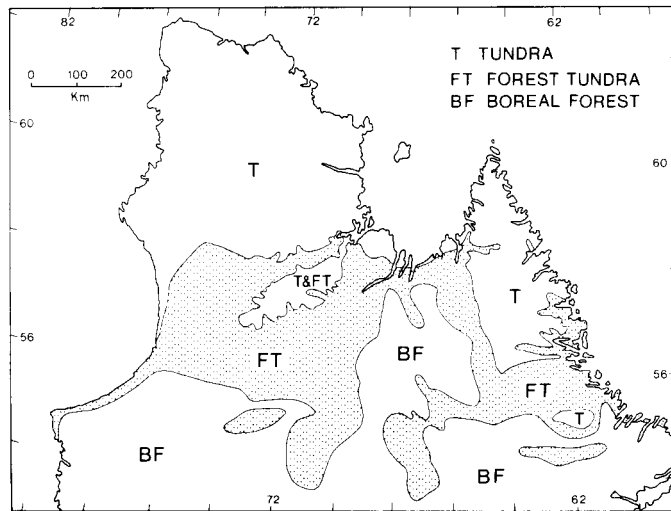


FIG. 1. Zonation of the tundra, the forest-tundra, and the boreal forest in northern Quebec/Labrador (modified after Payette, 1983).

The climate is continental, with cold winters (mean January temperature -21° to -23°C) and relatively warm summers (mean July temperature 10° to 13°C). Total annual precipitation in water equivalent ranges from 400 to 800 mm, of which nearly half falls as snow.

METHODS

Caribou of the George River herd were counted at irregular intervals since 1954. Different methods have been used, which resulted in various biases and errors. Details of each survey have been described by Goudreault (1985). Early counts were based on standard strip census methods in winter (Table 1). Since 1976, estimates were derived from quadrat sampling to count adult females on the calving ground. In 1984, aerial photographs were used with the quadrat sampling method. For all estimates since 1976, precalving populations were determined by dividing the total number of females ≥ 2.0 yr of age censused on the calving ground by the proportion of these females in the herd the previous autumn. An unsuccessful survey in 1986 (M. Crête, pers. comm. 1987) is not considered here.

Maps of 41 aerial reconnaissances conducted between 1970 and 1985 provided some information on the general distribution of the herd. The flights were originally designed to document population status, migration routes, herd structure, and calving biology. In 1973-74, 303 caribou were marked and 73 were equipped with radio collars. A total of 69 caribou relocations were obtained (Dauphiné *et al.*, 1975; Drolet and Anderka, 1977). An on-going telemetry project was initiated in October 1982 by Quebec and Newfoundland-Labrador government organizations. By December 1984 we had 812 locations from 156 radio-collared animals to more precisely define herd range.

Sex and age classifications of caribou were conducted during the rut (late October) and prior to or during calving (early June). In general, observers were positioned in proximity to natural trails and recorded, with the aid of binoculars and spotting scopes, the number of maturing calves (0.5-1.0 yr of age), adult females (> 1.0 yr), and adult males. Because of the difficulty in classifying animals 1.5-2.0 yr old (Parker, 1972), we incorporated counts of these animals into the adult age class.

A standing age structure was obtained from a sample of 875 female caribou systematically examined after a mass drowning of 10 000 caribou on 28-29 September 1984 along the Caniapiscou River. Because track observations revealed that few animals survived, we assumed that this mass drowning provided a representative sample of the whole population. The 875 caribou sub-sample was taken across the entire group of drowned animals. Also, 10 000 caribou would represent numerous aggregations of caribou and thus would ensure that all age classes were properly represented despite possible age segregation among groups. Aging was performed via microscopic inspection of cementum annuli in incisor teeth (Matson's, P.O. Box 308, Milltown, Montana, U.S.A.), after examination of 49 known-age incisors (1.5-8.5 yr old).

The life-table analysis follows the approach and terminology of Caughley (1977:81-97). Age class frequency data of adult females were converted into logarithmic values (Varley and Gradwell, 1970) and multiplied by the correction factor e^{rx} , where r is the estimated population growth rate and x the age class. Such transformation is required to derive the stationary age distribution from a standing age distribution when r differs from zero (Caughley and Birch, 1971). The resulting time-specific frequency data were further smoothed by a non-linear regression procedure for best fit. Such smoothing would dimin-

TABLE 1. Pre-calving population estimates of the George River caribou herd, 1954-84

Year	Month	Population estimate	CI at $\alpha = 0.10^a$	Census method	Citation
1954-56	Jan-Mar	4 700	—	Nonsystematic aerial survey	Banfield and Tener (1958)
1958	Mar	15 000	—	Strip census and extrapolation to total area	Bergerud (1967)
1963	Mar	61 800	—	Same as above	Unpubl. ^b
1973	Mar	105 000	—	Same as above	Unpubl. ^{b,c}
1975	Feb	205 000	—	Same as above	Unpubl. ^c
1976	Jun	176 600	$\pm 30\%$	Stratified random sampling of the calving ground	Unpubl. ^b
1980	Jun	294 510	$\pm 29\%$	Same as above	Unpubl. ^b
1982	Jun	271 060	$\pm 26\%$	Two-stage random sampling of the calving ground	Unpubl. ^b
1984	Jun	472 200	$\pm 6\%$	Stratified systematic sampling by aerial photographs of the calving ground	Unpubl. ^{b,c}

^aAs calculated by the investigators from counts of adult females in randomly spaced quadrats over the calving ground; does not include the variance associated with the observed proportion of adult females in the herd the previous autumn.

^bMin. Loisir Chasse et Pêche du Québec, data in files.

^cNewfoundland-Labrador Wildlife Division, data in files.

ish the effect of over- or under-representation of a given age class because of sampling errors, as well as possible inter-annual variations in fecundity and survival. Time-specific frequency data were used to estimate survivorship of females. The critical assumption here was that the rate of population increase remained constant, as a trend, over a period of time that included most age classes (i.e., 1970-84). Based on the available demographic data, the assumption appears to be justified (data herein).

The constructed life-table was centered on the season of births (early June). The original calf production (age class zero) was derived from the standing age distribution of females and their age-specific reproduction rate (i.e., the summation of $f_x m_x$). We assumed for age classes 1-15 that the distribution in June could be satisfactorily deduced from the observed distribution in September based on our sample of drowned animals (i.e., that a non-differential mortality occurred during the summer months for caribou > 1 yr of age).

RESULTS

Population Trends

Historical information suggests that caribou numbers in northern Quebec/Labrador were fairly high in the 1880s but declined sharply until 1920-30 (Low, 1896:318-319; Elton, 1942; Lutich, 1983). Exact causes for this decline are unknown and remain inevitably speculative. Audet (1979) suggested that overhunting for subsistence and habitat deterioration were implicated.

Between 1954 and 1984, there were nine surveys of the George River herd (Table 1). Estimates of spring population increased from 4700 to 472 200 animals during this period. In 1984, 586 000 caribou were estimated to be present after the parturition period. The quality of censuses varied through the years, and the recent ones are considered more accurate and precise than the early counts in the 1950s and 1960s (Goudreault, 1985). Despite changes in census methodology, the interpretation is that the herd has continued to increase from the low population level of 1954.

The rate of population increase (r) from 1955 to 1984 is estimated at 0.14 (Fig. 2). If we consider only the period 1970-84, r equals 0.11 (Fig. 2). This last estimate seems more realistic because population sizes for the period 1954-63 were likely underestimated, therefore inflating the rate of increase when considering the entire study period. There is little indication that the rate of increase declined from 1970 to 1984, but it probably did so afterward (see below).

Range Expansion

The total area occupied by the herd increased concomitantly with population size (Fig. 3). Mapped distributions of the herd covered 160 000 km² in 1971-75, 195 000 km² in 1976-80, and 442 000 km² in 1981-84 (Messier and Huot, 1985). The overall density increased from 0.2 to 1.1 caribou·km⁻² during the 1971-84 period, assuming a range size of 442 000 km². Range expansion occurred primarily during the winter season, when animals migrated farther west toward the Hudson Bay coast. A southern expansion also occurred during the period 1980-84, causing animals to forage more extensively at the fringe of the boreal forest.

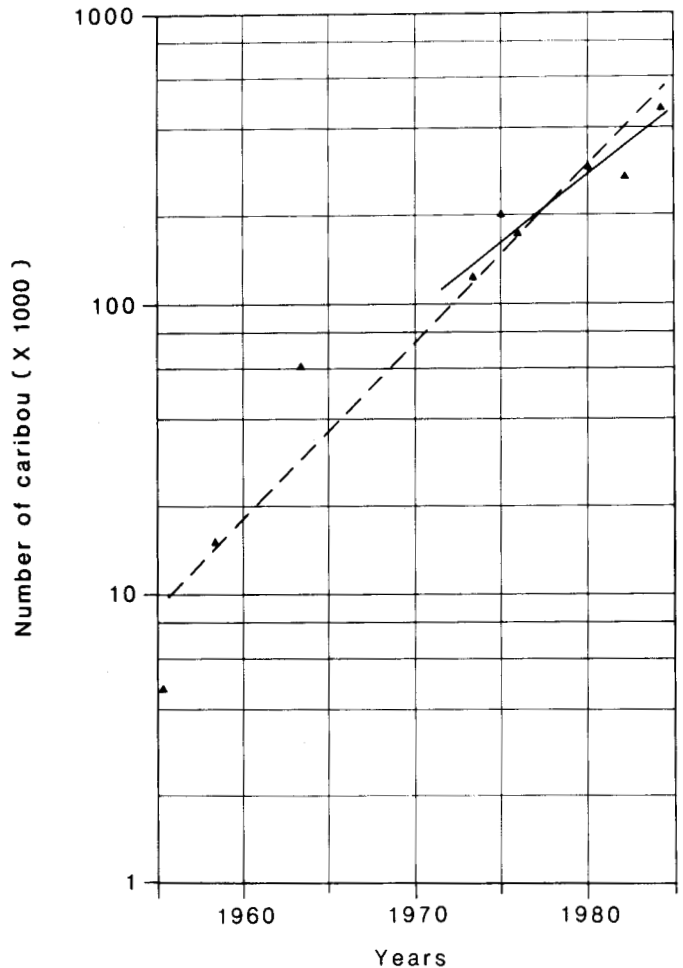


FIG. 2. Population growth of the George River caribou herd 1955-84. The regression line for the entire set of data is $Y = 8920 e^{(0.140)x}$, where Y represents the population size and x the number of years span since 1955 ($r = 0.96, n = 9, P$ of zero slope < 0.01). Using only the 1970-85 data set (solid regression line), the corresponding relationship is $Y = 17\ 370 e^{(0.110)x}$ ($r = 0.93, n = 6, P < 0.01$).

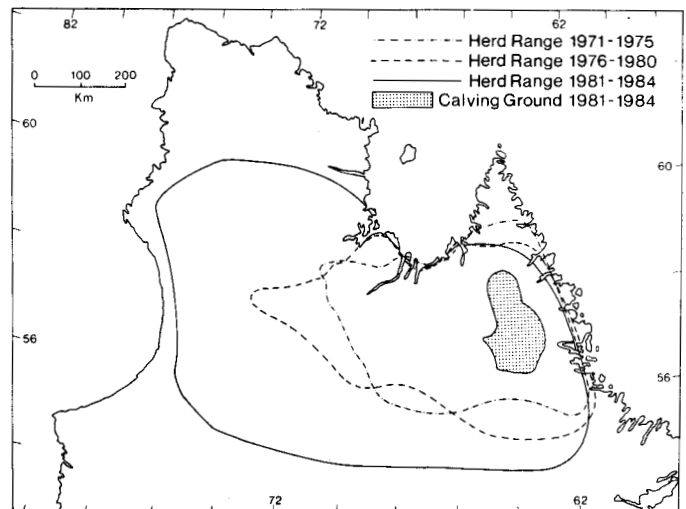


FIG. 3. Range expansion of the George River caribou herd 1971-84, and composite calving ground area 1981-84.

Population Structure

In October 1973-86, caribou > 1 yr of age formed 76.9% of the total population (Table 2). Neither the percentage of adult males (mean = 29.6%) nor the percentage of adult females (mean = 47.3%) was correlated with time ($r = 0.27$ and 0.08 respectively; P of zero slope > 0.05). Calves accounted for 19.6-27.3% (mean = 23.1%) of the autumn population (Table 2). The calf:female ratio, which may represent the best index of recruitment at 6 months of age, averaged 0.49 through the study period. However, this ratio decreased from an average of 0.52 in 1973-83 to 0.39 in 1984-86 (Table 2).

In spring (April-June), adult females and maturing calves from the previous year were classified near the calving ground. The calf:female ratio showed relatively large variations among years (0.18-0.73), mean = 0.37; Table 3). Its coefficient of variation (CV = s/x) was 38%, compared with 12% in autumn. In an attempt to explain this greater variability, we correlated the spring calf:female ratio with the total precipitation of snow the previous winter (Nitchequon weather station, 53°12'N,

70°54'W). The correlation analysis revealed no trend ($r = 0.21$, P of zero slope > 0.05). Equally important, the calf:female ratio in spring was not correlated with that reported the previous autumn ($r = 0.10$; P of zero slope > 0.05).

Reproduction

Parker (1981) provided pregnancy rates for 142 females sampled in April 1980. In addition, we examined 63 females killed from December to June 1983-86 in connection with other projects (Huot and Goudreault, 1985; Messier *et al.*, 1987; unpubl. data).

Pregnancy rate of females ≥ 1.5 yr of age declined from 0.85 to 0.67 between these two sampling periods (Table 4; G-test = 7.7, $P < 0.01$). We also noted a significant interaction between pregnancy rate and age (G-test = 4.1, $P = 0.04$), indicating that the reduction in pregnancy rate between sampling periods was more apparent in young than in fully mature females (see Table 4). Thus, there is an indication that the average age of first reproduction was significantly delayed in recent years.

TABLE 2. Sex and age composition of the George River caribou herd in autumn, 1973-86

Date	% males > 1.0 yr	% females > 1.0 yr	% calves	Ratio calves:females > 1.0 yr	N total
10-23 Oct 73 ^a	29.8	45.1	25.1	0.56	2 092
4- 5 Oct 74 ^a	29.1	48.4	22.5	0.46	1 593
4-19 Oct 75 ^a	27.9	47.8	24.3	0.51	24 060
20-31 Oct 76 ^a	24.0	50.9	25.1	0.49	7 619
12-22 Oct 77 ^a	23.8	48.8	27.3	0.56	2 900
1- 8 Oct 78 ^b	36.9	42.6	20.4	0.48	27 769
21-24 Oct 79 ^b	31.3	46.6	22.1	0.47	13 938
23-25 Oct 80 ^b	30.7	44.8	24.5	0.55	9 079
19-20 Oct 81 ^b	29.9	44.6	25.5	0.57	6 338
19-25 Oct 82 ^b	29.5	45.8	24.8	0.54	4 050
24-26 Oct 83 ^b	35.0	43.0	22.1	0.51	7 034
22-24 Oct 84 ^a	28.8	51.6	19.6	0.38	5 527
21-29 Oct 85 ^a	29.2	51.0	19.8	0.39	8 388
30 Oct-10 Nov 86 ^{a,b}	28.7	50.8	20.6	0.41	6 049
\bar{x} (SD)	29.6 (3.5)	47.3 (3.1)	23.1 (2.4)	0.49 (0.06)	

^aNewfoundland-Labrador Wildlife Division, data in files.

^bMin. Loisir Chasse et Pêche du Québec, data in files.

TABLE 3. Age structure of female caribou from the George River herd in spring, 1974-86

Date	% females > 22 mo	% calves 10-12 mo	Ratio calves: females > 22 mo	N total
1- 3 Jun 74 ^a	67.4	32.6	0.48	2 147
5- 7 Jun 75 ^b	74.7	24.3	0.34	3 093
3- 8 Jun 76 ^b	78.1	21.9	0.28	5 287
18-26 Apr 77 ^b	70.4	29.6	0.42	5 988
29 Apr-5 May 78 ^b	73.5	26.5	0.36	4 984
27 May-11 June 78 ^a	83.3	16.7	0.20	11 376
26 Apr-5 May 79 ^b	76.4	23.6	0.31	1 032
7 Jun 79 ^a	65.4	34.6	0.53	684
18-20 Apr 80 ^b	77.4	22.6	0.29	18 999
17-18 Apr 81 ^b	84.9	15.1	0.18	5 128
8- 9 Jun 82 ^a	72.6	27.4	0.38	1 552
14-18 Apr 83 ^b	69.3	30.7	0.44	10 409
26-29 Apr 84 ^b	81.2	18.8	0.23	5 806
8-10 Jun 84 ^a	73.9	26.1	0.35	5 357
13-16 Jun 86 ^{a,b}	57.7	42.3	0.73	1 505
\bar{x} (SD)	73.8 (7.1)	26.1 (7.1)	0.37 (0.14)	

^aMin. Loisir Chasse et Pêche du Québec, data in files.

^bNewfoundland-Labrador Wildlife Division, data in files.

TABLE 4. Pregnancy rate of female caribou from the George River herd in 1980 (Parker, 1981) and in 1983-86

Age at breeding season (yr)	Proportion pregnant (n)	
	1980	1983-86
0.5	0.00(16)	0.00(5)
1.5	0.43(23)	0.11(9)
2.5	0.90(20)	0.70(10)
3.5+	0.95(83)	0.80(39)

Life-Table Analysis

Mortality rate per year was estimated at 28.6% for calves, 5.4% for animals 1-8 yr of age, and 27.6% for older individuals (Table 5). The weighted mortality rate for all females was 13.4%; this figure is also the population turnover rate for females. Adult females (1-15 yr old) had a weighted mortality rate of 11.0%. The l_x schedule was used to compute future life

TABLE 5. Apparent life-table of female caribou from the George River herd following the season of births of 1984

Age x	Sampled frequency f_x	Corrected frequency $f_x e^{rx}(r=0.11)$	Smoothed frequency # F_x	Survival l_x	Proportion dying d_x	Mortality rate q_x	No. female calves per female m_x
0	236.1 \emptyset	236.1	236.1	1.000	0.286	0.29	0.00
1	138	154.0	168.5	0.714	0.007	0.01	0.00
2	156	194.4	167.0	0.707	0.017	0.02	0.06
3	113	157.2	163.0	0.690	0.027	0.04	0.35
4	94	145.9	156.6	0.663	0.037	0.06	0.40
5	83	143.9	147.9	0.626	0.044	0.07	0.40
6	65	125.8	137.3	0.582	0.053	0.09	0.40
7	63	136.1	125.0	0.529	0.057	0.11	0.40
8	57	137.4	111.4	0.472	0.063	0.13	0.40
9	40	107.6	96.6	0.409	0.065	0.16	0.40
10	24	72.1	81.2	0.344	0.067	0.19	0.40
11	18	60.4	65.4	0.277	0.067	0.24	0.40
12	12	44.9	49.5	0.210	0.066	0.31	0.40
13	7	29.2	33.9	0.144	0.064	0.44	0.40
14	1	4.7	18.8	0.080	0.061	0.76	0.40
15	4	20.8	4.4	0.019	0.019	1.00	0.40

Adjusted by a non-linear least-square technique for best fit. The relationship was $\ln(y + 100) = 5.589 + 0.00858(\text{age}) - 0.00475(\text{age})^2$.
 + Data from Table 4 (1983-86); the sex ratio was taken as 1:1 and litter size as one.
 \emptyset Computed as the summation of $f_x m_x$.

expectancy (Downing, 1980:257). Future life expectancy peaked for yearlings (8.6 yr), followed by a gradual decline with age (Fig. 4).

A key parameter in a demographic analysis is the reproductive value of a female as a function of its age. This parameter represents a female's age-specific expectation of producing female offspring in that year and in all future years (Emlen, 1970). The reproductive value reaches its maximum (2.9 at the age of first reproduction (2-3 yr) and gradually declines thereafter (Fig. 4).

Hunting

Human-induced exploitation, through subsistence and sport hunting, has been reviewed recently for the period 1973-83

(Quebec, 1984). Total harvest by the Inuit, Quebec sport hunters, and Labrador residents was best documented in six years (1975-80) when 5700-7700 caribou were killed per year (Table 6). The subsistence harvest of the Naskapi and the Montagnais from Schefferville was estimated at 800 caribou per year in the early 1980s (Quebec, 1984). If we assume an annual harvest of 9000 animals, the exploitation rate is estimated at 3% in the early 1980s.

The total harvest in 1984-86 is not known reliably and may be substantially higher. For example, the recent western range expansion of the herd has made it susceptible to hunting by various native groups along the Hudson Bay coast. Moreover, traditional users from Schefferville, the Ungava Bay region, and northern Labrador are fully aware that the caribou resource is now abundant, thus creating an incentive to intensify hunting for subsistence. The government of Newfoundland-Labrador also initiated an experimental commercial hunt in 1985 that accounted for 270 and 960 caribou in 1985 and 1986. The kill by sport hunters in Quebec increased in 1986 to about 8500 caribou due to more liberal regulations (Table 6). Overall, we best estimate the total harvest in 1986 at 5-7% of the herd.

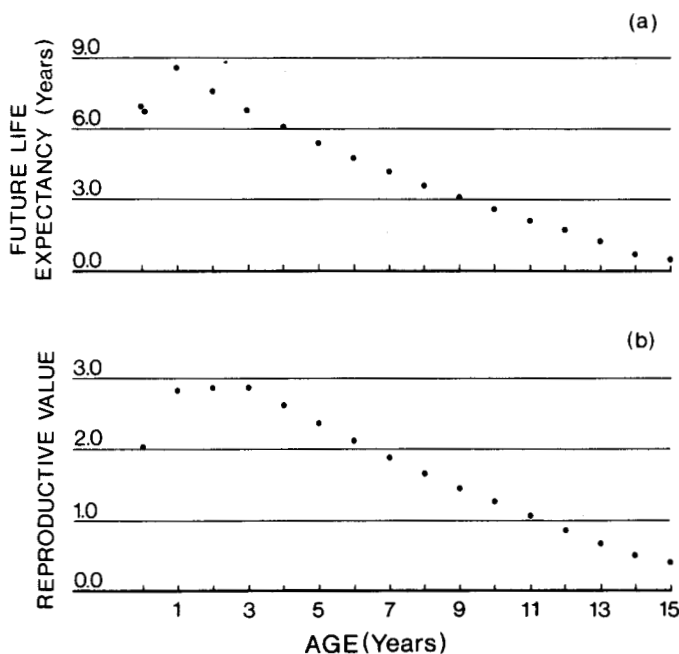


FIG. 4. Age-specific future life expectancy (a) and reproductive value (b) of female caribou from the George River herd in 1984.

TABLE 6. Reported harvest of caribou from the George River herd, 1973-86 (Quebec, 1984, and unpubl. data)

Year	Inuit (Quebec)	Sport hunters (Quebec)	Labrador residents	Total
1973	n.a.	n.a.	2485	> 2 485
1974	3161	n.a.	2230	> 5 391
1975	3478	1331	2230	7 039
1976	2949	1695	1179	5 823
1977	2629	1611	1479	5 719
1978	2662	1893	1627	6 182
1979	2679	2424	2320	7 423
1980	2436	2820	2456	7 712
1981	n.a.	3362	2597	> 5 959
1982	n.a.	2872	3670	> 6 542
1983	n.a.	4022	3415	> 7 437
1984	n.a.	4416	n.a.	> 4 416
1985	n.a.	6054	5871	>11 925
1986	n.a.	8593	n.a.	> 8 593

n.a. = not available.

DISCUSSION

Demography

From 1954 through 1984, the George River caribou herd experienced a rapid and steady growth. From the census data, the rate of increase (r) was estimated at 0.11, with a hunting rate of $\approx 3\% \cdot \text{yr}^{-1}$. Bergerud (1980) reviewed the demography of 30 herds with different wolf densities and hunting harvests and concluded that a rate of increase of this magnitude is expected if both hunting and predation have limited population consequences.

More recently, Bergerud *et al.* (1983) reported on the demography of the expanding Avalon Peninsula herd, Newfoundland ($r = 0.12$). Demographic parameter values of that herd were remarkably comparable to the ones found in this study. For the Avalon and the George River herds respectively, the mean adult sex ratio (M:F) was 64:100 and 63:100; the pregnancy rate of females ≥ 1.5 yr old was 73 and 67%; the calf percentage in the autumn population was 25 and 23%; and the natural adult mortality was estimated at 6% (both sexes included) and 8% (females only; i.e., 11% as calculated from the life-table minus 3% for harvest). Thus, the two herds offer a range of demographic values that may be typical of an expanding caribou population.

Since 1984, the rate of increase of the George River herd may have been reduced appreciably. Although direct supporting data are not available yet, we suggest two factors that are potentially involved. First, calf:female ratios in autumn dropped by about 20% in 1984-86 compared to the recorded levels in 1973-83 (Table 2). Second, hunting for subsistence, sport, and commercial use has been intensified in recent years. In this context, special efforts are being made to document the evolution of the total harvest. Davis *et al.* (1980) gave the example of the Western Arctic herd to illustrate that an originally expanding caribou population could be overharvested when modern techniques of hunting are employed without careful monitoring.

Data on pregnancy rates indicate a 20% reduction between 1980 and 1983-86, with yearlings and 2 yr olds showing the greatest change over the time period. Although a general reduction in pregnancy rate may have occurred, the differences in sampling between the two study periods likely created a bias in the results. In 1980 Parker (1981) collected female caribou when they were approaching the calving ground, whereas the majority (87%) of the females examined in 1983-86 were collected from December through March, before the spring migration. Non-pregnant females are less prone to migrate to the calving ground (Parker, 1972), so that a sample secured near such an area (e.g., Parker, 1981) would overestimate the proportion of breeding females in the herd.

The calf:female ratio in autumn was relatively consistent from 1973 to 1983 ($x = 0.52$), but decreased to about 0.39 in 1984-86. This lower rate of recruitment in recent years may be attributable to lower pregnancy rate (above) and/or greater post-natal mortality. It is not known if perinatal mortality has increased in recent years. Density-dependent food limitation associated with increasing population densities may cause a reduction in pregnancy rate, as well as a lower calf survival in wild reindeer (Leader-Williams, 1980; Reimers, 1983; Skogland, 1985, 1986). Summer weather may also affect calf survival due to differing level of insect harassment (Helle and Tarvainen, 1984).

There was more variability in short-yearling (10-12 months of age) percentage between years than there was in calf percentage the previous autumn. We considered the possibility of an associ-

ation between recruitment rate in spring and calf percentage the previous autumn; the analysis gave inconclusive results. The relationship between the recruitment rate in spring and total snow accumulation the previous winter was also non-significant. It is possible that, for practical reasons, the percentage of short-yearlings is difficult to estimate in April-June. Parker (1972) reported that in spring young of the previous year may form distinct groups, frequently segregated from adult females. There is some field evidence regarding the George River herd that short-yearlings tend to remain at the periphery of the calving ground prior to and during parturition time (D. Le Henaff and S. Luttich, pers. obs.). However, our sampling procedure was not designed to take into account such heterogeneity in distribution. Hence, it may be inappropriate at this stage to estimate overwinter calf mortality from changes in calf:female ratios (e.g., Couturier *et al.*, 1988).

Population Regulation

The density of an ungulate population may influence its demography in various ways: competition for vital resources, rate of predation, social interference, etc. (Clutton-Brock *et al.*, 1985; Messier and Crête, 1985; Skogland, 1985; Sinclair, 1985). Population regulation of caribou, in particular, may involve quite different population processes between biogeographic regions (Bergerud, 1983). We suggest that forage limitations represent the predominant mechanism of population regulation for the George River herd, and probably for other migratory herds in North America. However, three distinct features of caribou habitat interactions should be considered.

The first feature concerns the habitat structure. It is generally accepted that terricolous lichens represent the predominant forage resource for caribou (Miller, 1976; Skogland, 1984; Thomas and Hervieux, 1986). Lichens typically grow at a rate of 3-5 mm·yr⁻¹ (Pegau, 1968), so that the standing crop represents an accumulation of many decades of annual production. Under such habitat structure, the rate of increase of caribou population cannot be closely cued to the *annual* production of plant biomass, a prerequisite for long-term stability of plant-herbivore system (Caughley and Lawton, 1981). That is, any forage requirement exceeding the annual production of lichens would be compensated for by an exploitation of the lichen biomass "stored" in the standing crop. Consequently, an immediate feedback mechanism is not likely to be operative when a caribou population rapidly increases. True habitat limitations would become effective when the overall demand for lichens substantially exceeds the annual production of the habitat. Caribou-lichen interactions have the strong delayed density-dependent attributes that can promote population fluctuations (Klein, 1968; May, 1973; Gaare and Skogland, 1980). The relative high density of caribou in northern Quebec/Labrador in the turn of the century, followed by the seemingly rareness of caribou in 1920-30s, and the current rapid population increase, is consistent with this general interpretation.

The second feature of caribou-habitat interactions concerns range expansion by caribou (Fig. 3; Bergerud *et al.*, 1983). We still do not know what precise factors trigger the use of a greater range commensurate with increasing caribou numbers. Forage depletion or some form of social facilitation (Duquette and Klein, 1987) may prompt caribou to cover greater distances as the herd increases in size. Greater locomotion has an incremental cost in terms of energy expenditure (Fancy and White, 1986), and potentially in terms of reproduction and winter survival.

Consequently, range expansion *per se* may have a regulatory impact if total energy expenditure rises with herd size due to more extensive annual migrations. Even more important, range expansion may delay response to food limitations; the use of new ranges would provide additional forage, even if food resources are overexploited in the previously used habitats. Thus, food limitations will become apparent mainly when new ranges can no longer be colonized.

The third feature concerns the summer habitat. For most ungulate species living in a northern environment, food constraints are believed to be minimal in summer, because forage is normally readily available during the growing season. Moreover, summer habitats are often more extensive than the winter habitats. For caribou of the George River herd, summer habitats rather than winter ones appear to be particularly constraining in terms of foraging. The tundra plateaus along the Labrador Sea have been traditionally used over the years during June through August, seemingly because of dominant winds reducing insect harassment. Although not documented, this annual concentration of the herd in a relatively small proportion ($\approx 15\%$) of their annual range may have created high grazing pressure on the preferred plant species. The relatively low fat reserves of caribou in autumn (Huot and Goudreault, 1985; Messier *et al.*, 1987) and the earlier abandonment of the Labrador plateaus in recent years indicate that caribou are nutritively stressed in summer (Couturier *et al.*, 1988). In that context, caribou-habitat interactions may be especially critical in summer, because alternative ranges with similar characteristics in terms of wind exposure cannot be colonized following an increase in population size. This situation contrasts with the prevailing pattern in winter, where range expansion creates access to new foraging sites. Winter habitats do not appear to be limited in area, and indeed are much more extensive than summer habitats.

Bergerud (1980, 1983, 1985; Bergerud *et al.*, 1984) suggested that many caribou populations in North America are regulated by wolves. His hypothesis was originally presented in terms of space requirements (see Bergerud *et al.*, 1983:997). The implied predictions of Bergerud's hypothesis are that 1) the rate of predation increases with caribou density, 2) that wolf predation is sufficiently strong to halt population growth of caribou at densities near $0.4 \text{ caribou} \cdot \text{km}^{-2}$, and 3) that caribou are not food stressed at that threshold density.

Our data do not support the predation regulation hypothesis. The density of caribou of the George River herd exceeded by at least twofold the density of $0.4 \text{ animal} \cdot \text{km}^{-2}$. Wolves did not halt the growth of this herd even with the absence of any predator control program. There is no evidence that exploitation of wolves by native people is sufficiently strong to potentially maintain wolves at low densities (Parker and Lutich, 1986). Calf recruitment in autumn did not decline as caribou density was approaching $0.4 \text{ animal} \cdot \text{km}^{-2}$ (Fig. 5). Without observing such a general decline, it is difficult to argue that predation could be density dependent, and therefore be a regulatory mechanism. Calf recruitment did decline after 1984 (Table 2), but after some form of food limitation was apparent (Couturier *et al.*, 1988).

Two reasons may explain the relatively low abundance of wolves in northern Quebec/Labrador in association with the George River herd. First, there is no other ungulate species in this area that could sustain an expanding wolf population. Second, long-distance movements of caribou may prevent wolves from increasing because migrating caribou would become inac-

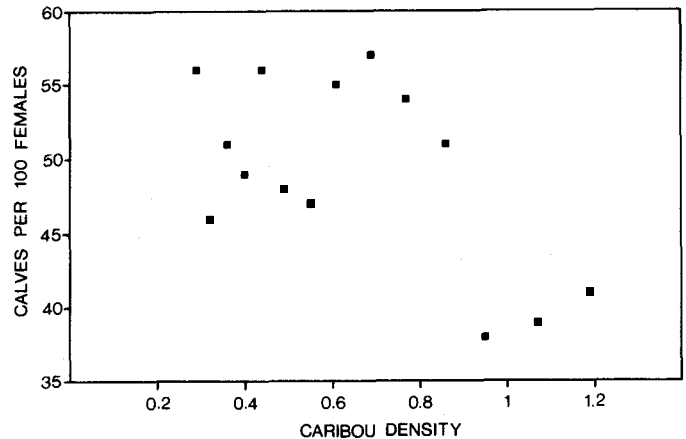


FIG. 5. Changes of calf:female ratios in autumn as a function of caribou density for the George River herd 1973-86.

cessible during the 4-5 months of wolf pup sedentariness in summer. Thus, long-distance migration of caribou can be interpreted as an effective antipredator strategy. In a spatially similar situation, large predators in the Serengeti ecosystem (Tanzania) also have minimal influence on the demography of migratory ungulate species (Sinclair, 1979). We conclude that the current expansion in numbers of the George River herd does not represent an anomaly of the predation regulation hypothesis, but may represent the norm for large barren-ground caribou populations not controlled by human hunting.

Although we suggest that wolf predation is not a regulatory factor for the George River caribou herd, such mortality factors should not be judged unimportant. Wolves are present in northern Quebec/Labrador and they use caribou as food sources (Parker and Lutich, 1986). Wolf predation may become particularly important if the caribou population eventually decreases. Both Keith (1974) and Gasaway *et al.* (1983) stressed that predators generally have an antiregulatory effect on prey numbers during a population decline. Thus, wolf predation rate should be expected to increase during a decline of a caribou population.

Management Implications

The possible deterioration of foraging habitats at high caribou densities may pose a threat to the George River caribou herd. Caughley and Lawton (1981) stressed that a rapid rate of increase of an ungulate population may generate a severe overshooting of the range carrying capacity if there is a time delay between food availability and food limitation on the population. We have stressed that both caribou-lichen interactions and range expansion may generate a time lag response. In addition, the vegetation recovery time following habitat degradation may be in the order of decades regarding caribou habitats. Overshooting of K carrying capacity (see Macnab, 1985) is a function of both the duration of the time lag and the initial rate of population increase (May, 1981). In Figure 6, we present the population projection of four hypothetical caribou herds assuming a logistic growth model based on food supplies and a time lag (T) of 20 years (a conservative estimate from our point of view). With an initial rate of increase of 0.10, the population would reach a density level of $3K$ before going through a catastrophic decline. A more

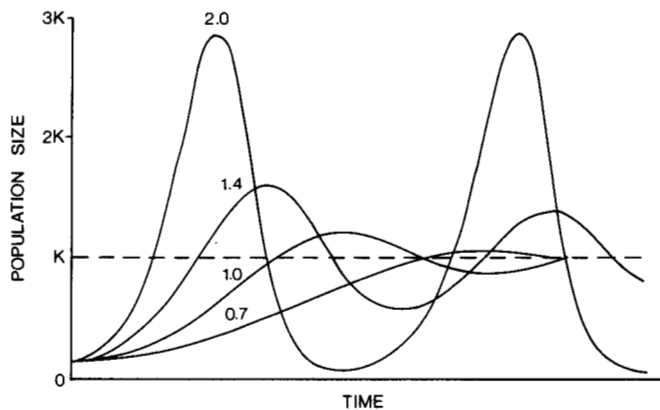


FIG. 6. Projected population size of a caribou herd assuming density-dependent food limitation (i.e., a logistic growth model) and a time delay (T) of 20 years for four different rates of increase (r): 0.10, 0.07, 0.05, 0.035. The overall model was $dN/dt = rN[1 - N(t - T)/K]$, where N is the population size and K the food carrying capacity. The values above the curve represent $T \times r$, a parameter determining the degree of overshooting of K .

acceptable adjustment at high densities would occur if $T \times r$ is smaller than 0.7, i.e., a rate of increase of 0.035 for a time lag of 20 years. This simplistic population model suggests that a reduced rate of increase, possibly by the manipulation of hunting, may be beneficial to the herd by favoring a smoother adjustment between available forage resources and food requirements by the herd.

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