Population dynamics of the Kaminuriak caribou herd, 1968 - 1985

Douglas C. Heard[1] and **George W. Calef**[2]

Abstract: The Kaminuraik caribou herd apparently declined from about 120 000 animals in 1950 to 63 000 in 1968. Beginning in 1968 documentation of herd trend was based on the estimate of the number of breeding (pregnant and post-partum) females on the calving ground during the birth peak. It appeared as if we understood the basic population processes responsible for the decline when we correctly predicted a drop from 14 800 breeding females in 1977 to 13 000 in 1980. However a three-fold increase, to 41 000 breeding females in 1982, and continued growth thereafter, was unanticipated. Most of that increase must have resulted from an immigration of cows to the herd's traditional calving ground around Kaminuriak Lake, although increased birth rates, and increased survival rates also contributed to herd growth. Immigrant cows probably came from the northeastern mainland of the NWT.

Key words: caribou (*Rangifer tarandus*), Kaminuriak herd, N.W.T., numbers, composition, hunting, predation

[1] Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada, X1A 2L9.
[2] Department of Wildlife and National Parks, Box 11, Maun, Botswana

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Introduction

The Kaminuriak caribou herd (KCH) is the easternmost of the four great herds of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) inhabiting Canada's Northwest Territories (NWT) (see Williams and Heard 1986). The KCH's traditional range encompasses the southern Keewatin District NWT, northern Manitoba and northeastern Saskatchewan and the herd calves near Kaminuriak Lake, NWT (Parker, 1972; Simmons *et al.*, 1979; Heard, 1983a).

Size of the KCH was estimated to be 120 000 in 1950 (Banfield, 1954), 149 000 in 1955 (Loughrey unpublished data) and 63 000 in 1968 (Parker, 1972). This paper describes changes in herd size, sex ratio, age composition, hunting pressure and wolf abundance between 1968 and 1985.

Methods

Four methods have been used to estimate size of the KCH since 1968 (Heard, 1985): 1) range-wide transect strip samples, 2) calving ground transect strip samples, 3) aerial photographic strip samples of calving grounds and 4) aerial photography of post-calving aggregations. The range-wide transect strip survey was conducted in March and April 1977 by Thompson and Fischer (1979). Transect strip surveys of the calving ground where caribou were counted visually were conducted in 1974 (Hawkins and Howard, unpublished data), 1976 (Calef and Hawkins, 1981), 1977 (Heard, 1981), 1980 (Heard, unpublished), 1983 (Gates, Heard and Kearney, unpublished) and 1985 (Heard and Stenhouse, unpublished). Photographic surveys of the calving ground were carried out in 1983 and 1985 and post-calving aggregations were

photographed in July 1983. The senior author participated in all surveys after 1974 except the 1977 winter survey by Thompson and Fischer (1979) and the 1982 calving ground survey by Gates (1985). Extrapolation of total herd size from calving ground estimates followed the method described by Heard (1985). All population estimates refer only to those animals 1-year-old and older and breeding females refers to pregnant and post-partum cows on the calving ground.

Herd composition was estimated in November 1979 and 1981, annually in April from 1979 through 1985 and on the calving ground each year a survey was conducted except for 1974 and 1976. Only calves (caribou less than 1-year-old) were distinguished from other caribou in November 1979 and in April 1980 and 1981 but during all other composition surveys the sex of all caribou over 1-year-old was also recorded. Observers recorded the presence or absence of distended udders on all females seen during calving ground composition counts. Classification was done primaily from the ground with the aid of a spotting scope but some samples also included observations made from fixed-wing aircraft (Nov 1979, Apr 1980, Apr 1981) and helicopters (Jun 1985).

The reporting year for hunter kill began in the summer, usually 1 July. In the NWT, kill estimates were based on annual interviews with each hunter from 1968/69 through 1975/76. In 1975/76 monthly interviews began in Eskimo Point and by 1979/80 they were carried out in all settlements (Gamble, 1984; Gates, 1985). Data were incomplete from 1976/77 through 1978/79. In Manitoba, the estimated kill was based on best guesses made by government biologists until 1976 when in each community a resident was hired to interview hunters when they returned from the field (Kearny, pers. comm.).

Results and discussion

Numbers

Between 1968 and 1980 the number of breeding females on the calving ground near Kaminuriak Lake declined from 22 000 in 1968 (Parker, 1972) to 13 000 in 1980 (Table 1). The 1982 estimate was more than three times higher than in 1980 and the 1983 and 1985 visual surveys confirmed that there had been a big increase and indicated that herd size was probably growing.

If visual calving ground surveys accurately indicated herd trend, as we believe they did, then all breeding females must have been included in the census zone each year and the variation in sightability among surveys must have been low relative to the actual change in numbers. We did extensive reconnaissance, that covered at least the areas used for calving in previous years, to ensure that the census zone was large enough to include almost all breeding females. For example, in 1980 we flew 11.3 h (1800 km) within a 25 000 km^2 area to define a census zone only 50 kmx50 km. In most years tracks in the snow helped to locate animals but there was always a possibility that some breeding females were missed.

Calving ground photography in 1983 and 1985 yielded estimates of 71 000 and 97 000 breeding females respectively (Table 1). The corresponding visual estimates were 31 000 and 50 000. Surveys of other calving grounds also indicated that density estimates based on photographic counts were about twice as high as those obtained visually (Heard, unpublished data). Thus the variation in sightability was probably low, at least relative to the increase in numbers between 1980 and 1982.

The four estimates not based on calving ground surveys were consistent with the calving ground data; showing a decline between 1968 and 1977 and an increase between 1977 and 1983 (Table 1).

Composition

The age ratio of the herd changed drastically with the 1979 cohort. The proportion of calves in the fall of 1979 and spring of 1980 were twice as high as earlier estimates and calf percentages remained high thereafter (Table 2). Problems with sampling to determine composition existed because age and sex classes were segregated, especially in the spring, but the magnitude of the change and the consistency of the results among seasons and from year to year suggest that there was a real increase in the proportion of calves. High calf proportions in the fall of 1979 and 1981 corresponded to high calf percentages the following springs and April calf percentages were positively correlated with the number of 12-month-old caribou on the calving ground ($r=0.66$, $n=5$). The abundance of yearlings on the calving ground was especially noticeable in 1980 when the calving ground estimate increased

Table 1. Kaminuriak caribou herd population estimates 1968 to 1985

Year	Calving ground estimate			Total herd size	Comments	Source
	Total	(±SE)	Breeding females			
1968	27 000	(± 4 500)	22 000	63 000		1
1968				51 000	Jan-Apr surveys	1
1968				40 000	post-calving photo	1
1974	23 000	(± 3 600)		54 000		2
1976	18 900	(± 2 800)		44 000		3
1977				31 000	March-April survey	4
1977	16 500	(± 1 940)	14 800	44 000		5
1980	20 000	(± 1 260)	13 000	39 000		
1982	54 000	(± 7 200)	41 000	180 000		6
1983	42 000	(± 3 600)	31 000	120 000		
1983	98 000	(±17 200)	71 000	230 000	calving ground photo*	
1983				126 000	post-calving photo	
1985	76 000	(± 5 700)	50 000	200 000		
1985	142 000	(±17 400)	97 000	320 000	calving ground photo**	

1. Parker (1972).
2. Hawkins and Howard (unpublished data).
3. Calef and Hawkins (1981).
4. Thompson and Fischer (1979).
5. Heard (1981).
6. Gates (1985).

* the standard error of 230 000 was about 50 000 based on estimates of the variances of the variables involved in the extrapolation.

** the standard error of 320 000 was about 60 000 based on estimates of the variances of the variables involved in the extrapolation.

because of the presence of large numbers of 1-year-olds, even though the number of breeding females declined.

The increase in the proportion of calves in the herd was probably due to both higher birth rates and higher calf survival. In the late 1960s Dauphine (1976) found only 2% of yearlings and 82% of older females were pregnant. Birth rates were higher in the 1980s. Collections by Gates (1985) between 1981 and 1983 indicated that 8 of 9 yearlings and all 140 older females were pregnant. Blood progesterone levels (Rehbinder *et al.*, 1981) indicated that all 25 cows live-captured in April and May 1985 were pregnant (Heard, unpublished data). Calf survival rates must have gone up because the increase in the proportion of calves in the herd was too large to be solely the result of increased pregnancy rates. The change in calf:cow ratios from the fall of 1981 to the spring of 1982 indicated that overwinter calf mortality was 40% and within the range found by Parker (1972; 50% in 1967/68 and 30% in 1968/69) but that estimate may not be representative because of the exceptionally high calf:cow ratio in the fall of 1981.

The increase in both birth and survival rates may be related to reduced wolf densities (see below). Calf survival has been shown to be related to wolf densities in other caribou herds (Bergerud, 1983). Bergerud (pers. comm.) suggested caribou may forage more efficiently when the risk of predation is reduced. Calef (unpublished data) observed wolves stampeding large post-calving aggregations for considerable distances near Kaminuriak Lake in 1976.

Increased foraging efficiency could result in superior body condition and therefore increased birth (and survival) rates.

Mortality from hunting

Of the 4700 people living on the KCH's range in 1983, 3500 in the NWT and 1200 in Manitoba, about 85% were native. (annual report of the Beverly and Kaminuriak Caribou Management Board 1983/84). Both Indian and Inuit populations were growing rapidly, with the annual finite rate of increase for Inuit estimated at 3.2% (Hamelin, 1979).

Caribou hunting by natives occurred throughout the year without restriction on age, sex or numbers shot. Hunting by non-natives was insignificant. The recorded kill increased between 1968/69 and 1984/85 (1968/69 - 2200, 1969/70 - 2700, 1970/71 - 2700, 1971/72 - 2900, 1972/73 - 3900, 1973/74 - 3100, 1974/75 - 3100, 1975/76 - 5200, 1976/77 to 1978/79 - no data collected from one or more communities, 1979/80 - 5300, 1980/81 - 4400, 1981/82 - 10 400, 1982/83 - 6300, 1983/84 - 5600 and 1984/85 - 5800) but part of that increase was probably the result of more accurate data collection. Prior to 1975/76 the kill was probably underestimated because hunters were asked to remember their entire year's kill. Monthly interviews should result in a higher and more accurate estimate of kill, but prior to 1981/82 the proportion of hunters contacted was sometimes quite low and no extrapolation for missing data was attempted (Gates, 1985). Large differences in the number of caribou shot between successive years (eg., 1981/82 vs. 1982/83) was a result of caribou wintering closer to villages in some years and therefore being more accessible to hunters. Regardless of winter distribution caribou were always accessible to some communities. There was no reason to believe that the kill from 1976/77 to 1978/79 was either exceptionally high or unusually low.

Table 2. Sex and age composition of the Kaminuriak caribou herd, 1966 — 1985

Date	% in sample			Sample size	Calves/ 100 cows	Estimate of % calves in the herd[3]	Source
	Cows[1]	Bulls[2]	Calves				
11/66			12	300			4
2/67			9	813			4
9-11/67			17	2 183			4
3-4/68			10	3 270			4
9/68			14	3 073			4
3/69			11	967			4
4/79	76	10	14	1 966	19	9	5
9/79			29	7 115			6
4/80			28	499			5
4/81			23	6 438			6
11/81	40	33	28	7 097	70	28	6
4/82	62	10	28	8 503	44	20	6
4/83	64	17	19	3 388	30	14	6
4/84	68	6	26	15 619	40	18	7
4/85	59	12	30	8 819	50	21	7

1. females over 1-year-old.
2. males over 1-year-old.
3. assumes that bulls were underrepresented in the spring samples and that there were 83 bulls/100 cows in the herd as determined in 11/81.
4. Parker (1972).
5. Kearney (pers. comm.).
6. Gates (1985).
7. Mulders (pers. comm.).

Calves comprised between 3 and 13% of the animals shot and males made up between 53% and 58% of the kill of caribou over one year old (Gates, 1985; Gamble, 1984). We assumed wounding losses accounted for an additional source of mortality equal to 25% of the reported kill.

Distribution changes

The amount of range used by the KCH during the year varied with population size. winter herd movements south into the Manitoba forests shrank from about 500 km in the 1950s (Banfield, 1954) to 300 km in the 1960s (Parker, 1972). By the mid-1970s most of the herd was wintering on the tundra and only small numbers crossed the Manitoba border short distances (Simmons *et al.*, 1979; Thompson and Fischer, 1979). The decline in the amount of range used was considered further evidence of declining numbers (Simmons *et al.*, 1979). In the winters of 1982/83 and 1984/85 the trend reversed as caribou moved over 100 km into Manitoba; into areas and in numbers not seen for 10 years (S. Kearney, pers. comm.). We predicted that caribou would continue to expand their distribution into Manitoba as numbers increased and they did. In the fall of 1985 large numbers of caribou moved 300 km into Manitoba and by January 1986 their distribution was similar to that Parker (1972) observed in the late 1960s (Kearney, pers. comm.).

In spite of major changes in winter distribution, ohservations during spring migration indicated that cows continued to migrate to the traditional calving ground at Kaminuriak Lake (Simmons *et al.*, 1979; Thompson and Fischer, 1979; Gates, pers. comm.). No calving was observed elsewhere on the range. Tag return locations between 1959 and 1973 did not indicate any significant interchange among herds (Heard, 1983a) but the absence of marked animals precluded any documentation of herd immigration or emigration after 1973. Many Inuit in Baker Lake believed that emigration was the cause of the herd's decline.

Relative wolf abundance

The number of wolves observed per hour of flying during all caribou related studies indicated that wolf densities declined between the late 1960s and 1985. Between 1966 and 1968, when caribou wintered in the forest, Parker (1973) observed 1400 wolves per 1000 flying hours in winter (Nov — Apr) and 250/1000 h in summer (May — Oct). During June and July 1971 Miller and Broughton (1974) saw 103/1000 h (n=311 h) and summer observations from 1978 through 1983 averaged only 15/1000 h (n=549 h). Between one and two hundered hours were flown during winter caribou work on the tundra from 1978 — 1984 but no wolves were seen. Over the same period Kearney (pers. comm.) saw an average of 123/1000 winter flying hours (n=154 h) in the forest. Kearney's observations suggested that wolf densities in the forest were higher than on the tundra (where most of the caribou were) but much lower than Parker found in the same forests in the late 1960s.

The frequency of wolf sightings on the calving ground did not decline over time. An average of 2.8 wolves were seen per calving ground survey (SE=0.60, n=8, 1971 — 1985); about 56/1000 h. However, wolves killed 35% of 52 neonates found dead on the calving ground in 1971 (Miller and Broughton, 1974) but only 3% of 31 calves found dead in 1985 (Heard, unpublished data).

Wolves were more common on adjacent caribou ranges. Wolf observations on the Beverly herd range averaged 134/1000 h (n=410 h, 1978 — 1983) in summer, 1027/1000 h (n=136 h, 1981 — 1984) in winter and an average of 27 wolves were seen per calving ground survey (SE=10.5, n=6); about 540/1000 h. Wolves accounted for 68% of 225 neonatal calf deaths on the Beverly calving ground (Miller, Gunn and Broughton, unpublished data). Seventy-nine wolves/1000 h (n=120 h) were seen on the Northeastern Mainland range in a May 1983 survey (see Williams and Heard, 1986 for range location).

The number of wolf pelts sold to fur buyers in the Keewatin, an index of the number shot, averaged about 90/yr from 1965/66 to 1971/72, 250/yr from 1972/73 to 1977/78 and 75/yr from 1978/79 to 1983/84. Few wolves were shot or trapped in northern Manitoba. The increase in kill in the mid 1970s was probably the result of the increase in pelt value, the increased use of snowmobiles and higher wolf densities. Pelt value rose from $80 in 1970, to $130 in 1977 and to $200 in 1980 (Heard, 1983b). Most wolves were shot after being tracked by hunters on snowmobiles. Snowmobiles were first introduced in the Keewatin in 1963 and by 1970 most hunters owned one (Bowden, pers. comm.). A

widespread wolf poisoning program was terminated in 1963 and wolf numbers probably recovered quickly (Heard, 1983b) ie. between 1963 and 1970. The low kill after 1977/78 suggests (as did the sighting frequencies) that wolf numbers declined during the 1970s. The kill was low even though pelt prices were at an all time high, caribou wintered close to Keewatin communities and the introduction of faster snowmobiles made wolf hunting an exciting and desirable sport. Hunting may have contributed to the wolf decline but it is also possible that the kill was largely a reflection of wolf abundance that was determined by other factors.

Another factor contributing to the decline in wolf numbers may have been the caribou's change in winter range use. We suggest the following mechanism for that relationship (see also Bergerud, 1983). The wolves associated with caribou on the tundra are migratory non-breeders recruited primarily from forest-resident productive wolves. The numerical response of forest-resident wolves is dependent on per-capita caribou densities. Reduced caribou densities in the forest result not only in fewer wolves in the forest but also in reduced recruitment to the migratory wolf population on the tundra. This scenario suggests that wolf numbers will increase over the entire KCH range as more caribou winter in the forest.

Population dynamics

The discussion of the Kaminuriak herd's population dynamics falls into two periods. In the late 1960s birth rates and calf survival were low and wolves were abundant. After 1980 birth rates and calf survival were high and wolves were rare. Between 1968 and 1980 the herd was small and declining. After 1980 the herd was large and increasing.

The conclusion of a Canadian Wildlife Service study in 1969 was that the KCH was stable (Parker, 1972; Miller, 1974; Walters *et al.*, 1975). However as we have shown in this paper, the herd declined. We suggest that the decline was not predicted by Parker because he underestimated natural mortality of adults (at 4.8%/yr). He assumed that wolves accounted for all natural mortality. In our opinion it was unlikely that all caribou dying of other causes were consumed by wolves. Bergerud (1983) showed that natural mortality of adult caribou in herds subjected to wolf predation was correlated with calf survival. Natural mortality of adults based on Bergerud's regression was 10%/yr and the best fit to the data (1968 — 1980) was 7.2%/yr.

The decline was not predicted by either Miller (1974) or Walters *et al.* (1975) apparently because they asumed calf survival was at least 40% (60% mortality) even though Parker's field data showed that it was only 22% (78% mortality). Miller's (1974) analysis demonstrated that survival to age 3 yr must have been at least 41% for stability. Walters' *et al.* (1975) computer simulation model indicated that 60% calf mortality produced a stable population. Their simulation of 75% mortality resulted in a decline that turned out to accurately describe herd trend from 1968 to 1980.

Before the June 1980 survey we modelled herd dynamics using 7.2% natural adult mortality, 75% calf mortality and an average hunter kill from 1977 to 1980 of 4000/yr and predicted that we would find 12 000 breeding females on the calving ground. The survey results indicated 13 000; the close agreement between the data and our prediction led us to believe we understood the basic population processes. Between 1968 and 1980 the KCH declined beeause the combined effects of hunting and natural mortality exceeded recruitment and we assumed that the decline would continue.

With the dramatic increase in numbers between 1980 and 1982 it was clear that herd population dynamics had changed. There is little doubt that internal herd growth, through recruitment and survival increases, was at least partially responsible for that increase. But the inerease was so large that inmigration must have contributed to herd growth. Using assumptions that maximized herd growth (eg. 100% pregnancy among 1-year-old and older caribou, 95% survival of all age classes including calves) we calculated that at least 15 000 cows must have immigrated after calving in 1980 in order to have 41 000 breeding females by 1982. If we assumed that the 1980 estimate was underestimated by 50% because of sightability bias (based on aerial photography of other calving grounds and other years) (Heard, unpublished data), we calculated that at least 13 000 immigrants would have been required to end up with 71 000 breeding females in 1983.

Both the Beverly and the Bathurst herds have also increased since 1980 (Williams and Heard, 1986) so substantial emigration from those herds

was unlikely. Immigrants probably came from the northeastern mainland of the NWT where unexpected fluctations in calving densities have occurred in the past and where there were enough caribou to provide the required number of immigrants (Calef and Heard, 1980; Heard *et al.*, 1986). Population estimates in 3 areas of the northeastern mainland (Melville Peninsula and north and south of Wager Bay) have varied by an order of magnitude between years. Emigration from the northeastern mainland was also implicated when the number of breeding females on the adjacent Bathurst herd's calving ground doubled from 72 000 in 1982 to 137 000 in 1984 (Heard, unpublished data).

Because there were no marked animals in any herd and the timing of surveys was not appropriate to document declines on the northeastern mainland coincident with the increases elsewhere, we considered explanations that did not involve immigration. If the 1980 estimate was too low (even after correction for sightability bias) and if we assumed that recruitment increased in the mid to late 1970s, the internal herd growth alone could explain the increase in numbers from 1977 to 1982. When we reviewed the 1980 survey data we could find no reason to reject the results. There were no unusual procedural problems during the field work and, as discussed above, reconnaissance was so extensive that it was unlikely significant numbers of cows calved outside of the census zone. If we rejected the 1982 estimate as being too high, immigration would still have been necessary to explain the 1983 and 1985 estimates.

Skoog (1968), Bergerud (1980, 1983) and Haber and Walters (1980) argued that periodic dispersal has been an important factor in caribou population dynamics. Haber and Walters (1980) suggested that competition for food causes caribou to disperse from herds that have obtained high densities (about 2 caribou/km^2). Herds receiving immigrants increase because the immediate reduction in the predator-prey ratio allows the herds to escape the controlling effects of wolf predation. The herd increases until competition for food again causes dispersel. In Bergerud's model, caribou disperse if they reach 2/km^2 but such high densities rarely occur 1. because wolf predation can halt herd increase before densities get that high or 2. because caribou expand their range to limit their own densities.

We have too few data to comment on the causal mechanism of dispersal but so far our data on the effects of immigration appear to fit Bergerud's second hypothesis. The decline in herd size from 1950 to 1980 resulted in a reduction in the amount of range used. With the abandonment of the forested portion of their winter range in the mid 1970s caribou made less contact with wolves and wolf numbers declined. Immigration provided a further decrease in the predator prey ratio, calf survival increased, caribou numbers increased and the herd began expanding its range.

In the fall of 1984 one of us (DH) began radio-collaring caribou in the KCH and on the northeastern mainland. We recognize that those marked animals cannot prove that immigration occurred between 1980 and 1982. But if we find significant interchange between calving grounds we would be more confident that immigration accounted for the increase in the Kaminuriak herd between 1980 and 1982 and we will be in a better position to test competing hypotheses of population control in caribou.

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