

Characteristics of the Wolf (*Canis lupus labradorius* Goldman) in Northern Quebec and Labrador

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ABSTRACT. Two hundred and twelve wolves (*Canis lupus labradorius*) shot by hunters in northern Quebec and Labrador during the winters of 1976-77 through 1983-84 were examined for various population parameters. An estimated annual adult survival rate of 55% and a recruitment rate of 49% suggest a population of moderate exploitation. The sex ratio did not differ significantly from 1:1. Fifty-five percent of yearling females were pregnant or in breeding condition. The average litter size for all females was 6.8. Internal fat deposits were greatest in young males and older females. Caribou (*Rangifer tarandus caribou*) was the most common food item found in stomachs. A sample of caribou killed by wolves in the winter showed a selection for older-aged caribou with fat deposits slightly below that of the general population.

Key words: wolf, caribou, northern Quebec, Labrador, predation

RÉSUMÉ. Un total de 212 loups (*Canis lupus labradorius*) tirés par des chasseurs dans le nord du Québec et au Labrador au cours des hivers de 1976-77 jusqu'à 1983-84 furent examinés afin d'établir divers paramètres relatifs à la population. Un taux de survivance annuel de 55% pour les adultes et un taux de recrutement de 49% suggèrent une exploitation modérée. Le taux de différenciation sexuelle ne s'éloignait guère de 1:1. Cinquante cinq pour cent des femelles âgées d'un an étaient enceintes ou en condition apte à la reproduction. La portée moyenne était de 6.8. Les dépôts de graisse interne paraissaient en quantité maximale chez les jeunes mâles et les vieilles femelles. Le caribou (*Rangifer tarandus caribou*) était la nourriture la plus communément trouvée dans les estomacs. Un échantillonnage de caribous tués par des loups durant l'hiver signala la sélection de caribous plus âgés avec des dépôts de gras quelque peu inférieurs à ceux de la population générale.

Mots clés: loup, caribou, nord du Québec, Labrador, activité prédatrice

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INTRODUCTION

The caribou (*Rangifer tarandus caribou*) of northern Quebec and Labrador, commonly referred to as the George River herd, represent one of the largest (~600 000 in 1984) and most rapidly expanding populations in North America. Cooperative research and management programs between Quebec and Newfoundland are directed toward averting a population decline, i.e., increasing annual harvests and reducing population growth. The George River population has increased 100-fold over the past 28 years (only 5100 caribou were estimated in 1956 by Banfield and Tener, 1958).

The factors contributing to natural control in the growth of free-ranging caribou populations are complex and contentious. Bergerud (1983) provided a summary of the theories relative to numerical control of caribou populations. He suggested that the primary means of control differs among biomes and that predation is the most frequent and consistent means of population control in the boreal forested regions of North America.

The most important predator of caribou other than man is the wolf (*Canis lupus*). Although considerable attention has been given to understanding the population dynamics of the George River caribou population (Parker, 1981), the wolf of northern Quebec and Labrador (*C. l. labradorius*) has been largely ignored. By 1958 the wolf in northern Labrador had been rare for 40-50 years (Bergerud, 1967). An increase in wolves was a natural and expected result of the increase in caribou numbers and is consistent with the predation control hypothesis presented by Bergerud (1983). However, as stated by Bergerud (1983), the failure to date for wolves to halt the rapid expansion of that population may disprove his predation limitation hypothesis.

Other than references to the description and records of several specimens of *C. l. labradorius* (Goldman, 1937; Anderson, 1943; Young and Goldman, 1944; Harper, 1961), there are no

quantified data in the literature describing any aspects of the ecology or population dynamics of the subspecies.

As part of the cooperative federal-provincial study of the George River caribou population, wolf carcasses were collected by the Newfoundland-Labrador Wildlife Division from hunters in various settlements within the range of that population. Canadian Wildlife Service was asked by the province of Newfoundland to examine the carcasses. This article reports on the examination of 212 wolf specimens collected from within the range of the George River caribou population during the winters of 1976-77 through 1983-84. Eighty-one of those specimens represented intact carcasses, the remainder skulls only.

Data were also collected from caribou killed by wolves. Information relative to the health of the caribou population is a result of a collection of caribou in spring 1980 (Parker, 1981).

METHODS

Wolf specimens were collected from hunters of the communities of Kuujuaq and George River, Quebec, and Nain, Labrador. Most wolves were shot by residents of those communities while hunting caribou. Several were shot near settlements or hunting camps. All specimens were frozen and transported to Goose Bay, Labrador. To facilitate transport, external measurements were taken of some prior to shipment (legs were then removed and in the case of males in 1982-83 and 1983-84 only the skulls were shipped to Goose Bay for aging).

Information on reproduction, diet and condition is from 136 wolves examined from 1980-81 through 1983-84; 43 stomachs from that sample were examined for food items. Teeth from an additional 76 skulls collected from 1976-77 through 1979-80 were used for overall age structure analysis.

Body weight is that of the skinned carcass. Total body length was from tip of the nose along the dorsal side to base of the tail

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(tails were missing from most carcasses). Two internal fat deposits were removed and weighed. They were: sternum, the pad of fat on the posterior end of the sternum; and, abdominal, the fat along the dorsal wall of the body cavity from the anterior end of the kidneys to the cavity formed by the pelvic girdle and vertebral column. Total fat weight was converted to a body fat index to minimize bias from differential body weights.

$$\text{fat index} = \frac{\text{fat weight (g)}}{\text{carcass weight (kg)}}$$

The lower right canine tooth was removed. Teeth with open root pulp canals were classified as pups. Teeth with closed roots were sawed in half at the gum line. The root portion was decalcified, and stained sections were mounted on slides. Sections were examined for cementum annuli. Ages were assigned by adding 1.5 years to the number of annuli (Matson, 1981). A second canine was removed from those specimens that had the root foramen closed but showed no discernible annuli. These teeth were also severed in half at the gum line. Measurements were taken of dentine thickness and maximum pulp cavity width. From a statistical analysis of those measurements it was determined that approximately one-half of those specimens with a closed root apical foramen, but no cementum annuli, were <1 year old (see Parker and Maxwell, 1986 — this issue). Those wolves would have been collected in late winter or early spring (February-April). The remaining specimens were aged as 1.5 years old.

Reproductive tracts were examined macroscopically for placental scars and embryos. Stomach contents were washed and examined for food remains. Food items were separated, identified to individual prey species, and weighed (wet weight) to the nearest gram.

Marrow fat values from femurs of wolf-killed caribou were determined by the dry-weight method (Neiland, 1970).

RESULTS AND DISCUSSION

Age Structure

Seventy-four percent of the sample was aged at 1.5 years old or less (Table 1). Forty-nine percent of the sample was <1 year old and only 7.5% was >4 years old.

We used the Chapman-Robson method (in Eberhardt, 1969) for estimating survival and age-class compatibility. First year survival (53%) was not compatible with survival in the older age classes ($\chi^2 = 86.98; p < 0.001; df = 1$). A survival rate of 55% for the 1.5 year and older age classes was compatible with the assumption of a constant survival rate ($\chi^2 = 1.99; p > 0.05; df = 1$). A second test of compatibility compared observed and expected relative frequencies by age class assuming the calculated survival rate (i.e., 55%) was correct (Eberhardt, 1969). The resulting χ^2 value of 3.95 with 5 degrees of freedom supported a survival rate of 55% for all adult (1.5 years and older) age classes.

A composite life table was constructed (Table 2) showing the age structure of the population with the usual assumptions relative to the dynamics of that population (e.g., unbiased sample, stable population, etc.). Following the approach by Mech (1970) and assuming a) an equal adult sex ratio, b) a breeding rate for females 1.5 years and older of 60%, and c) a mean litter size of 6.8, young wolves experience a first-year survival of 55%, identical to survival of older age classes. Earlier tests of age class compatibility found first year survival

TABLE 1. The sex and age structure of 212 wolves collected in northern Quebec and Labrador during the winters 1976-77 through 1983-84

Age (yr)	Number of specimens			Total	% of sample
	Male	Female	Unknown		
0.5	20	21	63	104	49.1
1.5	15	10	28	53	25.0
2.5	6	8	6	20	9.4
3.5	2	2	15	19	9.0
4.5	2	3	1	6	2.8
5.5	2	1	1	4	1.9
6.5	1		1	2	0.9
7.5			2	2	0.9
8.5					
9.5			1	1	0.5
10.5	1			1	0.5
Totals	49	45	118	212	100.0

TABLE 2. A composite life table (after Caughley and Birch, 1971) from the age distribution of wolves collected in northern Quebec and Labrador, 1976-77 through 1983-84

Age (yr) (x)	Sample size (f _x)	f _x Σf _x (d _x) ^a	Σ _x d _x (l _x) ^b	d _x l _x (q _x) ^c
0.5	104	0.49	1.00	0.49
1.5	53	0.25	0.51	0.49
2.5	20	0.09	0.26	0.35
3.5	19	0.09	0.17	0.53
4.5	6	0.03	0.08	0.38
5.5	4	0.02	0.05	0.40
6.5	2	0.01	0.03	0.33
7.5+	4	0.02	0.02	1.00

^ad_x = probability at 0.5 yr of dying in age interval x, x + 1.

^bl_x = probability at 0.5 yr of surviving to age x.

^cq_x = probability at age x of dying before age x + 1.

of 53%, slightly less than the average adult survival. The margin for error in these calculations is such that calculated mortality and rates of survival must be considered approximate only and statements on population change (r), positive or negative, can be estimates only.

The representation of pups in winter in unexploited wolf populations normally ranges from 13% (Kelsall, 1968) to 20% (Fuller and Novakowski, 1955) and in exploited populations from 35% (Pimlott *et al.*, 1969) to 55% (Fuller, unpubl. data). Statistics from this sample from northern Labrador and Quebec (i.e., 49% pups; 55% annual adult survival) suggest a population of moderate exploitation (Mech, 1970).

Sex Ratios

There was little variation from a 50:50 sex ratio for all age classes (Table 1). The exception was the yearling class (1.5 years old) for which from a sample of only 25 the male:female ratio was 75:50. However, the overall ratio of the 94 specimens of known sex was 54:50. The slight bias toward males for the total sample is typical of most wolf populations studied in North America (Mech, 1970). In Finland, Pulliainen (1965) found that an extreme bias toward males was associated with the tendency for males to immigrate into unoccupied range; sex ratios approach equality on established breeding range. We conclude that the wolves in the sample from northern Quebec and

Labrador represented established breeding populations with sex ratios approaching 1:1.

Reproduction

Thirty-four female reproductive tracts were examined for evidence of embryos or placental scars. Twelve were from females <1 year old; all were small and showed no evidence of precocial breeding. Of 10 females aged 1.5 years, 4 tracts were similar to those of pups, one was pregnant with 9 embryos and 5 had enlarged uteri. The latter were presumed to be in early stages of pregnancy or in breeding condition. All 12 uteri from females 2.5 years or older were enlarged. Seven contained either embryos or scars from previous pregnancies. Scars were not apparent in 5 of the 12 tracts. The mean number of scars and embryos was 6.8 (s.d. = 2.2; range = 4-10).

This sample suggests a breeding rate of 60% for yearlings (22 months). In Alaska, Rausch (1967) reported that ovulation by pups (8 months old) was extremely rare and that first breeding normally occurred at 22 months. Other references also suggest that breeding first occurs in the second year for captive wolves (Murie, 1944; Young and Goldman, 1944; Garceau, 1961; Pulliainen, 1965). Mech (1970) compiled average litter sizes for wolves in North America and Finland, and those averages ranged from a low of 2.8 in Finland (Pulliainen, 1965) to 6.5 in Alaska (Rausch, 1967), less than the average of 6.8 in this study.

Body Size and Condition

Male and female wolves reached adult body weight and length toward the end of their second year (Fig. 1a). Due to a large variance in weights for the 1.5 year class, differences between means for those two age classes were not significant. Differences between means for the 0.5 and 2.5 year classes were significant for both males ($t = 5.43$; $p < 0.005$) and females ($t = 2.14$; $p < 0.05$). Although female weights were slightly higher than males for the 0.5 year class, male weights were higher for the older classes (between sex differences not significant).

Wolves also reached adult body length by the end of their second year (Fig. 1b); differences in lengths between the first two age classes were significant for males ($t = 2.65$; $p < 0.02$) and females ($t = 2.85$; $p < 0.01$). Males were longer than females for all age classes, although not significantly so.

The two indices of physical condition (internal body fat) showed similar trends for males — i.e., maximum values for 1.5- and 2.5-year-old animals (Figs. 1c, d). In contrast, body fat index values for females were highest in the oldest age class (3.5 year +). Between-sex differences were significant only for the sternum fat index within the 3.5 year and older age class ($t = 2.52$; $p < 0.05$), which suggests that most young males are still with the pack at 1.5 years, share in the kill with the other pack members, and mobilize high body fat reserves. In later years, however, many males leave the family pack and, through competition for territory and social dominance, body condition declines. Only the alpha males would presumably maintain high body fat indices. It is also probable that wandering adult male wolves without established territories are more prone to mortality by hunting and that this sample contains few alpha males with high body fat reserves.

Females, due to the dominant status associated with breeding and raising of young, maintain an important role in the pack and sustain or increase body fat with age. The condition indices suggest that most older females in this sample were established alpha females within the pack.

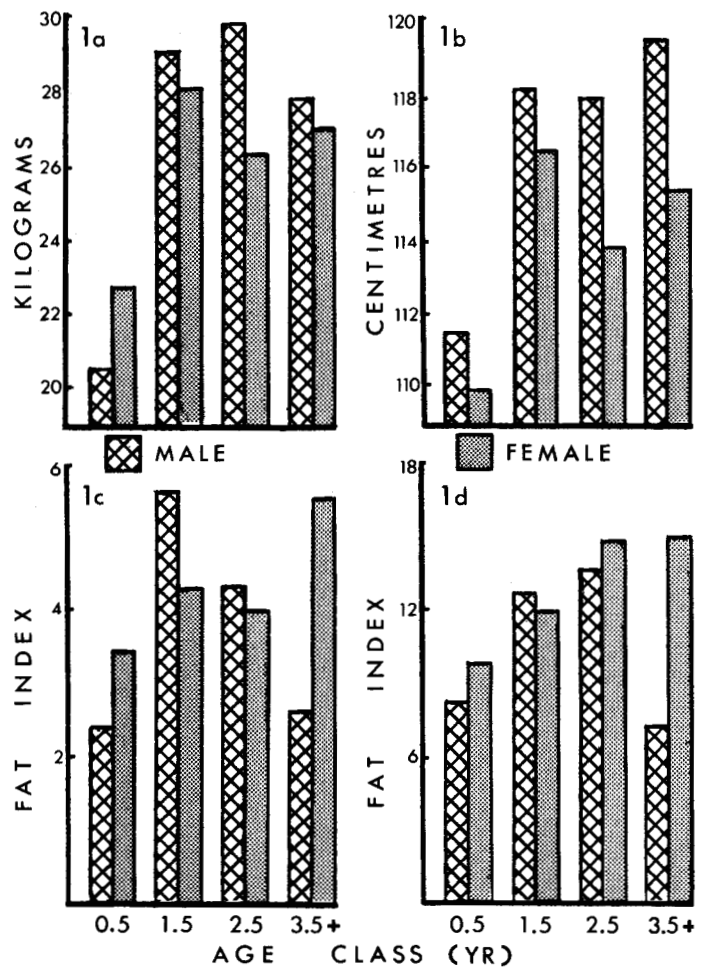


FIG. 1. Mean body measurements of wolf carcasses collected in northern Quebec and Labrador, 1980-81 through 1983-84: (a) carcass weight, (b) carcass length (to base of tail), (c) sternum fat index, (d) abdominal fat index.

Winter Diet

Stomach analysis. Fifty-three wolf stomachs were examined for food item identification: 10 (18.8%) of the stomachs were empty. Of the 43 samples analyzed with identifiable food items in them (Table 3), caribou was the most important in frequency of occurrence (86%).

Although the wolf is an opportunistic predator, the dependency of wolves upon caribou during winter in northern Quebec and Labrador is apparent. This close relationship between wolf and caribou is in agreement with studies in other regions of northern Canada (Kelsall, 1968; Kuyt, 1972).

TABLE 3. The percent frequency occurrence of food items in 43 wolf stomachs collected in northern Quebec and Labrador during the winters of 1980-81 through 1983-84

Food items	Number of stomachs	Frequency of occurrence (%)
Caribou	37	86
Red fox	3	7
Seal	2	5
Raven	1	2
Total	43	100

Wolf-Killed Caribou

Sex and age structure. During late winter aerial surveys of the George River caribou population in 1981-82 and 1982-83, 59 caribou presumably killed by wolves were found. The ages of 49 of them were determined by tooth eruption for calves (0.5 year) and yearlings (1.5 years) and a count of tooth cementum annuli for those caribou 2.5 years and older. Sex was determined for 45 of the carcasses.

In April 1980, 159 caribou were collected from the spring migration of the George River population near Nain, Labrador (Parker, 1981). The 1980 collection was considered a random sample of the age structure of the adult female-juvenile component of the population. Although caribou carcasses were collected throughout the wintering range of the George River population, the representation of age classes in the 1980 sample is used here as the expected age structure within the sample of wolf-killed caribou.

A Chi-square analysis showed that caribou ≥ 8.5 years old were overrepresented in the wolf-killed sample ($\chi^2 = 17.50$; $p < 0.005$). The young age classes (several were combined to increase individual cell size to five or more) were underrepresented, but not significantly so. A graphical depiction of the two samples is shown in Figure 2.

Miller (1974) provides sex and age structure data for the Kaminuriak Population from 1966 through 1968. A Chi-square test shows no significant difference in representation of the three age classes < 1 year, 1-7 years, and 8 years+ between the Kaminuriak sample and that from the George River population (Parker, 1981) ($\chi^2 = 2.19$; $p > 0.05$; $df = 4$).

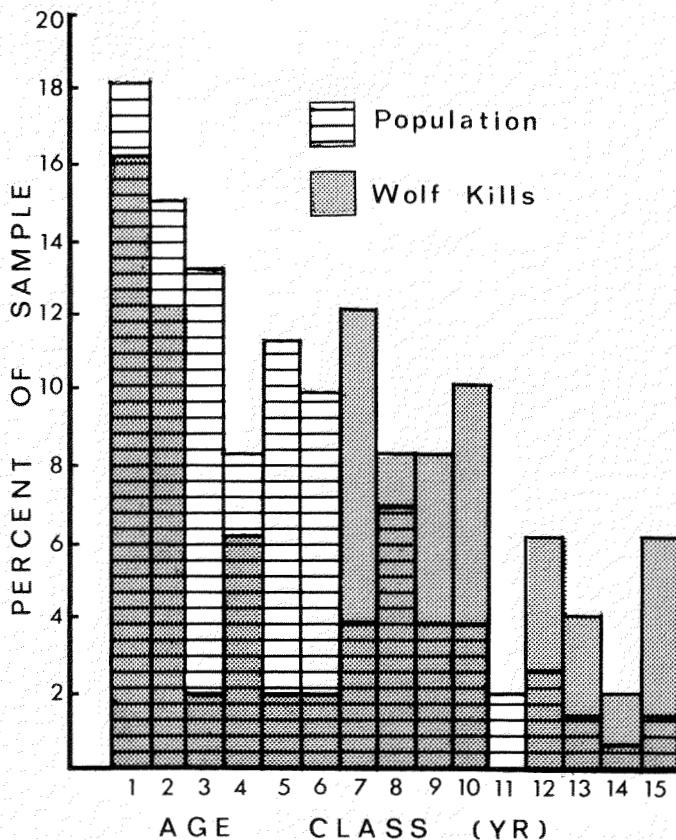


FIG. 2. Distribution of George River caribou by age class within a sample collected in spring 1980 (population) and within a sample of wolf-killed caribou collected in the late winters of 1981-82 and 1982-83.

However, a comparison of the age structure of wolf-killed caribou for the same three age classes between the two regions gave a different result ($\chi^2 = 60.5$; $p < 0.001$; $df = 4$). In northern Manitoba, Miller (1975) found only 6.8% of a wolf-killed sample ≥ 8 years old, while in Quebec-Labrador that age class represented 37.2% of the sample. The proportions of calves in this study and that by Miller (1975) were 11.6% and 18.0% respectively ($\chi^2 = 0.94$; $p > 0.05$; $df = 1$). Differences in representation of caribou 1-7 years old in the wolf-killed samples between the two studies was not significant ($\chi^2 = 3.28$; $p > 0.05$; $df = 1$).

The male:female ratio of the wolf-killed sample was 57:50. By age group the sex ratio was: 0.5-3.5 years = 75:50; 4.5-8.5 years = 64:50; 9.5-14.5 years = 50:50. The sex ratio favouring males in the younger cohorts reached equality for the older age classes.

Physical condition. The percentage fat in femur marrow was determined for 29 wolf-killed caribou. The percentage marrow fat values by caribou age class were: 0-1 year — 77.2%; 1-2 years — 86.9%; 2-5 years — 92.7%; 5-9 years — 75.2%; 9-15 years — 78.0%.

Compared to age-specific marrow fat values from healthy caribou collected in Labrador in spring 1980 (Parker, 1981), values for wolf-killed caribou were slightly high for the three younger age classes ($p > 0.05$) but significantly lower for caribou ≥ 9 years old ($t = 2.20$; $p < 0.05$; $df = 31$). The data suggest that wolves selected for older caribou and the physical condition of the selected prey was below that of the majority of the adult population. For younger caribou the size of prey rather than condition is probably the most important factor motivating a chase by wolves.

CONCLUSIONS

In the past 15 years, the George River caribou population of northern Quebec and Labrador has experienced a rapid expansion in total numbers and home range. The situation represents an anomaly relative to the predation limitation hypothesis (Bergerud, 1983). Wolf densities have not yet attained the capability of reducing recruitment below the rate of annual mortality.

This study shows that the productivity of wolves within the range of the George River caribou is high. Over one-half of females breed in their second year and the number of young per litter is high. Although statistics suggest that wolves in northern Quebec and Labrador represent a population of moderate exploitation, the high rate of productivity should ensure population growth. Although the representation of calves in the wolf-killed sample of caribou was not significantly different from that in the population, calves may be underrepresented in the sample because of their small size, greater use by wolves and subsequent rapid obliteration from view. Wolf-killed caribou in this study were first observed from aircraft; many had been dead for a considerable time.

Representation of old caribou (≥ 8 years), however, is significantly greater than in the 1980 spring sample and the wolf-killed sample from the Kaminuriak population. These data suggest that wolves within the range of the George River caribou population are selecting for older caribou and killing calves at least in proportion to, and probably higher than, their availability.

As wolf densities increase in response to increasing prey

availability, selection for calves may also increase. A switch from older caribou to calves commensurate with increasing caribou and wolf densities agrees with Bergerud's predation control hypothesis.

The calving grounds for most northern mainland caribou populations, especially the George River population, are not prime wolf denning habitat. This may explain why such areas have been selected for calving by northern mainland caribou populations. The prime denning areas for northern wolves is near the treeline. It is at the treeline that wolves are without caribou for the shortest period of time. As wolf populations increase, more subadult (non-breeding) wolves may follow the migrating caribou farther onto the tundra toward the calving grounds. More wolves on the calving area would mean more predation upon young calves (Miller and Broughton, 1974).

An increase in wolves and increased predator-prey contact at all seasons would increase predation upon caribou <1 year old. This scenario agrees with the predation limitation hypothesis. However, with a caribou population now approaching 600 000 animals and estimated rates of recruitment far exceeding estimated mortality, it seems unlikely that wolves alone will be responsible for termination of population growth. As both provinces are now considering commercial harvesting of caribou, thus substantially increasing mortality inflicted by man, the combined increased predation by man and wolf may succeed in controlling the growth of the George River population. Unchecked growth of caribou populations on islands with no predation by wolves or man leads to range deterioration and swift reductions in population size through depletion of available forage. This control of caribou numbers by the "food limitation hypothesis" has not been observed in free-ranging "continental populations."

The George River situation represents a unique opportunity to monitor the response of an expanding caribou population to increased predation by wolves and man.

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